ADVANCES IN CROP GROWTH AND PRODUCTIVITY

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Photo- stages of growth-seed germination to a complete plant
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Citation

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Plant density and crop productivity

Plant density is the number of plants per unit area in a cropped field. It indicates the size of the area available for individual plant. Yield of a crop is the result of final plant population which depends on the number of viable seeds, germination percent and survival rates. Establishment of optimum plant population is essential to get maximum yield. Under conditions of sufficient soil moisture and nutrients, higher population is necessary to utilize other growth factors efficiently. Once soil moisture and nutrients are not limiting, yield of crop is limited by solar radiation. The level of plant population should be such that maximum solar radiation is intercepted. In crops grown on stored soil moisture under rainfed conditions, plant population should not be high to deplete moisture before crop matures and not low to leave moisture unutilized.

FACTORS AFFECTING PLANT DENSITY

Optimum plant density is necessary to obtain maximum yield. Optimum plant density depends on size of the plant, elasticity, foraging area, nature of the plant, capacity to reach optimum leaf area at an early date and seed rate used. The factors affecting plant density are grouped into two as (a) genetic and (b) environment factors.

A. Genetic Factors (plant or internal factors)

(i) Size of plant - The volume occupied by the plant at the time of flowering decides the spacing of the crop. Plants of red gram, cotton, sugarcane etc., occupy larger volume of space in the field compared to rice, wheat, ragi, etc. Even the varieties of the same crop differ in size of plant.

(ii) Elasticity of the plant - Variation in size or plant between the minimum size of the plant that can produce some economic yield to the maximum size of the plant that can reach under unlimited space and resources is the elasticity of the plant. The optimum plant density range is high in indeterminate plants. For example, in indeterminate red gram varieties the optimum plant density ranges from 55 to 133 thousand plants/ha. The elasticity of plants is due to branching or tillering. For determinate plants like maize, sorghum etc., the elasticity is less and hence the optimum plant density range is small. The removal of auxiliary buds is done to get uniform and early maturity in castor.

(iii) Foraging area or soil cover - The crop should cover the soil as early as possible so as to intercept maximum sunlight. More interception of solar radiation leads to more dry matter production. Closely spaced plants intercept more radiation than widely spaced plants. Area of root spread also decides the density.

(iv) Dry matter partitioning - Dry matter production is related to the amount of solar radiation intercepted by the canopy, which depends on the plant density. As the plant density increases, the canopy expands more rapidly, more radiation is intercepted and more dry matter is produced.

B. Environmental Factors (management factors)

The primary management factor affecting the plant density of any crop varieties is the method of stand establishment/sowings like transplanting or broadcasting. For transplanting/direct drilling, the genetic factors are the deciding factors on the number of plants per unit area. For broadcasting, the factors are:
(i) **Time of sowing** - The crop is subjected to different weather conditions when sown at different periods. Among the weather factors, the most important factors that influence optimum plant density are day length and temperature. Photosensitive varieties respond to day length resulting in change in size of the plant. As low temperature retards the growth, higher density is established for quicker ground cover.

(ii) **Rainfall/Irrigation** - Plant density has to be less under rainfed than irrigated conditions. Under higher plant densities, more water is lost through transpiration. Under adequate irrigation or under evenly distributed rainfall conditions, higher plant density is recommended.

(iii) **Fertilizer application** - Higher plant density is necessary to fully utilize higher level of nutrients in the soil to realize higher yield. Nutrient uptake increases with increase in plant density. Higher density under low fertility conditions leads to development of nutrient deficiency symptoms. For example, rice does not respond to plant density without nitrogen application.

(iv) **Seed rate** - Quantity of seed sown/unit area, viability and establishment rate decides the plant density.

**CROP GEOMETRY**

**Crop geometry** is the pattern of distribution of plant over the ground or it refers to the shape of the space available for individual plants. It influences crop yield through its influence on light interception, rooting pattern and moisture extraction pattern. Crop geometry is altered by changing inter and intra-row spacing (Planting pattern).

- Wider spaced crops have advantage under this geometry
- Plants which requires no restriction in all directions are given square geometry
- Usually perennial vegetations like trees/shrubs are under this arrangement

(i) **Square planting** - Square arrangements of plants will be more efficient in the utilization of light, water and nutrients available to the individual plants than in a rectangular arrangement.

(ii) **Rectangular planting** - Sowing the crop with seed drill, wider inter-row and closer intra-row and closer intra-row spacing leads to rectangularity. Rectangular arrangement facilitates easy intercultivation. Rectangular planting mainly suits annual crops, crops with closer spacing etc., the wider section (row) is given for irrigation, intercultural operation etc.
  - It is an arrangement to restrict the endless growth habit in order to switch over from vegetation to the productive phase.
  - This method accommodate high density planting
  - It can facilitate intercropping also.

(iii) **Triangular planting** - It is a method to accommodate plant density under perennial/tree crops.

(iv) **Miscellaneous planting** - In rice and ragi transplanting is done either in rows or at random. Skipping of every alternate row is known as skip row planting. When one row is skipped the density is adjusted by decreasing inter-row spacing. When the
inter row spacing is reduced between two rows and spacing between two such pair are increased then it is known as paired row planting. It is generally done to introduce an inter crop.

**Yield of individual plant and community**

The full yield potential of individual plant is achieved when sown at wider spacing. When sown densely, competition among plants is more for growth factors resulting in reduction in the size and yield of the plant. Yield/plant decreases gradually as plant population/area increases (Fig 1 below). However, yield/area is increased due to efficient utilization of growth factors. Highest yield/area can, therefore, be obtained when the individual plants are subjected to severe competition.

![Graph showing the relationship between Yield and Plant population](image)

**Fig 1.** Yield of individual plant and community as influenced by plant population

**Plant population and yield**

Decrease in the yield of individual plants at higher plant density is due to reduction in the number of ears in indeterminate plants. In determinate plants, wherein the terminal bud ends in a flower or inflorescence, the reduction in yield is mainly due to the reduced size of ears or panicles. Highly branching or tillering plants behave as indeterminate plant and yield reduction is due to reduction in the number of seeds. Redgram produces about 20 pods/plant at 3.33 lakh/ha while it produces more than 100 pods/plant at 50000 plants/ha. Conversely, non-tillering or nonbranching plants produce less yield due to reduction in size of ears as in the case of maize and sorghum. Among all the yield attributes, test weight is the stable character under wide range of plant populations. Under very high population levels, plants become barren.

Efforts were made to quantify the relationship between plant population and yield. Holliday (1960) suggested two types of response curves, asymptotic and parabolic.

**Asymptotic response**

He said that the asymptotic relationship was characteristic of crops having a vegetative form of yield, and cited results from studies with potatoes, rape and kale to support this contention.
Similarly entire plant dry matter as in the case of fodder crops and tobacco is the economic product, the response to increasing plant population is asymptotic (Fig 2). Dry matter of individual plant increases with increase in plant density to a certain level. This indicates lack of appreciable competition between neighbouring plants. Further increase in density, increases the dry matter of individual plant at a diminishing rate. It signifies that competition between plants is felt and that the dry matter production of individual plants is reduced. However, this reduction is more than compensated by the increase in the number of plants. A further increase in plant population results in a plateau i.e. with increase in plant population there is no increase in dry matter per unit area. It shows that increase in production due to increased plant population compensates almost equally for the reduction in the production of the individual plant. The plateau continues for large increases in plant population. That is why, for fodder crops, dense stands are recommended to get maximum yield. The extra expenditure is the seed cost only. In addition, dense stands provide for lean stems and more leafy fodder compared to sparse population where stem dry matter is high. The type of response gives the asymptotic curve which is expressed as follow

\[ Y = Ap + \frac{1}{1 + Abp} \]

Where, \( Y \) is dry matter yield/area; \( A \) apparent maximum yield per plant, \( p \) number of plants per unit area and \( b \) is linear regression coefficient.

The term \( 1/(1+Abp) \) represents the maxima in which the maximum plant yield (\( A \)) is reduced by increasing competition resulting from greater plant density. It is termed as competition factor. Maximum yield that is obtained in particular condition when the plants are widely spaced with practically no competition is denoted as \( A \) or apparent maximum yield per plant.

![Fig 2 Asymptotic and parabolic response curves](image)

**Parabolic response**

Holiday added that the parabolic relationship was typical of crops having a reproductive form of yield. The kernel yield of corn has shown this response (Duncan 1958). Therefore, when the economic yield is the part of the total dry matter or the reproductive parts, parabolic curve is used to describe plant population yield relationship. In this case also yield increases with increase in population, then reaches a maximum. However, unlike in asymptotic curve, yield decreases with further increase in population (Fig 2). Holiday (1960) suggested that the curve can be fitted to the quadratic equation

\[ Y = a + bp + cp^2 \]
Where $Y$ is yield/area, $p$ plant population and $a$, $b$ and $c$ are regression coefficients.

There is a drawback in representing plant population-yield response as a quadratic function. With increase in plant population, after reaching a maximum, yield does not fall suddenly. There is a plateau for some range of plant population. The extent of plateau depends on elasticity of plants. This aspect is not considered in the quadratic equation.

**Square root function**

The disadvantage of quadratic function can be overcome by square root function.

$$Y = a + bp + c\sqrt{p}$$

It is almost similar to quadratic function except that root of $p$ is taken instead of square (Fig 3).

![Square root and quadratic curves](image)

Fig 3 Square root and quadratic curves

The relationship between bush snap bean yields and plant population density has been asymptotic in some studies and parabolic in others. The results of the several studies are difficult to compare however, because of differences in the range of densities examined, in the method of harvest and in the maturity of the crop.

Nelder has criticized the use of tests of significant difference for interpreting the crop yield-population density relationship and has advocated the use of quantitative models. Reciprocal equations, based on the relationship between the inverse of weight per plant and the plant population density, have been the most commonly used models because of their flexibility and possible biological significance. The first reciprocal model was derived independently by Shinozaki and Kira in Japan, and by Holliday in Great Britain. The basic form is:

$$w^{-1} = \alpha + \beta p \quad (A)$$

where $\alpha$ and $\beta$ are constants, $w$ is the yield per plant and $p$ is the population density (plants per unit area).

Although this model can describe an asymptotic relationship, it cannot describe the parabolic. To remedy this shortcoming, Holliday proposed an extension of the model to:

$$w^{-1} = \alpha + \beta p + \gamma p^2 \quad (B)$$

where $\gamma$ represents a third constant. He said that this empirically derived reciprocal quadratic model was only an approximation to the true parabolic situation. Willey and Heath demonstrated, however, that this equation could describe a wide range of yield-population...
density data. Nelder discussed the general usefulness of inverse polynomial models for describing a variety of quantitative relationships in crop research.

Bleasdale and Nelder proposed a modification of equation A to:

\[ w^{-\theta} = a + \beta p^\phi \]  

(C)

where \( \theta \) and \( \phi \) are additional constants. Experience demonstrated, however, that data were usually not sufficiently accurate to permit determination of specific values of both \( \theta \) and \( \phi \). In addition, Mead showed that the ratio of \( \theta \) and \( \phi \), rather than their absolute values, determines the fit of the model. Therefore, workers assumed \( \phi = 1 \), and simplified equation C to:

\[ w^{-\theta} = a + \beta p \]  

(D)

where \( \theta \leq 1 \). Bleasdale pointed out that when \( \theta = 1 \), the model describes the asymptotic yield-population density relationship, and when \( \theta < 1 \) it describes the parabolic one.

Biological significance has been attached to the variation of the constants in the reciprocal models. Willey and Hearth reasoned that since:

\[ Y = wp \]  

(E)

where \( Y \) is the yield per unit area, then equation A could be expressed as:

\[ Y = \frac{p}{\alpha + \beta p} \]  

(F).

They pointed out that as \( p \) approaches 0, \( Y \) approaches \( \alpha^{-1} \). Therefore, \( \alpha^{-1} \) has been interpreted as being indicative of the genetic potential of the plant. Willey and Heath acknowledged, however, that this interpretation failed to take into account the fact that yield per plant would level off at a \( p > 0 \).

Willey and Heath further demonstrated that as \( p \) increased, \( Y \) approached the asymptote, \( \beta^{-1} \). The \( \beta^{-1} \) has been considered a measure of environmental potential because it defined the limit of yield obtainable on a unit area of land.

According to Mead, the interpretation of \( a \) remains the same for equation D as for equation A. He said, however, that no simple practical interpretation of \( p \) can be made when \( \theta \neq 1 \). Nevertheless, it has still been viewed as a reflection of environmental potential.

Bleasdale was the first to present experimental evidence supporting the proposed biological significance of \( a \) and \( \beta \). Comparing three onion cultivars, he found they had a common \( \beta \) but different values of \( \alpha \). He also found the \( P \) varied from year to year for any given cultivar. Nichols, working with snap beans, and Hearn, working with cotton, found that soil fertility influenced \( p \) but did not affect \( a \). Bunting used equation A to compare the effects of plant population density on the shoot dry matter yields of three cultivars of maize. Although the cultivars differed greatly in the time of flowering, they had a common \( \beta \). The later flowering cultivars had, however, lower values of \( a \). When results from different years were compared, the \( P \) was found to be higher in dry seasons.

Contrary to the previous results, Jones found differences in both the \( a \) and \( \beta \) when he compared two bush snap bean cultivars. Bleasdale and Thompson reported similar results from a study with parsnips.

When equation D is used, \( a \) and \( \beta \) values from different treatments cannot be compared unless \( \theta \) is invariant. Although common values of \( \theta \) were found in the reports previously discussed, some studies have shown systematic variation in this parameter. Fery and Janick
found that the θ for the yield of marketable tomatoes declined for later dates of harvest. When the total fruit yield, green as well as ripe, was considered, the θ stayed near 1 regardless of harvest date. They concluded the changes in the θ for marketable fruit yield were related to yield concentration, earliness and the ability to maintain ripe fruit on the vine in a marketable condition. Hearn, working with cotton, found that θ declined when the plants lost young fruit due to insect infestation, periods of drought, or mechanical removal. The θ value was not influenced by soil fertility.

**Plant distribution**

The organisms are influenced by their environment in a number of ways. These environmental factors govern the survival and growth of individuals at all phases of their life cycle. The distribution or physical location of individuals within a population at a particular time is called dispersion. Wynne Edwards (1962) defined dispersion as comprising the placement of individuals and groups of individuals within the habitat they occupy, and the processes by which this is brought about. In other words, dispersion is the internal distribution pattern of individuals within a population. The distribution of individuals in a population may follow three broad patterns (Fig 4):

- **Random distribution** – in this case, the individuals in a population are scattered over an area without regularly or any degree of affinity for each other. The probability of locating an individual at a point in the populated area is equal for all the point. Random distribution is relatively rare in nature and is expected to occur only when the environment is uniform and the resources are evenly spread. There must also not be any interactions among individuals to repel each other or social attractions causing tendency to aggregate. When many small environmental factors are acting together on population, random distribution is expected in nature. However, when a few major factors are dominating, random distribution is not expected.

- **Uniform distribution** – In this case, the individuals are evenly spaced and tend to be as far apart from each other as possible within a particular density. The distribution of individuals is more regular than random. It may be found in places where there is severe competition among individuals or where positive antagonism is predominant leading to even spacing.
Clumped distribution – Here the individuals of a population are found scattered in groups here and there. This is perhaps the most common pattern of distribution and may result from nonuniformity of the habitat or attraction among individuals. This is also called irregular or nonrandom distribution. There may be variations in the intensity of clumped distribution and it may be present only at certain times of the individual’s life cycle. The seeds from annual or perennial plants will normally drop nearer to the parent and hence clumps of genetically related individuals may characterize the distribution. However, the distribution of groups may tend to be random or even uniform if the individuals of the population have a tendency to form groups of certain size viz. vegetative clones in plants or groups in animals. Depending upon the distribution of groups, clumped distribution may therefore, be

a. Random clumped (groups randomly distributed)
b. Uniform clumped (groups uniformly distributed) or
c. Aggregated clumped (groups aggregated among themselves).

The type of distribution is extremely important in selecting the appropriate method of sampling. The sample size in case of clumped population should be larger than the nonclumped, and the sampling techniques should be more carefully planned. A small sample would tend to give either too low or too high estimate of density of population.

The pattern of distribution and the degree of clumping are crucial in determining the interaction between members of the same or different species. The degree of clumping depends on the nature of habitat, seasonal changes, reproductive patterns and social attractions. Aggregation may increase competition among individuals for food, shelter etc. Nevertheless, it may increase the survival rate of individuals in the group due to their better ability to defend, find resources or modify the microclimate. Therefore, the growth rate of individuals in the population is less at lower as well as at very high densities. The highest growth rate is attained at intermediate densities in these populations. As a result of this phenomenon, both undercrowding (low density) and overcrowding (high density) are deleterious and limiting to the growth rate of the population. This phenomenon has come to be known as Allee’s principle after WC Allee, who put forth, this hypothesis in 1931. Group survival is an important feature which is the outcome of aggregation. Many plants are able to withstand the action of wind better in a group rather than as individuals.

The distribution and abundance of plants are influenced by the biotic and abiotic factors of the environment. Temperature, moisture, light, biogenic salts, soil (texture, OM, microorganisms, nutrients, pH), fire, concentration of O$_2$ and CO$_2$ are the important abiotic factors limiting to plants.

**Environmental factors affecting growth and yield**

**Temperature** - The growth of plant occurs in the range of about 0 to 35 °C. Within most of this range, raising the temperature by 10 °C increases the growth by 2-3 times. There are three temperatures known as the cardinal points for growth, the minimum or the lowest temperature at which growth can be detected; the optimum or temperature of maximum range of growth; and the maximum or the highest temperature at which growth can be detected.
These are not very sharp temperatures and they vary from species to species. It must be mentioned that the optimum temperature for growth may be different for a particular plant and also at a particular stage of development of the same plant. The growth depends on other processes such as photosynthesis and respiration and these processes also have their cardinal temperatures. Since the whole process of plant growth is due to chemical reactions which are enzymatically controlled. This implies that cardinal temperatures for growth, therefore, must be controlled by the denaturation temperature of a plant enzyme.

The amount of water present inside the cell and the conditions of protoplasm are closely related with its resistance to extremes of temperature. The values for three cardinal temperatures vary from plants of arctic, temperate and tropical zones.

**Light** – although growth of higher plants eventually depends upon photosynthesis, light as such is not essential for the process of plant growth as long as sufficient amount of organic materials are available. Some plants can complete their life cycle in the dark e.g. tuberous or bulbous plants. The higher plants grow in dark show a weak growth known as etiolation. Usually the leaves remain free of chlorophyll and the colour is therefore pale yellow, although some ferns, gymnosperms, seedlings and algae can synthesize chlorophyll in the dark. Light effects variously and depends upon its intensity, quality and periodicity.

**Light intensity** – Weak light promotes shortening of internodes and expansion of leaf. Very weak light reduces the rate of overall growth and also photosynthesis. Development of chlorophyll is dependent on light and in its absence etiolin compound is formed which gives yellow colour to the plant. Similarly high light intensity affecting indirectly increases the rate of water loss and reduces the rate of growth.

**Light quality** – Different wavelengths of light affect the growth of plant. Blue violet light enhances the intermodal growth while green light reduces the expansion of leaves as compared with complete spectrum of visible light. Red light favours growth. Infrared and ultraviolet lights are detrimental to growth.

**Light duration** – Duration of light remarkably affects vegetative as well as reproductive structures. The induction and suppression of flowers are dependent on duration.

**Water** – Since all growth depends on a hydrostatic turgor pressure, a water deficiency ill of course, retard or completely stop it. On the other hand excess water may result in an abnormal type of growth. So in a saturated atmosphere the development of leaves is poor and the differentiation of tissues is retarded. This is the result of excessive stretching of the cell walls because of the abnormally high turgor pressure. Plants adapted to adequate conditions have low osmotic pressures and therefore cannot develop such excessive turgor pressure even when tissues are saturated.

**Chemical stimulants and inhibitors** – Even nutrient salts required by the plants for normal growth may inhibit growth or actually kill the plant if applied in an unbalanced state. On the other hand, they stimulate growth when applied in suitable quantities and in balanced solutions. Growth is frequently inhibited by non-nutrient mineral elements. Salts of heavy
metals are toxic. Even the metabolic products of a plant like oxalic acid may be poisonous when supplied to the protoplasm instead of being stored in the vacuole. Several of the poisons when applied in very weak doses stimulate growth. Thus phenol is poisonous in 1: 1000 concentration but stimulates when used in 4 to 8 : 100000; ethyl alcohol checks growth in 25 to 75 : 1000 and stimulate it in 25 to 75 : 100000. Mercury compounds used to disinfect seeds sometimes stimulate growth.

**Pollutants** - Air pollution, in particular, has been recognized for well over 100 years as influencing plant growth. Ethylene, sulphur dioxide and fluorides have been shown to damage a wide variety of plants. Recently, several new classes of air pollutants have been recognized: hydrocarbons from motor vehicle exhausts and photochemical products resulting from the interaction of hydrocarbons with nitrogen oxides in the presence of sunlight.

**Oxygen supply** – Oxygen causes increase in growth because it helps in respiration which ultimately provides energy for vital activities of the plant during growth and development.

**Ionizing radiation** – During the growth, plants are also exposed to very short wavelength, high energy radiations known as ionizing radiations and some of these are part of the natural energy environment to which all living things are exposed, while other radiations are manmade.

**Nutrition supply** – the supply of nutritive materials is directly proportional to the rate of growth and with deficient food supply to growing regions, the rate of growth decreases and ultimately stops. Photosynthetic processes supply the growing plant with carbon skeletons which are incorporated into amino acids, proteins, phospholipids, nucleic acids, carbohydrates and other cytoplasmic and structural constituents. These metabolic processes require adequate supplies of inorganic elements.

**Soil structure and composition of soil air** – soil structure and texture determine the bulk density of a soil. As a rule, the higher the bulk density, the more compact is the soil, the more poorly defined the structure, and the smaller the amount of pore space. Such conditions are frequently reflected in restricted plant growth. Higher bulk densities inhibit the emergence of seedlings and offer increased mechanical resistance to root penetration. They reduce the rate of $O_2$ diffusion into the soil pores and the root respiration is directly related to a continuing and adequate supply of this gas.

Under field conditions, $O_2$ diffusion into the soil is determined largely by the moisture level of the soil if bulk density is not a limiting factor. On well drained soils with good structure, $O_2$ content is not likely to retard plant growth except during periods of flooding, when reduced $O_2$ supply may restrict ion uptake. The $O_2$ supply at the root absorbing surface is critical. Hence not only is the gross $O_2$ level of the soil air important, but also the rate which $O_2$ diffuses through the soil to maintain an adequate partial pressure at the root surface.

**Soil reaction** – Soil reaction or pH may affect plant development by influencing the availability of certain plant nutrients. Examples are the reduced availability of phosphorus in acid soils high in Fe and Al and of Mn in high organic matter soils with high pH values. A
decline in the availability of Mo results from a decrease in soil pH. Acid mineral soils are frequently high in soluble Al and Mn, and excessive amounts of these elements are toxic to plants.

When NH$_4$ – N fertilizers are left on the surface of soil with pH values greater than 7, NH$_3$ may be lost by volatilization. Soil pH values lower than 5.0 and above 7.5 will favour the conversion of water – soluble fertilizer P into forms of lower availability to crops. Certain soil borne diseases are influenced by soil pH. Scab of Irish potatoes, pox of sweet potatoes, and black root rot of tobacco are favoured by neutral to alkaline conditions.

The importance of soil acidity to crop growth and the availability of plant nutrients have greater value to growers. Soil acidity is one that can be easily altered.

**Biotic factors** – Many biotic factors can limit plant growth and reduce crop yields. Heavy fertilization may encourage greater vegetative growth and better environmental conditions for certain disease organisms. The imbalance of nutrients may also be a reason for the increased incidence of disease. Certain pests may impose an added fertilizer requirement. Viruses and nematodes, for example, attack the roots of certain crops and reduce absorption, requiring a greater supply of nutrients. Insect infestation may also seriously limit plant growth. Heavy fertilization may encourage certain insects, such as the cotton boll weevil, by greater vegetative growth. Definite advances have been made in breeding insect – resistance strains of certain crops in developing insecticides. Weeds are another serious deterrent to efficient crop production, for they compete for moisture, nutrients and in many instances light.

**Strategies for maximizing solar energy utilization, leaf area, interception of solar radiation and crop growth**

Solar radiation is the set of electromagnetic radiation emitted by the Sun. The Sun behaves almost like a black body which emits energy according to Planck’s law at a temperature of 6000 K. The solar radiation ranges goes from infrared to ultraviolet. Not all the radiation reaches Earth’s surface, because the ultraviolet wavelengths, that are the shorter wavelengths, are absorbed by gases in the atmosphere, primarily by ozone.

The atmosphere acts as a filter to the bands of solar spectrum, and at its different layers as solar radiation passes through it to the Earth's surface, so that only a fraction of it reaches the surface. The atmosphere absorbs part of the radiation reflects and scatters the rest some directly back to space, and some to the Earth, and then it is irradiated. All of this produces a thermal balance, resulting in radiant equilibrium cycle (Fig 5).
Fig. 5. Effects of clouds on the Earth’s Energy Budget. This image is from a NASA site Depending on the type of radiation, 324 Wm\(^{-2}\) reaching the Earth in the upper atmosphere (1400 Wm\(^{-2}\) is the solar constant), 236 Wm\(^{-2}\) are reissued into space infrared radiation, 86 Wm\(^{-2}\) are reflected by the clouds and 20 Wm\(^{-2}\) are reflected by the ground as short-wave radiation. But part of the re-emitted energy is absorbed by the atmosphere and returned to the earth surface, causing the “greenhouse effect”.

The average sun energy that reaches the outside edge of the atmosphere is a fixed amount, called ‘solar constant’. The energy contained between the 200 and 4000 nm wavelengths and it is divided into ultraviolet radiation, visible light and infrared radiation (Fig 6).

**Ultraviolet radiation**: Consists of the shorter wavelengths band (360 nm), it has a lot of energy and interacts with the molecular bonds. These waves are absorbed by the upper atmosphere, especially by the ozone layer.

**Visible Light**: This radiation band corresponds to the visible area with wavelengths between 360 nm (violet) and 760 nm (red), it has a great influence on living beings.

**Infrared radiation**: Consists of wavelengths between 760 and 4000 nm, it corresponds to the longer wavelengths and it has little energy associated with it. Its absorption increases molecular agitation, causing the increase of temperature.

Fig. 6. Spectrum of solar radiation above the atmosphere and sea level. Prepared by Robert A. Rohde as part of the Global Warming Art project
Solar radiation on the earth can be classified as:

**Direct radiation:** This radiation comes directly from the sun without any change in its direction. This type of radiation is characterized by projecting defined shadow onto the objects that intersect.

**Diffused radiation:** This radiation comes from all over the atmosphere as a result of reflection and scattering by clouds, particles in the atmosphere, dust, mountains, trees, buildings, the ground itself, and so on.

**Global radiation:** Is the total radiation. It is the sum of the two radiations above. On a clear day with a clear sky, the direct radiation is predominant above the diffused radiation. Animals with thermoregulatory abilities and mobility can seek or avoid certain features of current weather. In contrast, terrestrial plants are rooted in place and must accept that the rates of their metabolic processes are determined by the ambient conditions. Crop communities exert a strong influence over their local microenvironment. Nearly all cropping practices are geared toward, or have the effect of, modifying chemical and physical aspects of that environment (aerial and soils properties).

One of the most important factors that influences plants development is the solar radiation intercepted by the crop. The solar radiation brings energy to the metabolic process of the plants. The principal process is the photosynthetic assimilation that makes synthesize vegetal components from water, CO$_2$ and the light energy possible. A part of this, energy is used in the evaporation process inside the different organs of the plants, and also in the transpiration through the stomas.

Photosynthesis is a chemical process that converts carbon dioxide into organic compounds, especially sugars, using the energy from sunlight. Depending on how carbon dioxide is fixed the plants can be grouped into three types: C$_3$, C$_4$, and CAM. The C$_3$ plants are the more usual superior plants, which are the temperate weather crops (wheat, barley and sunflower, etc); the C$_4$ category are species from arid weathers or hotter or tropical weathers (corn, sugar or sorghum). The C$_3$ type are generally considered less productive than C$_4$ (Fig 7).

![Fig. 7. Typical theorized relationships between cumulated aboveground biomass and cumulated intercepted solar radiation for C$_4$ and C$_3$ species. From Gosse et al. 1986.](image)
Interception of radiation

In the interception of light (LI) by a canopy, the difference between the solar incident radiation and reflected radiation by the soil surface (Villalobos et al., 2002), is a determining factor in crop development and provides the energy needed for fundamental physiological processes such as photosynthesis and transpiration.

Plants intercept direct and diffuse sunlight. The upper leaves receive both types of radiation, while the lower leaves intercept a small portion of direct radiation. Diffuse radiation therefore, becomes more significant in the lower leaves due to radiation transmitted and reflected from the leaves and the soil surface. Solar radiation transmitted by the leaves is predominantly infrared. From a practical point of view, the solar radiation spectrum is divided into regions, each with its own characteristic properties. Appropriate procedures and sensors must be chosen according to the specific objectives of the radiation measurements. Visible radiation, between the wavelengths of 400 and 700 nm, is the most important type from an ecophysiological viewpoint, as it relates to photosynthetically active radiation (PAR). Only 50% of the incident radiation is employed by the plant to perform photosynthesis (Varlet-Gancher et al., 1993). The quantity of radiation intercepted by plant cover is influenced by a series of factors such as leaf angle, the properties of the leaf surface affecting light reflection, the thickness and chlorophyll concentration, which affect the light transmission, the size and shape of the leaf phyllotaxis and vertical stratification, and the elevation of the sun and distribution of direct and diffuse solar radiation. Of the 100% total energy received by the leaf only 5% is converted into carbohydrates for biomass production later. Losses of energy are:

- By non-absorbed wavelengths: 60%.
- Reflection and transmission: 8%.
- Heat dissipation: 8%.
- Metabolism: 19%.

Of the global radiation incident on the plant canopy only a proportion is used to carry out photosynthesis: PAR (photosynthetic active radiation). The plant’s response differs with different wavelengths. Chlorophyll is the main pigment that absorbs the light, other accessory pigments are the b-carotene, red isoprenoid compound which is the precursor of vitamin A in animals and the xanthophyll, a yellow carotenoid.

Essentially the entire visible light is capable of promoting photosynthesis, but the regions from 400 to 500 and 600 to 700 nm are the most effective (Fig 8). In addition, pure chlorophyll has a very weak absorption, between 500 and 600 nm. The accessory pigments complement the absorption of light in this region, supplementing the chlorophylls.

- 620-700 nm (red): A greater absorption bands of chlorophyll.
- 510-620 nm (orange, yellow- green): Low photosynthetic activity.
- 380-510 nm (purple, blue and green): Is the most energetic. Strong absorption by chlorophyll.
- < 380 nm (ultraviolet). Germicides effects, even lethal < 260 nm.
Leaf area index
For an efficient use of solar radiation by crop, the great part of the radiation must be absorbed by the photosynthetic tissues. Leaf is the principal photosynthetic functional unit, therefore its efficiency on the capture and use of solar energy determines the vegetable productivity. The area and arrangement of foliage (the canopy architecture), determine the interception of solar radiation (LI) by a crop and the distribution of irradiance among individual leaves (Loomis and Connor, 2002). Leaf area and arrangement change during the life of a crop and, by leaf movement, even during the course of a single day. Maximum crop production requires complete capture of incident solar radiation and can only be achieved with supporting levels of water and nutrients (Loomis and Connor, 2002).
Watson (1947). Because it is a dimensionless quantity, LAI can be measured, analyzed and modeled across a range of spatial scales, from individual tree crowns or clusters to whole regions or continents. As a result, LAI has become a central and basic descriptor of vegetation condition in a wide variety of physiological, climatological, and biogeochemical studies. LAI is a key vegetation characteristic needed by the global change research community. For example, LAI is required for scaling between leaf and canopy measurements of water vapour and CO₂ conductance and flux, and for estimates of these variables across the global biosphere–atmosphere interface. Because solar radiation covers the entire surface of the ground, the LAI is a robust measure of leaf area per unit of solar radiation available.

**Effect of intercepted radiation and leaf area index on growth and crop production**

The productivity of a crop depends on the ability of plant cover to intercept the incident radiation, which is a function of leaf area available, the architecture of vegetation cover and conversion efficiency of the energy captured by the plant into biomass. Most production strategies are directed towards maximizing the interception of solar radiation. In the case of crops, this implies adapting agricultural practices in such a way as to obtain complete canopy cover as soon as possible. Deficiencies in water and nutrient inputs may reduce the rate of leaf growth, reducing yield below optimum levels due to insufficient energy capture (Gardner et al., 1985).

The efficiency of interception of PAR depends on the leaf area of the plant population (Varlet-Grancher et al., 1989) as well as on the leaf shape and inclination to the canopy. Gallo & Daughtry (1986) observed that the difference between the intercepted and absorbed PAR, along the maize crop cycle, was lower than 3.5%. According to this, Müller (2001) showed that maize leaves absorb 92% of the intercepted radiation by the canopy. The efficiency of interception of a canopy corresponds to the capacity of the plant population in intercepting the incident solar radiation, which is the main factor influencing the photosynthesis and the transpiration processes (Thorpe, 1978). The efficient crops tend to spend their early growth to expand their leaf area; they make a better use of solar radiation. Agronomic practices, such as fertilization boot, high stocking densities and better spatial arrangement of plants (eg narrow rows) are used to accelerate ground cover and increase light interception.

Solar radiation also has an important role in the processes of evaporation and transpiration. Evaporation takes place mainly from the soil surface and transpiration is the evaporation that occurs across different plant organs, mainly leaves. Because both processes are closely linked, they are often considered together (evapotranspiration); water consumption account, linked to the crop itself, is considered "crop water needs" and is a fundamental aspect in the planning and designing irrigation strategies. Apart from the availability of water in the surface horizons, the cultivated soil evaporation is determined mainly by the fraction of solar radiation reaching the soil surface. This fraction decreases over the growing season, and at the same time the crop canopy cover grows (Fig 10). The development of a crop can be divided into four stages (Allen et al., 1998):

**Initial Stage:** The early growth of individual plants, with little plant-plant competition is very
fast. As the LAI develops, there is a shade of lower leaves, so that descriptions of crop growth are based on leaf area depending on the soil surface (Gardner et al., 1985). The water lost during this phase is mainly due to direct soil evaporation.

Crop Development Stage: LAI grows exponentially, changing the dominant component of evapotranspiration, predominating evaporation in the initial period and the plant transpiration at the end of the stage. As the leaf area grows, the radiation intercepted by leaves increases. At flowering time, leaf area development ends, with the goal of cultural practices to maximize crop photosynthesis intercepting virtually all of the incoming solar radiation.

Mid-season stage: The late season stage runs from the start of maturity to harvest or full senescence. In the vegetative period radiation interception does not increase, starting from fruit ripening to leaf senescence. (Late season stage).

From the point of view of optimizing the use of irrigation water, it is important to have an accurate estimate of the needs of the plant at any time. All of this will be determined in the development stage, which affect the distribution of solar energy in the process that occurs in the water consumption. Crop conditions (cultural practices, climate, soil, etc) that modify the development of vegetation cover along the life cycle change the water needs of the plant, which would imply a change in the watering schedule when the goal is to meet in those needs. There are different procedures to determine the needs of the crop (ETc): the most popular is that proposed by (Doorenbos & Pruitt, 1977) \[ \text{ETc} = \text{ETo} \times Kc[1] \]

Where ETo is the evapotranspiration reference, (Kc) is the crop coefficient, which varies with the state of crop development and is adapted as the reference evapotranspiration (ETo) for each crop. It is related directly to the LI or the PGC, since it determines the distribution of energy available from plant surfaces and bare soil.

Because the leaf surface is the main photosynthetic organ of the plant, it is sometimes convenient to express the growth per unit leaf area. The rate of accumulation of dry
matter per unit leaf area and per unit time is called net assimilation rate (NAR) and is usually expressed in g/m² (leaf area) day. The NAR is a measure of average photosynthetic efficiency of leaves in a population. This is high when the plants are small and most of the leaves are exposed to direct sunlight. As the plant grows and the leaf area index increases, the leaves begin to shade, causing a decrease in NAR. For covers with a high LAI, the young leaves at the top take the highest proportion of absorbed radiation, thus having a high rate of CO₂ assimilation and also assimilate many other parts translocated. In contrast, the older leaves at the bottom of the cover, which are shaded, have a low rate of assimilation of CO₂ and provide a small assimilation to other parts of the plant.

Under no-stressed environmental conditions, the amount of dry matter produced by a crop is linearly related to the amount of solar radiation, specifically photosynthetically active radiation (PAR), intercepted by the crop. The slope of the regression between biomass and cumulative radiation intercepted by a crop has been used to determine the radiation use efficiency (RUE), which is calculated as the ratio of the biological yield (kg/ha) to the intercepted PAR (MJ) by the crop plants. Monteith (1977), demonstrated that cumulative seasonal light interception for several crops grown with adequate soil water supply was closely related to biomass production. He formalized and fully established the experimental and theoretical grounds for the relationship (RUE) between accumulated crop dry-matter and solar radiation, arguing that this approach is robust and theoretically appropriate to describe crop growth. RUE is highly dependent on the photosynthetic performance of crop canopies and can be influenced by several factors, namely, extremes temperature, water, and nutrient status. This is indicated by the variation reported in RUE among and within crop species and across locations and growing environments (Subbarao et al 2005). The literature reported quite a large number of RUE values for different crops and locations (Gallagher & Biscoe, 1978; Gosse et al., 1986; Kiniry et al., 1989). Stockle & Kemanian (2009) at intervals showed the value of RUE in g/MJ for large groups of plants: C₃ Annuals (1.2-1.7), C₄ Annuals (1.7-2.0), C₃ Oil crops (1.3-1.6), Legumes (1.0-1.2) and Tuber and root (1.6-1.9). Moreover, the radiation use efficiency (RUE) approach that relates dry mass accumulation to the amount of intercepted PAR (Monteith, 1994; Kiniry, 1999) is widely used to estimate biomass accumulation in horticultural crops, fruit trees and forest (Landsberg & Hingston, 1996; Kiniry et al., 1998; Mariscal et al., 2000).

The efficiency of radiation interception is also influenced by the levels of nutrients in plants, mainly by nitrogen (Dewar, 1996; Scott Green et al., 2003). High crop RUE is directly dependent on obtaining the maximum leaf photosynthetic rate (Sinclair and Horie, 1989; Hammer and Wright, 1993). Nearly 70% of the soluble protein in leaf is concentrated in the carboxylation enzymes (i.e., Rubisco). A positive relationship between leaf nitrogen content per unit area (specific leaf nitrogen) and photosynthetic rates has been reported for a number of crops including wheat, maize, sorghum, rice, soybean, potato, sunflower, peanut, and sugarcane (Muchow & Sinclair, 1994; Sinclair & Shiraiwa, 1993; Sinclair & Horie, 1989; Hammer and Wright, 1993; Evans, 1983; Marshall and Vos, 1991; Giminez, et al 1994; Anten, et al, 1995; Peng, et al, 1994 and Vos & Van Der Putten, 1998 as cited in
Subbarao et al. 2005). The quantum yield of CO₂ assimilation, which is one of the major determinants of the photosynthetic efficiency of crop canopies, reportedly decreases under N deficiency (Meinzer and Zhu, 1998). Levels of photoinhibition also increase under N deficiency (Henley et al., 1991). Thus, a favorable crop nitrogen status appears to be necessary for the realization/expression of maximum RUE in a given crop species. Several studies have reported a positive response of RUE to N fertilization in a number of crops (Muchow & Sinclair, 1994; Hall et al., 1995; Green, 1987). Nitrogen deficiency should decrease the range where there is a linear response between PAR and increased light and thus the range of maximum RUE (Sinclair, 1990; Muchow, 1988). A substantial decrease in RUE under nitrogen stress has been reported for maize (Muchow & Davis, 1988; Muchow, 1994), sorghum (Muchow, 1988), kenaf (Muchow, 1992), wheat (Green, 1987), sunflower (Hall et al., 1995 and Bange et al., 1997), and peanut (Wright et al., 1993). Uhart & Andrade (1995) showed the differences in RUE produced in a crop of corn with nitrogen and without nitrogen, the latter being 40% lower (Fig 11).

The water deficit reduces the interception of solar radiation due to rolling up the leaves (Müller, 2001). If the water deficit is prolonged, the number and size of leaves may be reduced or the total leaf area may decrease, reducing as a result, the interception of radiation (Collinson et al., 1999). Soil water and the resulting plant water status play a key role in determining stomata conductance and canopy photosynthesis. Soil water deficit results in plant water deficits that lead to stomata closure and reduced photosynthesis, and results in loss of photosynthetic efficiency of the canopy and thus to a decrease in RUE (Monteith, 1977). Plants have developed a number of adaptive mechanisms to cope with water deficits to minimize the impact on their productivity (Subbarao et al 1995 and Tunner, 1997). Nearly a 70% decline in RUE due to drought stress was observed in a number of grain legumes (Subbarao et al 2005). Though RUE of C₄ crop species is generally higher than that of C3 crop species, the photosynthetic advantage disappears as the water stress increases.
When drought stress is imposed from flowering until physiological maturity, a 25% decline in RUE occurred in pigeonpea (Nam et al., 1998). The growth of many field crops can be slowed down or even stopped by a relatively moderate water stress (Boyer, 1970). Stress of this magnitude develops following only a few days without rain, resulting in stomata closure, thus limiting photosynthesis (Sheehy et al., 1975). For rice, wheat, maize, sorghum, and pearl millet, drought stress has been reported to decrease RUE (Gallagher and Biscoe, 1978; Lecoeur & Ney, 1991; Inthapan & Fukai, 1988; Muchow, 1989; Whitfield & Smith, 1989; Robertson and Giunta, 1994; Jamieson et al, 1995 as cited in Subbarao et al 2005). A variety of mechanisms that include leaf movements (that can reduce the radiation load on the canopy when exposed to water deficits) and osmotic adjustment, and root attributes (that can maintain water supply during drought spells) play a major role in maintaining high levels of RUE during water stress (Subbarao et al., 2005). Otegui (1992) compared two maize crops under irrigation and no irrigation, LAI experienced a decrease in cultivation without irrigation (Fig 11).

According to crop (processing tomato crop irrigated with two doses) requirements (T100) and a deficit treatment of 75% of crop needs throughout all crop cycle (T75), LAI measurement and the evolution of dry biomass (aerial biomass) deficit treatment has a lower accumulation of biomass and LAI throughout the crop cycle. This aspect affected the final crop production. Reductions in RUE due to water deficits have been reported by Hughes and Keatinge (1983) and Singh and Sri Rama (1989) in grain legumes. Tesfaye et al., (2006) indicated that dry matter production in grain legumes is highly associated with the fraction of PAR intercepted, which in turn is highly associated with LAI. Li et al. (2008) showed that furrow planting pattern should be used in combination with deficit irrigation to increase the RUE and grain yield of winter wheat in North China. Miralles and Slafer (1997) indicated that post-anthesis RUE appeared to be closely and positively associated and with the number of grains set per unit biomass at anthesis in winter wheat, and Uhart & Andrade (1995) found that stresses reduced the leaf photosynthetic rate and could result in lowering RUE. Whitfield and Smith (1989), Chen et al. (2003), and Li et al. (2008) showed that crop yield was positively related to RUE in winter wheat.

In the modern agricultural research one of the methods in analyzing the crop production along the growth season is simulation by means of the crop production model (Aquacrop, Cropsys, CERES,…); mathematical crop simulation models can quantify the different processes that lead to the yield formation. Once calibrated and validated for a zone, a theoretical harvest with different types of soil management and certain climatic conditions is obtained. The predictive ability of these models can be significantly improved by adjusting the model input data on biomass generated at certain stages of crop development (Baret et al., 1989; Chistensen & Goudriaan, 1993). Water stress and nutrition reduces LAI for a smaller size and greater leaf senescence. The smaller size of LAI agrees with light capture and thus crop growth, decreasing the efficiency of radiation.

The measurement of the radiation intercepted by a crop for the formation of leaf area is an important factor in monitoring crops, water relations studies, nutrition and crop simulation models. A good measurement of both parameters will be important in studying the effects of solar radiation on crops.
Intercepted radiation measurement

Quantifying the intercepted radiation (LI) is therefore an important consideration when studying the different agricultural or environmental factors on yield; it is the main source of data in the most widely used methods for estimating crop water needs.

The LI measurement methods are not necessarily destructive, since the provision of plants on the ground plays a key role. However, there are differences between the different methods in terms of the changes introduced into the covers to make measurements, direct methods and indirect methods.

LI measurement with direct methods

A direct method for determining the percentage of intercepted radiation (LI) is to measure PAR both above and below the canopy at noon on completely cloudless days (Board et al., 1992; Purcell, 2000; Reta-Sánchez y Fowler, 2002):

\[ LI = 1 - \frac{\text{PAR below canopy}}{\text{PAR above canopy}} \] ..............................(1)

Commercially available lineal PAR sensors are used to take these measurements which are based on PAR values registered by the sensor. These measurements can be taken either by locating sensors perpendicular to the crop rows (Egli, 1994) or by taking multiple measurements parallel to them (Board et al., 1992). The latter method can be costly, according to the number of measurements needed to characterize the study area, especially in the case of low-lying crops, where it may be necessary to remove vegetation in order to place sensors under it, which also has the drawback of introducing alterations during data collection. Using the percentage of shaded soil at solar noon or the percentage of ground cover (PGC) to estimate LI, is an easier and more economical way to obtain the required data. It is generally assumed that the shaded area at soil level corresponds to the fraction of incident radiation which has been intercepted by the crop. This is an approximation that is valid as long as the percentage of light transmission through the leaves is small in comparison to its absorption. The precision with which PGC estimates LI will therefore depend on how well the shaded area is defined and on the capacity of the canopy to capture all of the radiation within the shaded area. In this second case, estimates could be improved by taking complementary measurements of radiation at a sufficient number of points within the shaded area to characterize the radiation traversing the canopy (Lang et al., 1985).

Some of the methods used to determine PGC involve visual estimates (Olmstead et al., 2004; Ortega-Farias et al., 2004). Methods such as the “interception line” (Gallo y Daughtry 1986; Mohillo y Moran, 1991), the analysis the intersection of shadows on metric strips and paper drawings of the sampling areas were used to determine PGC in a non-destructive way (García et al., 2001). However, to apply these last three methods, cloudless days are needed, as a sufficient number of measurements at different orientations are needed to allow a reliable characterization of the area (Ewing y Horton, 1999). The precision of the visual estimation method varies, because it depends on the skill of the operator; results will not be comparable when several people are involved (Olmstead et al., 2004). Furthermore, it has been shown that coverage values tend to be overestimated (Olmstead et al., 2004). In the cases of the interception line and metric strip methods, similar problems are encountered as those associated with the use of PAR bars in the case of low-lying crops and it is difficult to take measurements below the canopy. Finally, making paper drawings is very costly when working under field conditions and when a relatively large area must be characterized.
LI measurement with indirect methods

In indirect methods, different apparatus for estimating the different components of radiation, such as direct radiation, diffuse, land, atmospheric... are used which consider the net radiation balance in order to know how much available radiation reaching the surface. The inherent difficulties in measuring PAR throughout a canopy and advances in radiometric techniques have led to the development of methods for remotely sensing radiation capture. Radiometric methods rely on differences in the spectral reflectance of vegetation and soil. Vegetative indices based on reflectance in broad wavebands have provided good estimates of radiation capture and yield in crop plants (Gallo et al., 1985; Hatfield et al., 1984). Vegetation indices have also provided good estimates of fractional ground cover (Boissard et al., 1992; White et al., 2000). More recently, spectroradiometers capable of measuring narrow band radiation have been used to monitor plant stress (Elvidge & Chen, 1995). Radiometric satellite data are now available for the evaluation of large areas, and small portable radiometers are becoming less expensive as the technology progresses. In this respect, good results have been obtained with measurements using digital photographic images to determine crop cover and radiation interception in soybean (Purcell, 2000) and lettuce (Klassen et al., 2003), crop cover in turfgrass (Richardson et al., 2001), and canopy and soil cover with straw mulch (Bennet et al., 2000; Beverly, 1996; Olmstead et al., 2004). Other important points are that the area of soil exposed to the sun can be differentiated from that covered by leaves while the angle of the camera is close to that of the sun (Purcell, 2000). With regards to differentiating between the green parts of the crop and the soil surface, results could vary in the case of soils of different colors as a result of their different behavior with respect to the reflection and absorption of radiation; this is particularly the case for different kinds of mulches. In this case, the validity of the method will largely depend on the capacity of the software to discriminate between parts of the crop’s green canopy. In the presence of weeds or green cover, it may be necessary to prescreen images.

Digital images offer a series of additional advantages over other methods for estimating LI, assuming that the soil background can be distinguished from leaves, light transmission of leaves is small relative to light absorption, and that the angle of the camera to the horizon approximates the solar angle (Purcell, 2000) such as the direct treatment of images by computers. Moreover, a graphic record of the crop is generated in the case of studies of canopy evolution. This can be used for phonological monitoring (Shelton et al., 1988) to determine differences in color and fertility in maize (Ewing and Horton, 1999) and to study the incidence of pests and diseases.

Automated methods of digital image analysis are indirect methods of LI measurement. Initially they were not widely used because they generally require complex and expensive instrumentation, as well as making mistakes with the changing colors of soil and plant (Hayes & Han, 1993; Van Henten & Bontsema, 1995; Beverly 1996). However, no alteration of vegetation cover and the automation of image analysis have allowed the elimination of many subjective decisions of the observer.

Recent advances in high-resolution digital cameras and associated image manipulation software provide enhanced methods of visual discrimination and computer thresholding that are user-friendly and inexpensive. Three recent studies have demonstrated the accuracy of

A seemingly key advantage of using digital cameras is that they allow for continuous monitoring of vegetation (White et al., 2000), in the case of low-lying horticultural crops. These measures do not alter the disposition of the crop. Replacing standard procedures, such as the width of cultivation, direct quantification of the shadows or linear PAR sensors, are subjective and costly, and often inaccurate (Campillo et al., 2008). Taking advantage of the latest developments in digital technology, it is now possible to measure the evolution of vegetation cover through digital photography and to determine the PGC using image interpretation techniques (Campillo et al., 2008; Rodríguez et al., 2000).

Fig. 12a. Digital images of processing tomato measure with a area method.

Campillo et al (2008), compared LI methodology (PAR) with various methods of PGC measurement. They used three methodologies to measure PGC in two low-lying crops, a winter crop (cauliflower) and a summer crop (processing tomato) in two consecutive years (2005 and 2006) and (2005) in cauliflower crop.

**Area method (SA):** In this method, crop row width was estimated by simulation based on measurements taken at three points within the marked area using a metric strip. The data were then used to estimate average row width and the PGC (Adams & Arkin, 1977; Giménez, 1985). Both row and frame width were determined in pixels using the measuring tool
(IMAGE J 1.33). The sampling area was delimited by the width (X) and length (Y) of the reference frame (Fig. 12a) and the three measurements of row width were: x1, x2, x3. PGC was calculated using the expression:

$$PGC = \left[ \frac{x_1 + x_2 + x_3}{3} \right] \cdot \frac{Y}{(X+Y)} \cdot 100$$

(2)

Fig. 12b. Digital images of processing tomato measure with a contour method.

Contour method (SC): In this method, the technique of drawing the crop’s shade contour on paper and the subsequent measurement of the area in question is simulated (Kvet & Marshall, 1971). Fig 12b shows the processing of the digital image. To measure the area, the crop’s contour was previously delimited using the IMAGE J 1.33 program. Areas with no vegetation cover that were within the canopy were measured and omitted from the surface area count. The crop surface area (S) was measured in pixels using the same program. This area was then related to the sampling area to estimate the PGC according to the following expression:

$$PGC = \left[ \frac{S^2}{(X+Y)} \right] \cdot 100$$

(3)

Fig. 12c. Digital images of processing tomato measure with a reclassification method.
Reclassification method (SR). With this method (Fig. 12c), the crop area (S) is determined by classifying the image according to the range of radiation levels shown on an RGB image of the crop (0 to 255 colors); this was done using a RGB max reclassification tool (GIMP 2.2). After the classification process, it is possible to measure the surface area occupied by green parts (crop) and to differentiate them from the soil or plastic. In contrast to the other two methods, here the crop must be subjected to homogeneous lighting conditions, because the presence of shadows may reduce a crop’s color and impede subsequent color reclassification. PGC was calculated according to formula [3].

PGC measurements were compared with measurements made with a LI PAR bar. Intercepted radiation: LI measurements were made using a 100-cm linear PAR sensor (LICOR Li-190; LI-COR, Lincoln, NE). They were made at solar noon, perpendicular to the crop row, in the same area in which the photographs had been taken. Samples taken from below the crop were compared with reference measurements taken above the crop row (ref). Percentages of LI were calculated by applying Eq. [4], in which it was necessary to know the percentage of radiation that was not intercepted by the crop (RP) as a quotient of the PAR measurements taken both above and below the canopy. According to the degree of plant development two situations for measurement of RP were proposed:

1. When the crop row width was less than 100 cm, RP was calculated by applying Eq. [5] as the average of five measurements taken under the crop (r1, r2, r3, r4, r5). Measurements were taken every 20 cm using the total length of the PAR bar (100 cm) and adding 50 cm to the reference measurement to include the total width of crop (150 cm). In this situation, ref was measured using the total length of the PAR bar.

2. When the crop row width was greater than 100 cm the maximum length of the PAR sensor, RP was calculated applying Eq. [6] as the average of three measurements taken beneath the crop on each side of the crop row (r1, r2, r3 left side and r4, r5, r6 right side). Measurements were taken at 20-cm intervals using a half-length PAR bar (50 cm).

The sensor was covered with a material that blocks light and average measurements were taken in the center of the row (r7, r8), also using a half-length PAR bar (50 cm). This was done in a way that included the total width of culture (150 cm). In this situation, ref was measured using a half-length PAR bar (50 cm).

\[
LI = [1 - RP] * 100  \quad \text{..................................................(4)}
\]

\[
RP = \left[ \frac{\text{mean} (r_1, r_2, r_3) + 0.5 \times \text{mean} (r_{ef})}{\text{mean} (r_{ef}) + 1.5} \right]  \quad \text{.................................(5)}
\]

\[
RP = \left[ \frac{\text{mean} (r_1, r_2) + \text{mean} (r_3, r_4, r_5) + \text{mean} (r_6, r_7, r_8)}{\text{mean} (r_{ef}) + 3} \right]  \quad \text{.................................(6)}
\]

There was a close relationship between the fraction of light intercepted by the canopy at solar noon and estimated PGC for all three methodologies. This indicates that any of the described methods would have been valid for estimating the amount of radiation intercepted by the crop. However, SR and SC methods are stronger than SA.

**Leaf area index measurement**

Determination of LAI is often the most expensive in a field study, because direct measurement (destructive methods) is time-consuming. We can classify in the same way as with LI, in direct methods (which can be destructive or non-destructive) and indirect, based on properties of vegetation cover, being non-destructive.

**LAI measurement with direct methods**
Direct methods for determining leaf area have so far been restricted to the use of an automatic area-integrating meter. Tracing, shadow graphing, and the use of a planimeter to measure the total leaf area attached to shoots are all time-consuming and are tedious approaches; furthermore, in some experiments, there is not enough time to make such measurements (Manivel & Weaver, 1974). All direct methods are similar in that they are difficult, extremely labor-intensive, require many replicates to account for spatial variability in the canopy, and are therefore costly in terms of time and money and also destructive.

**LAI measurement with indirect methods**

Many indirect methods for measuring LAI have been developed. Methods based on empirical relationships between leaf area and easily obtainable parameters such as the size of the leaves are available. In any case, the empirical relationship should always be check with direct action as they may vary during the crop cycle and some other varieties. Some used are \( S = A \cdot L \cdot I \) and \( S = A \cdot L \cdot B \), where \( S \) is the area, \( L \) the length and \( I \) the maximum width plant element, \( A \) and \( B \) are empirical elements. Also can estimate the leaf area through relationships with the weight. A first group of methods is based on the \( S = \frac{M}{\omega} \) where \( M \) is the leaf weight in grams and \( \omega \) is the specific weight \((\text{g/m}^2)\) (Patón et al., 1998). Techniques based on gap-fraction analysis assume that leaf area can be calculated from the canopy transmittance (the fraction of direct solar radiation which penetrates the canopy) (Ford, 1997). Optical methods are indirect, non-contact, and are commonly implemented. They are based on the measurement of light transmission through canopies (Jonckheere et al., 2004). These methods apply the Beer-Lambert law, taking into account the fact that the total amount of radiation intercepted by a canopy layer depends on the incident irradiance, the canopy structure, and its optical properties (Breda, 2003). Monsi & Saeki (1953) expanded the Beer-Lambert extinction law to apply it to plant canopies. The Beer-Lambert law expresses the attenuation of radiation in a homogenous turbid medium. In such a medium, the flux is absorbed in proportion to the optical distance. The LAI is related to the incident solar radiation intercepted by the crop \((LI)\) and extinction coefficient \((K)\), which describes the angle of the blades in relation to the sun, through the formula proposed by Monsi and Saeki (1953):

\[
LI = 1 - e^{-(K \cdot LAI)}
\]

This approach could also be used to estimate LAI using Eq. [7]; however, we would need to know the extinction coefficient for each crop and variety (Campbell, 1986). Several authors have discussed how to determine \( K \) (Hassika et al., 1997; Ledent, 1977; Smith, 1993; Vose et al., 1995) and the accuracy of methodology to be applied (Nel & Wessman, 1993). It is also important to consider that the extinction coefficient also depends on stand structure and canopy architecture (Smith et al., 1991; Turton, 1985) and that the canopy extinction coefficient is a function of wavelength (Jones, 1992), radiation type, and direction (Berbigier & Bonnefond, 1995). It is also important to maximize spatial integration by using large, linear and/or mobile sensors. Extinction coefficient, which varies with species, season and environmental conditions (Hay & Walter, 1989), take values in terms of leaf angles: spherical \((0.5-0.7)\), conical \((1)\), vertical or erectofila \((0.3-0.7)\). The distributions of leaf angles have agronomic and ecological implications. Horizontal distribution implies a high \( K \), allowing for
increased intercepted radiation by small plants. The disadvantage is that when the LAI is high the light distribution is very unequal, the lower leaves receive little light, which tends to accelerate senescence. In the opposite, erectofila distribution can be advantageous to intercept radiation when the zenith angle is large (winter, high latitudes) and represents a more homogeneous distribution of radiation when the LAI is high.

This method involves ground-based measurements of total, direct, and/or diffuse radiation transmittance to the forest floor and it makes use of line quantum sensors or radiometers (Pierce and Running, 1988), laser point quadrats (Wilson, 1963), and capacitance sensors (Vickery et al., 1980). These instruments have already proven their value in estimations of LAI for coniferous (Marshall and Waring, 1986; Pierce and Running, 1988) as well as broad-leaved (Chason et al., 1991) stands. In comparison with allometric methods, the approach provides more accurate LAI estimates (Smith et al., 1991). However, the light measurements required to calculate LAI require cloudless skies, and there is generally a need to incorporate a light extinction coefficient that is both site and species-specific as a result of leaf angle, leaf form, and leaf clumping, etc. (Vose et al., 1995). Measurements can be taken either by locating the sensors perpendicular to the crop rows (Egli, 1994) or by taking multiple measurements parallel to them (Board et al., 1992). This determination can, however, be costly; it depends on the number of measurements needed to characterize the study area, especially in low-lying crops, where vegetation must be moved to place sensors under it, which implies introducing alterations during data collection. There are several commercial systems available to measure indirectly the structure of vegetation and LAI, based on the Beer-Lambert law, including analyzer plant canopy (plant canopy analyzer LiCor LAI-2000) (Li-Cor, 1989); (Cintra et al., 2001; Malone, 2002). El LiCor LAI-2000 has an optical sensor and a control box easily manipulated by an operator. The LAI is estimated according to a model developed by Miller (1967), based on gap-fraction analysis (Barclay et al., 2000). Similar instruments is the CI-100 (Digital plant canopy imager). It consists of a digital camera with a lens of "fish eye" with a 180 degrees field of view.

The analysis of remote estimation methods, provides a temporal and spatial information. The new technologies, provide LAI data from digital cameras (Adamsen et al., 1999), video images (Beverly, 1996), multispectral digital sensors (Bellairs et al., 1996; Shanahan et al., 2001), aerial imagery (Blackmer et al., 1996; Flowers et al., 2001) and satellite images (Wiegand et al., 1979; Thenkabail et al., 1992; Green et al., 1997). One of the remote methods most used is Normalized Difference Vegetation Index (NDVI). These spectral reflectances are themselves ratios of the reflected to the incoming radiation in each spectral band individually, hence they take on values between 0.0 and 1.0. By design, the NDVI itself thus varies between -1.0 and +1.0. It should be noted that NDVI is functionally, but not linearly, equivalent to the simple infrared/red ratio (NIR/VIS). The advantage of NDVI over a simple infrared/red ratio is therefore generally limited to any possible linearity of its functional relationship with vegetation properties (e.g. biomass). This method is sensitive to background soil and weather conditions (Gilabert et al., 1997). There are different satellite sources where one can get the values of NDVI with different resolutions; AVHRR (Advanced Very High Resolution Radiometer), MODIS (Moderate Resolution Imaging Spectroradiometer), SPOT. Vegetation indices are widely used for the calculation of biomass
Campillo et al. 2010, compared a winter crop (cauliflower) and a summer crop (processing tomato) in two consecutive years (2005 and 2006) for measurements of PGC (non-destructive method) and LAI (destructive method). The objective was relations of two parameters and the possibility of using a PGC methodology as a LAI measurement in vegetable crops.

A polynomial relationship \( r^2 > 0.88 \) was observed between the two variables in both crops. PGC increased with leaf area development in a curve-linear pattern composed of an initial linear phase followed by a saturating phase, and lately a maximum asymptotic value at full groundcover.

In cauliflower, significant differences were observed between the curves obtained for each year \( r^2 = 0.89 \) and 0.95 for the first and second years, respectively). This difference was the result of a significant change in the prevailing weather conditions during the crop cycle that affected the morphology of the leaves. Temperatures in the first year were lower than in the second and frequent frosts caused the curling of leaf margins, resulting in a lower PGC for the same LAI. The PGC–LAI curve adjustments for the tomato crop were significant. The curves coincided for both years, although with differences in the adjustment \( 0.89 \) and 0.93 for 2005 and 2006, respectively). In this case, a single curve would have enabled us to estimate the LAI by nondestructive methods using digital images. Although, in principle, the factors that can modify the arrangement of leaves could alter this relationship, this trial included treatments with different water statuses that could have induced changes in plant leaf angle, but this aspect did not affect the goodness of fit. It still remains to be seen how this equation would be influenced by morphological (plant height and leaf type) differences between varieties. The PGC of a crop depends on the leaf area development and on the distribution of the plant leaves on the space (plant architecture). PGC is therefore the dependent variable in the relationship between LAI and PGC. The equations obtained for these two crops are highly significant with a narrow adjustment; they therefore provide a method for estimating LAI based on known PGC values.

From the data obtained when comparing LAI values with those of PGC, and from that obtained by Campillo et al. (2008) relating to PGC as a good estimator of LI, from Eq. [7], we obtained extinction coefficients for growing tomatoes and cauliflower with values ranging between 0.75 and 0.85 and 0.60 and 0.70, respectively. These data are consistent with the value of 0.75 obtained by Heuvelink et al. (2005) for the cultivation of tomato and of 0.55 for growing cauliflower proposed by Olesen & Greven (1997). Tei et al. (1996) obtained similar extinction coefficients for other horticultural crops with morphological similarities to cauliflower such as beets and lettuce (0.68 and 0.60, respectively). Campbell (1986) made an overall estimate of extinction coefficients for various crops based on the angle distribution of their leaves; considering average values for crops with leaf angles that were mainly almost horizontal, the values obtained ranged between 0.50 and 0.70.

The method of estimation of LAI was applied on four crops: Tobacco, pepper, soybean and eggplant. The crops chosen for evaluation sought validation of the method in species with very different morphological architectures, both in distribution and area occupied by the
plant, as well as the height of it. It turned to be an exponential relationship between the results derived from photography method and leaf area calculated with the planimeter. Linear correlation coefficients obtained for the various crops were 0.89 for eggplant, 0.91 for pepper, soya and 0.87 to 0.88 for tobacco. The correlations obtained in this evaluation were quite heterogeneous despite the morphological disparity and architecture of the different species tested, yielding correlations above 0.87 in all cases. In the case of crops of eggplant, pepper and tobacco, the growth of the canopy crop growth and leaf area occurred at the same time, the highest percentage agreeing with the largest canopy leaf area indices. This dynamic growth was not followed in the case of soybean, where the plant develops its canopy in great haste once covered. The development was apical exponential until reaching a constant height. Therefore, the feasibility of this approach is restricted to the early stages of soybean development, until it reaches the highest percentage of land shaded.

**Photosynthesis**

All living things need **energy**, which is defined as the ability to do work. We can often see energy at work in living things—a bird flies, a fire fly glows in the dark, a dog wags its tail. These are obvious ways that living things use energy, but living things constantly use energy in less obvious ways as well.

**Why Living Things Need Energy**

Inside every cell of all living things, energy is needed to carry out life processes. Energy is required to break down and build up molecules and to transport molecules across plasma membranes. All life’s work needs energy. A lot of energy is also simply lost to the environment as heat. The story of life is a story of energy flow—its capture, its change of form, its use for work, and its loss as heat. Energy, unlike matter, cannot be recycled, so organisms require a constant input of energy. Life runs on chemical energy. Where do living organisms get this chemical energy?

**How Organisms Get Energy: Autotrophs and Heterotrophs**

The chemical energy that organisms need comes from food. **Food** consists of organic molecules that store energy in their chemical bonds. In terms of obtaining food for energy, there are two types of organisms: autotrophs and heterotrophs.

**Autotrophs** - Autotrophs are organisms that make their own food. Most autotrophs use the energy in sunlight to make food in a process called **photosynthesis**. Only three types of organisms—plants, algae, and some bacteria—can make food through photosynthesis. Examples of each type of photosynthetic organism are shown in **Fig 13**.

![Fig 13: Photosynthetic autotrophs, which make food using the energy in sunlight, include (a) plants,](image-url)
(b) algae, and (c) certain bacteria.

Autotrophs are also called **producers**. They produce food not only for themselves but for all other living things as well (which are known as consumers). This is why autotrophs form the basis of food chains, such as the food chain shown in Fig 14.

![Food Chain Diagram](image)

**Fig 14**: A food chain shows how energy and matter flow from producers to consumers. Matter is recycled, but energy must keep flowing into the system. Where does this energy come from?

**Heterotrophs** - Heterotrophs are living things that cannot make their own food. Instead, they get their food by consuming other organisms, which is why they are also called **consumers**. They may consume autotrophs or other heterotrophs. Heterotrophs include all animals and fungi and many single-celled organisms. In Fig 14, all of the organisms are consumers except for the grass. What do you think would happen to consumers if all producers were to vanish from Earth?

**Energy Molecules: Glucose and ATP**

Organisms mainly use two types of molecules for chemical energy: glucose and ATP. Both molecules are used as fuels throughout the living world. Both molecules are also key players in the process of photosynthesis.

**Glucose**

Glucose is a simple carbohydrate with the chemical formula $C_6H_{12}O_6$. It stores chemical energy in a concentrated, stable form. In your body, glucose is the form of energy that is carried in your blood and taken up by each of your trillions of cells. Glucose is the end product of photosynthesis, and it is the nearly universal food for life.

**ATP**

ATP (adenosine triphosphate) is the energy-carrying molecule that cells use for energy. ATP is made during the first half of photosynthesis and then used for energy during the second half of photosynthesis, when glucose is made. It is also used for energy by cells for most other cellular processes. ATP releases energy when it gives up one of its three phosphate groups and changes to ADP (adenosine diphosphate).
Why Organisms Need Both Glucose and ATP

Why do living things need glucose if ATP is the molecule that cells use for energy? Why don’t autotrophs just make ATP and be done with it? The answer is in the “packaging.” A molecule of glucose contains more chemical energy in a smaller “package” than a molecule of ATP. Glucose is also more stable than ATP. Therefore, glucose is better for storing and transporting energy. However, glucose is too powerful for cells to use. ATP, on the other hand, contains just the right amount of energy to power life processes within cells. For these reasons, both glucose and ATP are needed by living things.

Making and Using Food

The flow of energy through living organisms begins with photosynthesis. This process stores energy from sunlight in the chemical bonds of glucose. By breaking the chemical bonds in glucose, cells release the stored energy and make the ATP they need. The process in which glucose is broken down and ATP is made is called cellular respiration. Photosynthesis and cellular respiration are like two sides of the same coin. This is apparent from Fig 15. The products of one process are the reactants of the other. Together, the two processes store and release energy in living organisms. The two processes also work together to recycle oxygen in Earth’s atmosphere.

![Diagram of photosynthesis and cellular respiration](image)

**Fig 15:** This diagram compares and contrasts photosynthesis and cellular respiration. It also shows how the two processes are related.
Photosynthesis

Photosynthesis is often considered to be the single most important life process on Earth. It changes light energy into chemical energy and also releases oxygen. Without photosynthesis, there would be no oxygen in the atmosphere. Photosynthesis involves many chemical reactions, but they can be summed up in a single chemical equation:

$$6\text{CO}_2 + 6\text{H}_2\text{O} + \text{Light Energy} \rightarrow \text{C}_6\text{H}_{12}\text{O}_6 + 6\text{O}_2.$$  

Photosynthetic autotrophs capture light energy from the sun and absorb carbon dioxide and water from their environment. Using the light energy, they combine the reactants to produce glucose and oxygen, which is a waste product. They store the glucose, usually as starch, and they release the oxygen into the atmosphere.

Photosynthesis occurs in two stages, which are shown in Fig 16.

1. Stage I is called the **light reactions**. This stage uses water and changes light energy from the sun into chemical energy stored in ATP and NADPH (another energy-carrying molecule). This stage also releases oxygen as a waste product.

2. Stage II is called the **Calvin cycle**. This stage combines carbon from carbon dioxide in the air and uses the chemical energy in ATP and NADPH to make glucose.

Fig 16: The two stages of photosynthesis are the light reactions and the Calvin cycle. Do you see how the two stages are related?

Before we read about these two stages of photosynthesis in greater detail, we need to know more about the chloroplast, where the two stages take place.
**The Chloroplast: Theater for Photosynthesis**

The “theater” where both stages of photosynthesis take place is the chloroplast. Chloroplasts are organelles that are found in the cells of plants and algae. (Photosynthetic bacteria do not have chloroplasts, but they contain structures similar to chloroplasts and produce food in the same way.) Look at the Fig 17. The figure is a high power microscopic photo of the upper part of a Winter Jasmine leaf. If you could look at a single leaf of this plant under a microscope, you would see small green ovals, like those shown. These small green ovals are chloroplasts. These are microscopic organelles of varying sizes (4-6 µm in diameter) and shape (round to oval). Their fine structure can be distinguished from electron microscope. Contents of chloroplast are bounded by a double membrane system or envelop. These membranes are continuous with no perforations and are differentially permeable as the plasmalemma of the cell when exposed to solutions of different osmotic potentials.

![Fig 17](image)

Fig 17: High power microscopic photo of the upper part of a Winter Jasmine leaf. Viewed under a microscope many green chloroplasts are visible.

**Fig 18** shows the components of a chloroplast. Each chloroplast contains neat stacks called **grana** (singular, granum). The granum consist of sac-like membranes, known as **thylakoid membranes**. These membranes contain **photosystems**, which are groups of molecules that include **chlorophyll**, a green pigment. The light reactions of photosynthesis occur in the thylakoid membranes. The **stroma** is the space outside the thylakoid membranes. This is where the reactions of the Calvin cycle take place. Some of the thylakoids may be connected to other grana by membranes in the stroma. These connecting links between grana are the stroma lamellae. The chloroplast of algae usually lack grana and in the blue green algae the lamellae are found in the cytoplasm with no confining envelop. In higher plants chloroplast pigments are confined to the membranes. Granules, lipid droplets, starch grains and vesicles, in addition to the lamellae system, may be found in the stroma. Eye spots and pyrenoid bodies, often found in algae cells, are also found in the matrix.
Fig 18: A chloroplast consists of thylakoid membranes surrounded by stroma. The thylakoid membranes contain molecules of the green pigment chlorophyll.

**Photosynthesis Stage I: The Light Reactions**
The first stage of photosynthesis is called the light reactions. During this stage, light is absorbed and transformed to chemical energy in the bonds of NADPH and ATP. We can follow the process in the Fig as we read about it below.

**Steps of the Light Reactions**
The light reactions occur in several steps, all of which take place in the thylakoid membrane, as shown in Fig 19.

- **Step 1:** Units of sunlight, called photons, strike a molecule of chlorophyll in photosystem II of the thylakoid membrane. The light energy is absorbed by two electrons (2 e\(^{-}\)) in the chlorophyll molecule, giving them enough energy to leave the molecule.

- **Step 2:** At the same time, enzymes in the thylakoid membrane use light energy to split a part of a water molecule. This produces:
  1. two electrons (2 e\(^{-}\)). These electrons replace the two electrons that were lost from the chlorophyll molecule in Step 1.
  2. an atom of oxygen (O). This atom combines with another oxygen atom to produce a molecule of oxygen gas (O\(_2\)), which is released as a waste product.
  3. two hydrogen ions (2 H\(^{+}\)). The hydrogen ions, which are positively charged, are released inside the membrane in the thylakoid interior space.

- **Step 3:** The two excited electrons from Step 1 contain a great deal of energy, so, like hot potatoes, they need something to carry them. They are carried by a series of electron-transport molecules, which make up an **electron transport chain**. The two electrons are passed from molecule to molecule down the chain. As this happens, their energy is captured and used to pump more hydrogen ions into the thylakoid interior space.

- **Step 4:** When the two electrons reach photosystem I, they are no longer excited. Their energy has been captured and used, and they need more energy. They get energy from light, which is absorbed by
chlorophyll in photosystem I. Then, the two re-energized electrons pass down another electron transport chain.

- **Step 5:** Enzymes in the thylakoid membrane transfer the newly re-energized electrons to a compound called \( \text{NADP}^+ \). Along with a hydrogen ion, this produces the energy-carrying molecule NADPH. This molecule is needed to make glucose in the Calvin cycle.

- **Step 6:** By now, there is a greater concentration of hydrogen ions—and positive charge—in the thylakoid interior space. This difference in concentration and charge creates what is called a chemiosmotic gradient. It causes hydrogen ions to flow back across the thylakoid membrane to the stroma, where their concentration is lower. Like water flowing through a hole in a dam, the hydrogen ions have energy as they flow down the chemiosmotic gradient. The enzyme ATP synthase acts as a channel protein and helps the ions cross the membrane. ATP synthase also uses their energy to add a phosphate group (Pi) to a molecule of ADP, producing a molecule of ATP. The energy in ATP is needed for the Calvin cycle.

![Diagram of Photosynthesis](image)

**Fig 19:** This Fig shows the light reactions of photosynthesis. This stage of photosynthesis begins with photosystem II (so named because it was discovered after photosystem I). Find the two electrons (2 e-) in photosystem II, and then follow them through the electron transport chain to the formation of NADPH in Step 5. In Step 6, where do the hydrogen ions (H+) come from that help make ATP?

**Photosynthesis Stage II: The Calvin Cycle**

The second stage of photosynthesis takes place in the stroma surrounding the thylakoid membranes of the chloroplast. The reactions of this stage can occur without light, so they are sometimes called light-independent or dark reactions. This stage of photosynthesis is also known as the Calvin cycle because its reactions were discovered by a scientist named Melvin Calvin. He won a Nobel Prize in 1961 for this important discovery. In the Calvin cycle, chemical energy in NADPH and ATP from the light reactions is used to make glucose. We can follow the Calvin cycle in **Fig 20.**

**Steps of the Calvin Cycle**

The Calvin cycle has three major steps: carbon fixation, reduction, and regeneration. All three steps take
place in the stroma of a chloroplast.

- **Step 1: Carbon Fixation.** Carbon dioxide from the atmosphere combines with a simple, five-carbon compound called RuBP. This reaction occurs with the help of an enzyme named RuBisCo and produces molecules known as 3PG (a three-carbon compound, 3-Phosphoglyceric acid).

- **Step 2: Reduction.** Molecules of 3PG (from Step 1) gain energy from ATP and NADPH (from the light reactions) and re-arrange themselves to form G3P (glycerate 3-phosphate). This molecule also has three carbon atoms, but it has more energy than 3PG. One of the G3P molecules goes on to form glucose, while the rest of the G3P molecules go on to Step 3.

- **Step 3: Regeneration.** The remaining G3P molecules use energy from ATP to form RuBP, the five-carbon molecule that started the Calvin cycle. This allows the cycle to repeat.

![Figure 20: The Calvin cycle begins with a molecule named RuBP (a five-carbon sugar, Ribulose-1,5-bisphosphate) and uses the energy in ATP and NADPH from the light reactions. Follow the cycle to see what happens to all three of these molecules. Two turns of the cycle produce one molecule of glucose (called sucrose in the figure). In this diagram, each black dot represents a carbon atom. Keep track of what happens to the carbon atoms as the cycle proceeds.](image)

**Chemosynthesis**

Most autotrophs make food by photosynthesis, but this isn’t the only way that autotrophs produce food. Some bacteria make food by another process, which uses chemical energy instead of light energy. This process is called **chemosynthesis**. Some chemosynthetic bacteria live around deep-ocean vents known as “black smokers.” Compounds such as hydrogen sulfide, which flow out of the vents from Earth’s interior, are used by the bacteria for energy to make food. Consumers that depend on these bacteria to produce food for them include giant tubeworms, like these pictured in **Fig 21**. Why do bacteria that live deep below the ocean’s surface rely on chemical compounds instead of sunlight for energy to make food?
Factors essential for photosynthesis

Like any other physiological process, photosynthesis is affected by the conditions of the environment in which it occurs. According to the concepts of three cardinal points, there is a minimum, optimum and maximum for each factor in relation to photosynthesis. For example any species has a minimum temperature below which no photosynthesis takes place, and optimum temperature at which the highest rate takes place and a maximum temperature above which no photosynthesis takes place. However, external factors affecting photosynthesis cannot be treated individually but in relation to one another. The Blackman’s principle of limiting factors which is actually a modification of Liebig’s law of the minimum states that the rate of a process controlled by several factors is only as rapid as the slowest factor permits. At lower concentration of the limiting factor, a proportional relationship often appears to exist between rate and quantity of the limiting factor present, but at higher concentration this is not so. Therefore, an approximation of the effect of these factors can be obtained.

External factors
Light (Intensity, quality and duration), carbon dioxide, temperature, oxygen, water, mineral nutrients.

Internal factors
Chlorophyll contents, protoplasmic factors and accumulation of carbohydrates.

Light: The plant is capable of using only a very small portion of the incident electromagnetic radiation that fall on a leaf or the radiation that is absorbed by the pigment complex of the leaf. The chlorophylls absorb heavily in the blue and red regions of the spectrum and β-carotene absorbs mostly in the blue region. Most of the light reflected, then, is in the green region, thereby giving a leaf green colour. Thick leaves absorb more light than thinner leaves and have lower transmittance. The average green leaf will transmit only about 10% of the incident infrared free white light and 25-35% incident sunlight including infrared radiation.
Leaves, in general, are almost transparent to infrared and far-red radiation. There is a direct relationship between the rate of photosynthesis and the intensity of light, provided other factors are not limited. However, this relationship holds true at lower light intensities. As light intensity increases, the photosynthetic rate falls off because of some other limiting factor or because of the destructive effects of the high light intensity. Also, the point of saturation may be reached at which time the rate of photosynthesis will remain stationary.

On bright sunny days, the CO_2 concentration of the atmosphere, not the light intensity, is usually limiting the rate of photosynthesis. However, on cloudy days, light may be the limiting factor. Another variable that may be considered is the shading effect of one species on another or even the shading effect of outer leaves on the inner leaves of a tree. The intensity of light reaching the forest floor is greatly diminished, thereby making light a limiting factor under these conditions. Rate of photosynthesis by an apple tree was steadily increased with light intensity up to about full sunlight, even though saturation intensity for a single exposed leaf was a good deal lower (Heinicke and Childers). About one-fourth of full summer sunlight (2500 to 3000 footcandles) is all that is needed for maximum photosynthesis in a single, normally exposed leaf of corn. Undoubtedly, the need for higher light intensities for maximum photosynthesis of an entire tree is due to partial illumination of the inner leaves.

Approximately 90-95% of light absorbed by a leaf is lost as heat. The remainder is utilized by photochemical reactions. However, plants differ in respect to the radiant energy required to balance photosynthesis exactly with respiration. The intensity of light, in which the CO_2 utilized in photosynthesis is equal to that liberated by respiration, is called the light compensation point. The light compensation point is different for each species and must be appreciably exceeded for a plant to survive, grow, and develop.

Optimum or saturation intensities may vary considerably for different species. Some plants grow very well in shaded habitats (shade plant), other require exposure to full sunlight (sun plant). In contrast with sun plants (many crop plants), shade plants have low light compensation points. They photosynthesize at higher rates under low light intensity, with the photosystems seemingly saturated at relatively lower intensities than those of sun plants. Some plants adapt to shade – *Pinus taeda*. Young seedlings of this species become shade adapted when they grow under the canopy of older trees. However, older seedlings and young trees of the species are unable to survive under the same conditions.

The leaves of shade trees exhibit morphological and anatomical features that are different from the leaves of sun plants. Plants growing under forests have thinner leaves with more surface area and chlorophyll than those of sun plants. Shade plants exhibit elongated stems and growth orientation towards the light. C_4 plants most of which are sun plants or have high saturation points of their photo-synthetic light harvesting systems, show very high photosynthetic rates under appropriate light conditions. Conversely C_3 plants tend to exhibit photosynthetic rate saturation prior to one-half the intensity of full sunlight. We do not have the reasons for these differences but we can speculate based on our understanding of C_3 and C_4 physiology. We might expect that photosynthetic efficiency, among other characteristics of C_4 plants is related to very high light harvesting saturation points. Another viewpoint,
however, is that saturation of light harvesting is not the primary distinguishing feature of efficiency but rather it is the size ratio of the reaction center to light harvesting efficiency or the photosynthetic unit size (PSU). Photosynthetic size is small in C₄ and sun plants but larger in C₃ and shade plants.

Solarization - when the intensity of light incident on leaves is increased beyond a certain point, chlorophyll within it subject to photooxidation which is called as solarization. When shade plants are placed in sunlight, chlorophyll molecules that can possibly be utilized become excited and in the presence of oxygen are readily subject to oxidation. The leaves become chlorotic and finally die. Besides oxygen, presence of carotenoids and CO₂ also influences the extent of photo-oxidation. CO₂ will tend to inhibit the process. With high concentration of CO₂, the photooxidative consumption of O₂ occurs at much higher light intensities than it does at lower CO₂ levels. Carotenoids acts as antioxidants. They absorb light energy and divert it from chlorophyll through heat dissipation. In fact, in higher light more chlorophyll triplets appear to be formed and the energy is transferred to carotene triplet states. Thus, carotene provides a channel to dispose of excess energy absorbed by chlorophyll. However, may shade plants are still not sufficiently protected to survive in full sunlight.

**Carbon dioxide**

Stomata seem to be the primary path of entrance of CO₂ in the leaves. Stomatal behavior is much more important in regulating CO₂ availability to the leaves than in regulating O₂ penetration. O₂ penetrates the cuticle of the leaves readily, CO₂ is essentially impeded. Therefore, opening and closing of stomata have an important effect on the regulation of photosynthetic activity, particularly in C₃ plants. C₃ plants incorporate CO₂ directly into phosphorilated sugar intermediates. There is increase in the rate of photosynthesis when there is increase in the concentration of CO₂ irrespective of light intensity.

At a given low concentration of CO₂ and non-limiting light intensity, the photosynthetic rate of a given plant will be equal to the total amount of respiration (true respiration + photorespiration). The atmospheric CO₂ concentration under which photosynthesis just compensates for respiration is referred to as the CO₂ compensation point. The CO₂ compensation point is reached when the amount of CO₂ compensation point is reached when the amount of CO₂ uptake is equal to that generated at a non-limiting light intensity. Apparent photosynthesis under these conditions is zero. In C₃ plants the CO₂ compensation point is usually much higher (25 to 100 ppm CO₂) than it is in C₄ plants (< 5ppm). The obvious implication is that C₄ plants have high CO₂ levels in bundle sheath chloroplasts and high pool levels of CO₂ in the mesophyll cells. In C₄ plants CO₂ is distributed as organic acids that maintain high pool levels of CO₂. The amount of free CO₂ in the mesophyll of C₃ plants is not as high because there is no such mechanism of CO₂ fixation. Higher levels of CO₂ inhibit photorespiration in C₄ plants because at higher concentration CO₂ compete better than O₂ for RuBPcase active site and is fixed at a larger rate than O₂. Normally the CO₂ concentration in the atmosphere is constant. However, in areas of concentrated photosynthesis, such as above fores canopy or above maize or wheat field, the CO₂ concentration is significantly diminished during the daylight hours. Similarly at higher altitudes the partial pressure of CO₂ is less and
drops proportionately as the height increases. This results in unusual higher rates of photosynthesis for some alpine plants.

**Temperature**

As in all life processes, photosynthesis is restricted to a temperature range that corresponds roughly to the range tolerated by protein compounds, which are generally active at temperature above 0 °C and below 60 °C. Although the photochemical part of the photosynthesis is independent of temperature, the biochemical part, which is controlled by enzyme activity, is strictly temperature dependent. However, plants exhibit a wide variance and adaptability in their ability to tolerate temperature extremes.

Injury at temperature extremes- Cold temperature retards the rate of photosynthesis both directly and indirectly. Directly, cold temperature inhibits the rate of photosynthesis by lowering the activity of enzymes involved in the dark reactions of photosynthesis. Indirectly, the process of photosynthesis is affected in an adverse manner by the formation of ice outside and inside the cell. The formation of ice crystals causes dehydration of the cell, mechanical injury which destroy the permeability of the membranes and modification of the colloidal structure of the cytoplasm and chloroplasts.

All vital functions are terminated at higher temperature and at very high temperature thermal death is almost immediate. At temperature slightly above the temperature range of the organism, death is not immediate but is a slow process, which we can observe by noting the diminishing rate of some vital process e.g. photosynthesis.

Temperature effect on rate of photosynthesis – In general increase in temperature results in an acceleration of photosynthesis when other factors are not limiting. This increase is linear at the lower temperature, starts to drop off as higher temperatures are reached and finally reaches an optimum above which photosynthesis is inhibited. The optimum response depends on species and the length of time it is exposed. In C₃ plants the most likely inhibitory effects of high temperature on photosynthesis are due to a stimulation of photorespiration. CO₂ fixation in C₃ plants is often inhibited at 25-30 °C. The C₄ plants show proportional increases and reach an optimum photosynthetic rate above 35 °C because photorespiration is low in these plants.

The effect of temperature on the rate of photosynthesis is roughly comparable to the effect of temperature on enzyme reactions, a fact supporting the theory that the deactivation of enzymes is one cause of the inhibition of photosynthesis at high temperatures. The theory is most likely true. The rate of CO₂ absorption may be limiting at very high rates of photosynthesis, even though the optimum concentration of CO₂ is present. This fact is particularly true for C₃ plants.

Under natural conditions optimum photosynthetic response is very seldom reached. In most cases light or CO₂ concentration or both are limiting.

**Water**

It is hard to establish whether or not a deficiency in water supply has a direct inhibitory effect on photosynthesis. The amount of water actually needed for the process of photosynthesis is
very small in comparison to the amount needed to maintain the living plant. Water deficiency, of course, would retard photosynthesis along with the other vital processes of the biological mechanism. Many investigators have noticed reduced rate of photosynthesis in water deficient soils. The reduction was observed before evidence of wilting of the leaves could be seen. In pecan trees, the greatest reduction in photosynthesis coming when conditions favoured high transpiration rates. These inhibitory effects are primary because of decreased hydration of the protoplasm and stomatal closure. Removal of water from the protoplasm will affect its colloidal structure and its metabolic processes such as respiration and photosynthesis. Enzymatic efficiency is impaired by dehydration of the protoplasm which inhibits the rate of vital processes. Photosynthesis is more sensitive to dehydration than some other metabolic processes. One reason for this sensitivity might be the physical damage that dehydration may cause to the micromolecular structure of the photosynthetic system.

When a water deficit occurs in a plant, it causes the stomata of the leaves to close, thereby causing a decrease in the absorption of CO₂. A decrease in its absorption should slow the rate of photosynthesis. However, it is found that rate of photosynthesis remains unchanged until the leaf is wilted and the diffusion remains high and approximately uniform until the stomata are closed. Therefore, stomatal closure is only one of probably many factors involved.

**Oxygen and inhibition of photosynthesis and photorespiration**

In 1920s Warburg reported his observation that O₂ inhibited photosynthesis. O₂ is necessary component of respiration favours a more rapid respiration rate and allows the process of respiration to compete favourably for intermediates common to photosynthesis and respiration. Secondly O₂ might compete with CO₂ for hydrogen and become reduced in place of CO₂. Lately it was found that rate of respiration as measured by O₂ consumption or CO₂ liberation from the leaves of C₃ plants was often as much high as two times in light than in darkness. But in this type of respiration no energy liberation occurs and is termed as photorespiration because of its similarity to the true respiration in terms of gas exchange.

At high light intensity, high O₂, and high temperature, the mesophyll cells in the leaves of all C₃ plants exhibit high rates of photorespiration. C₄ plants, however, exhibit low rates of photorespiration in the bundle sheath cells where Calvin-Benson pathway is operative.

In 1971 Orgen and Bowes showed that in the presence of O₂, ribulose 1,5-bisphosphate carboxylase operates as an oxygenase catalyzing the oxidation (addition of O₂) of RuBP to phosphoglycolic acid, thus causing the net effect of reduced rate of CO₂ fixation and diminution of phosphorylated sugar synthesis. The entire process takes place in chloroplasts, peroxisomes and mitochondria. Photorespiration is essentially nonproductive photosynthetically because the carbon is used to regenerate RuBP, with no gain in carbohydrate synthesis for respiration or storage. The CO₂ release from photorespiring cells is a reflection of the amount of CO₂ not fixed due to O₂ fixation.

**Physiological limitations to crop yield**

Increase in the yield of crop plants can come from many quarters, such as better adaptation to environmental conditions, greater resistance to pests and diseases, improved agronomic
practices, increased genetic yield potential, and interactions between these. To comprehend the development of yield we need to treat photosynthesis, translocation, growth, and storage as an integrated whole, since these processes are linked by numerous interactions.

Changes that have occurred between wild species and modern cultivar may be grouped into four categories:

- changes conferring adaptedness to cultivation and systematic harvesting;
- modification of daylength and vernalization requirements;
- quality improvements by selection against undesirable, and for desirable, components; and
- increase in yield potential.

So far, increase in yield potential has been achieved by direct selection for ability to yield the organs of interest under progressively improved systems of agronomic inputs; changes in individual physiological characteristics have resulted only indirectly from such selection. Recently, however, there has been increased interest in the possibility of raising yield by direct selection for important physiological attributes.

Marked increase in the size of seeds, pods, fruit, or inflorescences (e.g. in maize) has occurred in many crops during their evolution. The diameter of sugarcane stems and of sugar beet roots has likewise increased. In some cases, as Charles Darwin observed, the increase in size has been confined to the organs or tissues harvested or eaten by man (e.g. in brussels sprouts and some stone fruits), but in others there has been a parallel increase in the size of several organs. In wheat there has been parallel increase in leaf and seed size. In sugarcane, both stem diameter and the area of the upper leaves have increased over a twentyfold range from *Saccharum spontaneum* through *S. robustum* to modern forms of *S. officinarum*.

Greater cell size, with increasing ploidy, has contributed to the parallel increases in organ size during the domestication of wheat and sugarcane, but a rise in cell numbers was also involved. Despite these changes, the relative growth rate (RGR) of young plants does not appear to have increased in the course of domestication, even when comparisons are made with seedlings of the same size. This has been shown for wheat, maize, tomato, and cowpea. The relative leaf area growth rate is an important determinant of the time taken for the crop canopy to close. Before the canopy achieves full interception of the light, variation in leaf area is a much more powerful determinant of variation in crop growth rate than is variation in photosynthesis rate per unit leaf area. After canopy closure, photosynthetic CO$_2$ exchange per unit leaf area may become an important determinant of canopy photosynthesis.

Yet there is no evidence to date of any indirect selection for increase in the maximum light-saturated CO$_2$ exchange rate per unit leaf area (CER) during the domestication and
improvement of wheat, maize, sorghum, pearl millet, sugarcane, cotton, or cowpea. Indeed, the highest CERs recorded for wheat, sorghum, pearl millet, and cotton have been found in the wild relatives, not in the modern cultivars. In wheat, the higher CER of the more primitive species were associated with higher stomatal and residual conductance and with higher Hill-reaction activity per unit of chlorophyll.

The lack of advance in leaf CER during crop evolution may have been due in part to negative relationships between CER and leaf area and the persistence of photosynthetic activity as discussed in the next section.

Also the need for increase in the genetic potential of CER may have been mitigated in some cropping environments by the use of nitrogenous fertilizers. In the absence of genetic increases in photosynthesis and growth, past improvements in yield potential have derived largely from increase in the proportion of accumulated dry weight which is invested in the organs harvested by man, i.e. in the harvest index. Both the size and the number of these organs have been increased, as have the rate and the duration of their growth in many species. Increases in duration have been associated with greater longevity of leaves, or with the storage phase making up a larger proportion of the crop life cycle. Increased rate of storage, on the other hand, has been shown, at least in wheat, to involve a greater allocation of photosynthetic assimilates to the grain during grain filling.

Associated with this greater allocation has been a parallel increase in the cross-sectional area of phloem in the peduncle. In sugarcane also, the phloem cross-sectional area serving the storage tissues has increased in parallel with the latter.

Clearly, many coordinated changes have occurred in the course of evolution from wild plant to modern cultivar. In general, developmental processes- such as those concerned with germination, flowering, plant form and composition, dehiscence, and shedding etc-appear to have been more readily modified by empirical selection than has photosynthesis.

Two lines of argument may be followed from the observation of improved carbon partitioning during crop evolution. One is that any remaining scope for further improvement in carbon allocation must be small, so it would be better now to aim at increasing photosynthetic and growth rates. The other is that since partitioning is where the flexibility has been in the past, it is better to aim for further increases in harvest index. We briefly examine the first argument before returning to the second one.

**IMPROVING PHOTOSYNTHETIC RATE**

Genotypic differences in components of photosynthesis have been found and used as selection criteria. The great genetic variation in chlorophyll content per unit leaf area seems generally to have little impact on variation in CER or productivity, as for example in barley, where even chlorophyll- deficient mutants have near-normal CER. The reduction in CER of soybean lines having abnormally low leaf chlorophyll (<35 µg cm⁻²) may be associated with low specific leaf weight in low chlorophyll genotypes. Similarly, there is no indication that variation in Hill activity or photophosphorylation per unit area is reflected in variation in CER. Determinations of Hill activity per unit chlorophyll cannot be interpreted in relation to CER without information on chlorophyll per unit leaf area.
In contrast to the light reactions, variation in ribulose bisphosphate carboxylase (RuBPC) in C3 species has often been found to correlate with leaf CER, as Randall et al found when comparing a high CER mutant of tall fescue with normal tall fescues. Since RuBPC represents 30-50% of the soluble protein of leaves, there is a risk that breeding for its high activity might be at the expense of other important enzymes. Selection for high specific activity forms of the enzyme might be better, but none have been found yet, although a ryegrass tetraploid with a lower than normal \(K_m\) (\(\text{CO}_2\)) for RuBPC has been described. Also, the oxygenase activity of the carboxylase protein yields a substrate for photorespiration, for which a function has not yet been established. The substantial effort to breed out photorespiration by several methods including screening seedlings for low \(\text{CO}_2\) compensation point has proved fruitless. There is no unequivocal evidence of C3 plant genotypes with low oxygenase and normal carboxylase activity.

A morphological character which often but not always, correlates with CER is specific leaf weight (SLW = leaf dry weight per unit area) or, more simply, leaf thickness. Inter-genotypic variation in SLW at a chosen ontogenetic stage can show stability of ranking from season to season and is heritable. Whether or not it is a good breeding strategy to select for high SLW depends on its relationship to leaf area development. Expansion of leaf area and thickening of leaves can be inversely related. A sound strategy might be to produce plants which expand large thin leaves early in the season and then thick leaves after the canopy intercepts all the light.

Selection for stomatal frequency and length has not met with success in changing CER through stomatal conductance, since frequency and length are inversely related and other countering compensations in leaf area and longevity can also occur. Further, stomatal aperture is a much more powerful determinant of stomatal conductance, and behaves as if it were continuously controlled to resolve optimally the conflict between the carbon needs of growth and the environmental demand on plant water through transpiration. So even if stomatal frequency were increased, it is likely that the water loss/carbon gain optimization process would lead to the same resolution in terms of stomatal conductance.

The complexity of the internal controls over CER, together with the little success at improving it by selection for component processes, suggests that direct selection for CER itself might be more effective. There is much evidence of heritable variation in leaf CER, and high and low lines have been selected in several species. Unfortunately, the relationship between CER and growth and yield is tenuous, so much so that it was possible to select tall fescues with high growth rate but low CER and vice versa. The fact that \(\text{CO}_2\) enrichment of the atmosphere will enhance growth and yield of C3 crops shows that growth is photo synthetically limited in some environments. So selection for high CER might be failing because of counterproductive associations.

Part of the problem is that CER is determined to some extent by sink growth rate in relation to leaf area, as will be discussed later. Ontogenic changes in the partitioning of leaf dry weight between leaf area and leaf thickness, together with sink demand effects, can result in poor correlation between CER at one onto genetic stage and at another. In wheat the persistence of flag leaf photosynthesis was greatest for the modern hexaploids, so that toward grain maturity they have higher CER than the primitive types despite a reverse ranking early
in grain filling. An inverse relationship between area per leaf and maximum CER among wheat species and within triticale, and in maize, alfalfa, and soybean, is partly a reflection of the inverse association between leaf thickness (SLW) and leaf area. It is also reflected in a negative relation between mesophyll cell size and CER.

It is likely that any manipulable physiological imbalances in crops which have, through long selection, become well adapted to their agronomic environment, will be subtle and small. Wilson identified one such imbalance in perennial ryegrass (*Lolium perenne*). He has selected genotypes with low rates of dark respiration in fully expanded leaves. The low respiration lines have about a 10% growth rate advantage in both simulated swards and field plots. There is indication that there may also be wasteful respiration, amenable to elimination, in maize and tall fescue. Given the disappointments in breeding for high CER and for low photorespiration, it is remarkable that a few cycles of selection were sufficient to eliminate completely an apparent inefficiency which nature or agricultural practice had not already overcome.

**CARBON PARTITIONING BETWEEN ORGANS**

Several stages exist in the partitioning of photosynthetic products. For a developing leaf, photosynthetic assimilate is partitioned within the leaf between exported material and further leaf growth or temporary storage. Assimilate exported is partitioned between different sinks, and within sinks the incoming carbon is partitioned between different chemical constituents.

We are concerned here with the partitioning of net assimilate (often approximated by dry weight) between organs which are separated by vascular transport channels. Sinks may be meristematic, elongation, or storage sinks, and the characteristics of storage sinks depend on the type of product stored - sucrose, starch, proteins, or lipids. There may also be respiratory sinks in some plants, involving cyanide-resistant respiration which is not an integral part of tissue growth and maintenance.

Although the biological yield of cereal cultivars has not been increased, grain yield continues to increase because partitioning of assimilate to grains (as measured by harvest index = grain yield/shoot yield) has increased over many years for oats, barley, and wheat. The same is true for lipid and protein-storing peanuts. Although there must be a limit to how high harvest index can go, [Austin et al suggest about 62% for wheat], progress still seems possible, the best wheats now having harvest indices around 50%.

The inadequacy of our understanding of the control of partitioning of photosynthetic assimilate is indicated by the empirical ways in which modelers of crop productivity handle it. It is sometimes handled by rules based on descriptive allometry, sometimes by "priority" concepts for sinks, sometimes by a "nutritional control" approach based on "functional equilibrium" between organs, and sometimes by transport resistance/substrate gradient/growth response curve models. The most appropriate viewpoint will depend on the purpose of the model and the type of sink of central interest.

**CHARACTERISTICS OF ESTABLISHED SOURCE-PATH-SINK SYSTEMS**

Photosynthesis in Relation to Sink Demand

The dominant primary sources of assimilate are leaves, although green stems and floral organs can sometimes make substantial contributions. While environmental factors have
strong direct influence on photosynthesis, the demand by sinks for assimilate can also
determine photosynthetic supply. Unfolding leaves, before photosynthetic autonomy, must
compete with other sinks for assimilate, and it is a common observation that heavily fruiting
or tuberizing plants experience reduced growth of vegetative parts including leaves though
less essential growth-like increase of stem diameter in apple-may suffer more than leaf
development by heavy fruiting. Countering this tendency, CER may be enhanced for a leaf
which developed and unfolded in a regime of intense competition from other sinks, whether
the intense competition is generated by the onset of fruit growth as in soybean or by removal
of other leaves.

After full leaf expansion, CER can still be increased or decreased by a natural or manipulated
change in sink demand. Responses occurring within hours may represent stomatal responses.
Longer term responses over several days can be due to parallel change in both stomatal and
internal mesophyll control of CER such that intercellular space CO$_2$ concentration is almost
constant. But also senescent leaves can be rejuvenated to full photosynthetic performance
when the sink: source ratio is increased substantially. By contrast, when sink growth is
competing with leaves for remobilizable nitrogen, senescence and the fall in CER may be
accelerated, as postulated by Sinclair & de Wit. Also, removal of fruits or meristematic sinks
may arrest senescence of older leaves for unknown but possibly hormonal reasons.

Thus, the quantity of assimilate available for partitioning to sinks is itself dependent on the
presence and properties of sinks in a complex way, involving opposing responses which
cannot yet be predicted. Evidence for the simplest explanation of photosynthetic stimulation
by sink demand—that assimilate level in the leaf controls photosynthesis by end-product
inhibition—remains equivocal. This uncertainty indicates that it is not a simple mechanism,
and involvement of growth regulators, perhaps emanating from sinks, seems likely in many
situations.

**Phloem Loading**

Movement of photosynthetic assimilate toward veins is considered to be in the symplast. A
downhill gradient of tissue sucrose concentration from the mid-interveinal region to the veins
was found in wheat, but an active cross-mesophyll transport could not be ruled out. However,
mesophyll cells have the capacity to release sucrose and hexoses into the free space, although
this capacity may not be expressed except by mesophyll cells close to the phloem. There
sugars are believed to be transferred to the apoplast close to the minor veins. There is no
direct evidence for this, but such a pathway would be advantageous in maintaining the large
differences in osmotic and turgor potentials and in discriminating between compounds during
transfer from mesophyll to phloem. This unloading into the vascular free space is stimulated
by K+ ions in sugar beet, suggesting that there may be an active proton co-transport
mechanism involved. Uptake into sieve tubes from the vascular free space is probably via
phloem parenchyma and/or companion cells and is an active carrier-mediated process having
saturation kinetics, with respect to the donor side of the membrane, in C3 species at least.
Transfer from the companion cells to the sieve tubes is probably symplastic. In the sieve
tubes, sugar (in most species almost solely sucrose) reaches very high levels, usually in the
range 200-800 mM. The weight of evidence suggests that sucrose is the molecule loaded
rather than hexoses in most species, though evidence for prior inversion in some species does exist. This active accumulation of sucrose in the sieve-tube--companion cell complex leads to osmotic uptake of water and hence to a considerable hydrostatic pressure in these cells.

**Inter-organ Transport**

That assimilate transport in sieve tubes occurs down the sucrose gradient, as originally found by Mason & Maskell, or at least down the osmotic pressure gradient—which for most species amounts to almost the same thing—still seems to be generally accepted. Fisher found in soybeans that there was a sufficient gradient in sieve-tube sucrose between source leaf and sink to create a hydrostatic pressure gradient to drive Munch-type mass flow at the observed rate. Assuming open sieve-plate pores, it would not take a large osmotic pressure gradient, relative to the absolute osmotic pressure in the tubes, to generate enough differential in hydrostatic pressure to drive translocation over the distances involved in crop species, but such small gradients are difficult to detect.

Minor vein sieve tubes extend into sterna as bundles and as isolated vascular strands. Numerous bridging strands occur between and within bundles in lamina, petiole, and stem, and in grasses many anastomoses also occur at the nodes. This continuous network of sieve tubes allows a molecule entering at any point to follow several routes to any sink organ, perhaps even without leaving the sieve-tube lumen. The pathway lacks directional valves. A severed vein is quickly by-passed, presumably via bridging strands, without the surrounding tissue being flooded with unloaded translocate. So there is the possibility of continuous traffic around the plant as seen with the reciprocal interchange of carbon between young tillers and main shoot of grass plants, and the simultaneous influx and efflux of phosphorus in the shoot apex. Nevertheless, labeled assimilate can follow specific routes to particular sinks, especially in the short term; for example, $^{14}$C is translocated specifically to younger leaves in the same orthostichy in tobacco, cotton, apple, and other species. This does not necessarily mean that there are no linking connections to other sinks along the path from source to favored sink, for in soybean such sink specificity was found even though functional cross-links were known to occur en route, and transport routes quickly adjust to changes in the pattern of supply. In terms of our assumptions about the mechanism of translocation, it simply means that for the configuration of competing sources and sinks any gradients in solute concentration across the links were insufficient to drive detectable flow through them in the period of the experiment (often a few hours). Over a long period some label can reach all parts of the plant, this being particularly evident in grasses which have many cross-links between bundles. Even where there is usually little net C translocation from one organ to another as between well-developed grass tillers, the vascular channel is still functional for long periods, as shown by repeatedly removing the source leaves from the tillers. Study of the short-term distribution of carbon from a particular source may tell us something of the preferred routes and the pattern of gradients, but it does not establish the control mechanisms underlying the long-term distribution of dry weight.

**Phloem Unloading**

Sieve-tube unloading has received little attention. Phloem retains its solutes with minimal radial exchanges except where remobilizable stores are being laid down or in growing
regions where unloading occurs. Autoradiographs of $^{14}$C assimilate moving from a mature tobacco leaf to recipient expanding leaves have shown that major veins in the exporting leaf can retain labeled assimilate without leakage detectable on the autoradiographic film, whereas major veins of the importing leaves are the first parts to show up, indicating some leakage or unloading before translocate reaches the minor veins.

One way that leakage out of the vascular bundle may be prevented en route is for a suberized lamella to form in cell walls of the layer of mesophyll cells which ensheath the vascular bundle in some species, as found by O'Brien & Carr in the mestome sheath of temperate cereals. But this would not prevent apoplastic leakage into xylem vessels. The transpiration stream rarely contains appreciable sugars where transport between well developed sources and sinks is involved. But for some woody perennials like grapevine and sugar maple, xylem sucrose can be very high before leaf development in spring, and in apple some xylem transport of carbon was evident for trees with developed leaves. Where the source leaf is immature, carbon export can be partly through the xylem, presumably before the leaf’s phloem has acquired full loading capability. There may be temporary storage depots enroute between source and final sink, but transfer to them does not represent leakage, depots being sinks too. It is possible, therefore, that the sieve-tube/companion cell/phloem parenchyma complex is countering leakage by actively loading sucrose along almost its entire length against the radial concentration gradient; the pH gradient from alkaline sieve tube to nearby acid xylem contents would assist that if proton co-transport were the loading mechanism [see below]. If so, unloading could occur by leakage wherever active uptake by the phloem ceases.

A simple possible corollary would be that sinks in some way locally inhibit the phloem-loading mechanism. This could take several forms according to the type of sink. In apical meristems it could simply be that the phloem is not developmentally mature enough to have acquired the sucrose-loading mechanism, or that the absence of xylem vessels adjacent to phloem termini leads to an inadequate proton gradient for loading. In storage tissues, such as sugarcane stem internode and maize endosperm, it may be that sink control over the activity of invertase, which is closely associated with the phloem or sieve-tube surfaces, prevents sucrose being reloaded by inverting it to hexoses. Whether or not the phloem actively unloads with a carrier-mediated process in any situation is unknown. It probably varies according to the type of sink, but for some sinks the necessity to unload water may constrain options for sugar unloading; apoplastic sucrose inversion could set up an osmotic gradient in a direction assisting water removal from the sieve tubes. Whether unloading into the apoplast be active or passive, there must be some feedback control over the process related to the sugar concentration in the recipient free space and to the "needs" of sink growth.

**Sink Properties**

Despite much work on prolonged tissue culture in vitro, only a restricted range of organs has been examined in terms of short-term sugar uptake. The latter is more relevant to defining properties of plant parts as sinks. Organs so studied include sugarcane internode segments, cotton hypocotyl segments, wheat kernels, expanding cotyledons of Ricinus seedlings, and developing barley embryos. Generally sucrose is found to be the preferred substrate for uptake and short-term growth or storage by these tissues, although the cotton hypocotyl
system could also utilize fructose, and in sugarcane stem, glucose is preferred even though it is sucrose which accumulates in the stem cells. The ready uptake of sugars from the bathing media by these tissues is suggestive that in vivo they may take up assimilate delivered by the phloem from the free space, and this apoplastic route is most commonly favored. In wheat kernels, the endosperm is separated from the vascular strand by a cell-free endosperm cavity containing sucrose and little hexose, suggesting uptake from the apoplast. In roots, where water flow through the free space occurs in the opposite direction, symplastic transport of sucrose from stele to cortex and apical cells seems more likely and is supported experimentally. In all the systems cultured in sucrose in vitro, except perhaps the wheat kernel, sucrose uptake by the cells of the tissue has saturation kinetics and can occur against a concentration gradient from the outside to the inside of the cells. This indicates that a membrane carrier mechanism is involved. In wheat kernels, Jenner found no evidence for active transport of sucrose into the cells, and he argues that the regulation of sugar uptake by grains lies not in the kinetics of uptake by the cells but in the concentration of sucrose in the vascular bundle running along the length of the groove in the grain. By contrast, in maize kernels the interpretation is that sucrose is cleaved to hexoses in the free space of the placento-chalazal region of the kernel as it diffuses from phloem to endosperm cells. And the invertase reaction is a control point in sugar uptake, and hence in starch synthesis, by the maize endosperm. Similarly, apoplastic invertase plays a regulatory role in the passage of sugar into sugarcane internode cells; the phloem delivers and the cells store sucrose, but the sugar enters the cells as hexose.

The apparent Michaelis-Menten constant for sugar uptake (Km) by the tissues varies widely from 0.9 mM for glucose uptake by cane internodes to 36 mM for sucrose uptake by barley embryos. In cotton hypocotyl, Km varied threefold, this probably being related to the season during which the plants were grown. The specificity of carriers varied between systems, although in general the sucrose carriers were not interfered with by other sugars. In both cotton hypocotyls and wheat kernels, the endosperm free-space sucrose concentration in vivo was low enough for the rate of uptake and storage by the cells to be considered a linear function of free-space sucrose concentration—a conclusion which simplifies the approach taken to modeling assimilate distribution. At free-space sugar concentrations higher than are generally found in vivo, several of the systems showing carrier-mediated uptake revealed a diffusional component of sugar influx.

Other phenomena observed in short-term sugar uptake studies add awkward complexity to the task of constructing source-path-sink models to interpret carbon distribution. First, in Ricinus cotyledon, cotton hypocotyl, and barley embryo systems, the rate of carrier mediated sucrose uptake was not only determined by substrate concentration in the free space but also by the concentration of transported moiety inside the cells. The higher the intracellular concentration, the less the transport. So although transport operates against the gradient in these systems, the rate is not independent of the steepness of the gradient across the cell membrane. Thus the rate of removal of cytoplasmic sucrose by accumulation in the vacuole or by conversion is not only determined by, but also influences the rate of sucrose transport into the cells. Second, in cotton hypocotyls, incorporation of sucrose into insoluble fractions
was dependent on current uptake of sucrose from the medium; sucrose taken up previously by the tissue was apparently unavailable for synthesis. Perhaps this is due to sequestering in the vacuole. When this occurs it is not meaningful to relate tissue growth rate simply to average cellular sucrose concentration.

The third feature found for cotton hypocotyl which creates difficulties in interpreting in vitro tissue culture studies in vivo was that the maximum rate of sucrose uptake exceeded the maximum rate at which insoluble compounds could be synthesized. This suggests that in vivo some kind of control over sucrose uptake might operate to prevent its concentration from rising to the very high levels possible in vitro.

The variety of strategies which the above sinks use to control their growth makes universal description of sink capabilities, in-so-far as they determine assimilate partitioning, difficult. But one variable which can be a powerful determinant of sink growth is the apoplastic sugar concentration in the free space of sink tissues.

REGULATION OF CARBON FLOW THROUGH SOURCE-PATH-SINK SYSTEMS
A Conceptual Framework
The following paragraph is a generalization of the above, intended as a working hypothesis onto which further details of the control of carbon partitioning can be built.

The amount of photosynthetic substrate available for distribution is in part determined by sinks themselves through feedback control of photosynthesis.

The same may be true of substrate from remobilizable reserves. The sieve tubes are separated from both source cells and sink cells by the free space of sources and sinks although for some sinks, such as growing roots, symplastic connections between phloem and sink cells may be more important than apoplastic ones. Phloem can actively take up sucrose from a low concentration solution in the source apoplast, accumulating high concentrations in the sieve tubes, the rate of accumulation being a function, among other things, of free-space sucrose concentration. The phloem may be actively loading against a steep sucrose concentration gradient along its entire length, except where unloading is somehow stimulated by the presence of sinks. Sinks can actively accumulate sugars from the free space of unloading phloem. In excised tissues, sink growth saturates with respect to free-space sugar at around 60-200 mM sucrose and typically operates in apoplastic solution less concentrated than that. Since sieve-tube contents can range up to 800 mM sucrose or higher, it is easy to envision that gradients could develop in these tubes between sources and sinks, creating hydrostatic pressure gradients sufficient to drive whatever mass flow is needed to equate supply and demand provided sieve-plate pores are not plugged in vivo. In this simple picture the average sucrose concentrations and the gradient within the sieve tube would automatically rise and fall, balancing supply and demand. Temporary storage in stems can also help reconcile inputs and outputs at each end of the sieve tubes. The observation that localized stem cooling in species not damaged by chilling causes no change in the rate of translocation after an hour or two of adjustment supports this passive, physical interpretation of sieve-tube transport. Passioura & Ashford have shown that rates of translocation (specific mass transfer) ten times greater than the highest previously recorded in the literature can be induced by restriction of
the sieve-tube cross-section available. They conclude that rate of transport in sieve tubes is unlikely to limit flow from source to sink.

**Additional Complexities**
Features which complicate the above picture include: the role of energy and light; evidence that the phloem exerts more directional and quantitative control over C flow than is credited to it above, including hormone-directed transport; buffering of flow between primary sources and ultimate sinks by temporary stores; claims that source leaves can exert control over destination; and the problem of whether the movement of carbon down sucrose gradients in the sieve tube's necessarily implies that it flows from high sucrose source organs to low sucrose sink organs.

**ENERGY AND LIGHT**
The energy requirements for the above model are primarily in the source, for loading sucrose into the phloem parenchyma, and in the sink, for loading the sink tissue cells. The only energy needed en route would be for tissue maintenance and for keeping the sieve tube loaded (leak prevention). The mechanism may be for a membrane ATPase to pump protons into the sugar donor side of the membrane, thereby maintaining a proton gradient necessary to allow a sugar-proton co-transport mechanism to operate across the membrane. Besides driving the photosynthetic supply of sucrose, light may play indirect roles in controlling translocation and partitioning at several steps.

Light has frequently been noted to foster active transport of solutes across membranes of living systems, though the mechanism is unknown. Light might be involved in controlling export of photosynthetic metabolites from the chloroplasts or generally from leaves. Similarly, there is evidence of light stimulation of uptake of sugars by sink tissues like apical meristems or cotton hypocotyls, but apparently not in young bean leaves. Such evidence is not strong, but if the processes of source supply, phloem loading, short-term storage, and sink uptake were influenced or attuned by irradiance, one might obtain reduced sink growth in low light without any change in free-space sugar concentration in source and sink. This would confound interpretations based on simple transport resistance/substrate concentration gradient models. Jenner tested that possibility by examining grain growth and grain endosperm sucrose concentration in shaded and well-illuminated wheat; in fact, both parameters declined with shading consistent with the simple picture.

**LIMITATIONS ON TRANSLOCATION CAPACITY**
Milthorpe & Moorby concluded that vascular transport does not usually exert any control over sink growth. Experiments involving incisions in the culm of wheat and sorghum have shown that dry-weight accumulation in the grain was not reduced by restricting phloem cross-section. In terms of our conceptual framework, phloem restriction would create an increased sucrose gradient in the sieve tubes across the restriction, causing flow to bypass through interconnecting strands. This change of gradient could reduce sink growth indirectly by reducing the sucrose concentration to which the sink is exposed while increasing the concentration that the source must work against.

One way that the transport mechanism could be inadequate to accommodate an enhanced rate of photosynthesis is if the carrier-mediated loading of sucrose at the phloem parenchyma plasmalemma reached the saturation point with respect to mesophyll apoplastic sucrose
concentration. Geiger believes this to be unlikely, saturation not occurring until mesophyll sucrose reaches about 100 mM. Moreover, for sucrose applied exogenously to the mesophyll free space of sugar beet leaves, a second uptake curve is superimposed which saturates at about 400 mM sucrose. For C4 grasses, it has been suggested that when leaf photosynthesis is driven high enough, the bundle sheath mesophyll may reach sucrose concentrations exceeding the sieve-tube contents such that loading occurs down a gradient. But even then the proportion of assimilate retained by the leaf did not increase, indicating that an upper limit to translocation capacity out of the leaf had not been reached.

So although the sieve tubes undoubtedly impose a resistance to mass flow, and they can channel the flow from particular sources to particular sinks, there is enough system flexibility for translocation not to limit flow from sources to sinks in most situations. The flexibility derives from the existence of alternative routes not necessarily having much higher resistances, the possibility of adjusting solute gradients at a small expense of energy, the potential for cycling of materials between organs having both source and sink attributes, occasionally the transport of carbon compounds in the xylem, and the possibility of turgor-dependent loading which might provide a mechanism, involving K+ pumping, for matching loading and transport-to-sink demand independent of any apparent impediments in the phloem channels.

Another reason why the vascular system may rarely exert appreciable control over flow of material from source to sink is that the vasculature may develop in such a way as to meet the "anticipated" needs for C flow as it does in the wheat peduncle, where the number and size of the vascular bundles correlates with the number of spikelets. During the most rapid phase of wheat stem elongation, vascular connections are being continually broken, but rate of differentiation of new sieve tubes exceeds the rate of destruction, and specific mass transfer of carbon compounds (per unit area of sieve-tube lumen) never rises to particularly high levels during stem extension.

Phloem develops in cultured tissues in response to IAA and sucrose in the medium. Primordia produce auxins and the extending end of a vascular bundle releases sucrose, so it is easy to envisage how vascular connections may extend to wherever they are needed. Indeed, complex venation patterns can be simulated by a mathematical model based on auxin diffusion from growing tissues. Moreover, callus cultured in media containing auxin can develop vascular tissues, and the ratio of phloem to xylem is a function of sucrose concentration in the medium and of no other sugar.

HORMONE-DIRECTED TRANSLOCATION

Growth regulators have long been implicated in assisting translocation in established source-pathsink systems. Although most discussion relates to growth regulators released from sinks, hormones from sources have also been considered. When IAA and other regulators like cytokinins, ethylene, and gibberellic acid are applied to a cut stem surface, or ABA is dissolved in the rooting solution of Phaseolus plants, assimilates accumulate in the region of application. Combinations of growth regulators can have additive, synergistic, or inhibitory effects. The idea that such IAA-directed transport (the most studied hormone in this regard) is due solely to stimulation of growth rate of tissue at the site of application was argued against
from the outset, and there is evidence for direct effects on transport. However, the systems studied usually involve very low translocation rates and may not reflect the most important controls for intact plants. In bean seedlings, which were regenerating root and shoot apices following their excision, the main control over the distribution of sucrose between root and shoot sinks was attributed to hormonal influences (IAA and cytokinin) on sink activity per se, although some superimposed influence on relative sucrose availability to the respective sinks could not be excluded. By contrast, the enhanced accumulation of 14C assimilate in peapods caused by pod warming was due both to an effect on ovule growth directly and to an influence on transport outside the warmed zone; this is suggestive of a hormonal effect emanating from the sink.

Each growth regulator might act primarily on different parts of source path- sink systems, and most steps in the overall sequence have been examined: phloem loading, long-distance transport in the sieve tubes, sieve-tube unloading, and sugar uptake by sink tissues. Such hormonal influences are yet too ill-defined to be able to generalize in relation to assimilate partitioning.

DESTINATION CONTROL BY LEAVES
It has been suggested occasionally that leaves can determine the destination of their assimilates. We know of no clear evidence on this.

DIRECTION OF INTERORGAN ASSIMILATE GRADIENTS
Although there is little doubt that phloem transport occurs down pressure potential and solute gradients in the sieve tubes, this does not mean that assimilate distribution necessarily occurs from organs of high to organs of low average soluble carbohydrate. Phloem loading and uptake by sink cells and vacuoles against the gradient mitigate against that. If a sink stores sucrose in its symplasm and vacuoles and has a capacity to accumulate sugars against a steep gradient, then the sink apoplast could have a lower sugar concentration than the sieve-tube contents in the source leaves despite a higher sucrose concentration in the sink as a whole. This presumably is what happens in sugar beet, sugarcane, and sugary fruits. Another mechanism of maintaining a downhill solute gradient in the phloem, despite an uphill sucrose gradient between source and sink organs, is to convert soluble carbohydrate from one form to another. Sucrose is inverted in cane-stem apoplast and taken into the cells as hexoses; Rosaceae translocate sorbitol but store sucrose in the fruits. The possibility of loading being controlled more by sieve-tube turgor than by sieve-tube or apoplastic sucrose concentrations can, in the presence of K+ pumping.

SINKS AS DETERMINANTS OF CARBON PARTITIONING
It is difficult therefore to avoid concluding that it is phenomena in the sinks which largely determine the distribution of assimilate between them. Although in the very short term label moves from certain sources to certain sinks, in the longer term it is the ability of sinks to take up sugars from the sink free space which determines partitioning, not the relative adequacy of vascular connections between sources and sinks nor the relative activity of various sources. From studies on competition between two wheat ears containing different numbers of grains but receiving assimilate from a common source leaf equidistant from the two sinks, a similar conclusion could be drawn; dry weight growth of the ears was more or less proportional to
the number of grains in the ear, but in the short term the ear with the larger number of grains drew a disproportionately large share of its growth from the source leaf equidistant from both ears. These findings are consistent with the notion that a rapidly growing sink generates a steeper gradient in sieve-tube assimilate concentration leading to flow from more distant sources than does a weakly growing competing sink.

If sinks control partitioning of dry weight, then a corollary is that it is factors determining the setting up and relative activity of sinks which determine the pattern of assimilate distribution. This implicates the entire fields of environmental and developmental plant physiology. Among the many factors determining the existence and activity of sinks is the supply of photosynthetic assimilate at an earlier ontogenetic stage. For example, the development of lateral meristems in grasses is strongly influenced by the light and also by the carbon dioxide level. The number of grains set in wheat is determined by the adequacy of the photosynthetic environment before anthesis, especially during the phase of ear development between 10 days after terminal spikelet formation and ear emergence.

Solar radiation concept and agro-techniques for harvesting solar radiation

In the last section we have studied in brief about solar radiation. Here in the foregoing pages we are performing in depth analysis of solar radiation.

THE SUN: THE SOURCE OF ENERGY

The sun is the nearest star to the earth. Its radiant energy is practically the only energy source to the earth. The mean sun-earth distance (one astronomical unit, AU), is $1.496 \times 10^8$, km or, more accurately, $149,597,890 \pm 500$ km. The earth revolves round the sun in an elliptical orbit. The minimum sun-earth distance is about 0.983 AU and the maximum approximately 1.017 AU. The earth is at its closest point to the sun (perihelion) on approximately January 3 and at its farthest point (aphelion) on approximately July 4. The visible disk or photosphere has a radius of $6.599 \times 10^5$ km, and the solar mass is $1.989 \times 10^{30}$ kg (Goody and Yung, 1989; Iqbal, 1983).

The sun is a completely gaseous body. The chemical composition of the outer layers is (by mass) 71% hydrogen, 26.5% helium, and 2.5% heavier metals. Its physical structure is complex, although several regions, including the core, photosphere, reversing layer, chromosphere, and corona, are well recognized.

The innermost region, the core, is the densest and hottest part of the sun. It is composed of highly compressed gases at a density of 100 to 150 g·cm$^{-3}$. The core temperature is in the range of $15 \times 10^6$ to $40 \times 10^6$ °C. Outside the core is the interior which contains practically all of the sun’s mass. The core and interior are thought to be a huge nuclear reactor in which fusion reactions take place. These reactions supply the energy radiated by the sun. The most important reaction is the process by which hydrogen is transformed to helium. The energy is first transferred to the surface of the sun and then radiated into space. The radiation from the core and interior of the sun is thought to be in the form of X rays and gamma rays.
The surface of the sun, called the *photosphere*, is the source of most of the visible radiation arriving at the earth’s surface. The photosphere is the crust that is visible to the naked eye when looking at the sun through a blue glass. It is composed of very low density gases. The temperature in this region is 4,000 to 6,000 °C. In spite of the fact that it has low density (10⁻⁴ that of air at sea level), the photosphere is opaque because it is composed of strongly ionized gases. The photosphere is the source of radiation flux to space because it has the capability to emit and absorb a continuous spectrum of radiation.

Outside the photosphere is the *solar atmosphere*, which is several hundred kilometers deep and almost transparent. This solar atmosphere is referred to as the *reversing layer*. This layer contains vapors of almost all of the known elements found on the earth. Outside the reversing layer is the *chromosphere*, which is about 25,000 km deep. It is seen from the earth only during a total eclipse when it appears as a rosy color layer. It is in this zone that the short-lived, brilliant solar flares occur in the clouds of hydrogen and helium. These flares are a source of intense bursts of ultraviolet (UV) and radio wave radiation. The solar flares also eject streams of electrically charged particles called *corpuscles*, which, on reaching the earth’s surface, disturb its magnetic field. The temperature in the chromosphere is several times higher than that of the photosphere.

The outermost portion of the sun is the *corona*, which is composed of extremely rarefied gases known as the *solar winds*. These winds are believed to consist of very sparse ions and electrons moving at very high speeds and are thought to extend into the solar system. The corona can be seen during a total eclipse. It has a temperature on the order of 1,800,000 °K. There is no sharp boundary to this outermost region.

These zones suggest that the sun does not act as a perfect black body radiator at a fixed temperature. The radiation flux is the composite result of its several layers. For general purposes, however, the sun can be referred to as a black body at a temperature of 5,762 °K. The sun rotates at a rate that is variable in depth and latitude. As measured by the motion of sunspots, the synodic period (as seen from the earth) is 26.90 + 5.2 sin²(latitude) days. The sun is a variable star. It is estimated to be about 5 × 10⁹ years old.

Theories of climatic changes on geological time scales indicate definite changes that must have taken place during the lifetime of the sun. According to widely accepted theories, when the sun was formed it was 6% smaller and 300 °K cooler, and its irradiance was 40% lower than present-day values (Goody and Yung, 1989). Some of the variations occurring in the sun are monitored on a regular basis. These variations are associated with magnetic activity resulting from interactions between convective motions, the solar rotation, and the general magnetic field of the sun. Magnetic fields and electric currents penetrate the chromosphere and corona, where magnetic variations have far greater influence because of the low densities.

The most striking visual disturbances are on the photosphere, and these are known as *sunspots*. These are patches varying in diameter from a few thousand to 100,000 kilometers, with an emission temperature in the center about 1,500 °K lower than that of the undisturbed photosphere. The fraction of the photosphere covered by spots is never more than 0.2%, and their average persistence is about a week. For most of the period for which the observations are available, a *sunspot cycle* averages 11.04 years. The number of spots is only one
characteristic feature of the sun that changes in this rhythmic manner. Just after the minimum, spots first appear near 27° latitude in both hemispheres. As the cycle proceeds, they drift equatorward and disappear close to 8° latitude. They are rarely observed at latitudes higher than 30° or lower than 5°.

When a sunspot is near to the extremity it can be seen to be surrounded by a network of enhanced photospheric emission, patches which are called faculae. These photospheric emissions have longer lifetimes than the associated sunspot group, appearing before and disappearing after the spots themselves.

Floculi or plages are other disturbances that are typical features in hydrogen light (H-alpha). Floculi are the most prominent features, and they occur at high latitudes, where spots do not. Occasionally, a hydrogen flocculus near a spot will brighten up. In extreme cases, the brightening is visible to the eye. These brightenings are known as solar flares, and they are associated with great increases of Lyman alpha and other ultraviolet radiations that influence the upper atmosphere.

Prominences are photospheric eruptions extending into the chromosphere. Many different forms occur, but a typical prominence might be 30,000 km high and 200,000 km long, with a temperature of 5,000 °K. Large changes in the corona are well established. Coronal ultraviolet emission is the heat source for levels in the upper atmosphere where the density is very low. The thermosphere, above 150 km, is greatly influenced by variable conditions on the sun. Coronal disturbances are closely related to the sunspot cycle. In visible light the corona appears more jagged at the sunspot maximum than at the minimum. Solar radio emission from the corona shows a marked variation with the sunspot cycle and is also correlated with shorter period changes in sunspot number.

Solar Constant
The sun is the source of more than 99% of the thermal energy required for the physical processes taking place in the earth-atmosphere system. The solar constant is the flux of solar radiation at the outer boundary of the earth’s atmosphere, received on a surface held perpendicular to the sun’s direction at the mean distance between the sun and the earth. The value of the solar constant is 1,370 W m⁻² (about 2 cal·cm⁻²·min⁻¹), giving an average flux of solar energy per unit area of the earth’s surface equal to 350 W m⁻². The solar constant is only approximately constant. Depending on the distance of the earth from the sun, its value ranges from approximately 1,360 to 1,380 W m⁻².

Of this energy, approximately 31% is scattered back to space, 43% is absorbed by the earth’s surface, and the atmosphere absorbs 26%. The ratio of outward to inward flux of solar radiation from the entire earth’s surface (termed albedo) is about 0.31, leaving an average around 225 W m⁻² (range 220 to 235 W m⁻²) that is available for heating, directly and indirectly, the earth-atmosphere system (Goody and Yung, 1989; Kiehl and Trenberth, 1997; Roberto et al., 1999). The irradiation amount at the earth’s surface is not uniform, and the annual value at the equator is 2.4 times that near the poles. The solar energy incident upon a surface depends on the geographic location, orientation of the surface, time of the day, time of the year, and atmospheric conditions (Boes, 1981).
NATURE AND LAWS OF RADIATION
The behavior of electromagnetic radiation may be summed up in the following simplified statements:

- Every item of matter with a temperature above absolute zero emits radiation.
- Substances that emit the maximum amount of radiation in all wavelengths are known as black bodies. Such bodies will absorb all radiation incident upon them. A black body is thus a perfect radiator and absorber.
- Substances absorb radiation of wavelengths, which they can emit.
- The wavelengths at which energy is emitted by substances depend on their temperature—the higher the temperature, the shorter the wavelength.
- Gases emit and absorb radiation only in certain wavelengths.
- The amount of radiation absorbed by a gas is proportional to the number of molecules of the gas and the intensity of radiation of that wavelength.

Wavelength
The wavelength of electromagnetic radiation is given by the equation

$$\lambda = \frac{c}{v}$$

(I)

where $\lambda$ is the wavelength, the shortest distance between consecutive crests in the wave trans; $c$ is the constant equal to the velocity of light, $3 \times 10^{10}$ cm·sec$^{-1}$; and $v$ is the frequency, the number of vibrations or cycles per second.

Planck’s Law
Electromagnetic radiation consists of the flow of quanta or particles, and the energy content (E) of each quantum is proportional to the frequency given by the equation

$$E = hv$$

(II)

where $h$ is Planck’s constant (having a value of $6.625 \times 10^{-27}$ erg·sec$^{-1}$) and $v$ is the frequency. The equation indicates that the greater the frequency, the greater is the energy of the quantum.

Kirchhoff’s Law
Any gray object (other than a perfect black body) that receives radiation disposes of a part of it in reflection and transmission. The absorptivity, reflectivity, and transmissivity are each less than or equal to unity.
This law states that the absorptivity $a$ of an object for radiation of a specific wavelength is equal to its emissivity $e$ for the same wavelength. The equation of the law is

$$a(\lambda) = e(\lambda)$$

(III)

Stefan-Boltzman Law
This law states that the intensity of radiation emitted by a radiating body is proportional to the fourth power of the absolute temperature of that body:

$$\text{Flux} = \sigma T_a^4$$

(IV)

where $\sigma$ is the Stefan-Boltzman constant ($5.67 \times 10^{-5}$ erg·cm$^{-2}$·sec$^{-1}$·K$^{-4}$) and $T_a$ is the absolute temperature of the body.
**Wein’s Law**
The wavelength of maximum intensity of emission from a black body is inversely proportional to the absolute temperature (T) of the body. Thus,
Wavelength \( \lambda \) of maximum intensity (µm) = \( \frac{2897}{T} \) \( \text{V} \)
For the sun the wavelength of the maximum emission is near 0.5 m and is in the visible portion of the electromagnetic spectrum.

**Lambert’s Law**
This law states the permeability of the atmosphere to solar radiation. The intensity of solar radiation on a vertical irradiation at the earth’s surface is given by the equation
\[ I_m = I_o q m \] \( \text{VI} \)
where \( I_o \) represents the solar constant, \( q \) is the transmission factor for the layer thickness 1 (solar angle 90°), and \( m \) represents distance of the air transversed. When the transmission factor \( q \) is replaced by the extinction coefficient \( a \) (\( a = \ln q \)), the equation takes the form
\[ I_m = I_o e^{-am} \] \( \text{VII} \)
About 95% of the sun’s radiation is contained between 0.3 and 2.4 µm, 1.2% in wavelengths < 0.3 µm, and 3.6% in wavelengths > 2.4 µm (Iqbal, 1983). A systematic division of solar radiation according to frequency and wavelength is given in Tables 1.1 to 1.3. An approximation of energy content in various segments of shortwave radiation is given in Table 1.2. A more detailed picture of the energy content and nature of the solar radiation spectrum is given in Table 1.3.

**EARTH’S ANNUAL GLOBAL MEAN RADIATIVE ENERGY BUDGET**
The global annual mean energy budget is determined by the net radiation flow of energy through the top of the atmosphere and at the earth’s surface.

**TABLE 1.1. Broad bands of the solar spectrum**

<table>
<thead>
<tr>
<th>Color</th>
<th>( \lambda ) (µm)</th>
<th>Irradiance W m(^{-2})</th>
<th>% of solar constant</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ultraviolet</td>
<td>&lt; 0.4</td>
<td>109.81</td>
<td>8.03</td>
</tr>
<tr>
<td>Visible</td>
<td>0.390-0.770</td>
<td>634.40</td>
<td>46.41</td>
</tr>
<tr>
<td>Infrared</td>
<td>&gt; 0.77</td>
<td>634.40</td>
<td>46.40</td>
</tr>
</tbody>
</table>

Source: Adapted from Iqbal, 1983.

**TABLE 1.2. Electromagnetic spectrum energy content in various color bands**

<table>
<thead>
<tr>
<th>Color</th>
<th>( \lambda ) (µm)</th>
<th>Irradiance W m(^{-2})</th>
<th>% of solar constant</th>
</tr>
</thead>
<tbody>
<tr>
<td>Violet</td>
<td>0.390-0.455</td>
<td>108.85</td>
<td>7.96</td>
</tr>
<tr>
<td>Blue</td>
<td>0.455-0.492</td>
<td>73.63</td>
<td>5.39</td>
</tr>
<tr>
<td>Green</td>
<td>0.492-0.577</td>
<td>160.00</td>
<td>11.70</td>
</tr>
<tr>
<td>Yellow</td>
<td>0.577-0.597</td>
<td>35.97</td>
<td>2.63</td>
</tr>
<tr>
<td>Orange</td>
<td>0.597-0.622</td>
<td>43.14</td>
<td>3.16</td>
</tr>
<tr>
<td>Red</td>
<td>0.622-0.770</td>
<td>212.82</td>
<td>15.57</td>
</tr>
</tbody>
</table>
TABLE 1.3. Partition of solar irradiation, 0.2 to 5.0 m wavelength

<table>
<thead>
<tr>
<th>Wavelength (µm)</th>
<th>% Irradiance</th>
<th>Wavelength (µm)</th>
<th>% Irradiance</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.20</td>
<td>0.003</td>
<td>0.55</td>
<td>6.675</td>
</tr>
<tr>
<td>0.22</td>
<td>0.024</td>
<td>0.60</td>
<td>6.300</td>
</tr>
<tr>
<td>0.24</td>
<td>0.102</td>
<td>0.65</td>
<td>5.858</td>
</tr>
<tr>
<td>0.26</td>
<td>0.477</td>
<td>0.70</td>
<td>4.972</td>
</tr>
<tr>
<td>0.28</td>
<td>0.817</td>
<td>0.80</td>
<td>3.882</td>
</tr>
<tr>
<td>0.30</td>
<td>1.873</td>
<td>0.90</td>
<td>3.031</td>
</tr>
<tr>
<td>0.32</td>
<td>2.520</td>
<td>1.00</td>
<td>2.418</td>
</tr>
<tr>
<td>0.34</td>
<td>3.031</td>
<td>1.10</td>
<td>1.975</td>
</tr>
<tr>
<td>0.36</td>
<td>3.542</td>
<td>1.20</td>
<td>1.635</td>
</tr>
<tr>
<td>0.38</td>
<td>4.019</td>
<td>1.40</td>
<td>1.090</td>
</tr>
<tr>
<td>0.39</td>
<td>4.257</td>
<td>1.60</td>
<td>0.715</td>
</tr>
<tr>
<td>0.40</td>
<td>4.904</td>
<td>1.80</td>
<td>0.511</td>
</tr>
<tr>
<td>0.42</td>
<td>6.198</td>
<td>2.00</td>
<td>0.368</td>
</tr>
<tr>
<td>0.44</td>
<td>6.879</td>
<td>2.50</td>
<td>0.167</td>
</tr>
<tr>
<td>0.46</td>
<td>7.356</td>
<td>3.00</td>
<td>0.89</td>
</tr>
<tr>
<td>0.48</td>
<td>7.390</td>
<td>4.00</td>
<td>0.031</td>
</tr>
<tr>
<td>0.50</td>
<td>7.152</td>
<td>5.00</td>
<td>0.014</td>
</tr>
</tbody>
</table>

Source: Adapted from Goody and Yung, 1989.

At the top of the atmosphere, the net energy output is determined by the incident shortwave radiation from the sun minus the reflected shortwave radiation. This difference determines the net shortwave radiation flux at the top of the atmosphere. To balance this inflow of shortwave energy, the earth atmosphere system emits longwave radiation to space. Satellite observations of the top of the atmosphere have made fairly accurate estimates of the global mean energy budget. According to these estimates, the global mean annual outgoing longwave radiation is 235 W m\(^{-2}\) and the annual mean absorbed shortwave flux is 238 W m\(^{-2}\). Hence, the measured top-of-atmosphere budget balances to within 3 W m\(^{-2}\). A part of this imbalance could be associated with the buildup of greenhouse gases and a part is probably associated with El Niño events (Kiehl and Trenberth, 1997).

** Incoming Shortwave Radiation **

Solar radiation that encounters matter, whether solid, liquid, or gas, is called incident radiation. Interactions with matter can change the following properties of incident radiation: intensity, direction, wavelength, polarization, and phase. Radiation intercepted by the earth is absorbed and used in energy-driven processes or is returned to space by scattering and reflection (Fig 22). In mathematical terms, this disposal of solar radiation is given by the equation

\[ Q_s = Cr + Ar + Ca + Aa + (Q + q)(1 - a) + (Q + q) a \] (VIII)

where \( Q_s \) is the incident solar radiation at the top of the atmosphere; \( Cr \) is reflection and scattering back to space by clouds; \( Ar \) is reflection and scattering back by air, dust, and water vapors; \( Ca \) is absorption by clouds; \( Aa \) is absorption by air, dust, and water vapors; \( (Q + q) a \)
is reflection by the earth; \((Q + q)(1 - a)\) is absorption by the earth’s surface, where \(Q\) and \(q\) are, respectively, direct beam and diffused solar radiation incident on the earth and \(a\) is albedo. The global disposal of shortwave radiation (W m\(^{-2}\) per year) is given in Table 1.4.

About a quarter of the solar radiation is reflected back to space by clouds. On average, the reflection is greatest in middle and high latitudes and least in the subtropics. A small portion of the incident radiation is scattered back to space by the constituents of the atmosphere, mainly air molecules, dust particles, and water vapors. About 30% of the radiation is scattered downward. Atmospheric scattering results from multiple interactions between light rays and the gases and particles of the atmosphere. The two major processes, selective scattering and nonselective scattering, are related to the size of the particles in the atmosphere. In selective scattering, the shorter wavelength of UV energy and blue light are scattered more severely than that in longer wavelengths (red) and infrared (IR) energy. Selective scattering is caused by fumes and by gases such as nitrogen, oxygen, and carbon dioxide. This is known as Rayleigh scattering and is the primary cause of the blue color of the sky. For larger sizes of particles, scattering is independent of the wavelength, i.e., white light is scattered. The phenomenon is known as Mie scattering. As the path length increases, the percentage of solar energy in the visible part decreases. Within the visible part itself, the ratio of the blue to the red part decreases with increased path length. This is because the part of the spectrum with higher frequency is scattered to a greater extent than the part with lower frequency. The red color of the sky at sunrise and sunset is because of increased path length in the atmosphere which scatters blue and green wavelengths so only red light reaches the viewer (Sabins, 1997).

The atmosphere absorbs about 20% of the solar radiation. The constituents of the atmosphere that absorb the solar radiation significantly are oxygen, ozone, carbon dioxide, and water vapors. This absorption is of great importance to life on the earth’s surface, because only a very small amount of this radiation can be tolerated by living organisms.

**Oxygen and ozone:** Solar radiation in the wavelengths <0.3 \(\mu\)m is not observed on the ground. It is absorbed in the upper atmosphere. Energy of 0.1 \(\mu\)m is highly absorbed by the atomic and molecular oxygen and also by nitrogen in the ionosphere. Energy of 0.1 to 0.3 \(\mu\)m is absorbed efficiently by ozone in the ozonosphere. Further but less complete ozone absorption occurs in the 0.32 to 0.36 \(\mu\)m region and at minor levels around 0.6 \(\mu\)m (visible part) and 4.75 \(\mu\)m, 9.6 \(\mu\)m, and 14.1 \(\mu\)m (infrared part).

**Carbon dioxide:** This gas is of chief significance in the lower part of the atmosphere. Carbon dioxide has a weak absorption band at about 4 \(\mu\)m and 10 \(\mu\)m and a very strong absorption band around 15 \(\mu\)m.

**Water vapor:** Among the atmospheric gases, water vapors absorb the largest amount of solar radiation. Several weak absorption bands occur below 0.7 \(\mu\)m, while important broad bands of varying intensity exist between 0.7 and 0.8 \(\mu\)m. The strongest water absorption is around 6 \(\mu\)m, where almost 100% of longwave radiation may be absorbed if the atmosphere is sufficiently moist (Barrett, 1992).
TABLE 1.4. Disposal of solar radiation

<table>
<thead>
<tr>
<th>Solar energy</th>
<th>W m$^{-2}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Incident on the top of the atmosphere</td>
<td>342</td>
</tr>
<tr>
<td>Reflected by clouds, aerosols, and atmosphere</td>
<td>77</td>
</tr>
<tr>
<td>Reflected from the earth</td>
<td>30</td>
</tr>
<tr>
<td>Total reflected</td>
<td>107</td>
</tr>
<tr>
<td>Absorbed by the atmosphere</td>
<td>67</td>
</tr>
<tr>
<td>Absorbed by the earth</td>
<td>168</td>
</tr>
<tr>
<td>Total absorbed by earth-atmosphere system</td>
<td>235</td>
</tr>
</tbody>
</table>

Source: Adapted from Kiehl and Trenberth, 1997.

Thus, after reflection, scattering, and absorption in the atmosphere, about half of the solar radiation reaches the earth’s surface. Out of this, about 6% is reflected back to outer space. This is known as albedo. The albedo is defined as the fraction of incoming shortwave radiation that is reflected by the earth’s surface. The albedo varies with the color and composition of the earth’s surface, the season, and the angle of the sun’s rays. The values are higher in winter as well as at sunrise and sunset. The albedo also varies with the wavelength of the incident radiation (Roberto et al., 1999). Very small values have been recorded in the ultraviolet part of the spectrum and higher values in the visible part. The albedo values of some selected surfaces are given in Table 1.5.

**Outgoing Longwave Radiation**

The surface of the earth after being heated by the absorption of solar radiation becomes a source of radiation itself (Fig 23). Because the average temperature of the earth’s surface is about 285 °K, 99% of the radiation is emitted in the infrared range from 4 to 120 µm, with a peak near 10 µm, as indicated by Wein’s displacement law. This is longwave radiation and is also known as terrestrial radiation. The average annual global disposal of infrared radiation is represented by equations IX, X, and XI.

\[
I(e) = I_a + I_s \quad \text{(IX)}
\]

\[
I(a) = I_b + I(a)s \quad \text{(X)}
\]

\[
I = I(e) - I_b \quad \text{(XI)}
\]

where \(I(e)\) is infrared radiation emitted by the earth’s surface; \(I_a\) is infrared radiation from the earth’s surface absorbed by the atmosphere; \(I_s\) is infrared radiation from the earth lost to space; \(I(a)\) is infrared radiation from the atmosphere; \(I_b\) is counter radiation; \(I(a)s\) is infrared radiation from the atmosphere lost in space; and \(I\) is the effective outgoing radiation from the earth. The quantitative disposal of longwave radiation (W m$^{-2}$ per year) from the earth-atmosphere system is summarized in Table 1.6. The earth’s atmosphere absorbs about 90% of the outgoing radiation from the earth’s surface. Water vapours absorb in wavelengths of 5.3 to 7.7 µm and beyond 20 µm; ozone in wavelengths of 9.4 to 9.8 µm; carbon dioxide in wavelengths of 13.1 to 16.9 µm; and clouds in all wavelengths. Longwave radiation escapes to space between 8.5 and 11.0 µm, known as the atmospheric window. A large part of the radiation absorbed by the atmosphere is sent back to the earth’s surface as counter radiation. This counter radiation prevents the earth’s surface from excessive cooling at night.
TABLE 1.5. Albedo of shortwave radiation

<table>
<thead>
<tr>
<th>Surface</th>
<th>Albedo (%)</th>
<th>Surface</th>
<th>Albedo (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fine sandy soil</td>
<td>37</td>
<td>Alfalfa</td>
<td>2-5</td>
</tr>
<tr>
<td>Dark black soil</td>
<td>14</td>
<td>Cotton</td>
<td>20-22</td>
</tr>
<tr>
<td>Moist black soil</td>
<td>8</td>
<td>Grass (dry)</td>
<td>31-33</td>
</tr>
<tr>
<td>Deciduous forest</td>
<td>17</td>
<td>Grass (green)</td>
<td>26</td>
</tr>
<tr>
<td>Pine forest</td>
<td>14</td>
<td>Lettuce</td>
<td>22</td>
</tr>
<tr>
<td>Prairie</td>
<td>12-13</td>
<td>Lucerne</td>
<td>23-32</td>
</tr>
<tr>
<td>Desert scrubland</td>
<td>20-29</td>
<td>Maize</td>
<td>16-23</td>
</tr>
<tr>
<td>Ice sheet with water</td>
<td>26</td>
<td>Rice</td>
<td>11-21</td>
</tr>
<tr>
<td>Sea ice</td>
<td>36</td>
<td>Sugar beet</td>
<td>18</td>
</tr>
<tr>
<td>Dense clean dry snow</td>
<td>86-95</td>
<td>Rye</td>
<td>11-21</td>
</tr>
<tr>
<td>Water surface at 30° latitude</td>
<td>6-9</td>
<td>Wheat</td>
<td>16-23</td>
</tr>
</tbody>
</table>

Source: Adapted from Barrett, 1992; Iqbal, 1983.

TABLE 1.6. Disposal of longwave radiation

<table>
<thead>
<tr>
<th>Longwave radiation</th>
<th>W m⁻²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Emitted by the earth’s surface</td>
<td>390</td>
</tr>
<tr>
<td>Lost to space</td>
<td>40</td>
</tr>
<tr>
<td>Absorbed by the atmosphere</td>
<td>350</td>
</tr>
<tr>
<td>Emitted by the atmosphere and clouds</td>
<td>519</td>
</tr>
<tr>
<td>Lost to space from atmosphere</td>
<td>195</td>
</tr>
<tr>
<td>Back radiation from atmosphere absorbed by earth</td>
<td>324</td>
</tr>
<tr>
<td>Total outgoing longwave radiation</td>
<td>235</td>
</tr>
</tbody>
</table>

Source: Adapted from Kiehl and Trenberth, 1997.

Radiation Balance in the Earth-Atmosphere System

When averaged over the globe, the earth’s surface absorbs about 168 W m⁻² of solar radiation every year and effectively radiates 66 W m⁻² of longwave energy to the atmosphere. The difference, +102 W m⁻², is the net radiation gain of the earth’s surface. Likewise, the net radiation balance of the atmosphere comes to −102 W m⁻² per year. Thus, the atmosphere loses as much radiative energy in a year as the earth’s surface gains. To keep the thermal balance in equilibrium, energy is transferred from the earth’s surface to the atmosphere. This vertical heat exchange occurs mainly through the evaporation of water from the surface of the earth (heat loss), through condensation in the atmosphere (heat gain), and by the conduction of sensible heat from the surface and transfer to the atmosphere through convection.
SOLAR RADIATION AND CROP PLANTS
Solar radiation is the energy source that sustains organic life on earth. Crop production is in fact an exploitation of solar radiation. The three broad spectra of solar energy described in this section are significant to plant life. The shorter-than-visible wavelength radiation segment in the solar spectrum is chemically very active. When plants are exposed to excessive amounts of this radiation, the effects are detrimental. However, the atmosphere acts as a regulator in this type of solar radiation, and none of the cosmic, gamma, and X rays reach the earth (Evans, 1973). The ultraviolet radiation of this segment reaching the earth’s surface is very low and is normally tolerated by plants.
Solar radiation in the higher-than-visible wavelength segment, referred to as infrared radiation, has thermal effects on plants. In the presence of water vapors, this radiation does not harm plants; rather, it supplies the necessary thermal energy to the plant environment. The third spectrum, lying between the ultraviolet and infrared, is the visible part of solar radiation and is referred as light. This segment of solar radiation plays an important part in plant growth and development through the processes of chlorophyll synthesis and photosynthesis and through photosensitive regulatory mechanisms such as phototropism and photoperiodic activity. Light of the correct intensity, quality, and duration is essential for normal plant development. Poor light availability is frequently responsible for plant abnormalities and disorders. Virtually all plant parts are directly or indirectly influenced by this part of the spectrum. It affects the production of tillers; the stability, strength, and length of the culms; the yield and total weight of plant structures; and the size of leaves and root development (Rodriguez et al., 1999). The length of day or the duration of the light period determines flowering and has a profound effect on the content of soluble carbohydrates present. The majority of plants flower only when exposed to certain specific photoperiods. It is on the basis of this response that the plants have been classified as short-day plants, long-day plants, and dayneutral plants. When other environmental factors are not limiting it, photosynthesis increases with longer duration of the light period (Salisbury, 1981).

Reflection, Transmission, and Absorption
Reflection and transmission from the leaves have similar spectral distributions as shown in Figs 24 and 25. The maxima for both are in the green light as well as in the infrared region. The impression of the green color of the plants depends on the high reflectivity, the relatively high intensity of solar radiation, and the greater sensitivity of the human eye for green light. The strong infrared reflection from plants is an important natural device for protection of plant life against damage due to overheating. On average, the plant canopy absorbs about 75% of the incident radiation, with about 15% reflected and 10% transmitted.
Due to their chemical components or physical structures, plants absorb selectively in discrete wavelengths (Fig 26). The transparent epidermis allows the incident sunlight to penetrate into the mesophyll, which consists of two layers: (1) the palisade parenchyma of closely spaced cylindrical cells and (2) the spongy parenchyma of irregular cells with abundant interstices filled with air. Both types of mesophyll cells contain chlorophyll, which reflects part of the incident green wavelengths and absorbs all the blue and red energy for photosynthesis (Sabins, 1997). Chlorophyll absorption is maximum in the blue (0.45 µm) and in the red (0.65 µm) regions (Table 1.7). The longer wavelengths of photographic IR energy penetrate...
into the spongy parenchyma, where the energy is strongly scattered and reflected by the boundaries between the cell walls and air spaces. The high near-infrared (near-IR) reflectance of leaves is caused not by chlorophyll but by the internal cell structure. Near the border of visible light, absorption by the plant decreases but then increases again in the infrared. Infrared radiation greater than 3 µm is completely absorbed by the plants.

<table>
<thead>
<tr>
<th>Wavelength (µm)</th>
<th>Reflection (%)</th>
<th>Transmission (%)</th>
<th>Absorption (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.34</td>
<td>9</td>
<td>0</td>
<td>91</td>
</tr>
<tr>
<td>0.44</td>
<td>11</td>
<td>2</td>
<td>87</td>
</tr>
<tr>
<td>0.51</td>
<td>14</td>
<td>10</td>
<td>76</td>
</tr>
<tr>
<td>0.58</td>
<td>14</td>
<td>10</td>
<td>76</td>
</tr>
<tr>
<td>0.64</td>
<td>13</td>
<td>9</td>
<td>78</td>
</tr>
<tr>
<td>1.0</td>
<td>45</td>
<td>50</td>
<td>5</td>
</tr>
<tr>
<td>2.4</td>
<td>7</td>
<td>28</td>
<td>65</td>
</tr>
</tbody>
</table>

Source: Adapted from Baumgartner, 1973.

It can be summed up that the plant leaf strongly absorbs blue and red wavelengths, less strongly absorbs the green, very weakly absorbs the near infrared, and strongly absorbs in the far-infrared wavelengths. Because the absorption of the near-infrared wavelengths (which contain the bulk of energy) by the leaf is limited, by discarding this energy it prevents the internal temperature from becoming lethal. At the infrared wavelengths, the plant leaf is an efficient absorber, but in these wavelengths the energy at the surface is small, with the result that the plant is a good absorber in the far-infrared. It is an equally a good radiator at these wavelengths.

The quality of radiation affects flowering, germination, and elongation. Red light with a wavelength of 0.66 µm is by far the most effective inhibitor of flowering in the case of long-day plants. Red light helps mature apples to turn red. Germination of seeds is inhibited when they are exposed to green, blue, and other short wavelength colors. However, germination is induced when seeds are exposed to the red portion of the spectrum. The red and infrared parts of the spectrum have reversible effects on seed germination. Stem elongation is promoted by exposure to far-red wavelengths, whereas the red part of the spectrum suppresses the elongation (Butler and Roberts, 1966; Takaichi et al., 2000).

The visible part of the spectrum also influences the orientation of shoots, phenomenon known as phototropism (Stowe-Evans, Luesse, and Liscum, 2001; Koller, Ritter, and Heller, 2001; Jin, Zhu, and Zeiger, 2001). When shoots turn toward the light, the phenomenon is known as positive phototropism. With increasing intensity of light, positive phototropism turns into negative phototropism. The strongest influence on phototropism is by the blue part of the spectrum (0.5 m) and the weakest influence is by red rays. The phototropism action of the visible spectrum increases from the red to the blue part; subsequently, it declines again in the ultraviolet part. However, Ruppel, Hangarter, and Kiss (2001) have demonstrated that, in addition to the previously described blue-light-dependent negative phototropic response in
roots, roots of wild-type and mutant (ACG 21) *Arabidopsis thaliana* display a previously unknown red-light-dependent positive phototropic response. The ultraviolet and gamma part of the spectrum has only a slight effect on the plant. This may be partly because very little of this part of the spectrum reaches the earth’s surface. However, it is well known that these rays have biological effects (Skorska, 2000; Predieri and Gatti, 2000). These rays may kill microorganisms, disinfect the soil, and eradicate diseases (Sharp and Polavarapu, 1999). Ultraviolet rays also influence the germination and quality of seeds. These rays lead to many irregularities in the growth and development of plants (Caldwell, 1981). Ultraviolet radiation leads to a strong in hibition of photosynthesis and metabolism (Karsten et al., 1999; Correia et al., 2000).

The solar spectrum can be divided into the following eight broad bands on the basis of the physiological response of plants:

1. Wavelength greater than 1.000 \( \mu \text{m} \): Most of this radiation absorbed by plants is transformed into heat without interfering with the biochemical processes.
2. Wavelength 1.000 to 0.700 \( \mu \text{m} \): Elongation effects on plants.
3. Wavelength 0.700 to 0.610 \( \mu \text{m} \): Very strong absorption by chlorophyll, the strongest photosynthetic activity, and in many cases strong photoperiodic activity.
4. Wavelength 0.610 to 0.510 \( \mu \text{m} \): Low photosynthetic effectiveness in the green segment and weak formative activity.
5. Wavelength 0.510 to 0.400 \( \mu \text{m} \): Strong chlorophyll absorption, strong photosynthetic activity, and strong formative effects.
6. Wavelength 0.400 to 0.315 \( \mu \text{m} \): Produces fluorescence in plants and a strong response by photographic emulsions.
7. Wavelength 0.315 to 0.280 \( \mu \text{m} \): Significant germicidal action. Practically no solar radiation of wavelengths shorter than 0.29 \( \mu \text{m} \) reaches the earth’s surface.
8. Wavelength shorter than 0.280 \( \mu \text{m} \): Very strong germicidal action. It is injurious to eyesight and when below 0.26 \( \mu \text{m} \) can kill some plants. No such radiation reaches the earth’s surface.

**Factors Affecting the Distribution of Solar Radiation Within the Plant Community**

The distribution of radiation in a plant canopy is determined by several factors, such as the transmissibility of the leaf, leaf arrangement and inclination, plant density, plant height, and the angle of the sun (Vorasoot, Tienroj, and Apinakapong, 1996; Cohen et al., 1999; Courbaud, Coligny, and Cordonnier, 2003). Leaves of deciduous trees, herbs, and grasses (including cereals) have transmissibility ranging from 5 to 10%. The broad leaves of evergreen plants have a value of 2 to 8%. Transmissibility varies slightly with the age of the leaf. The transmissibility of a young leaf is relatively high. With the maturing of the leaf, it declines but then rises again as the leaf turns yellow. The transmissibility of a leaf is directly related to its chlorophyll content. The logarithm of transmissibility decreases linearly with an increase in the chlorophyll content. If the leaves that transmit 10% of the radiation were horizontally displayed in
continuous layers, only 1% of light, mostly in the green region, could penetrate the second layer. However, leaves are rarely displayed horizontally. The relative light interception of horizontal and erect foliage is calculated in the ratio 1 to 0.44. Therefore, the actual light gradient within the canopy is not as steep as the transmissibility will suggest. On average, when the total leaf area equals the area at the ground, the mean transmissibility is around 75% for the more upright leaves and 50% for the more horizontal leaves. In weak light, any departure of the leaves from the horizontal position reduces the net photosynthesis.

In full sunlight, the optimum leaf inclination for efficient light use is 81° (Fig 27). At full sunlight, a leaf placed at the optimum inclination is 4.5 times as efficient in using light as a horizontal leaf (Fig 28). For more efficient use of light, the upper leaves in a plant canopy should have a near-vertical orientation, whereas the lower foliage should be almost horizontal.

An ideal arrangement of the plant canopy is for the lower 13% of the leaves to be oriented at an angle of 0 to 30°, the middle 37% of the leaves should be at 30 to 60°, and the upper 50% leaves should be at 60 to 90° with the horizontal (Chang, 1968).

In the case of young plants, the percentage of light interception is not only small but also variable with the time of day. It is at a minimum at noon and at maximum during the morning and evening hours. When the plant height increases, the interception of light by the canopy also increases, with only a small variation at different times of the day.

Numerous investigators have studied the radiation distribution in a plant canopy and put forward equations for determining light at a particular height in a canopy (Monteith and Elston, 1983; Kull and Kruijt, 1998; Mariscal, Orgaz, and Villalobos, 2000; Marques, Filho, and Dallarosa, 2000). So far, the equation for Beer’s law is thought to be the most appropriate. The equation of the law is written as

\[ I = I_a e^{-k f} \] (XII)

where \( I \) is the intensity of light at a particular height within the canopy, \( I_a \) is the intensity at the top, \( k \) is the extinction coefficient of the leaf, \( f \) is the leaf area index (LAI), and \( e \) is the base of natural log. The extinction coefficient can be defined as the ratio between the light loss through the leaf to the light at the top of the leaf. The extinction coefficient varies with the orientation of the leaf. Its value is low in stands with upright leaves and high in stands with more or less horizontal leaves.

Roujean (1999) made actual measurements of solar radiation profiles in black spruce canopies on typical summer days and compared those with Beer’s law values (Fig 29). He observed certain deviations from the Beer’s law extinction and assigned those to seasonal effects, such as the angle of the sun’s rays.

**Spectral Composition of Radiation in a Plant Canopy**

As solar radiation penetrates the canopy, its quality undergoes transformation in different layers (Baumgartner, 1973). After every reflection and transmission, red and infrared radiation increases relative to the other wavelengths. In the interior of the canopy there is a relatively greater decrease of light in the chlorophyll absorption bands at 0.45 µm and 0.65
µm, and a relatively small decrease in green at 0.55 µm and infrared at 0.80 µm. In less tall crops such as, about 30% of the total radiation and 20% of light reaches the ground. For a tall maize crop, the transmission of infrared radiation to the ground is 30 to 40%. In the visible part of the spectrum, the transmission is only 5 to 10%.

Flint and Caldwell (1998) measured global (total) and diffuse solar radiation in canopy gaps of a semideciduous tropical forest in Panama. Compared to unobstructed measurements taken outside the forest, the sunlit portions of gaps were depleted in the proportion of UV-B relative to PAR, especially at midday. Shaded areas, in contrast, were always richer in UV-B relative to PAR, but the magnitude of the change varied greatly. It was suggested that this variation was due to the differences in the directional nature of diffuse solar UV-B radiation as compared to diffuse PAR. Measurements in the gaps showed substantial reductions in the proportion of radiation in the diffuse components of both the UV-B and PAR wavebands. However, because of the greater proportion of UV-B that is diffuse, it tended to predominate in shaded areas. Similar patterns were seen in measurements taken at temperate latitudes.

The composition of solar radiation changes with the angle of the sun. The maximum visible spectrum penetration is at noon. Penetration of infrared radiation is comparatively high soon after sunrise and just before sunset. The early morning and evening values are higher because of the greater amount of diffused light. Anisimov and Fukshansky (1997) measured the spectral composition of incident solar and diffuse sky PAR as well as the spectral scattering coefficient of PAR for a green leaf. The results are shown in Figs 30 and 31.

**PHOTOSYNTHETICALLY ACTIVE RADIATION (PAR)**

The visible region (approximately 0.385 to 0.695 µm) of the solar spectrum is generally referred to as photosynthetically active radiation. Although the global radiation is expressed in terms of W m\(^{-2}\), the unit of PAR measurement is µE m\(^{-2}\) s\(^{-1}\). Photosynthetic photon flux density (PPFD) is the number of photons in the photosynthetically active band of solar radiation.

It is usually defined in moles of photons per unit surface and per unit time (mol m\(^{-2}\) s\(^{-1}\)). 1 µmol photons m\(^{-2}\) s\(^{-1}\) = 6.022 \times 10\(^{17}\) photons m\(^{-2}\) s\(^{-1}\) = 1 µE m\(^{-2}\) s\(^{-1}\). For conversion sake, 2.02 µmol photons m\(^{-2}\) s\(^{-1}\) of PAR is treated as equivalent to 1 W m\(^{-2}\) of global radiation (Berbigier and Hassika, 1998; Alados et al., 2002).

PAR is often calculated as a constant ratio of the broadband solar irradiance. Many reports are available in the literature to estimate PAR from the more routinely measured parameters of solar radiation, light intensity, and cloud amount. Several of these reports indicate the desirability of local calibration for the relationship between PAR and solar irradiance to account for local climatic and geographic differences such as cloudiness, day length, and diurnal pattern of solar radiation. A wide range of values has been quoted for the ratio (fe) of PAR (W m\(^{-2}\)) to global solar radiation (W m\(^{-2}\)).

Several researchers suggest that this variation can be ascribed to differences in the waveband limits chosen to define PAR and in part to the different methods used to measure or calculate fe (Olesen, 2000). On the other hand, many people argue that different lower and upper waveband limits have no significant influence on the ratio received at the earth’s surface.
At higher and middle latitudes, the daily average value of $fe$ is little affected by atmospheric and sky conditions. Systematic differences from day to day are largely a function of cloudiness. Even in the tropics, $fe$ should be a conservative quantity on clear days. For a clear day, $fe = 0.51$, and for very cloudy skies, $fe = 0.63$ have been measured in tropical countries. Udo and Aro (1999) made measurements of global solar radiation ($Rs$) and global photosynthetically active radiation for a period of 12 months at Ilorin, Nigeria, to find the relationship between them. The results of the measurements showed that the average ratio of PAR to $Rs$ for the year was 2.08 E MJ$^{-1}$, with the dry and rainy season values of 2.02 and 2.12 E MJ$^{-1}$, respectively. The minimum monthly mean daily ratio of 1.92 E MJ$^{-1}$ was in January, representing a typical dry season month, while the maximum was 2.15 E MJ$^{-1}$ in May, representing a rainy season month. The ratio values in the rainy season months and even dry season months remain constant at about 2.1 E MJ$^{-1}$. On a daily basis, the maximum and minimum ratios were 1.86 and 2.31 E MJ$^{-1}$, respectively. Hourly values of the ratio increased as the sky conditions changed from “clear” to “cloudy.” Hassika and Berbigier (1998) made continuous measurements of global and diffuse PAR throughout the year, within and above a forest. On clear sky days, roughly 65% of the incident PAR was absorbed by the needles, stems, and branches, 20% was reflected, and the understory absorbed the remaining 15% (Fig 32).

PAR interception in actively growing wheat crops was studied by Prasad and Sastry (1994). Two wheat varieties were grown with irrigation during the 1985-1986 winter season and assessed for total solar radiation interception, PAR, net radiation, and albedo. Maximum solar radiation and PAR interception was at 100 days after sowing (milk ripeness stage). For high values of crop net photosynthesis, the number of rows is more important at high light than at low light, whereas crop height is more important at low light than at high light (Thornley, Hand, and Wilson, 1992). The distribution of leaf angles (more vertical than horizontal angles) is important for maximizing whole-plant photosynthesis (Herbert, 1991).

**SOLAR RADIATION USE EFFICIENCY**

The conversion coefficient, defined as the quantity of biomass produced per unit of intercepted radiation (g MJ$^{-1}$), provides a measure of the efficiency $e$ with which the captured radiation is used to produce new plant material. The alternative term, radiation use efficiency (RUE), is also commonly used (Black and Ong, 2000). Corlett and colleagues (1992) measured the $e$ values for a millet crop under varying agronomic practices (Table 1.8).

As the values in Table 1.8 indicate, solar radiation use efficiency under the current crop production systems is very low. It is much below the theoretically estimated (8 to 10%) upper limit (Mavi, 1994). The efficiency of the conversion of photosynthetically active radiation by C$_3$ plants falls off with increasing intensity. This decrease is caused by finite resistance to diffusion of CO$_2$ through the leaf to the chloroplast. However, an increase in the productivity of direct solar energy can be achieved if, by redistribution, it is intercepted at more uniform and lower intensity by a greater portion of the leaf area of a crop. Aikman (1989) developed a model which predicts that redistributing direct solar radiation over twice the leaf area at half the intensity would give an increase of 22% of annual productivity.
TABLE 1.8. Intercepted solar radiation, aboveground biomass production, and biomass production per unit of intercepted radiation (e)

<table>
<thead>
<tr>
<th>Season/crop</th>
<th>Intercepted radiation (MJ m−2)</th>
<th>Biomass (t ha−1)</th>
<th>e (g MJ−1)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rainy season (July-August 1986)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sole millet</td>
<td>581</td>
<td>4.7</td>
<td>0.81</td>
</tr>
<tr>
<td>Alley millet</td>
<td>300</td>
<td>3.1</td>
<td>1.03</td>
</tr>
<tr>
<td>Sole L. leucocephala</td>
<td>520</td>
<td>4.0</td>
<td>0.77</td>
</tr>
<tr>
<td>Alley L. leucocephala</td>
<td>510</td>
<td>4.0</td>
<td>0.77</td>
</tr>
<tr>
<td>Total alley system</td>
<td>810</td>
<td>7.1</td>
<td>0.81</td>
</tr>
<tr>
<td>Rainy season (July-August 1987)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sole millet</td>
<td>504</td>
<td>5.0</td>
<td>0.98</td>
</tr>
<tr>
<td>Alley millet</td>
<td>180</td>
<td>0.9</td>
<td>0.050</td>
</tr>
<tr>
<td>Sole L. leucocephala</td>
<td>861</td>
<td>7.1</td>
<td>0.82</td>
</tr>
<tr>
<td>Alley L. leucocephala</td>
<td>748</td>
<td>6.4</td>
<td>0.86</td>
</tr>
<tr>
<td>Total alley system</td>
<td>928</td>
<td>7.3</td>
<td>0.79</td>
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Source: Adapted from Corlett et al., 1992.

The model gives reasonable values for the reduction in productivity reported for shade regimes. The results of this study suggest that in protected cultivation, screens of partially reflective material could be used to redistribute solar radiation from leaves exposed to high intensities onto shaded leaves and so raise the photosynthetic efficiency. Assuming absorption of direct light by the screens of 0.1, the increase in productivity is estimated to be 17%. Li, Kurata, and Takakura (1998) also demonstrated that solar radiation enhancement through reflected radiation on the cultivated area could be achieved to raise the photosynthetic productivity throughout the winter.

When water or nutrient supplies do not limit growth, the quantity of biomass produced by monocrops is limited primarily by the quantity of radiation captured, and seasonal biomass accumulation for a given species may be expressed as the time integral of the product (Monteith, 1990, 1994). Numerous studies of annual crops, and some with perennial species, have demonstrated the existence of close correlations between dry matter production and cumulative intercepted radiation. For example, Stirling and colleagues (1990) examined the impact of artificial shade imposed on groundnut between the onset of peg initiation and pod filling, and final harvest using bamboo screens. A close linear correlation between aboveground biomass and cumulative intercepted radiation was found in all treatments, although the quantity of biomass produced per unit of intercepted radiation was substantially greater when shading was imposed from peg initiation onward. In the absence of stress, e is often conservative, typically ranging between 1.0 and 1.5 g MJ−1 for C3 species in temperate environments, 1.5 to 1.7 g MJ−1 for tropical C3 species, and up to 2.5 g MJ−1 for tropical C4 cereals under favorable conditions (Squire, 1990). However, the work of Stirling and colleagues (1990) showed that e may vary substantially within a single season between 0.98 g MJ−1 in the unshaded control and 2.36 g MJ−1 in crops shaded from peg initiation onward. Thus, plants in the latter treatment intercepted approximately one-quarter of the radiation.
received by the unshaded control but converted this to dry matter 2.4 times more efficiently (Monteith and Elston, 1983; Russell, Jarvis, and Monteith, 1988). Choudhury (2000) also observed a strong linear relationship between RUE and diffuse fraction of the incident solar radiation.

The observed variability in experimentally determined e values contrasts with earlier views that e is highly conservative except during severe water stress but complies with more recent suggestions that the assumption of a constant value within species or cultivars may be incorrect (Demetriades Shah et al., 1994; Sumit and Kler, 2000; Bonhomme, 2000).

This leads to criticism of the concept that biomass accumulation may be linked directly with cumulative intercepted radiation, and those meaningful e values may be derived from such correlations. It is argued that the concept of radiation use efficiency is oversimplistic, cannot improve our understanding of crop growth, and is of limited value in predicting yield. This argument concludes little evidence exists that incident radiation is a critical limiting factor determining crop growth under normal field conditions.

Demetriades Shah and colleagues (1992) advocated that analysis of crop growth in terms of cumulative intercepted radiation and the conversion efficiency of solar energy during dry matter production should be approached with caution. A major plank in this argument was that photosynthesis, and hence crop growth rate, depends on numerous soil, atmospheric, and biological factors, of which radiation is only one component. They suggested that good correlations would always be found between radiation interception and any growing object, even when radiation is not the limiting variable.

So a close correlation between crop growth and radiation interception may be expected even when light is not a major limiting factor. Therefore, although solar energy may be the most fundamental natural resource for crop growth from a physical viewpoint, from a biological viewpoint it is no more important than water, nutrients, CO₂, or any other essential commodity. As such, analysis of crop growth in terms of its radiation conversion coefficient may be inappropriate when variables other than radiation are the primary limiting factor.

Further experimental support for this view was provided by Vijaya Kumar and colleagues (1996), when they showed that the conversion coefficient for rainfed castor beans (Ricinus communis) was less stable than previously suggested. The values obtained varied from year to year and were influenced by sowing date, decreasing with lateness of planting within the range 0.79 to 1.10 g MJ⁻¹. Values recorded prior to flowering were more stable than those obtained after flowering began. Campbell and colleagues (2001) also demonstrated that RUE steadily declined during growth of the rice crop and suggested that when RUE is used as a model parameter, it must be changed for differing LAI and for pre- and postanthesis periods.

Monteith (1994), however, defends the validity, generality, and robustness of correlations between intercepted radiation and growth and the conservativeness of e. Monteith concludes that few of the arguments advanced against conversion coefficient e are not convincing, and errors involved in measuring intercepted radiation can be minimized. In contrast to the view of Demetriades Shah et al. (1992), he saw no reason to abandon the concept, but instead highlighted the need to test and improve methodology as new information becomes available.

Monteith’s arguments are supported by Kiniry (1994) and Arkebauer and colleagues (1994), who suggested that Demetriades Shah and colleagues (1992) had overlooked the fact that
many environmental stresses that limit growth act through physiological pathways directly involving the photosynthetic process and its products. Arkebauer and colleagues (1994) argued that $e$ cannot be expected to be constant, even within a single species or genotype, in the face of changes in other environmental variables. They argued that the definition of $e$ involves three separate factors. First, the type and energy content of the carbon involved, i.e., net CO$_2$ uptake by the canopy, total aboveground dry matter production, or total plant dry matter including roots and storage organs. Second, the way in which radiation is characterized, i.e., total incident solar radiation, intercepted shortwave radiation, intercepted PAR, or absorbed PAR. Third, the time scale over which $e$ is calculated is extremely important and may range from instantaneous to hourly, daily, weekly, or seasonal estimates. Because widely differing definitions of $e$ have been adopted, the values obtained may be expected to show substantial variation.

Weighing arguments for and against the concept of solar radiation use efficiency, it can be concluded that RUE is likely to remain as a tool in understanding and predicting crop growth and yield.
FIG 28. Rate of photosynthesis in a leaf placed at two different angles (Source: Mavi, 1994.)

FIG 29. Solar radiation profile in a spruce forest (Source: Reprinted from Agricultural and Forest Meteorology, 93, J. L. Roujean, Measurement of PAR transmittance within boreal forest stands during BOREAS, pp. 1-6, 1999, with permission from Elsevier Science.)


# Unit – II

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Growth analysis

Growth is one of the important properties of living organisms. Many physiological processes play an important role during growth of plants and animals. In plants seed germinates and develops into a seedling and later it assumes the shape of an adult plant. Plants show indefinite and diffuse growth while animals show fixed and uniform growth.

Growth – Quantitative change during development which may be defined as an irreversible change in the size of a cell, organ or whole organism. External form of an organ is primarily the result of differential growth along certain axis.

Types of growth

Primary and secondary growth - The mitotic division of meristematic cells presents at the root and shoot apex increases the length of the plant body. This is called the primary growth. The secondary meristem increases the diameter of the plant body and it is called the secondary growth.

Unlimited Growth- The root and the shoot system of plants grow continuously from germination stage to the death or throughout the life span of the plant. It is called ‘Unlimited’ or ‘indeterminate’ type of growth.

Limited growth - The leaves, fruits and flowers stop growing after attaining certain size. This is called ‘limited’ or ‘determinate’ type of growth.

Vegetative growth- The earlier growth of plant producing leaves, stem and branches without flowers is called ‘vegetative growth/Phase’.

Reproductive growth- After the vegetative growth, plants produce flowers which is the reproductive part of the plant. This is called reproductive growth/phase.

Growth stages: When we plot growth (increase in weight, height etc) against time an ‘S’ shaped curve called growth curve is obtained (Fig. 33). It is also called ‘sigmoid ‘curve. This curve mainly shows four phases of growth-

1. initial slow growth (Lag phase),

2. the rapid period of growth (log phase/grand period of growth/exponential phase) where maximum growth is seen in a short period and

3. The diminishing phase where growth will be slow and

**Development** – Whole series of changes which an organism (or individual organ, tissue or even cell) goes through during its life cycle. Plant development involves both growth and differentiation. Development is governed by both environmental and internal factors. One of the internal factors that regulate growth and development is ‘plant hormones’.

**Differentiation** – During development there appear not only quantitative differences in number and arrangement of cells within different organs, but also qualitative differences between cells, tissues and organs to which the term differentiation is applied e.g. differentiation of plant body into shoot and root.

**Dedifferentiation and redifferentiation of cells**
The three phases of cell growth are **cell division**, **cell enlargement** and **cell differentiation**. The first two stages increase the size of the plant cell while the 3rd stage brings maturity to the cells. **Differentiation**, is a process during which cells undergoes structural changes in the cell wall and protoplasm (Fig. 34). A differentiated cell cannot divide.

![Phases of Cell growth](image)

**Fig 34- Phases of Cell growth-Cell division, cell elongation and cell differentiation phases**

An undividable differentiated cell, however, sometimes regains the power of division. This process is called **dedifferentiation**. Dedifferentiation is a common process in plants during secondary growth and in wound healing mechanisms. A dedifferentiated cell can divide and produce new cells. Thus produced new cells again loose the power of division and become a part of permanent tissue. This process is called “**redifferentiation**’. Tumour cells form good example for redifferentiated cells.

The dynamics of growth – For individual cells or organs growth is potentially unlimited and begins as an exponential pattern. However, mutual interaction within an individual impose limitations on growth, the actual growth curve becomes sigmoid in nature. The overall growth of an organism includes an early exponential phase. Growth of a higher plant during its exponential phase is analogous to accumulation of capital at continuous compound
interest. If the plants initial weight is $W_0$, and the rate of compound interest is $r$, the total weight after a certain time $t$ will be

$$W_t = W_0(1 + r)^t$$

Growth analysis – Growth analysis is a technique of quantifying components of plant growth from a series of mathematical equations.

The expression *CROP Growth Analysis (CGA)* generally refers to useful set of quantitative methods describing and interpreting the behaviour of whole plant/crop systems under natural, semi-natural or controlled conditions. CGA can provide an explanatory, holistic, and integrative approach to interpreting plant morphology, physiology, phenology and functions often required in research and education activities. The bases for CGA are primary data such as weights, areas, volumes and contents/components of plants/crops elaborated dynamically for describing the entire system behaviour. Two distinct approaches to CGA have evolved: *classical* (or intervals) and *functional* one.

**Classical (or intervals) approach:** This is the oldest methods of plant growth analysis, introduced in the beginning of last century (Blackman 1919, West et al. 1920). In the past, the interval method was utilized to compute the growth analysis components (e.g. RGR, NAR and LAR), by using average plant weight, leaf weight, and leaf area. In this method a relative growth rate (RGR) is calculated by dividing the difference in ln-transformed plant weight at two harvests by the time difference between those harvests. Although straightforward, this approach has been considered unsatisfactory. Firstly, the time course of the growth rate may be severely obscured by fluctuations in RGR between adjacent harvest intervals (Causton and Venus 1981). Secondly, in the calculation of the net assimilation rate (NAR), a fixed relation between leaf area and plant weight has to be assumed (Evans 1972). Third, it is difficult to statistically evaluate differences in RGR (Poorter and Lewis 1986). The problems with the interval method are that it computes the growth analysis indices using two sampling dates and therefore assumes linear growth between the two sampling dates and that sampling errors can have a relevant effect on the value of indices itself, so a high number of replication is required.

**Functional approach:** Functional approach typically is more robust functional approach, even if some small time scale effect can be hidden because original values of crop data are substituted by their interpolated values. Thanks to the availability of powerful software and hardware tools and numerical methods, Functional Growth Analysis (FGA) is now the commonly accepted method for growth analysis. For FGA the first step is to fit (by varying numerical technique) a function to plant growth over the season. Through this approach, a function must be fit for root, shoot, leaf biomass and leaf area over time. Once obtained a mathematical dynamic expression of an appropriate growth model, it is possible to calculate the instantaneous value of growth rate at any (and all) time, in terms of Relative Growth Rate (RGR) and derive different parameters required for crop growth models.

The ‘functional’ approach, developed in the 1960’s (Vernon and Allison 1963, Hughes and Freeman 1967), has been presented as a solution to these problems. In this approach a
polynomial of the form \( Y = b_0 + b_1X + b_2X^2 + \ldots + b_nX^n \) is fitted through the growth data. The dependent variable \( Y \) is the ln-transformed weight of the plant, the independent variable \( X \) is the time of harvest. By differentiating this equation, an equation for RGR is obtained. NAR may also be computed fairly easily.

In his work on the functional approach, Hunt (1982) mentions 12 advantages of this method. Among them are the following: (1) The functional approach provides a clearer perception of ontogenetic drift; (2) Assumptions involved in the calculation of mean values of NAR are avoided; (3) Statistical analyses may be integrated into the same analytical procedure as the calculation of the derived quantities. Despite these valid claims the functional approach does not necessarily result in correct values for RGR, NAR and the confidence limits of these parameters. Poorter and Lewis (1986) showed that the testing of differences in RGR had only limited biological meaning. Wickens and Cheeseman (1988) argued that the functional approach is of limited value if plants are subjected to short-term environmental changes. But even when plants are grown in a constant environment, the functional approach has some pitfalls.

The relationship between growth and time is not conveniently used in following concepts:

i) Relative growth rate (RGR) – Increase in weight per unit of original weight of a time interval \( t = \frac{1}{w} \frac{dw}{dt} = \frac{\log_e W_2 - \log_e W_1}{t_2 - t_1} = \frac{L_n W_2 - L_n W_1}{t_2 - t_1} \), where \( w \) is the dry weight of plant, \( dw \) change in weight and \( dt \) time interval. \( W_2 \) and \( W_1 \) are dry weight of plant at time \( t_2 \) and \( t_1 \) and \( L_n \) is natural log. It is expressed as g/g/day or per week. \( \log_e = 2.3026 \).

ii) Leaf area ratio (LAR) – It may be defined as the ratio of leaf area (L) to whole plant dry weight and is expressed as \( LAR = \frac{L_1 + L_2}{W_1 + W_2} = \frac{L_2 - L_1}{\log_e L_2 - \log_e L_1} \times \frac{\log_e W_2 - \log_e W_1}{W_2 - W_1} \), where \( L_1 \) and \( L_2 \) is leaf area at time \( t_1 \) and \( t_2 \) and \( W_1 \) and \( W_2 \) is dry weight of plant at time \( t_1 \) and \( t_2 \), respectively. It is expressed as \( \text{cm}^2/\text{g} \).

iii) Unit leaf rate (ULR) – It is defined as rate of increase in dry weight per unit leaf area assuming both dry weight and leaf area are increasing exponentially. Photosynthesis tissues other than leaves are also taken into account. It is expressed as \( ULR = \frac{W_1 + W_2}{L_1 + L_2} [\log_e L_2 - \log_e L_1] \), where \( L_1 \) and \( L_2 \) is leaf area at time \( t_1 \) and \( t_2 \) and \( W_1 \) and \( W_2 \) is dry weight of plant at time \( t_1 \) and \( t_2 \), respectively.
iv) Relative leaf growth rate (RLGR) – Analogous to RGR of whole plant and is expressed as \( \frac{1}{w} \frac{dw}{dt} = \frac{\log_e L_2 - \log_e L_1}{t_2 - t_1} \) where \( L_1 \) and \( L_2 \) is leaf area at time \( t_1 \) and \( t_2 \), respectively.

v) Absolute growth rate (AGR) – Growth rate of a plant is measured in terms of height and dry matter over a period of time. It is calculated as 

\[
AGR (\text{plant height}) = \frac{H_2 - H_1}{t_2 - t_1} \quad \text{and} \quad AGR (\text{Dry weight}) = \frac{W_2 - W_1}{t_2 - t_1},
\]

where \( H_1 \) and \( H_2 \) is plant at time \( t_1 \) and \( t_2 \) and \( W_1 \) and \( W_2 \) is dry weight of plant at time \( t_1 \) and \( t_2 \), respectively. It is expressed as cm/day or g/day.

vi) Net assimilation rate (NAR) – rate of increase in whole plant dry weight per unit leaf area. It indicates rate of net photosynthesis and is expressed as 

\[
NAR = \frac{\log_e LW_2 - \log_e LW_1}{t_2 - t_1},
\]

where \( LW_1 \) and \( LW_2 \) is leaf weight at time \( t_1 \) and \( t_2 \), respectively. It is expressed as g/cm\(^2\)/day.

vii) Leaf relative growth rate (LRGR) - 

\[
LRGR = \frac{\log_e LW_2 - \log_e LW_1}{t_2 - t_1},
\]

where \( LW_1 \) and \( LW_2 \) is leaf weight at time \( t_1 \) and \( t_2 \), respectively.

viii) Relative leaf area growth rate (RLAGR) - 

\[
RLAGR = \frac{\log_e LA_2 - \log_e LA_1}{t_2 - t_1},
\]

where \( LA_1 \) and \( LA_2 \) is leaf area at time \( t_1 \) and \( t_2 \), respectively.

ix) Leaf area ratio (LAR) - 

\[
LAR = \frac{1}{2} \left( \frac{LA_1}{W_1} + \frac{LA_2}{W_2} \right),
\]

where \( LA_1 \) and \( LA_2 \) is leaf area at time \( t_1 \) and \( t_2 \) and \( W_1 \) and \( W_2 \) is dry weight of plant at time \( t_1 \) and \( t_2 \), respectively.

x) Specific leaf area (SLA) - 

\[
SLA = \frac{1}{2} \left( \frac{LA_1}{LW_1} + \frac{LA_2}{LW_2} \right),
\]

where \( LA_1 \) and \( LA_2 \) is leaf area and \( LW_1 \) and \( LW_2 \) is dry weight of leaf at time \( t_1 \) and \( t_2 \), respectively.

xi) Specific leaf weight -

\[
SLW = \frac{1}{2} \left[ \frac{LW_1}{LA_1} + \frac{LW_2}{LA_2} \right],
\]

where \( LA_1 \) and \( LA_2 \) is leaf area and \( LW_1 \) and \( LW_2 \) is dry weight of leaf at time \( t_1 \) and \( t_2 \), respectively.

xii) Leaf area index (LAI) -

\[
LAI = \frac{\text{Leaf area}}{\text{Ground area}}
\]

xiii) Relative leaf area expansion rate (RLAER) - 

\[
RLAER = \left( \frac{1}{LA} \right) \left( \frac{dLA}{dt} \right),
\]

where \( L_A \) is leaf area, \( dLA \) is change in leaf area with time \( t \).

xiv) Leaf area partitioning factor (LAPF) -

\[
LAPF = \frac{dLA}{dLW},
\]

where \( dLA \) is change in leaf area and \( dLW \) is change in leaf weight.
xv) Average area per leaflet (APL) – APL = \( \frac{A}{N} \) mm\(^2\) leaf area per kg, where A is leaf area index (m\(^2\) leaf area/m\(^2\) land area), N is number of leaflet (no./m\(^2\) land area)

xvi) Leaf weight ratio (LWR) = \( \frac{LW}{W} \) (kg/kg), where LW is leaf weight and W is phytomass dry weight gm\(^{-2}\) land area.

xvii) Crop growth rate (CGR) = \( \frac{dw}{dt} \) gm\(^{-2}\) land area day\(^{-1}\). CGR represents total dry matter productivity of the community per unit land area over a certain time span. CGR = NAR \times LAI, Since LAI is simply a ratio of leaf area/land area, it becomes a fulcrum between NAR and productivity.

xviii) Harvest index = \( \frac{\text{Economic yield (grain)}}{\text{Biological yield (grain+straw)}} \)

xix) Leaf area duration (LAD) – Ability of plant to produce leaf area on unit area of land throughout its life. Leaf area integrated over time is called LAD. It equals active L and time. It is expressed as, \( LAD = \frac{L_i + (L_i + 1)}{2} (t_2 - t_1) \), where \( L_i \) is LAI is at first stage, \( L_i + 1 \) is LAI at second stage and \( t_2 - t_1 \) is time interval between the successive stages. If the value of LAD is more, it indicates the plant is more potent for photosynthesis for a long period.

xx) Dry matter partitioning – It is partitioning of total dry matter into different components. It is expressed as \( dL = \frac{L}{W} \times 100 \), where \( dL \) is dry matter of leaf, \( L \) is leaf dry matter and \( W \) is total dry matter of plant.

xxi) Biomass duration (BMD) – it is the area curve for biomass production. It is expressed as g/day. BMD = \( (BM_1 + BM_2) \times (t_2 - t_1)/2 \), where \( BM_1 \) and \( BM_2 \) is the dry matter at time \( t_1 \) and \( t_2 \), respectively.

xxii) Leaf production rate (LPR) – It gives an idea of producing number of leaves over a period of time. It is calculated as \( LPR = \frac{Ln_2 - Ln_1}{t_2 - t_1} \), where \( Ln_1 \) and \( Ln_2 \) are number of leaves produced at time \( t_1 \) and \( t_2 \), respectively. It is expressed as number of leaves per day. Indirectly, it gives photosynthetic efficiency of leaves in unit time.

xxiii) Panicle emergence rate (PER) – Rate of number of panicles emerged over a period of time. It is important under moisture stress conditions. \( \text{PER} = \frac{Pn_2 - Pn_1}{t_2 - t_1} \), where \( Pn_1 \) and \( Pn_2 \) are emerged panicles at \( t_1 \) and \( t_2 \), respectively.
xxiv) Rate of flowering (FR) – rate of appearance of flowers over a period of time.

\[ \text{FR} = \frac{F_{n2} - F_{n1}}{t_2 - t_1}, \]

where \( F_{n1} \) and \( F_{n2} \) are emerged flowers at \( t_1 \) and \( t_2 \), respectively for the crops like cotton, pigeonpea etc.

xxv) Unit area efficiency (UAE) – It is expressed as \( r/m^2/day \).

(a) \( \text{UAE (Kapas yield)} = \frac{\text{Seed cotton}}{\text{DMP}} \times \frac{1}{\text{Duration of the crop}} \)

(b) \( \text{UAE (total DMP)} = \frac{\text{Total DMP}}{\text{Land area}} \times \frac{1}{\text{Duration of the crop}} \)

xxvi) Boll setting percentage – It is calculated on 120 DAS as follow,

\[ \text{Boll setting (\%)} = \frac{\text{Total bolls on 120th day}}{\text{Total fruiting points on 120th day}} \times 100 \]

xxvii) Barlett’s earliness index (BI)

\[ BI = \frac{P_1 + (P_1 + P_2) + (P_1 + P_2 + P_3) + (P_1 + P_2 + P_3 + \ldots + P_n)}{(P_1 + P_2 + P_3 + \ldots + P_n) \times n} \]

Where, \( P_1, P_2, P_3, \ldots, P_n \) are the seed cotton yield at the first, second, third and nth pickings, respectively. \( n \) is number of pickings.

xxviii) Moisture deficiency index (MDI) – It is the measure to estimate dryness of a region and is expressed by the formula

\[ MDI = P - PE \times \frac{100}{PE} \]

P is precipitation, PE is potential evapotranspiration. MDI ranges from -20 to -80.

xxix) Monetary advantage index (MAI) – It indicates the relative remunerativeness of a system.

\[ MAI = Value \ of \ combined \ intercrop \times \frac{LER - 1}{LER} \]

Where, LER is land equivalent ration. Higher the index value better is the cropping system.

xxx) Relative dominance (RD) – The actual area occupied by a species expressed as a percentage of total area occupied by all species in a given area.

\[ RD = \frac{\text{Total basal area of species ‘a’}}{\text{Total area of all species}} \]
xxxii) Dry matter production efficiency (DMPE)

\[
DMPE = \frac{\text{Kapas yield}}{\text{DMP}} \times \frac{1}{\text{Duration of crop}}
\]

xxxii) Light interception – Interception of light within a plant is more important as it aids in increasing photosynthetic efficiency.

\[
\text{Light interception} = \frac{\text{Light interception at top} \times \% - \text{light interception at bottom} \times \%}{\text{Light interception at bottom} \times \%} \times 100
\]

Validity and limitations in interpreting crop growth and development

The two distinct approaches to the growth analysis have evolved. In classical approach, events are followed through a series of relatively infrequent, large, often destructive harvest (with much replication of measurements). In the so-called functional approach, the individual harvests supply data for curve fitting, but they are each smaller (having less replication of measurements) and often much more frequent. The two approaches are not mutually exclusive if time and space are no object (harvest may be large and frequent), but in most cases, the experimenter is forced to choose one or other in advance, as this influences the design of the experiment.

The stock of trade of plant growth analysis is a collection of simple primary data, the measured quantities upon which the subsequent analyses depend. These data may be determined either for the whole plant or for different components such as roots, stems or for different components such as roots, stems and leaves, as required. Naturally all of the analytical and statistically techniques should be chosen before practical work is begun. In the growth analysis of individual plants, the primary data are used to calculate values of one or more of four distinct types of derivate.

Absolute growth rates

Absolute growth rate in size/number

This is the simplest index of plant growth: a rate of change in size/number, which is an increment in size/number per unit of time. The absolute growth rates can be valuable comparative tools when they are used within like bodies of data. When used to compare unlike systems, however, their usefulness declines. To compare the overall performance in such circumstances requires other approaches. For example, if two species are grown for equal periods of time and both put on equal amounts for equal periods of time and they will both exhibit the same absolute growth rate even if the species differ in initial dry weight.
Some measures of growth is needed that also takes into account this original difference in size. That measure is relative growth rate.

**Relative growth rate**

This was originally termed an ‘efficiency index’ because it expresses growth in terms of a rate of increase in size per unit of size. As such, it permits more equitable comparisons between organisms than does absolute growth rate. Normally, relative growth rate deals with total dry weight per plant, though other measures of size have also been used. In the financial world, relative growth rate is analogous to the rate of compound interest earned on capital. Negative relative growth rates are called relative decay rates.

Relative growth rate is useful wherever current size realistically controls current increase in size. It provides a convenient integration of the many component processes that contribute to the performance of the whole plant, but it depends upon the assumption that all parts of the relevant size are equally capable of producing further amounts of the same quantity (in the same way that invested capital grows through the accrual of compound interest). However, as most plants grow, the proportion of their mass that is largely supporting material (i.e. not directly productive) increases, for much the same reason that larger animals develop proportionally more bulky bones than smaller ones. So, relative rate soon declines with time and the interest then passes to the components of relative growth rate in the hope of explaining how this decline comes about.

**Simple ratios**

Mathematically these ratios (leaf area ratio, specific leaf area, leaf weight ratio, root-shoot allometric coefficients) are alone capable of instantaneous evaluation without recourse to fitted growth curves. However, if he functional approach is followed, the component ratio $Z/Y$ should always be evaluated from the separate functions $\ln Z = f_Z(t)$ and $\ln Y = f_Y(t)$, rather than directly from $Z/Y = f_{Z/Y}(t)$, which can have difficult statistical properties. Where, $Z$ and $Y$ are like quantities, their ratio is simply an index of allocations; where they are unlike quantities, the ratio is a ‘snapshot’ of the functional balance between two related or antagonistic components. In the case of the allometric coefficient, there is the added advantage that it often remains approximately constant across substantial intervals of time, which increases its value as a comparative tool.

**Compound growth rates**

These (Unit leaf rate and specific absorption rate) are rates of production of something per unit of something else. In plant growth analysis, provided that the ‘something’ $Y$ is of interest to the experimenter and that the ‘something else’ $z$ may reasonably be held responsible for its production, then $(1/Z)(dY/dt)$ is an analytical tool of fundamental importance. As such, it has been used to describe plant processes from the molecular level, through organs and whole herbaceous plants up to perennial woody crops. There is no reason why such applications should not flourish still further.
Interrelations

In general

Although the terms involved in plant growth analysis have the individual meanings, their strength as analytical tools owes much to their interrelations with one another, or the ways in which an individual term may be decomposed into others. Various types of interrelation can occur, but they all have the status of mathematical identities, not conditional equations. (A mathematical identity states a logical truth, not an hypothesis that is open to disproof).

Simple

Where both parts of a simple ratio or fraction bear the same units, they provide an index of the importance of one component of the plant in relation to another. All such components can be linked into a single scheme. As a simple example, in young grasses if Rw/W is the root weight ratio (where Rw is the total root dry weight of the plant), Sw/W is the stem weight ratio (where Sw is the total stem dry weight of the plant), and Lw/W is the leaf weight ratio (where Lw is the total leaf dry weight of the plant), then the three are related by the expression Rw/W + Sw/W + Lw/W = 1.

Interrelations between more heterogeneous quantities can also occur. For example, a subdivision of leaf area ratio is LA/W=LA/LW x LW/W, where LA/LW is the specific leaf area and LW/W is the leaf weight ratio. By looking simultaneously at all three of these terms it is possible, for example, to establish that the much less leafy nature of Scots pine (Pinus sylvestris), in comparison to sunflower, is due almost entirely to the relatively greater density of the pine needles and hardly at all to variation in leaf weight ratio (the productive investment of the plant), which, in fact, shows a small difference in favour of pine.

More complex

It is often useful to subdivide an index of overall performance, such as relative growth, into indices that represent the individual performances of components of the system. In fact, unit leaf rate and leaf area ratio originally evolved as subdivisions of relative growth rate. So, it is by definition that (1/W)(dW/dt) = (1/LA)(dW/dt) x LA/W. Simply expressed, the growth rate of the plant depends simultaneously upon the efficiency of its leaves as producers of new material and upon the leafiness of the plant itself (Except in very special circumstances, this relation holds only approximately for the three mean values of these quantities; instantaneous values are needed for the interrelation to be exact). Also as LA/W=LA/LW x LW/W, these subdivisions of leaf area ratio may be inserted into the equation for relative growth rate to give (1/W)(dW/dt) = (1/LA)(dW/dt) x LA/LW x LW/W otherwise, relative growth rate expressed as the product of unit leaf rate, specific leaf area and leaf weight ratio.
Tools for performance

Classical approach

The instantaneous mathematical definitions of the various terms are usually not amenable to direct substitution of experimental data. That is why the harvest interval mean formulae, however, if there has been any replication of the measurements that require logarithmic transformation and it is wished to work with harvest mean value of these variables, it is important to calculate these as (for example) mean(\(\ln W\)) and not \(\ln(\text{mean } W)\).

The statistical properties of the harvest interval means are important and often neglected. It is incorrect simply to calculate, say, the variance of a group of several unit leaf rates spanning the same harvest interval. Not only does this involve difficult decisions as to how to ‘pair’ the primary data across the harvest interval, but it also ignores the fact that the statistical properties of a derived term depend upon those of its primary data and not upon those of its sibling values. Spreadsheet tools are available within the growth analytical literature that will perform these calculations correctly.

Functional approach

The great advantages are that the instantaneously defined terms can be obtained directly from the fitted curves, seen in their exact interrelation to one another, and provided with statistics derived only from the primary data. The disadvantage is that an appropriate type of fitted curve has to be selected and applied, without under-fitting (forcing the data into too simple a strait jacket) or over-fitting (chasing off after outliers, which should really be eliminated or smoothed). The growth analytical literature contains tools for fitting low-order polynomials, nonlinear asymptotic functions with up to four parameters, and splined curves (smoothly joined polynomials) which offer almost unlimited flexibility.

Growth curves

Growth curve, in biology, a curve in graph form that shows the change in the number of cells (or single-celled organisms) in an experimental culture at different times. Growth curves are also common tools in ecological studies: they are used to track the rise and fall of populations of plants, animals, and other multicellular organisms over time. The classic growth curve, as exemplified by a newly established bacterial colony, is divided into four phases, in order of their appearance: (1) lag phase; (2) log (logarithmic), or exponential, phase; (3) stationary phase; and (4) death, or decline, phase.

The pattern of dry matter accumulation of a crop canopy is characterized by a sigmoid curve. Three more or less distinct phases can be distinguished (Fig. 33b and Fig 35): (i) a period of exponential growth during early development, followed by (ii) a period of more or less constant rate dry matter accumulation, and (iii) a period of declining crop growth rates during the final phase of development when green leaf area declines due to leaf senescence and leaf photosynthesis declines due to leaf aging. It is important to realize that the parameters SGR and NAR are only relevant during the first phase.
(i) Early phases of development. Rate of dry matter accumulation during early development is directly related to LAI and as LAI is closely associated with plant dry matter during this phase, rate of dry matter accumulation of a crop is a function of its own weight:

\[ \frac{dW}{dt} = SGR \times W \]

Integrating Equation [1] gives:

\[ W_t = W_0 \times e^{SGR \times t} \quad \text{[2]} \]

\[ \frac{W_t}{W_0} = e^{SGR \times t} \quad \text{[2a]} \]

Where, \( W_0 \) and \( W_t \) are the crop weights at times \( t = 0 \) and \( t = t \), and SGR is the slope of the natural log of crop dry matter vs. time, i.e.:

\[ \ln \left( \frac{W_t}{W_0} \right) = \ln e^{SGR \times t} = SGR \times t \quad \text{[3]} \]

The increase in LAI, and, consequently, the increase in rate of dry matter accumulation, is proportional to rate of dry matter accumulation per unit leaf area (NAR). During this phase of development, an increase in leaf area leads to an increase in rate of dry matter accumulation (because light interception is directly related to leaf area during this phase of development) and an increase in dry matter accumulation leads to an increase in leaf area (because proportion of dry matter allocated to leaves remain fairly constant). Various equations are used to estimate mean net assimilation rate \( \text{NAR}_{\text{mean}} \). NAR is the ratio of rate of dry matter accumulation and leaf area index and a mean ratio should take into account the rate of change of each of its components. During exponential dry matter accumulation, and assuming an equal exponential rate of increase for LAI and dry matter, mean NAR can be estimated as follows:

\[ \text{NAR}_{\text{mean}} = \left[ \frac{(W_2 - W_1)}{(t_2 - t_1)} \right] ÷ \left[ \frac{(LAI_2 - LAI_1)}{(LAI_2 - LAI_1)} \right] \quad \text{[4]} \]

where \( \text{NAR}_{\text{mean}} \) is the mean net assimilation rate during a period from \( t = t_1 \) to \( t = t_2 \). The second part of Equation [4] expresses the inverse of mean LAI from \( t = t_1 \) to \( t = t_2 \). In contrast to mean NAR, instantaneous NAR can be estimated by calculating rate of dry matter accumulation at time \( t \) (i.e., by differentiating the "growth curve" at time = \( t \)) and measuring LAI at time = \( t \).

Instantaneous NAR at time = \( t \) is rate of dry matter accumulation divided by LAI. The NAR will decline once mutual shading among leaves in the canopy will occur. Rate of dry matter accumulation will become "constant" when a change in LAI will not influence absorbance of incident irradiance: the canopy has attained the phase of "constant" growth.
Similarly, a crop will have attained the phase of "constant" growth when leaf-area expansion has been completed, even if PAR absorptance is less than 100%. Dry matter accumulation during this period is relatively unimportant in the context of dry matter accumulation during the growing season. For instance, a maize crop will accumulate less than 15% of dry matter at maturity during this period.

(ii) The period of a relatively constant rate of dry matter accumulation. This period is the most important phase of development for dry matter accumulation and grain yield of most crops. For instance, maize may accumulate up to 75% of its dry matter at maturity during this period and, consequently, this period contributes most to final yield. Rate of dry matter accumulation during this period is fairly constant and, consequently, CGR is the appropriate parameter to use. CGR will vary with incident solar irradiance and abiotic stresses may reduce CGR. Because CGR is relatively constant, total dry matter accumulated during this period is closely related to the duration of the period.

(iii) Final phase of development. Rates of dry matter accumulation per day start to decline due to aging during the final phase of development. The decline in the rate of dry matter accumulation during this phase is associated with functional and visual leaf senescence. Functional leaf senescence is the decline in photosynthesis per unit leaf area due to aging. Visible leaf senescence is the loss of chlorophyll in the leaf. Whereas no photosynthesis will occur in a leaf that has lost all its chlorophyll, a leaf that has retained all its chlorophyll does not necessarily maintain it rate of photosynthesis. For instance, Echarte et al. (2008) depicted that leaf photosynthesis (CER) declines during the grain-filling period of maize, even if chlorophyll content remain constant under a high N fertilizer level. The sevenfold increase in grain yield of corn hybrid in North America during the last 70 years has been attributed, in part, to increased functional and visual "stay green".

Types of growth models

Growth models can be classified under two broad headings: those that assume that an asymptotic final size exists and those that do not. The idea of asymptotic final size is somewhat problematic for individual plants (Hunt 1982), but is well-established in zoology and for the resource-limited growth of populations (McMahon & Bonner 1983). Plant size may approach an asymptote because of limiting below ground resources or ontogenetic changes, such as the onset of flowering. Choosing between asymptotic and non-asymptotic functional forms depends in part upon the response variable of interest and the time scale of the study. For example, canopy trees may be considered to grow asymptotically in terms of height, even as their girth and biomass may increase without limit (Thomas 1996; Chave et al. 2003; Muller-Landau et al. 2006; Sillett et al. 2010). Asymptotic models are also appropriate for analyses that include the entire lifespan, as is frequently the case for studies of annual plants. Non-asymptotic models make the implicit (and in the extreme case, unrealistic) assumption that growth continues indefinitely. Even so, they can be appropriate for modeling the initial stages of the life-span, such as seedlings of long-lived trees. This is not an absolute dichotomy, however. Biomass can be log transformed, allowing non-asymptotic forms to be fit, usually with the added benefit of reducing heteroscedasticity. We include models that can
be fitted within a linear model framework for completeness and to illustrate that their performance is frequently poor. Details of all model forms are provided in Table 2.1.

Table 2.1. Basic functional forms for plant growth modelling.

<table>
<thead>
<tr>
<th>Name</th>
<th>Form</th>
<th>Model dM/dt biomass</th>
<th>Biomass M time basis</th>
<th>AGR dM/dt time basis</th>
<th>RGR (dM/dt)/M time basis</th>
<th>RGR (dM/dt)/M Mass basis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Linear</td>
<td>(\frac{dM}{dt})</td>
<td>(M_0 + rt)</td>
<td>(r)</td>
<td>(\frac{r}{M_0 + rt})</td>
<td>(\frac{r}{M_0})</td>
<td></td>
</tr>
<tr>
<td>Exponential</td>
<td>(rM)</td>
<td>(Me^{rt})</td>
<td>(M_0e^{\mu})</td>
<td>(M_0e^{\mu})</td>
<td>(r)</td>
<td>(r)</td>
</tr>
<tr>
<td>Power law</td>
<td>(rM^\beta)</td>
<td>(\frac{M}{M_0 + rt})</td>
<td>(\frac{r}{M_0 + rt})</td>
<td>(\frac{r}{M_0})</td>
<td>(rM^\beta)</td>
<td>(rM^\beta)</td>
</tr>
<tr>
<td>Monomolecular</td>
<td>(r(K-M))</td>
<td>(K - e^{(K-M)\mu})</td>
<td>(\frac{r}{K} + e^{(K-M)\mu})</td>
<td>(\frac{r}{K} + e^{(K-M)\mu})</td>
<td>(r(K-M))</td>
<td>(\frac{r(K-M)}{M})</td>
</tr>
<tr>
<td>Three-parameter logistic</td>
<td>(rM(1-M/K))</td>
<td>(\frac{M}{M_0 + (K-M_0)e^{rt}})</td>
<td>(\frac{r}{M_0 + (K-M_0)e^{rt}})</td>
<td>(\frac{r}{M_0})</td>
<td>(r(1-M/K))</td>
<td>(r(1-M/K))</td>
</tr>
<tr>
<td>Four-parameter logistic</td>
<td>(rM(1-M/L))</td>
<td>(\frac{M_0 + (K-L)(LPe^{rt})}{(M_0 + (K-L)e^{rt})})</td>
<td>(\frac{r}{M_0 + (K-L)e^{rt}})</td>
<td>(\frac{r}{M_0})</td>
<td>(r(1-M/L))</td>
<td>(r(1-M/L))</td>
</tr>
<tr>
<td>Gompertz</td>
<td>(rM(K/M)^{\mu})</td>
<td>(\frac{M_0}{M})</td>
<td>(\frac{r}{M_0})</td>
<td>(\frac{r}{M_0})</td>
<td>(rln\frac{K}{M})</td>
<td>(rln\frac{K}{M})</td>
</tr>
</tbody>
</table>

The models are autonomous first-order differential equations expressing the change in
biomass, M, as a function of time, t. The solution of each differential equation provides an expression for M at any time t. Absolute growth rate (AGR) is the derivative of M with respect to time. Relative growth rate (RGR) can be expressed either as a function of mass or as a function of time. Note that in the linear model, AGR is constant with respect to time, and in the exponential model, RGR is constant with respect to both time and mass. Also it is to be noted that if log-transformed biomass $M_t = \ln(M)$ is modelled, RGR is simply $\frac{d(M_t)}{dt}$, because $\frac{d\ln(F(t))}{dt} = \frac{1}{F(t)} \frac{dF(t)}{dt}$. AGR is, correspondingly, $\exp(M_t) \frac{d(M_t)}{dt}$, because $\frac{d\exp(F(t))}{dt} = \exp(F(t)) \frac{dF(t)}{dt}$. These models may be parameterized in many ways, and we have chosen naming conventions that facilitate comparisons among models. The parameters L and K indicate lower and upper horizontal asymptotes, respectively.

**Linear forms – non-asymptotic**

**(LOG -) LINEAR MODELS**

In linear models, AGR is constant, i.e. the same quantity of biomass is added in each unit of time (Table 2.1). Thus biomass acquisition is independent of current biomass. Assumption is implausible, as biomass acquisition should depend on leaf area, and hence biomass at least initially, when resources are unlikely to be limiting. There are two parameters in the linear model: $M_0$, initial biomass, and r, the absolute increase in biomass per unit time. A problem with the standard linear model is that it frequently predicts negative biomass at early time points. This biologically impossible prediction may be avoided by constraining the intercept to pass through the origin ($M_0 = 0$). In such a ‘no-intercept’ linear model, biomass is always positive, and seed mass is implicitly ignored. With only one parameter, r, the no-intercept model is less flexible than the standard linear model, so it is no surprise that it fits the data even less well. Owing to their notable defects, linear models appear rarely in the current growth-analysis literature and are included here primarily for completeness.

Fitting a linear regression to the logarithm of biomass yields the exponential (loglinear) model, in which the rate of biomass acquisition is proportional to current biomass (Blackman 1919). In the unlikely event that neither environmental nor physiological factors slow the rate of biomass acquisition, the exponential model may be appropriate (for example, in the initial portion of a plant’s lifespan). There are two parameters: $M_0$, initial biomass, and r, the relative growth rate. The exponential model is the only one, in which the estimated parameter $r$ is equivalent to RGR, and constant with respect to time and biomass. The AIC and $R^2$ of the exponential model are far superior to either of the linear fits. However, the exponential model is only appropriate when growth is unconstrained (e.g. algal blooms) and is not flexible enough to account for the slowing of biomass acquisition that can occur with increasing structural biomass. In contrast to the linear models, exponential models are frequently used to analyse growth data. Although they may be useful in cases where growth is authentically exponential, we generally discourage their use in favour of more flexible nonlinear models.
POLYNOMIAL

In the polynomial model, growth follows a smooth curve, potentially of great complexity (Poorter 1989; Heinen 1999). They were once widely used because they can be fit in a linear model framework. However, polynomial functions tend to make spurious upward or downward predictions, especially at the extremes of the data. Furthermore, it is difficult to determine the proper order of polynomial to use and to interpret the model parameters.

Nonlinear forms – non-asymptotic

POWER LAW (AKA ALLOMETRY)

A power-law model allows RGR to slow with increasing time and biomass, according to the value of the exponent \( b \). \( b = 0 \) yields the linear model, \( 0 > b > 1 \) corresponds to progressive decreases in RGR, \( b = 1 \) yields the exponential model (RGR is constant through time), and \( b > 1 \) corresponds to the case of RGR increasing with increasing biomass. Recently, the metabolic theory of ecology has focused attention on power-law functions for their ability to predict relationships among many aspects of individual survival and growth. Specifically, it predicts that biomass AGR should scale with (biomass)\(^{3/4}\) and that diameter AGR should scale with (diameter)\(^{1/3}\) (West, Brown & Enquist 1999). A test of these predictions was conducted in 10 tropical rainforests, encompassing >1.7 million trees, but were only upheld in one forest (Muller-Landau et al. 2006). Among the non-asymptotic models, the power law is preferred in terms of \( R^2 \) and AIC. It effectively captures the rapid initial growth and the slowing over time. Despite continuing discussion regarding the value of the exponent \( b \) to be expected from theory, the power law is frequently useful for non-asymptotic data, as it allows RGR to decrease as biomass increases.

Nonlinear forms – asymptotic

MONOMOLECULAR (AKA Mitscherlich)

The monomolecular model was originally derived from physical chemistry, where it describes the progress of first-order chemical reactions (Richards 1959; Zeide 1993; Heinen 1999). There is no point of inflection; unlike the other asymptotic forms it is always concave-down. Correspondingly, AGR is fastest initially, and slows thereafter. It can be appropriate, therefore, for log-transformed data but it can predict negative biomass at early time points for untransformed data. In the limit, as the asymptotic mass (K) approaches zero, the monomolecular becomes the exponential. It has been occasionally applied to plant growth (Scanlan & Burrows 1990; Paul-Victor et al. 2010) and is implemented in R with the SSasympt function (Pinheiro & Bates 2000).
THREE-PARAMETER LOGISTIC (AKA VERHULST, AUTOCATALYTIC GROWTH) AND FOUR-PARAMETER LOGISTIC

The logistic is the most commonly utilized asymptotic form (Winsor 1932; Fresco 1973; Hunt 1982; Zeide 1993; Heinen 1999). In the three-parameter version, the lower horizontal asymptote is fixed at 0 and the inflection point – the time at which AGR is maximized – falls rigidly at $M = K/2$. Four-parameter versions loosen one or the other of these strictures (Nelder 1961; R function SSfpl in Pinheiro & Bates 2000). The five-parameter version provides maximum flexibility and alleviating both restrictions (Gottschalk & Dunn 2005). The three-parameter version collapses to the exponential in the limit as $K$ approaches infinity. For some data sets, the additional flexibility of the four-parameter version greatly increases the variance explained by the model, although the three-parameter version provides a more parsimonious and equally adequate fit in other situations. The three- and four-parameter logistic models are implemented in R with the SSlogis and SSfpl functions, respectively (Pinheiro & Bates 2000).

GOMPERTZ

In the Gompertz model, RGR declines exponentially over time (Heinen 1999; Gompertz 1825; Winsor 1932; Zeide 1993). The Gompertz model differs from the three-parameter logistic in that the inflection point of the former occurs at approximately 37% of the asymptotic mass $K$ (Winsor 1932), whereas in the latter, the inflection point occurs at one-half the maximal biomass (Hunt 1982). The Gompertz and logistic models provide similar fits to the Cerastium data. The three-parameter logistic is preferred on the basis of AIC, whereas the Gompertz is preferred on the basis of $R^2$. Like the logistic, the Gompertz model can be generalized to allow non-zero initial masses and variation in the inflection point (Winsor 1932). It is implemented in R with the SSgompertz function (Pinheiro & Bates 2000).

Calculating and comparing growth rates

For proper inference, the uncertainty surrounding the estimated growth rates must be quantified. If experimental groups (such as species or treatment levels) only vary in a single parameter, then the standard error of the growth rate is simply the standard error for that parameter, and comparisons are easily made. However, if groups vary in two or more parameters, then the covariance among parameters must be accounted for to generate confidence intervals for the growth rates. We present the method of population prediction intervals, which is easily implemented and is considered reliable, although it lacks a strong statistical justification. Bolker (2008) reviews this and other techniques of error propagation, including the delta method. To calculate population prediction intervals, we first examine the square-root transformed likelihood profiles for each parameter to check that they are approximately V-shaped, and thus that the corresponding sampling intervals are approximately multivariate normal. If this is the case, we randomly draw parameter combinations from a multivariate normal distribution centred on the maximum-likelihood parameter estimates and variance–covariance estimates (as determined by the R functions nls, gnl$ or nlsList). These sets of parameter combinations are used to calculate replicates of the desired growth rate using the expressions in Table 2.1. Confidence
intervals for a significance threshold $\alpha$ can be extracted by taking the $\alpha/2$ and $(1-\alpha)/2$ quantiles at every point in time (or biomass). For comparisons among experimental groups, for example between a wild type and various mutants, it is frequently more interpretable to calculate the difference in growth rates and compare that difference to zero, corresponding to the null expectation of no difference between groups (see Züst et al. 2011). This can be accomplished with population prediction intervals, except that one calculates differences in growth rates between groups, rather than the growth rates themselves.

The fluctuating nature of growth rates derived from nonlinear growth models encourages a reconsideration of comparisons of growth rates (whether AGR or RGR) among experimental groups. Rather than comparing point estimates of growth rates, one compares time-(or biomass-) specific functions. For example, the best form for modelling Cerastium and Geranium growth was the three-parameter logistic. Using the traditional approach, one could hypothesize that their growth rates would differ. Using function-derived growth rates, we can refine this hypothesis, testing the degree to which they differ in terms of the timing and magnitude of peak AGR and RGR. To visualize these comparisons, we plot biomass, AGR and RGR as functions of time and mass for both species. In this case, the peak AGR of Geranium precedes that of Cerastium by 46 days and is 29% greater in magnitude. In the middle of the growing season, Cerastium has a 37% greater RGR than does Geranium. The differences in magnitude are significant, as the confidence intervals around the differences in AGR and RGR between species do not overlap zero. Time-based comparisons of RGR can be misleading, however, as physiological and environmental conditions change over time, and experimental groups may vary widely in initial size (Britt et al. 1991). Differences in initial size among groups are especially common when comparisons are made among species (Turnbull et al. 2008; Rees et al. 2010). Thus, it can be more illuminating to express RGR on the basis of biomass, rather than that of time. Standardized for mass, Geranium has a significantly greater RGR than does Cerastium. Analyzing RGR on a biomass basis corrects for variation in initial size, which can be substantial.

It is important to carefully select the times or biomasses at which growth rates are compared among experimental groups. For example, Paul-Victor et al. (2010) compared RGR among inbred recombinant lines of Arabidopsis thaliana at the average mass of plants half-way through their experiment, whereas Rees et al. (2010) compared growth rates at the smallest size common to all studied species. Here, at a common size of 5 g, Geranium has a greater RGR than does Cerastium. The choice of comparison times is particularly important when values of two or more model parameters differ among experimental groups, because crossovers in growth rates among experimental units may then occur (e.g. Hautier et al. 2010). For example, Cerastium and Geranium differ in both initial and asymptotic biomass ($M_0$ and $K$, respectively), and their AGR trajectories correspondingly intersect. Comparisons performed at different times would therefore lead to different conclusions. Compared at day 75, Geranium had significantly greater AGR, whereas at day 100, Cerastium’s AGR was significantly greater. These patterns are not obvious in the trajectory
of biomass through time. For these reasons, we recommend plotting AGR and RGR against time or biomass to allow a more holistic understanding of the variation in growth rates as time passes and biomass increases (Heinen 1999; Hautier et al. 2010).

**Root system and root-shoot relationships**

The size of root systems has been studied extensively however, the physiology of roots received less attention until recently, at least partly because they are usually underground and more difficult to study. Nevertheless, even casual consideration of their functions indicates that physiologically vigorous root systems are as essential as vigorous shoots for successful plant growth because root and shoot growth are so interdependent that one cannot succeed without the other. Knowledge of root structure is important because it affects the pathway and resistance to water and solute movement, while the extent of root systems affects the volume of soil available as a source of water and mineral nutrients.

**FUNCTIONS OF ROOTS**

The functions of roots include anchorage, the absorption of water and mineral nutrients, synthesis of various essential compounds such as growth regulators, and the storage of food in root crops such as sugar beet and cassava (*Manihot* sp.).

**Anchorage**

The role of roots in anchorage often is taken for granted, but it actually is very important because the success of most land plants depends on their ability to stand upright. For example, part of the success of the Green Revolution resulted from development of cereal crops with short, stiff stems that resist blowing over by wind and rain (lodging), but stiff stems are useless unless they are firmly anchored in the soil by vigorous root systems. The mechanical strength of roots also is important in preventing overthrow of trees by wind and winter injury to crops such as winter wheat by frost heaving. Resistance to uprooting by grazing animals may also be important for small herbaceous pasture plants. Roots also increase the stability of soil on slopes (Hellmers et al., 1955). Coutts (1983) discussed the relationship between tree stability and their root systems. Ennos et al. (1993) and Crook and Ennos (1993) pointed out that resistance to lodging in maize and wheat is improved by increased spread and bending strength of roots.

**Roots as Absorbing Organs**

The importance of deep, wide spreading root systems for absorption of water and minerals cannot be overemphasized.

**Synthetic Functions**

Root cells possess many of the synthetic functions of shoot cells and some aerial roots even produce functional chloroplasts. Flores *et al.* (1993) cited examples of photosynthesis in aerial roots of orchids and mangroves and reported that roots of several genera of *Asteraceae*
and Orchidaceae can become adapted to photoautotrophy in solution culture by exposure to light and high concentrations of \( \text{CO}_2 \). According to Johnson \textit{et al.} (1994), phosphorus deficiency stimulates dark fixation of \( \text{CO}_2 \) in proteoid roots of lupine and increases production of citrate and its secretion into the rhizosphere where it increases the availability of phosphorus. Bialzyk and Lechowski (1992) observed significant absorption of \( \text{CO}_2 \) from the root medium and transport of carbon compounds from roots to shoots in tomato.

Most roots are dependent on shoots for thiamin and sometimes for niacin and pyridoxine, and receive auxin from the shoots. The nitrogen-fixing role of \textit{Rhizobium} bacteria in root nodules is important and the activities of microorganisms in the rhizosphere may also be important (Box and Hammond, 1990; Cud and Truelove, 1986; Wild, 1988, pp. 526-530).

Nicotine is synthesized in the roots of tobacco and is translocated to the shoots and tobacco shoots grafted on tomato root systems contain no nicotine (Dawson, 1942). Ammonia also is converted to organic compounds in roots, but in most species much of the nitrate is translocated to the shoots and reduced. According to a review by Oaks (1992), nitrate reduction in roots differs in legumes and cereals because legume roots export asparagine to their shoots, but cereals do not. Biles and Abeles (1991) found peroxidases and other proteins synthesized in the roots in the xylem sap of several species of plants. According to Rao (1990), flavonoids produced in roots protect them against pests such as fungi and nematodes and have allelopathic effects.

It was suggested long ago that roots probably synthesize hormones essential for shoots (e.g., Went, 1943). Among these are cytokinins (Kende, 1965; Skene inToney and Clarkson, 1975), gibberellins (Skene, 1967), and abscisic acid (Davies and Zhang, 1991). It has been suggested that reduced shoot growth of plants whose roots have been subjected to stress such as deficient soil water, deficient aeration, high salinity, or low temperature is caused at least in part by a change in the amount and kind of growth regulators supplied from the roots (Blum \textit{et al.}, 1991; Davies and Zhang, 1991; Itai and Vaadia, 1965; O'Leary and Prisco, 1970; Skene in Torrey and Clarkson, (1975). However, Jackson \textit{et al.} (1988) claimed that stressed pea roots are not a source of excess abscisic acid (ABA) and Munns (1990) argued against ABA as a chemical signal. In contrast, Khalil and Grace (1993) reported that when one-half of a split root system of sycamore maple was water stressed there was a large increase in ABA in the drying roots and the xylem sap, and a decrease in stomatal conductance in the shoots. Of course these stresses are likely to also reduce the supply of water and minerals, which likewise reduces shoot growth. The relative importance under field conditions of decreased absorption of water and minerals versus changes in root metabolism and in the supply of hormones to the shoots deserves further study (McIntyre, 1987).

**Roots as Sensors of Water Stress**

In recent years considerable attention has been given to the possibility that roots of plants in drying soil function as primary sensors of water stress. According to this view, as the soil dries changes in root metabolism such as a decrease in cytokinin production, an increase in ABA production, and a disturbance of nitrogen metabolism send biochemical signals to the
shoots that produce physiological changes such as a decrease in growth, stomatal conductance, and rate of photosynthesis, regardless of the water status of the leaves. The root sensor effect has been demonstrated in pot experiments with split root systems (Khalil and Grace, 1993), with roots in pressure chambers (Davies et al., 1986; Passiourea, 1988a; Schulze, 1986a; Turner, 1986 and others), and with maize under field conditions (Tardieu et al., 1991). Tardieu et al. (1991) reported that in the field the entire root system of maize must be in dry soil before the ABA concentration in the xylem sap increases.

Under field conditions in areas with adequate rainfall and many sunny days shoots of plants often are subjected to water stress even though the roots are in moist soil. Examples are the curling of leaves of corn plants in moist soil and the midday water stress in flooded rice reported by Tazaki et al. (in Turner and Kramer, 1980). It therefore seems doubtful if roots usually are primary sensors of water stress under those conditions (Kramer, 1988), although opposing arguments are presented by Zhang and Davies (1990), Davies et al. (1990), and Tardieu et al. (1991). Davies and Zhang (1991) and Davies et al. (1994) have good reviews of the role of roots as sensors.

Experiments of Kitano and Eguchi (1992a,b) seem to demonstrate that a change in shoot water status can directly affect stomatal conductance. Cramer and Bowman (1991) approached this problem by comparing leaf elongation of intact maize plants and shoots from which the roots have been removed, when placed in a saline solution. The short-term response of leaves on shoots without roots was similar to that on shoots with roots. This led them to conclude that signals from roots are not necessary for the occurrence of short-term reduction of leaf elongation by high salinity in maize. Day et al. (1991) reported that chilling one-half of a split root system of Pinus taeda did not decrease photosynthesis, suggesting that no nonhydraulic signal originated in the chilled roots.

Of course as the soil dries both roots and shoots dehydrate, altering the biochemistry in both and changing the biochemical and hydraulic communications between them. This makes it difficult to determine the relative importance of chemical and hydraulic messages.

**ROOT GROWTH**

Root growth results from cell division and the pressure developed by enlargement of newly formed cells. Bret-Harte and Silk (1994) question how sufficient carbon for growth reaches root meristems, which are several millimeters beyond the termination of the phloem. The older portions of
roots are anchored in the soil and the tips are pushed forward through the soil by cell enlargement at rates of a few millimeters to a few centimeters daily, often following a tortuous path of least resistance through crevices and around pebbles and other obstructions. Generally, root tips tend to return to their original direction of growth after passing around obstacles, a characteristic observed in the 19th century by Darwin and others, which is known as exotropy (Wilson, 1967). Despite numerous temporary deflections, branch roots of many plants tend to grow outward for a time before turning downward (Wild, 1988, Fig. 36). The cause of this change in sensitivity of roots to gravity deserves more study.

During growth and maturation roots undergo changes in anatomy at various distances behind the apex that affect the permeability to water and solutes. The approximate order of maturation of tissues is indicated in Fig. 37, but the length of the various zones varies widely, depending chiefly on the species and the rate of growth. In slowly growing roots, differentiation of new tissues occurs much closer to the root tips than in rapidly growing roots (Peterson and Perumalla, 1984). A diagram of a cross section through a fully differentiated dicot root is shown in Fig. 38, and a scanning electron micrograph of a cross section of a young barley root is shown in Fig. 39.

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**Fig. 37** The location of primary tissues in an elongating root and relative amounts of absorption at various distances behind the apex. The distance from the apex at which various stages of maturation occur depends on the species and the rate of root elongation. According to McCully and Canny (1983) the metaxylem of maize and soybean roots becomes capable of significant water conduction 15 to 30 cm behind the root apex. From Kramer (1983).

**Fig. 38** Cross section through a squash root in the region where salt and water absorption occur most rapidly. The endodermal cell walls usually become much thickened, except for passage cells opposite the xylem which often remain unthickened. The pericycle usually gives rise to branch roots and the cork cambium found in older roots (Kramer 1983; Crafts and Broyer 1938).

**Fig. 39** Scanning electron microscope of a young barley root showing numerous root hairs, a large central xylem vessel and a few small vessels. The endodermal cell walls are not yet thickened from Kramer 1983.
Enlarging roots often develop pressures sufficient to lift sidewalks and crack masonry walls. Enlargement of tap roots and large branch roots of pine compresses the soil in their immediate vicinity sufficiently to increase its bulk density. This might decrease infiltration of water around the base of tree trunks. The large number of roots produced beneath grasses (Dittmer, 1937; Pavlychenko, 1937) might temporarily reduce the pore space, but their death and decay would soon increase it.

**Epidermis and Root Hairs**

The epidermis and associated root hairs have received considerable attention because they make direct contact with the soil and are the surfaces through which most of the water and minerals usually enter roots. The epidermis is composed of relatively thin-walled, elongated cells, which produce protrusions from the epidermal cells, or from cells of the hypodermis lying beneath it, termed root hairs.

Root hairs greatly increase the root surface in contact with the soil and decrease the distance that ions and water must travel to reach root surfaces. This presumably facilitates absorption of water and minerals, at least in some situations (Itoh and Barber, 1983). Because of their small diameter they can penetrate soil pores too small to be penetrated easily by roots. On growing roots the root hair zone moves forward as the roots elongate and the older root hairs usually are destroyed by suberization of epidermal cells. However, they persist for months on some herbaceous plants (Dittmer, 1937; Scott, 1963; Weaver, 1925) and indefinitely on some woody plants (Hayward and Long, 1942). The number of root hairs varies widely among species and with soil conditions, generally being most abundant in moist, well-drained, well-aerated, loamy soils (Itoh and Barber, 1983; Kramer, 1983, Meisner and Karnok, 1991). Their formation usually is inhibited by oxygen deficiency and by the presence of ectotrophic mycorrhizae. The number of root hairs reported varies from 20 to 500 per cm$^2$ of root surface on roots of trees to 2500 on roots of winter rye (Kramer, 1983).

The importance of root hairs in the absorption of water and minerals seems to vary among species and cultivars, and perhaps with the growth stage of the plant. For example, Bole (1973), using cultivars of wheat known to differ in root hair frequency, found that the amount of root hair development did not significantly affect phosphorus uptake from a clay loam soil with either a low or high phosphorus content. He also found that rape and flax roots, which bear few or no root hairs, absorbed more phosphorus per unit of length than wheat roots with numerous root hairs. In contrast, Itoh and Barber (1983) reported that root hairs clearly contribute to the phosphorus uptake of Russian thistle and tomato and to a lesser extent lettuce, but not of wheat. Perhaps some of the discrepancies in the literature result from differences in plant demand for minerals at the time of the experiment, which depends on rapidity of growth (Raper et al., 1977; Vessey et al., 1990). Also, if root density is high roots may compete with one another for water and minerals, even if no root hairs are present. It seems that the contribution of root hairs to water and mineral absorption is variable.

The epidermal cells and root hairs are covered by thin films of cutin wherever they are exposed to air (Scott, 1963, 1964), and the root cap and adjacent epidermal cells are covered by a layer of mucigel consisting of polysaccharides secreted by root cells and perhaps partly
by associated microorganisms. The mucigel acts as a lubricant to elongating roots and improves contact with the soil (Foster, 1981; Jenny and Grossenbacher, 1963; Oades, 1978). It may also protect roots from aluminum toxicity (Hecht-Buchholz and Foy, 1981; Horst et al., 1982), but Delhaize et al. (1993) attribute aluminum tolerance of wheat to the excretion of malic acid. Roots release large amounts of organic matter (Barber and Martin, 1976) which stimulate microorganisms and result in formation of a unique layer high in organic matter in the soil around them, called the rhizosphere (Box and Hammond, 1990; Curl and Truelove, 1986; Wild, 1988, pp. 526-530). Root exudates may use 2 to 20% of the carbon fixed by photosynthesis (Clarkson, 1985, p. 102, and Lambers in Gregory et al., 1987)

A conspicuous part of the primary structure of many roots is the endodermis, the innermost layer of the cortex, the walls of which often become conspicuously thickened, plus strips of suberized tissue on the radial walls, the Casparian strips. A similarly thickened layer of cells, the exodermis, sometimes develops beneath the epidermis of roots (Esau, 1965; Peterson, 1988). This decreases their permeability and presents a barrier to inward apoplastic movement of water and solutes in the cell walls. However, there is considerable evidence that some water and minerals enter roots even where the endodermis is suberized. Thickening of the endodermis often is quite uneven, with pits and plasmodesmata in the walls which permit symplastic movement of materials from cell to cell (Clarkson and Robards in Torrey and Clarkson, 1975), and the endodermis often is pierced by branch roots that may provide openings for apoplastic radial water movement (Dumbroff and Peirson, 1971; McCully in Gregory et al., 1987; McCully and Canny, 1988; Peterson and Perumalla, 1984; Peterson et al., 1981; Queen, 1967). The development and functioning of the endodermis are discussed in Torrey and Clarkson (1975) and in Clarkson (1993), and there is much interesting information on tissue development during root growth in books on plant anatomy. Benfey and Schiefelbein (1994) stated that a number of mutants have been identified in roots of Arabidopsis that affect growth and reaction to environmental stimuli.

Secondary Growth
Secondary growth of roots, resulting from cambial activity, increases root diameter, but causes loss of primary tissues such as the epidermis and cortex, including the hypodermis and endodermis, and development of a suberized outer layer of bark which must significantly modify the pathway of and increase resistance to water and solute entrance. According to Addoms (1946), the entrance of water into suberized roots occurs through lenticels, gaps around branches, and wounds in the bark. The variation in root structure with age and stage of development means that there are large variations in permeability and uptake of water and ions along roots, making it difficult to estimate average uptake per unit of root length.

Root Contraction
A seldom mentioned aspect of root growth that has been observed in many species is their contraction (Esau, 1965, pp. 519-521). It is said to occur in over 450 species, including alfalfa, sugar beet, carrot, and various bulbous monocots. In at least some instances it is brought about by longitudinal contraction and radial expansion of parenchyma cells, resulting
in distortion of the vascular tissue. Its importance is uncertain, although Esau speculated that it might pull the shoot apex into the soil surface where the environment is more favorable for growth and the development of adventitious roots.

**Rate and Periodicity of Root Growth**

The rate of root elongation varies widely among species, with the season, with variation in such soil conditions as water content, aeration, and temperature, and with variations in the shoot environment that affect the supply of carbohydrates.

The principal roots of maize were observed to grow 5 or 6 cm per day for 3 or 4 weeks (Weaver, 1925). A rate of 10 or 12 mm per day is said to be common in grasses, but rates of 3 to 5 mm seem to be more common in tree roots (Barney, 1951; Reed, 1939; Wilcox, 1962). A few studies indicate that roots sometimes elongate more rapidly at night than during the day (Lyr and Hoffman, 1967; Reed, 1939). Such behavior is most likely to occur when high rates of transpiration produce daytime water stress.

Reich *et al.* (1980) reported that in a constant environment flushes of oak root growth occurred between flushes of shoot growth. There also are seasonal cycles in root growth of perennial plants at least partly related to soil temperature (Lyr and Hoffman, 1967; Romberger, 1963). Turner (1936) and Reed (1939) observed root growth every month of the year in loblolly and shortleaf pine, with the most growth occurring in the spring and summer and the least in the winter. Periods of slow root growth in the summer coincided with periods of low soil moisture. According to Teskey and Hinckley (1981), physiologically optimum soil temperatures and water potentials never occurred simultaneously in the Missouri oak-hickory forest that they studied.

Root extension into previously unoccupied soil is important because it makes additional water and minerals available. Thus the ability of roots to resume growth promptly after transplanting, known as the root growth potential (RGP), is very important to the success of transplants. Conditions in the nursery such as water supply, fertilization, density of seedlings, and time of lifting affect the capacity of seedlings to generate new roots when outplanted. Evidence that roots can grow on water mobilized from stem tissue after transplanting exists and this may aid in establishment (Matyssek *et al.*, 1991a,b). Occasionally, warm winter weather reduces the root growth potential of seedlings of some cooler climate species (Stone and Norberg, 1979). The factors involved in root growth potential of forest tree seedlings are discussed in detail by Kramer and Rose (1986).

**Depth and Spread of Roots**

In deep, well-aerated soil, roots penetrate to great depths and spread widely. Peanut roots reached a depth of 120 cm in 40 to 45 days, but after attaining a certain density showed no further increase (Ketring and Reid, 1993). In prairie soils, corn and sorghum roots regularly penetrate to 2 m, alfalfa roots have been found at depths of 10 m, and Wiggans (1936) found that roots of 18-year-old apple trees penetrated to a depth of at least 10 m and fully occupied the soil between the rows, which were about 10 m apart. Jaafar *et al.* (1993) describe a study of sunflower root development in relation to shoot growth and flowering in a well-watered deep silt loam. The roots penetrated to a depth of 1.8 m at the beginning of disk flowering.
and 2.0 m by the end of flowering. Roots of several kinds of fruit trees growing in a deep loam soil in California penetrated at least 5 m and the greatest number of roots occurred between 0.6 and 1.5 m (Proebsting, 1943). Hough et al. (1965) placed $^{131}$I in a forest soil and found that it was absorbed in detectable amounts from as far away as 16 to 17 m by longleaf pine and turkey oak. Hall et al. (1953) used uptake of $^{32}$P to measure root extension of crop plants, and a study of corn root extension is shown in. The situation is very different in heavy, poorly aerated soils. For example, Coile (1937) found that over 90% of roots less than 2.5 mm in diameter occurred in the top 12.5 cm of soil under pin and oak stands in the heavy clay soil of the North Carolina Piedmont. Pears growing in an adobe soil in Oregon had about 90% of their roots in the upper meter (Aldrich et al., 1935). Even in sandy soils trees often form root mats near the surface because the surface soil contains more mineral nutrients released by decomposition of leaf litter and is wetted by summer showers (Woods, 1957).

The branching and rebranching of root systems often produce phenomenal numbers of roots. Pavlychenko (1937) estimated that a 2-year-old crested wheat grass plant possessed over 500,000 m of roots occupying about 2.5 m$^3$ of soil. Nutman (1934) estimated that a 3-year-old coffee tree growing in the open bore about 28,000 m of roots, 80% of which occurred in a cylinder 1.5 m deep and 2.1 m in diameter. Kalela (1954) estimated that a 100-year-old pine bore about 50,000 m of roots with 5,000,000 root tips. Considerable further information on the extent of root systems has been summarized by Miller (1938, pp. 137-148) and by Weaver (1926). Much information on conifer root systems has been summarized by Sutton (1969).

**Longevity of Roots**

Although the larger roots of perennial plants are perennial and some are approximately as old as the plants, mortality is heavy among the smaller roots. The short mycorrhizal roots of pine often die over winter and some of the small roots on apple and other fruit trees live only a week or two (Kinman, 1932; Rogers, 1929). Grier et al. (1981) reported a high turnover of roots in a mature forest of *Abies amabilis* in the Washington Cascades, and Caldwell (in Lange et al., 1976) found high rates of root replacement in mixed deciduous forests and cool desert shrub communities. According to Reid et al. (1993), most of the fine roots on *Actinidia deliciosa*, a woody vine, survive less than 60 days.

A considerable variation in longevity also exists among the roots of herbaceous plants. It often is stated that the primary roots of grasses live only a few weeks and are succeeded by adventitious secondary roots, but this is not always true. The primary roots of barley, rye, wheat, and various wild grasses are the only roots present and maintain the plants for an entire season. Weaver and Zink (1946) found that the seminal roots of several species of prairie grasses survived two seasons and that some were alive after three seasons.

**THE ABSORBING ZONE OF ROOTS**

Consideration of root anatomy suggests that entrance of water and minerals into young roots probably occurs chiefly in a region a few centimeters behind root tips, approximately where root hairs are most abundant. However, this is questioned by observations that the xylem is
not yet fully functional in the root hair zone of maize and soybean (McCully and Canny, 1988). This situation deserves study in roots of other kinds of plants. Little water enters through the meristematic regions (Frensch and Steudle, 1989), probably because of a lack of functional xylem to carry it away. Farther back the xylem becomes functional, but suberization and lignification of the hypodermis and endodermis usually reduce the permeability in older regions.

It formerly was believed that mineral absorption occurred chiefly near the root apex. However, this was based on mineral accumulation studies, and experiments in which radioactive tracers were supplied to roots of transpiring plants at various distances behind the tips indicate that absorption and translocation often occur far behind the apex (Clarkson et al., 1975; Richter and Marschner, 1973; Wiebe and Kramer, 1954). Research by Lazof et al. (1992), using secondary ion mass spectrometry, indicates slow influx of NO$_3$ into root tips and emphasizes the importance of finely branched lateral roots in absorption. Absorption through Suberized Roots

Most discussions of absorption deal with young roots and leave the impression that absorption through older, suberized roots is unimportant. Haussling et al. (1988), for example, quite properly stressed the importance of growing roots for water and ion uptake of conifers, but absorption through suberized roots must be important in perennial plants where unsuberized roots are often scarce or absent, especially in cold or drying soil. For example, on sunny winter days evergreens such as conifer and citrus trees lose large amounts of water that must be replaced by absorption through suberized roots because few or no unsuberized roots are present (Reed, 1939; Reed and MacDougall, 1937; Roberts, 1948). Kramer and Bullock (1966) found that less than 1% of the root surface in the upper 10 cm of soil under pin and yellow poplar stands in North Carolina was unsuberized in midsummer. Chung and Kramer (1975), Kramer and Bullock (1966), and Queen (1967) all observed a significant uptake of water and phosphorus through suberized roots growing in solution cultures. It seems that the unsuberized root surfaces are too limited in extent, too short lived, and occupy too small a volume of soil to supply all of the water and minerals required by many perennial plants (Chung and Kramer, 1975) and that older, suberized roots must play an important role in absorption, despite their lower permeability.

Passioura (1988b) objected to conclusions based on uptake from solution cultures, but MacFall et al. (1990, 1991a), using NMR imaging, observed depletion of soil moisture around suberized pine roots growing in fine sand. This occurs because water sometimes is absorbed more rapidly than it moves toward roots.

**Mycorrhizae**

The roots of many plants are invaded by fungi that form symbiotic associations called mycorrhizae. These are of two types: endotrophic (VAM, for vesicular arbuscular mycorrhizae) in which the fungus penetrates the root cells, but has little effect on external appearance, and ectotrophic in which the fungus covers the external surface and causes marked hypertrophy and extensive branching of roots. Mycorrhizae seem to increase the rate of mineralization and solubilization, increasing the supply of minerals, especially phosphorus, available to roots (MacFall, 1994). The presence of mycorrhizal roots also appears to increase the absorption of water and increase drought tolerance, at least in some
circumstances (Dixon et al., 1983; Duddridge et al., 1980; Huang et al., 1985; Lamhamedi et al., 1992; MacFall, 1994; Sylvia et al., 1993). Fungal hyphae extend out into the soil and increase the absorbing surface. However, Graham et al. (1987) reported that the inoculation of citrus trees with a VAM fungus did not improve their water status, and Harmond et al. (1987) found no increase in tolerance of flooding or salinity. Danielset al.. (1987) found that although inoculation with a mycorrhizal-forming fungus improved the growth of well-watered corn, sudan grass, and big bluestem, only the growth of big bluestem was improved by mycorrhizae under water stress.

Endotrophic or VA Mycorrhizae. The role of VA(vesicular-arbuscular) or endotrophic mycorrhizae is discussed by Safir (1987), in McMichael and Persson (1991), and in Waisel et al. (1991, Chapters 33 and 34). Some factors controlling VAM symbiosis are discussed by Koide and Schreiner (1992) and Volpin et al. (1994), and McArthur and Knowles (1992) suggest that phosphorus deficiency makes plants more susceptible to VAM fungi. Johansen et al. (1993) reported that colonization of subterranean clover with VAM fungi increased the uptake of 32p and 15N. According to Syvertsen and Graham (1990), VAM colonization of roots of citrus seedlings did not affect gas exchange, stomatal conductance, or water-use efficiency. They cited work indicating that VAM infection increased the hydraulic conductance of roots of citrus and green ash seedlings only if the plants were deficient in phosphorus (also see Safir et al., 1971, 1972). According to Anderson et al. (1988), the colonization of roots of green ash seedlings with VAM fungi did not increase root hydraulic conductance.

Of course beyond a certain root density, a further increase in absorbing surface does not increase overall absorption because the new root surface merely competes with the existing surface. Although endotrophic mycorrhizae are more common on herbaceous plants, Janos (1980) reported that they also are important on many species of tropical lowland trees. Occasionally, both types of mycorrhizae occur on the same plant.

Ectotrophic Mycorrhizae. According to Bowen (1984, p. 170) and others, ectotrophic mycorrhizae increase the competitive capacity of trees (and presumably some other plants) and compensate for unfavorable soil conditions such as high pH, excess salt, toxic elements such as aluminum, and deficient aeration. For example, inoculation with mycorrhizal-forming fungi improves tree seedling growth on mine dumps (Marx, 1980; Walker et al., 1989) and increases tolerance of aluminum (Cumming and Weinstein, 1990; Kasuga et al., 1990). Mycorrhizal roots are said to be less susceptible to disease and live longer than the average nonmycorrhizal short root. The beneficial effects of inoculating tree seedlings with mycorrhizal-forming fungi, especially Pisolithus tinctorius, are discussed by Marx et al. (1984,1985). MacFall et al. (1991b) reported that the of red pine seedlings was greatly increased in phosphorus-deficient soil inoculation with the mycorrhizal-forming fungus Hebetoma arenosa, but that the effect on growth decreased as the phosphorus concentration of the soil increased. Iron was accumulated and copper, calcium, cobalt, boron, and sodium were excluded in mycorrhizal roots in low phosphorus soil as compared with nonmycorrhizal seedlings. Apparently the fungus increases the supply of phosphorus to tree seedlings in
phosphorus-deficient soil and regulates compartmentalization of poly phosphorus in mycorrhizal roots (MacFall et al., 1992). Auge and Duan (1991) reported that the presence of mycorrhizae on roots hastened stomatal closure when the mycorrhizal-infected half of a split root system was water stressed. They suggested that mycorrhizal roots supply a nonhydraulic signal that affects stomatal aperture.

Although most attention has been given to mycorrhizae in connection with trees and other woody plants (Perry et al., 1987), they may be important in improving water and mineral absorption of herbaceous plants, including cultivated crops, especially on infertile soil (Gerdemann in Torrey and Clarkson, 1975; Safir, 1987; Safir et al., 1972). For example, Bethlenfalvay et al. (1987) concluded that mycorrhizal infection increased legume nodule activity and decreased water stress in soybean. However, mycorrhizae require considerable carbohydrate, estimated at 7-10% of that translocated to the roots, and that might reduce yield (Gregory et al., 1987, pp. 140-141, 161-162). Bjorkman (1942) and Wenger (1955) found that girdling and shading decrease the development of mycorrhizal roots, presumably by reducing the supply of carbohydrate.

Mycorrhizae are discussed in more detail in Harley and Smith (1983), by Marks and Kozlowski (1973), and by Munkerji et al. in McMichael and Persson (1991). The latter state that there is evidence that the presence of mycorrhizae increases nodulation and nitrogen-fixation by legumes. In contrast, Johnson et al. (1992) suggest that the yield decrease accompanying continuous cropping of corn and soybean may be caused by an increase in detrimental VAM fungi.

MacFall (1994) has an interesting review of ideas concerning the role of mycorrhizae in forestry and agriculture. She suggests that they play a role in accelerated mineralization and soil biogeochemistry as well as in nutrient uptake through increased absorbing surface. Norris et al. (1994) provide a summary of methods for research on mycorrhizae.

DEVELOPMENT OF ROOT SYSTEMS

The amount of water and mineral nutrients available to plants depends on the volume of soil occupied by their roots, and it is well established that plants with deep root systems are more tolerant of drought than shallow-rooted plants. Coile (1940) concluded that the inability of loblolly pine seedlings to compete with hardwood seedlings under closed canopies results from their reduced photosynthesis in the shade (Kramer and Decker, 1944), resulting in failure to produce the deep taproots characteristic of oak and hickory seedlings.

Thus pine seedlings are more dependent than hardwood seedlings on water in the surface soil, which is quickly depleted during summer droughts. Fayle (1978) observed that poor growth of red pine plantations was associated with poor vertical root development, and Meyer and Alston (1978) stated that wheat yield in semiarid regions depends on the geometry of the root system in relation to the distribution of soil water at various depths. Boyer et al. (1980) concluded that newer soybean cultivars yield better than older cultivars because they have a higher root density and therefore are less subject to afternoon shoot water deficits than older cultivars. Frederick et al. (1990) questioned this but used only leaves stored for various times to measure water potentials, which may have obscured the differences.
There are some limitations to the concept that very high root density is always favorable. For example, Andrews and Newman (1968) removed 60% of the roots from densely rooted wheat plants without reducing transpiration, even in drying soil, and Eavis and Taylor (1979) reported that treatments increasing the ratio of root length to leaf area did not significantly increase transpiration or leaf water potential. Also, Newman and Andrews (1973) found that although uptake of phosphorus by wheat was well correlated with root growth, uptake of the more mobile potassium was not. Raper and Barber (1970) observed an increased uptake of potassium per unit of root surface in a soybean genotype with lower root density than in one with higher root density. Presumably, as root density increases, competition between roots of the same plant for water and minerals also increases as well as competition between roots of adjacent plants, decreasing the uptake per unit of root surface and the benefits from further increase in root length density.

The depth and lateral spread of root systems depend on both heredity and environment. Taylor and Terrell (1982) give extensive data describing the spread, depth, and density of root systems in various plant species.

**Root-Shoot Interrelationships**

The optimum growth of plants depends on maintenance of an efficient balance of functions between roots and shoots, such that neither suffers serious deficiencies in supplies of essential substances contributed by the other. Borchert (1973) suggested that rhythmic shoot growth in a uniform environment may result from cyclic feedback between root and shoot growth, tending to maintain a constant root-shoot ratio. However, it is doubtful if a constant root-shoot ratio is generally maintained in most growing plants.

Roberts and Struckmeyer (1946) concluded that the composition and reserve conditions in the shoot were a large and perhaps controlling factor in the production of roots. Sachs _et al._ (1993) proposed that a plant can be regarded as a colony of shoots and roots competing for vascular connections with the remainder of the plant, and their success in this is important for their development.

**Effects of Shoots on Roots.** Roots are dependent on shoots for carbohydrates, growth regulators, and some other organic compounds, and severe reduction in leaf area by pruning, insect defoliation, grazing, or diversion of food into fruit and seed production is likely to reduce root growth. The development of fruits and seeds sometimes reduces root growth significantly, and Fig. 40 shows the effect of seed filling on root growth of maize.
There was steady increase in root density at all depths until pollination, after which roots began to die more rapidly than they were produced, resulting in a decrease in root density, especially of the older roots in the surface soil, and a decrease in total root weight (Mengel and Barber, 1974). In another experiment, Loomis (1935) found that if the ears were removed corn root growth continued until frost. Figure 41 shows that as apple shoot growth increased, root growth decreased and vice versa and that pruning stimulated shoot growth, but reduced root growth (Head, 1967). Buwalda (in McMichael and Persson, 1991), pp. 431-441) found that most of the root growth of kiwi vines (*Actinidia deliciosa*) occurs after shoot and fruit growth is nearly completed. Also, partial defoliation reduces root growth more than fruit growth, suggesting that, as might be expected, kiwi fruits are stronger sinks for photosynthate than roots.

A heavy crop of coffee is said to sometimes reduce the carbohydrate supply to the roots so severely that some die, resulting in injury to the trees (Nutman, 1933), and fruiting of a tropical palm also is said to reduce root growth (Piiero et al., 1982). Root growth of tomato is reduced during fruiting (Hudson, 1960, and others), and Eaton (1931) reported that both root dry weight and root-shoot ratio of cotton were nearly tripled by preventing boll and branch formation. These effects on root growth usually are explained in terms of diversion of carbohydrates from roots to shoot growth or to fruit and seed development. For example, Tripp et al. (1991) reported that the increased yield of
tomato fruit on plants supplied with a high concentration of CO₂ results from the diversion of photosynthate from roots to fruits because high CO₂ increases seed number in tomato fruits and makes them stronger sinks. However, Van der Post (1968) reported that the appearance of flowers on cucumbers stopped root growth before the fruits were large enough to be important sinks for carbohydrates, suggesting hormonal controls. Wilson (1988) reviewed the extensive literature on root-shoot ratios and concluded that Thornley's (1972) model explains reactions of the root-shoot ratio to environmental factors such as water deficits, light, CO₂, and mineral supply, also to defoliation and root pruning. This model was simplified by Johnson and Thornley (1987) who put more emphasis on the carbon and nitrogen status of plants in the vegetative stage than on hormones. However, as Bingham and Stevenson (1993) state, the carbohydrate supply is only one component of the complex of factors controlling root growth.

**Effects of Roots on Shoots.** It is not surprising to learn that damage to root systems severe enough to reduce water and mineral absorption inhibits shoot growth. In addition, shoots are dependent on roots for growth regulators such as abscisic acid, cytokinins, and gibberellins. However, it is somewhat surprising to find that the mineral content of the leaves and the quality of citrus fruit are affected by the kind of rootstock on which the trees are growing, yet those effects have been observed worldwide (Haas, 1948; Sinclair and Bartholomew, 1944). For example, more soluble sugar and total acids are found in fruits from orange trees grown on citrange and trifoliate orange roots than in fruits from trees grown on rough lemon roots. Also, the juice from the Washington navel orange is less bitter in fruit grown on trifoliate orange roots than in fruit grown on other rootstocks such as sour orange, sweet orange, or its own roots. Gregoriou and Economides (1993) found that rootstocks affected fruit size and composition of ortanique tangor, but the differences were too small to be of practical importance. The reasons for these differences are not fully understood. Horticulturists know that rootstocks differ in disease resistance and tolerance of flooding, salinity, and low temperature, which affect the success of the shoots growing on them. For example, trifoliate orange rootstocks tend to exclude sodium from the shoots grafted on them (Walker, 1986), and Lloyd et al. (1987) state that the uptake of sodium and chloride by Valencia oranges varies with the rootstocks on which they are grown. Apparently trifoliate orange rootstocks sequester sodium at the root-shoot transition zone. Maas (1993) surveyed the recent literature on the effects of salinity on citrus. Reciprocal root and shoot grafts between bean genotypes differing in drought tolerance indicated that the differences in tolerance were in the roots (White and Castillo, 1989). In contrast, Delves et al. (1987) concluded from reciprocal grafts that the shoot controls supernodulation in soybeans. It has been known for centuries that the kind of rootstock affects the size and vigor of trees grafted on it. Pears are dwarfed by grafting them on quince roots, and apples are not only dwarfed to one-third of their normal size, but begin to fruit at a younger age when grafted on a dwarfing root system such as M9. Also, on the M9 rootstock about 70% of the photosynthate goes into fruits compared to 40 or 50% in normal trees. However, in California, apple trees on M9 root systems grow too small and M7a and M106 are better for early bearing (Micke et al., 1992). (Numbers with the prefix M indicate that the root systems
originated at the horticultural research station at East Malling, England). The physiology of these root-shoot interactions are not well understood, but some information has been provided in reviews by Lockard and Schneider (1981) and (1973). The role of roots as sensors of water stress was mentioned earlier in this chapter and will come up again in later chapters. The importance of chemical signals from roots in controlling shoot processes was reviewed by Davies and Zhang (1991), ans Gowing et at. (1993).

There seems to be renewed interest in electrical potentials as coordinating signals in plants. They received considerable attention a few decades ago, and their role in relation to leaf movement in plants sensitive to touch is well known.

Fromm and Eschrich (1993) claimed that electrical signals from roots affect photosynthesis and transpiration in the shoots of willow trees. Hamada et al. (1992) reported that there is a decrease in electrical potential on the surface of roots at the point where branch roots will emerge, about 10 hours before. While the role of electrical potentials over distances of a few centimeters seems well established (see references in Fromm and Spanswick), their effectiveness over long distances is more speculative. Perhaps the use of modern technology will result in clarification of their importance. Malone (1993) regards hydraulic signals as important.

The increase in wood production of trees accompanying fertilization usually is attributed to an increase in leaf area and photosynthesis. However, Axelsson and Axelsson (1986) state that there is increasing evidence that the decreased allocation of photosynthate to fine root production by well-fertilized trees is an important factor contributing to increased shoot growth. King (1993) supported the view that increasing the supply of nitrogen decreases root production relative to shoot growth.

**Root-Shoot Ratios.** The preceding discussion of the interdependence of roots and shoots suggests that there might be some optimum ratio of roots to shoots. However, root-shoot ratios vary widely among species, with age, and with environmental conditions. Table 2.2 summarizes some data from Bray (1963) giving ratios varying from 0.15 to 0.20 for various trees, 0.5 for maize, and 3.0 for the storage roots of beets. Such data are not very accurate because of differences in methods and amounts of roots recovered, but they indicate the wide range of root-shoot ratios found among plants in the field. This variation results in part from the wide variations in water supply and other environmental factors to which plants often are subjected during a growing season, as well as to genetic variations among plants such as grasses and root crops. Perhaps the root-shoot ratio should be considered in terms of root and leaf surface but it is difficult to measure root surface. Fiscus (1981) found that there was a linear relationship between root and leaf surface in growing bean plants. A correlation exists between the sapwood area and leaf area in trees and Kaufmann and Fiscus (1985) state that the amounts of conducting tissue in roots, stems, and leaves are strongly correlated. Various aspects of root-shoot relations have been reviewed by Klepper (in Waisel et al., 1991).
Table 2.2— amount of dry matter in t/ha incorporated annually into roots and shoots of various plant species

<table>
<thead>
<tr>
<th>Species</th>
<th>roots</th>
<th>shoots</th>
<th>Root-shoot ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Zizania aquatic (wild rice)</td>
<td>0.6</td>
<td>4.0</td>
<td>0.15</td>
</tr>
<tr>
<td>Hordeum</td>
<td>3.0</td>
<td>12.0</td>
<td>0.25</td>
</tr>
<tr>
<td>Andropogon scoparium (first year)</td>
<td>3.5</td>
<td>14.2</td>
<td>0.25</td>
</tr>
<tr>
<td>Triticum (average)</td>
<td>2.0</td>
<td>6.8</td>
<td>0.29</td>
</tr>
<tr>
<td>Medicago sativa (average)</td>
<td>3.2</td>
<td>7.4</td>
<td>0.43</td>
</tr>
<tr>
<td>Zea mays (average)</td>
<td>4.5</td>
<td>8.7</td>
<td>0.52</td>
</tr>
<tr>
<td>Solanum tuberosum (average)</td>
<td>4.0</td>
<td>2.6</td>
<td>1.54</td>
</tr>
<tr>
<td>Beta (average)</td>
<td>9.5</td>
<td>3.1</td>
<td>3.06</td>
</tr>
<tr>
<td>Pinus syysvestris (average)</td>
<td>1.6</td>
<td>8.9</td>
<td>0.17</td>
</tr>
<tr>
<td>Picea abies (average)</td>
<td>2.1</td>
<td>11.9</td>
<td>0.18</td>
</tr>
<tr>
<td>Fagus sylvatica (average)</td>
<td>1.6</td>
<td>8.2</td>
<td>0.19</td>
</tr>
<tr>
<td>Ghana rain forest</td>
<td>2.6</td>
<td>21.7</td>
<td>0.12</td>
</tr>
</tbody>
</table>

From Bray (1963)

METHODS OF STUDYING ROOT SYSTEMS

The oldest method of studying root systems was to excavate them, a method that requires much time, energy, and a disregard for getting dirty. One form of excavation requires cutting a trench and then removing soil by hand or by a stream of water or air, while mapping the roots on the face of the trench. This was used effectively on fruit trees by Oskamp and Batjer (1932) and on forest trees by Coile (1937) and many others (see Bohm, 1979). Occasionally soil is removed in the horizontal plane to expose the spread of tree root systems. Another approach, the monolith method, is to remove large blocks of soil and wash out the roots. Sometimes these blocks are enclosed in steel boxes driven into the soil to hold the soil mass together while removing it. Boards covered with spikes, called pin boards, are sometimes driven into the soil mass to preserve the root arrangement while the soil is washed away. Root frequency sometimes is sampled in cores of soil removed with various kinds of soil augers, which frequently are driven into the soil and removed by tractor power (Jaafar et al., 1993). Clark (1875), who made the first measurements of root growth in the United States, known to the authors, grew plants in greenhouse benches and washed out the roots.

Another method, apparently introduced by Sachs in 1873, is to install glass plates in the soil and observe root growth against them. From this has developed the elaborate rhizotrons at East Malling, Auburn, Alabama, Ames, Iowa, and elsewhere which have large underground observation tunnels and observation windows large enough to follow the development of tree root systems. Mini-. rhizotrons also have come into use, consisting of plastic tubes about 5 cm in diameter and 2 or 3 m long which are driven into the ground, usually at an angle. A camera and a fiber optic illumination system can be lowered down the tube to record root growth over time. An example is described by Upchurch and Ritchie (1988) and another by Box and Ramseur (1993). Buckland et al. (1993) discussed the problems involved in
converting minirhizotron observations into root length density data. The advantages and disadvantages of various methods are discussed by Bohm (1979, pp. 75-76) and by Glinski and Lipiec, (1990, Chapter 7). Heeramon and Juma (1993) concluded that destructive sampling is still the best method to study root growth. Couchat et al. (1980) used neutron radiography to study root growth in sand, and nuclear magnetic resonance imaging shows promise for some purposes (Brown et al., 1986, 1991; Omasa et al., 1985b; Rogers and Bottomley, 1987). MacFall et al. (1990, 1991a) showed development of a water depletion zone around suberized pine roots by NMR imaging and Omasa et al. (1985b) used it to show changes in root and soil water content. The use of nuclear magnetic resonance technology for research on plants has been discussed by Kramer et al. (in Hashimoto et al., 1990) and for plants and soil by MacFall and Johnson (1994). An example of its use is described in a paper by Zimmermann et al. (1992). Hegde and Miller (1992) reported that scanning electron microscopy is useful for studying root anatomy and morphology. However, these methods cannot provide images of large root systems. Several indirect methods have been used to estimate root density and the rate of root extension in the soil. One method is to measure the decrease in soil water content, assuming that a decrease is closely related to root density. This is most useful if rainfall is infrequent or if rain shelters are available. Root extension also has been followed by injecting small quantities of a radioactive isotope of phosphorus, sulfur, or rubidium into the soil at various depths below and distances from seedlings and noting when it appears in the plant. Sometimes the tracer is injected into the plant and is recovered from root samples in soil cores (Fusseder, 1983). Some success has been attained in using $^{14}$C as a tracer of carbon transport to the roots and to distinguish between living and dead roots. These methods are discussed in Chapter 8 of Bohm (1979). Measurement of the ratio of deuterium to hydrogen (D/H ratio) in xylem sap has proven useful in studying plant-soil water relations (White in Rundel et al., 1988). For example, White et al. (1985) found that bald cypress growing in a swamp showed no isotopic change in response to rain because most of its roots were below the surface of the water table, whereas trees on a dry site used rainfall water exclusively for several days after a rain. Trees on intermediate sites used both at first, but a few days after a rain they were using groundwater exclusively. In another study, Flanagan et al. (1992) used the difference in the D/H ratio between rain water and soil water to determine the relative uptake of rain and groundwater by woody plants in a pinyon-juniper woodland.

**Metabolic Cost of Root Systems**

A large amount of photosynthate goes into root growth. Some is used in the production of new tissue, some in the respiration supplying energy for the metabolic processes involved in growth, and some in the maintenance respiration of existing tissue (Amthor, 1989; Lambers in Gregory et al., 1987). Caldwell (in Lange et al., 1976) reported that 50% of the annual net primary dry matter production of a deciduous forest and a fescue meadow and 75% of the annual production of short grass prairie and shrub steppe communities goes into the production of new roots. Woods (1980) concluded that the turnover in root biomass of a New
England deciduous forest exceeds that of leaves, and Harris *et al.* (1977) reported that root dry matter production is 2.8 times that of aboveground wood production in pine and hardwood forests of the southeastern United States. The economics of root systems are discussed in detail in Givnish (1986).

There has been considerable discussion of why plants often produce more roots than seems necessary and Caldwell (in Lange *et al.*, 1976) was unable to find a satisfactory explanation. It has been argued that death and replacement of roots are efficient because they reduce root respiration at times when they are not needed, but this is doubtful. Part of the problem is the difficulty in determining what constitutes an adequate root system. For example, Teskey *et al.* (1985) reported that they could remove one-fourth of the roots from forest trees in the Pacific Northwest without increasing tree water stress, but Carlson *et al.* (1988) found that removal of any roots from 5-year-old loblolly pine seedlings in Oklahoma increased tree water stress. The benefits of large root systems seem to depend on soil water storage capacity in the root zone and on rainfall patterns, and may vary from year to year. The role of root density and the extent of root systems in the success of plants have been discussed by Kummerow and by Taylor in Turner and Kramer (1980), by Barley (1970), by Fitter (1987), and also in Waisel *et al.* (1991, Chapter 1). Passioura (1972) discussed the configuration, i.e., branching patterns and depth of rooting, in relation to water and mineral absorption and plant success in competition. The data of Newman and Andrews (1973) indicate that at high densities wheat roots compete with each other for potassium; they probably also compete for water. In their experiments the distance between roots ranged from 4 to 1.5 mm at root length densities of 4 to 16 cm/1 cm³ of soil.

Natural selection probably favored survival of plants with large root systems because they are most likely to survive occasional severe droughts. They also are more likely to encounter the nutrients that are distributed irregularly in many soils. This probably resulted in evolution of root systems that are larger than necessary for most cultivated crop plants in humid regions. It therefore seems probable that plant breeders should consider the possibility that selection for smaller root systems would be practical for crops grown in fertile soil in regions with dependable rainfall or with irrigation. According to O'Toole and Bland (1987) the extensive genotypic variation in root systems of various crop plants provides opportunities for selecting root systems with characteristics suitable for special situations.

**Environmental factors affecting growth**

Root growth is greatly affected by environmental factors such as soil texture and structure, aeration; moisture, temperature, pH, salinity, the presence of toxic elements such as Al, lead and copper, competition with other plants and the presence of bacteria, fungi and soil inhabiting animals such as nematodes. Root growth often is inhibited by soil resistant to root penetration; by deficient aeration, low pH, or an excess of toxic elements such as aluminum; and by competition with other roots. Roots of a few species of plants produce substances toxic to other plants (allelopathy), and growth sometimes is retarded when orchards and vineyards are replanted to the same species. Small containers that restrict root growth often inhibit shoot growth, even when well watered and fertilized. In conclusion, conditions
favorable for root growth are just as important to the success of plants as conditions favorable for shoot growth.

**Mixed and intercropping**

**Mixed cropping**

It is the process of growing two or more crops together in the same piece of land. This system of cropping is practiced in areas where climatic hazards such as flood, drought, frost etc are frequent and common. The farmers always fear that their crops will fail. Mixed cropping is also practiced with a view to achieve multiple requirements of food and fibre. Farmers generally sow sarson on the borders of wheat fields to harvest sarson for greens during the initial stages. Under mixed cropping, the time of sowing of all the crops is almost the same. However, they may mature either together (wheat + gram, wheat + barley or wheat + mustard) or they may mature at different times (arhar + Jowar, til + mung or bajra + ground nut).

Based method of sowing mixed cropping can be classified into the following groups:

1. **Mixed crops** – In this case, the seeds of different crops are mixed together and then sown either in lines or they are broadcasted. The system is not scientific and it causes problems in performing all the agricultural operations and harvesting of the crops.
2. **Companion crops** – Under this method the seeds of different crops are not mixed together but different crops are sown in different rows i.e. between two rows of mustard five to eight rows of wheat or between two rows of arhar two-three rows of groundnut are sown. This method of sowing facilitates in weeding, interculture, plant protection operation and even in harvesting.
3. **Guard crops** – Under this system of cropping, the main crops is grown in the centre, surrounding by hardy or thorny crops such as safflower around pea or wheat, mesta (patsan) around sugarcane, jowar around maize etc with a view to provide protection to the main crop.
4. **Augmenting crops** – When sub crops are sown to supplement the yield of the main crop, the sub crops are called as augmenting crops such as Japanese mustard with berseem. Here the mustard helps in getting higher tonnage of fodder in spite of the fact that berseem gives poor yield in fist cutting.

**Principles of mixed cropping**

The most important point is the selection of crops. Crops which compete with each other should not be chosen. The following points should be considered while selecting crops.

1. Legumes should be sown with non-legumes (arhar with jowar and gram with wheat).
2. Tall growing crops should be sown with short growing crops (maize with soybean/mung/mash)
3. Deep rooted crops (tap rooted crops) with shallow rooted crops (adventitious crops)
4. Bushy crops with erect growing crops
5 Crops being attacked with similar insects, pests and diseases should not be sown together.
6 Mixture should consist of short and long duration crops.

**Advantage of mixed cropping**

Mixed cropping has the following advantages

1 All crops do not fail under adverse climate conditions e.g. frost kills only legume, floods kill only dicot plants and drought kills the monocot plants or shallow rooted crops. Thus, the farmer gets some crop instead of losing the entire crop.
2 An epidemic attack of any insect, pest or disease kills only one crop without affecting the rest of the crops.
3 The farmers grow different crops which fulfil their daily need or demand for cereals, pulses and oilseeds.
4 Mixed cropping checks soil erosion, weeds etc.
5 It improves or maintains the soil fertility.
6 Family labour and cattle are employed throughout the whole year.
7 Legume and non-legume mixture increase the fodder quantity and quality both.
8 It reduces cost of cultivation.

**Intercropping**

This is the process of growing subsidiary crops between two widely spaced rows of main crop. The main objective of this type of cropping is to utilize the space left between two rows of main crop and to produce more grain per unit area. Intercropping has long been practiced by small scale farmers. In particular, cereal and legume intercropping is recognized as a common cropping system in developing tropical countries (Ofori and Stern, 1987). Typically, C4 cereal crops such as maize (*Zea mays* L.), pearl millet (*Pennisetum glaucum* (L.) R.Br.) and sorghum (*Sorghum bicolor* (L.) Moench) are the dominant plant species, whereas *C₃* legume crops such as beans (*Phaseolus vulgaris* L.), cowpea (*Vigna unguiculata* (L.) Walp.), groundnut (*Arachis hypogaea* L.), pigeonpea (*Cajanus cajan* (L.) Millsp.) and soybean (*Glycine max* (L.) Merr.) are the associated or secondary species. Canopy structures and rooting systems of cereal crops are generally different from those of legume crops. In most cereal–legume intercropping, cereal crops form higher canopy structures than legume crops, and the roots of cereal crops grow to a greater depth than those of legume crops. This suggests that the component crops probably have differing spatial and temporal use of environmental resources. Intercrops may make use of environmental resources such as radiation, water and nutrients more efficiently than monocrops (Willey, 1990).

Crop productivity mainly depends on the amount of radiation intercepted by crops when other factors, such as water, nutrients, disease and weeds, are not limiting (Loomis and Williams, 1963). Many studies have shown a positive correlation of crop production to the amount of radiant energy intercepted by the crop (Monteith, 1977; Tsubo et al., 2001). Compared with sole cropping, intercropping has greater radiation capture potential and utilisation because of the effect of combination of differing spatio-temporal use of radiation among component crops (Willey, 1990).
Agronomic considerations for inter-cropping system are different due to inclusion of more than one crop as in intercropping. Thus, principles involved in management of intercropping system are different.

**Principles of intercropping**

- The crops grown in association should have complementary effects rather competitive effects.
- The subsidiary crop should be of shorter duration and of faster growing habits to utilize the early slow growing period of main crop and they must be harvested when main crop starts growing. Faster sesamum, sawan, urd or ming grown with red gram picks up branching and attains rapid growth. Autumn planted sugarcane remains dormant after germination until February during which potato, berseem, lucerne, mustard could be taken successfully as companion intercrops. Cotton could be intercropped with onion, green or blackgram; and chillies and tomato could be intercropped with onion.
- Component crops should have similar agronomic practices.
- Erect growing crops should be intercropped with cover crops like pulses. These check the weeds and reduce soil erosion. The losses of water due to evaporation are also reduced.
- The component crops should have different root depths. This will minimize competition for nutrients, water and root respiration.
- A standard plant population of main crop should be maintained whereas that of subsidiary crops the plant population could increased or decreased as per demand of the situation.
- The planting method and management should be simple, less time consuming, less cumbrousive, economical and profitable so that it may have wider adoptability.
- Component crops of similar pests and disease pathogens and parasite infestations should not be chosen.

**Types of intercropping**

i) **Parallel Cropping:** Under this cropping two crops are selected which have different growth habits and have a zero competition between each other and both of them express their full yield potential. e.g. 1) Green gram or black gram with maize 2) Green gram or soybean with cotton.

ii) **Companion Cropping:** In companion cropping the yield of one crop is not affected by other. In other words, the yield of both the crops is equal to their pure crops. That the standard plant population of both crops is maintained. e.g.1) Mustard, wheat, potato, etc. with sugarcane 2) Wheat, radish, cabbage, sugar beat etc., with potato.

iii) **Strip Inter-cropping:** Growing two or more crops simultaneously in different strips wide enough to permit independent cultivation but narrow enough for the crops to interact ergonomically.
iv) **Relay inter-cropping:** Growing two or more crops simultaneously during part of the life cycle of each. A second crop is planted after the first crop has reached its reproductive stage but before it is ready for harvest.

v) **Multistoried Cropping or Multi-tire cropping:** Growing plants of different height in the same field at the same time is termed as multistoried cropping. It is mostly practiced in orchards and plantation crops for maximum use of solar energy even under high planting density. e.g. 1) Eucalyptus + Papaya + Berseem, 2) Sometimes it is practiced under field crops such as Sugarcane + Potato + Onion 3) Sugarcane + Mustard + Potato 4) Coconut + Pineapple + Turmeric/Ginger.

**Multi-tire Cropping:** Inter-cropping is mostly prevalent in plantation crops like coconut and areca nut. The practice different crops of varying heights, rooting pattern and duration are called multi-tire cropping. The objective of this system of cropping is to utilize the vertical space more effectively. In this system, the tallest components have foliage tolerant of strong light and high evaporative demand and the shorter component(s) with foliage requiring shade and or relatively high humidity. e.g. Coconut + black pepper + cocoa + pineapple.

The multi-tire cropping plan is shown in Fig. 42. below. In this system, coconut is planted with a spacing of 7.5 m. Rooted cutting of black pepper are planted on either side of coconut about 75 cm away from the base. On the coconut trunk at a height of about one meter from the ground level, the vines of pepper are trailed. A single row of cacao is planted at the center of space between coconut rows. Pineapple is planted in the inter-space. Coconut growing to a height of more than 10 m. Cacao with its pruned canopy of about 2.5 m height and pineapple growing to about 1 m height form the first and ground floors, respectively.

In another multi-tier system in coconut, ginger or turmeric and partial shade loving vegetables form the first tier, banana is second tier, pepper in third tier and coconut or arecanut in the final tier.
In the arecanut plantation, tuber crops are predominantly intercropped. Elephant yam, tapioca, greater yam and sweet potato are common inter-crops in humid tropics. Banana and pineapple also cultivated as intercrops in arecanut gardens.

In coffee based multi-tier cropping systems, first tier is with pineapple, second tier with coffee, third tier with cacao/mandarin orange and final tier with fast growing shade trees necessary for coffee plantation.

Management of Intercropping Systems

In intercropping system crops are grown simultaneously. Management practices aim to provide favorable environment to all the components, exploit favorable interaction among the component crops and minimize competition among the components.

a. **Seedbed Preparation:** The objective of land preparation is to establish an ideal zone for the seedling that minimizes the stress. Potential stress condition include inadequate or excess moisture, unfavorable temperature for a given species, soil crusting, weeds, residue of preceding crop and insect or pathogen attack. Important of seedbed is the same in both conventional (monoculture) and in multiple cropping. Seedbed preparation depends on the crop. Deep rooted crops responds to deep ploughing while for most of cereal shallow tillage is sufficient. The crops with small seed require fine seedbed, cotton, and maize, planted on ridges, certain crops on flat seedbed. Since more than one crop is planted in intercropping, the seedbed is generally prepared as per the needs of base crop. Sugarcane planted in furrow and intercrop sown on ridges. In Groundnut + red gram intercropping system, flat seedbed is prepared for sowing crops. However, ICRISAT is recommending broad bed and furrow for black soils. In rice + maize intercropping system, ridges and trenches are formed. Maize is planted on ridges and rice in trenches.

b. **Varieties:** The varieties of component crop in intercropping system should be less competitive with the base crop and peak nutrient demand period should be different from the base crop. Minimum difference between the maturity periods of two components should be of 30 days. Hybrids varieties of sorghum like CSH - 6, CSH - 9 are suitable for intercropping with long duration variety of red gram like C11 and LRG 30 because of wider gap between maturity periods. The varieties selected for intercrop should have thin leaves, tolerant to shading and less branching. If the base crop is shorter than intercrop, the intercrop should be compact with erect branching and its early growth should be slow. The characteristics of the base crop should be as in sole crop.

c. **Sowing:** Practices of sowing are slightly altered to accommodate inter - crop in such a way that it cause less competition to the base crop. Widening inter row spacing of cereal component to accommodate more rows of component legume crop improves legume yield and efficiency of the intercrop system. Sowing of base crop is done either as paired row, paired – wider row or skip row of base crop are brought close by reducing inter row spacing. The spacing between two pairs of rows is increased to accommodate the inter crop. Such row arrangement of base crops within the rows improves the amount of light transmitted to the lower component crop, which can enhance legume yield in cereal + legume intercropping system. For example – the normal row spacing in Rainfed cultivation is 30 cm. The row spacing is reduced to 20 cm between paired rows and 50 cm spacing in two pairs. The spacing in paired row planting designed as 20/50 cm indicates that the spacing between two rows in pairs is 20 cm and among the pairs 50 cm. Similarly, pearl millet is planted with row spacing 30/60 cm in paired row planting. These
changes in crop geometry do not alter the yield of base crop, but intercrops are benefited to some extent. When alternating pairs of sorghum rows 90 cm with two rows of an associated legume, Singh (1972) found that LER was greater compared at 60 cm between rows with two rows of the legume in between. Planting in fixed ratio of intercrop is most common. The intercropping system of groundnut + red gram is either in 5:1 or 7:1 ratio and sorghum + red gram in 2:1 ratio. In these cases the normal three tined or four tined seed drill can be used without any modification. The hole(s) pertaining to intercrop row in the hopper(s) are closed with a piece of cloth in that row, intercrop is sown with alkali or kera. For higher yields, base crop population is maintained at its sole crop population and intercrop population is kept at 80 percent of its sole crop population. Relative sowing time of component crop is important management variable manipulated in cereal + legume intercropping system but has not been extensively studied. Sowing may be staggered to increase the temporal difference, which might result in higher yield advantage (Singh et al. 1981).

d. **Fertilizer Application:** The nutrient uptake is generally more in intercropping system compared to pure crops. When the legume is associated with a cereal crop in intercropping system, legume supplement a portion of nitrogen required of cereal crop; the amount may be of 20 kg/ha by legumes. Application of higher dose of nitrogen to the cereal + legume intercropping system not only reduce the nitrogen fixation capacity of legumes, but also growth of the legume is suppressed by aggressive fast growth of cereals. Cereal + legume intercropping, therefore is mainly advantageous under low fertilizer application. Considering all the factors, it is suggested that the nitrogen dose recommended for base crop as pure crop is sufficient for intercropping system with cereal + legume or legume + legume. With regards to phosphorus and potassium, one eighth to one fourth of the recommended dose of intercrop is also added in addition to recommended dose of base crops to meet the extra demand. Basal dose of nitrogen is applied to rows of both components in cereal + legume intercrop. Top dressing of nitrogen is done only in cereal rows. P & K are applied as basal dose to both crops.

e. **Water Requirement:** The technique of water management is the same for sole cropping and intercropping or sequential cropping. However, the presence of an additional crop may have an important effect on evapo-transpiration. With proper water management, it is possible to grow two crops where normally only one crop is raised under rain fed condition. Intercropping system is generally recommended for rain fed situations to get the stable yields. The total water requirement of intercrop does not increase much compared to sole cropping. At ICRISAT, the water requirement of sole sorghum and intercropping with red gram was almost similar (584 and 585 mm, respectively). However in a more competitive crop like onion as intercropped in groundnut increase the total water requirement by about 50 mm. The total water used in intercropping system is almost same as in sole crops, but yields are increased. Thus water use efficiency of intercropping is higher than sole crops.

Scheduling of water: If one of the crop is irrigated based on its requirement, the other crop may suffer due to excess water stress, sometimes leading to total failure of crop. In cotton + black gram intercropping system, cotton is irrigated once in 15-20 days. The intercrop black gram is often affected by excess water and gives poor yield. In such situations, skip furrow method of irrigation is advocated. Scheduling irrigation at IW/CPE ratio of 0.60 to 0.80 or irrigation at one bar soil moisture tension is suitable for most of the systems.

f. **Weed Management:** Generally it is believed that intensive cropping reduces weed problems. Weed infestation depends on the crop, plant density and cultural operation done. Weed problems is less in intercropping system compared to the sole crops. This is due to complete crop cover
because of high plant density in intercropping which cause severe competition with weeds and reduce weed growth. The weed suppressing ability of intercrop is dependent upon the component crops selected, genotype used, plant density adopted, proportion of component crops, their spatial arrangement and fertility moisture status of the soil. Experiment carried out at ICRISAT, Hyderabad, indicated that there was 50 - 75 % reduction in weed infestation by intercropping. Pigeon pea + sorghum intercropping system, which is extensively practiced in Karnataka, M.S and A.P is known to reduce weed intensity. The higher plant population and complete covering of the soil earlier in intercropping system reduce weed infestation. In late maturing crops that are planted in wide rows, presence of early maturing crops helps to cover the maturing crops that are planted at wide rows. Presence of early maturing crops helps to cover the vacant inter-row space and keeps weed under check. Quick growing non- competitive, compact legumes like green gram and black gram act as another crop due to their good canopy coverage. In certain situations, intercrops are used as biological agents to control weeds. Black gram, green gram, cow pea in sorghum and cowpea in banana reduce weed population. One hand weeding can be avoided by this method. However, in some intercropping systems like maize + groundnut, rice + tapioca, maize + tapioca, weed problem is similar to their sole crops. The growth habit of genotype used in intercropping has a great influence on weed growth. Weed infestation in intercropping is influenced by early growth and competitive additives of the component crops. If one or both the component crops are vigorous and cover the land area rapidly, weed infestation is greatly reduced. Early crop canopy to cover the soil is more important than rapid increase in plant height. It is well known that, different species of weeds are associated with different crops, but weeds present in sole crops are different than those present in intercropping system. At Hyderabad, in pearl millet as sole crop mixed weed flora was observed as Celosia, Digitaria and Cupreous in sole crop of groundnut. In pearl millet + groundnut intercropping system type of weeds changes with proportion of component crops. As more rows of groundnut are introduced in place of pearl millet of rows, there is a striking increase in both numbers and biomass of the tall and competitive Celosia, especially in groundnut rows. Weed problem is less; weed control is necessary in intercropping system. But labour required for weeding is less; second weeding is not necessary because of crop coverage and limited weed growth. Normally two hand weeding are required, but it may restrict to one hand weeding under intercropping in sorghum + red gram or sorghum + cowpea. Just one weeding is sufficient to get high yield as in weed-free check. The critical period of weed free condition may be extended a little longer in intercropping than in sole cropping. This is because the critical growth stages of the component crops vary temporally in intercropping. For example, critical weed free period has to be extended to first 7 weeks in sorghum + red gram intercropping while sole sorghum crop requires only 2- 4 weeks weed free period.

Chemical weed control is difficult in intercropping system because the herbicide may be selective to one crop but non-selective to another. Atrazine control weeds in sole sorghum, but it is not suitable for sorghum + red gram intercropping system, as it is toxic to red gram. Herbicides suitable for intercropping systems as-

* Maize + green gram & Maize + cowpea. Alachlor (pre-emergence) (Lasso)
* Sorghum + pulse – fluchloralin (PPI) (Basalin) or Alachlor (pre-emergence) (Lasso)
* Sorghum + red gram – prometryne (pre-emergence)
* Sugarcane + groundnut – nitrofen (pre-emergence) (TOK E -25).
g. **Pest and Disease in Intercropping System:** Pest and diseases are believed to be less in intercropping system due to crop diversity than sole crops. Some plant combination may enhance soil fungicide and antibiotics through indirect effects on soil organic matter content. The spread of the diseases is altered by the presence of different crops. Little leaf of Brinjal is less when Brinjal is sheltered by maize or sorghum, as the insect-carrying virus first attacks maize or sorghum; virus infestation is less on Brinjal. Non-host plant in mixtures may emit chemicals or odor that affects the pests, thereby protecting host plants. The concept of crop diversification for the management of nematode population has been applied mainly in the form of decoy and trap crops. Decoy crops are non-host crops, which are planted to make nematode waste their infection potential. This is affected by activating larva of nematode in the absence of hosts by the decoy crops.

<table>
<thead>
<tr>
<th>Crop</th>
<th>Nematode</th>
<th>Decoy crops</th>
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<tbody>
<tr>
<td>Brinjal</td>
<td>Meloidogyne incognita</td>
<td>Sesamum orientale</td>
</tr>
<tr>
<td>Tomato</td>
<td>Meloidogyne pratylenchus alleni</td>
<td>Caster, groundnut</td>
</tr>
<tr>
<td>Soybean</td>
<td>Pratylenchus sp</td>
<td>Crotalarias spectabills</td>
</tr>
</tbody>
</table>

Trap crops are host crops sown to attract nematode but destined to be harvested or destroyed before the nematode manage to hatch. This is advocated for cyst nematode. The technique involves is sowing in pineapple plantations; tomatoes are planted and ploughed in to reduce root knot nematodes. There is also evidence that, some plants adversely affect nematode population through toxic action. Marigold reduces the population of *Pratylenchus* species.

**Mixed versus intercropping**

Intercrops differ from mixed crops in the following ways

<table>
<thead>
<tr>
<th>SN</th>
<th>Intercrop</th>
<th>Mixed crop</th>
</tr>
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<tbody>
<tr>
<td>1</td>
<td>The main objective to to utilize the space left between two rows of main crop especially during early growth period of main crop.</td>
<td>The main objective is to get atleast one crop under any climate hazards (flood, drought or frost occurrence)</td>
</tr>
<tr>
<td>2</td>
<td>More emphasis is given to care ain crop and subsidiary crops are not grown at the cost of the main crop. Thus there is no competition.</td>
<td>Here all the crops are equal and there is no main or subsidiary crop.</td>
</tr>
<tr>
<td>3</td>
<td>Subsidiary crops are of short duration and they are harvested much earlier than the main crop.</td>
<td>The crops are almost of the same duration.</td>
</tr>
<tr>
<td>4</td>
<td>Both the crops are sown in rows. The sowing time may be the same or the main crop is sown earlier than the subsidiary crop.</td>
<td>The crops may be broadcasted or sown in row but the sowing time for all the crops is the same.</td>
</tr>
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</table>

**Advantage of intercropping**

It offers similar benefits to that from rotational cropping. The nutrients from different layers of the soil are evenly used. A cereal + legume mixture is beneficial because of an efficient
fixation of atmospheric N into the soil. Leaf shedding and their subsequent decomposition reduces the chances of micro-nutrient deficiency in shallow or surface rooted crops like cereals as the legumes absorb such nutrients from lower layer and return them to the surface soil through shedding of leaves and decomposition. Total biomass production/unit area/time is increased because of fullest use of land as the inter-row space will be utilized which otherwise would have been used for weed growth. The farmer gets all his required agriculture commodities from a limited space. Thus the profit/unit area becomes higher. The fodder value becomes higher when a legume is intercropped with a non-legume e.i. Napier + cowpea – Napier + beerseem. It offers best employment and utilization of labour, machine and power throughout year.

**Mechanism of yield advantage in intercropping**

The most important index of biological advantage is the relative yield total (RYT) introduced by De wit or Land van Den Bergh (1965) or land equivalent ratio by Willey (1979).

1. The mixture yield of a component crop expressed as a portion of its yields as a sole crop from the same replacement series is the relative yields of the crop and sum of relative yields of component crop is called Relative yield total (RYT).
2. The total land area required under sole cropping to give the same yields obtained in the intercropping is called Land equivalent ratio (LER). Both the expressions (RYT and LER) are similar.

**Land Equivalent Ratio (LER):**

This is the most frequently used efficient indicator. LER can be defined as the relative land area under sole crop that would be required to produce the equivalent yield under a mixed or an intercropping system at the same level of management.

\[
LER = L_a + L_b = \frac{Y_{ab}}{Y_{aa}} + \frac{Y_{ba}}{Y_{bb}}
\]

Where, \(L_a\) and \(L_b\) are LER of crop a and crop b, respectively; \(Y_{ab}\) = yield of crop an in intercropping, \(Y_{ba}\) = yield of crop b in intercropping, \(Y_{aa}\) = yield of crop an in pure stand and \(Y_{bb}\) = yield of crop b in pure stand.

LER of more than 1 indicates yield advantage, equal to 1 indicates no grain or no gain or no loss and less than 1 indicates yield loss. It can be used both for replacement and additives series of intercropping.

LER is the summation of ratios of yields of intercrop to the yield of sole crop.

LER gives a better picture of the competitive abilities of the component crops. It also gives actual yield advantage of intercropping. In other words LER is the measure of production efficiency of different system by convening the production in terms of land acreage. LER gives an accurate assessment of the biological efficiency of intercropping.
Example: Let the yields of groundnut and red gram grown, as pure crops are 1,200 and 1,000 kg/ha, respectively. Let yields of these crops when grown, as intercrop be 1,000 and 600 kg/ha, respectively. The land equivalent ratio of groundnut + red gram intercropping system is

\[
\text{LER of groundnut} = \frac{\text{Yield of intercrop}}{\text{Yield of sole crop}} = \frac{1000}{1200}
\]

\[
\text{LER of red gram} = \frac{\text{Yield of intercrop}}{\text{Yield of sole crop}} = \frac{600}{1000}
\]

\[
\text{LER of system} = \frac{1000}{1200} + \frac{600}{1000} = 1.43
\]

LER of 143 indicates that a 43 percent yields advantage is obtained when grown as intercrop compared to growing as sole crops. In other words the sole crops have to be grown in 1.43 ha to get the same yields level that is obtained from 1.00 ha of intercropping.

Relative Yields Total (RYT):

The mixture yields of a component crop expressed as a portion of its yields as a sole crop from the same replacement series is the relative yield of crop and sum of the relative yields of component crop is called Relative Yields Total (RYT). Or When LER is compared at uniform overall plant density of sole and intercrops then it is known as RYT. In RYT yields advantages is to measure not only unit area, but also on unit population. This is mainly used for replacement series.

\[
\text{RYT} = \frac{Y_{ab}}{Y_{aa}} + \frac{Y_{ba}}{Y_{bb}}
\]

Where \( Y_{aa} \) = yields of component a as sole crop \( Y_{bb} \) = yields of component b is a sole crop \( Y_{ab} \) = yields of component a as intercrop in b \( Y_{ba} \) = Yield of component b as intercrop in a.

Example: in pasture mixture, Stylo and anjan grown in 1:1 ratio with 50% sole crop population of both crops. In I/C, mixture yield (50%) for Stylo and anjan is 6 and 4 tons/ha of fodder, respectively. The yield of these crops in sole stand with 100% plant population is 10 and 8 ha of green fodder, respectively.

\[
\text{RYT} = \frac{12+8}{10+8} = \frac{20}{18} = 1.11
\]

So RYT 1.11 indicates 11% extra fodder yields obtained by mixture.

Two crops yields in the intercrop mixture are MA and MB and the yield of crops grown as pure crop are SA and SB then the combined index is
The intercrop embodied in LER is that L represents the land required for sole crops to reduce yields achieved in the intercropping mixture. A value of L greater than (1) indicates overall biological advantages of intercropping. The two component of total index LA and LB represent the efficiency of yields production of each crop when grow in mixture, relative to crop performance.

**Relative Crowding Coefficient (K or RCC):** It is proposed by de Wit (1960). It is used in replacement series of intercropping. It indicates whether a species or crop when grown in mixed population has produced more or less yield than expected in pure stand. In 50:50 mixture Relative crowding coefficient can be defined as

\[ K_{ab} = \frac{\text{Mixture yield of } a}{\text{Pure yield of } a - \text{mixture yield of } a} = \frac{Y_{ab}}{Y_{aa} + Y_{ab}} \]

But when population differ from 50:50 then,

\[ K_{ab} = \frac{Y_{ab} \cdot Z_{ba}}{(Y_{aa} - Y_{ab})Z_{ab}} \]

Where, K = coefficient of each crop species  
Yaa = Yield of pure stand of a  
Ybb = Yield of pure stand of b  
Yab = Mixture yield of a in combination with b  
Yba = Mixture yield of b in combination with a  
Zab = Sown proportion of a in mixture with b  
Zba = Sown proportion of b in mixture with a  
Kab = Values indicate the following conclusions:  
K>1 = there is yield disadvantage  
K=1 = there is no difference  
K<1 = there is yield advantage in mixing

Crowding coefficient and LER give the yield advantage but only LER give the magnitude of advantage. Therefore LER is preferred to assess the competition effects and yield advantage in intercropping situations.

The two main indices of dominance are the aggressivity and competition index. Aggressivity is proposed by Mc Gihrist (1965). It gives a simple measure of how much the relative yield increase in species A is greater than that for species B. It is an index of dominance.

\[ A_{ab} = \frac{\text{mixture yield of } a}{\text{Expected yield of } a} - \frac{\text{mixture yield of } b}{\text{Expected yield of } b} = \frac{Y_{ab}}{Y_{aa} \cdot Z_{ab}} - \frac{Y_{ba}}{Y_{bb} \cdot Z_{ba}} \]
Sown proportion of species A and B are represented of ZA and ZB, respectively. An aggressively value Zero indicates that the component species are equally competitive. A positive sign indicates the dominant species and a negative sign the dominated.

The basic process in the competition index is the calculation of two equivalence factors, one each component species. It is the product of two equivalent factors, one for each component species. It is a measure to find out the yield of various crops when grown together as well as separately. It indicates the yield per plant of different crops in mixture and their respective pure stand on an unit area basis. If the yield of any crop grown together is less than its respective yield in pure stand then it is harmful association but an increased yield means positive benefit. CI is proposed by Donald (1963).

\[
CI = \frac{(Y_{aa} - Y_{ab}) \times (Y_{bb} - Y_{ba})}{Y_{aa} \times Y_{ab}}
\]

**Effective Land Equivalent Ratio (ELER):** Mead and Willey (1980) showed that any required ratio could be achieved by growing the intercrop of the land area and one of sole crops the remainder.

\[
P = \frac{(La + E)}{(LER + E)}
\]

LER is a measure of the net advantages from the combined intercrop determined by adding the crop and sole crop relative yields.

\[
ELER = \frac{Lb}{((1 - La) + (LER - 1)P)}
\]

**Staple Land Equivalent Ratio (SLER):** In situation, where the primary objective is to produce yields of one component (staple crop) usually a cereal and some yields of the legume, the concept of SLER is composed.

\[
SLER = \frac{MDA}{SA} + P\left(\frac{MB}{SB}\right)
\]

Where, MDA is derived yield of A in mixture yield and P, the proportion of land devoted for intercropping. The two crop yields in the intercrop mixture are MA and MB and yield of crops grown as sole crop are SA and SB.

**Land Equivalent Coefficient (LEC):**

It was proposed by Adetilaye and Ezedinma (1986) the product of ler of intercrop components.

\[
LEC = \frac{MA \times MB}{SB \times SB}
\]

It can therefore, be regarded as a measure of association or interaction when crop with the strength of relationship for a two crop mixture the minimum expected product by yield advantage is obtained and
LEC greater than 0.25 (25%). This was obtained from the 50:50 yields where inter-specific competition equaled intra-specific competition.

\[ \text{LEC} = \text{La} \times \text{LB} = 0.5 \times 0.5 = 0.25. \]

The LEC is developed to assess the interaction and potential of crop mixture. It is derived from the understanding that in intercrop yields, as compared to optimum sole crop yield is due to competition assuming that the inter competition is absent.

**Area Harvest Equivalency Ratio (AHER):**

This was proposed by Bal Subramanian and Sekayange (1990). It indicates resource efficiency. The concept of AHER combines the area time factors in a practical sense quantifying intercrop yield advantage particularly in multi-season.

**Crop Performance Ratio and Its Types**

It is defined as the productivity of an intercrop per unit area of ground compared to what was expected from sole crops sown in the same proportions (Azam Ali et al 1990). For each same then productivity in the intercrop can be expressed as a partial CPR.
## Unit – III

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Competitive relationship and competition functions

**Competition** in biology, ecology, and sociology, is a contest between organisms, animals, individuals, groups, etc., for territory, a niche, or a location of resources, for resources and goods, mates, for prestige, recognition, awards, or group or social status, for leadership. It is opposite to cooperation. It arises whenever at least two parties strive for a goal which cannot be shared or which is desired individually but not in sharing and cooperation. Competition occurs naturally between living organisms which co-exist in the same environment. For example, animals compete over water supplies, food, mates, and other biological resources. Humans compete usually for food and mates, though when these needs are met deep rivalries often arise over the pursuit of wealth, prestige, and fame. Competition is also a major tenet in market economy and business is often associated with competition as most companies are in competition with at least one other firm over the same group of customers, and also competition inside a company is usually stimulated for meeting and reaching higher quality of services or products that the company produces or develops.

Competition occurs in virtually every ecosystem in nature. This type of relationship develops when more than one organism in an environment requires the same thing in order to survive. When food and shelter are plentiful, there is no competition. It only takes place when there is not enough to go around. Competition often results in the survival of the fittest.

Competition within, between, and among species is one of the most important forces in biology, especially in the field of ecology. Competition between members of a species ("intraspecific") for resources such as food, water, territory, and sunlight may result in an increase in the frequency of a variant of the species best suited for survival and reproduction until its fixation within a population. Competition is also present between species ("interspecific"). When resources are limited, several species may depend on these resources. Thus, each of the species competes with the others to gain access to the resources. As a result, species less suited to compete for the resources may die out unless they adapt by character dislocation, for instance. As per evolutionary theory, competition within and between species for resources plays a significant role in natural selection. At shorter time scales, competition is also one of the most important factors controlling diversity in ecological communities, particularly in plant communities where asymmetric competition and competitive dominance frequently occur.

**Intraspecific**

Competition often occurs between members of the same species. This is known as intraspecific competition. It is a common type of competition because animals of the same species often live in great numbers in a particular area. These individuals compete for limited resources like food, shelter and mates.

This type of competition acts to keep the population under control. If there is a limited amount of food to go around, the environment can only feed certain individuals of the same species. This results in the survival of those most capable of competing and winning. Similar regulation occurs when individuals compete over shelter, especially dens necessary for
Interspecific competition occurs when members of more than one species compete for the same resource. For example, woodpeckers and squirrels compete for nesting rights in the same holes and spaces in trees, while the lions and cheetahs of the African savanna compete for the same antelope and gazelle prey.

Even though individual animals are competing for the same shelter or food, interspecific competition is usually less critical than intraspecific competition. For example, the antelope is not the lion's only prey. Because of this, the lion can choose whether to compete for antelope or to look elsewhere. Animals of different species typically compete with each other only for food, water and shelter. However, they may compete with members of their own species for mates and territory as well.

Competition Among Plants

Plants also compete for space, nutrients and resources such as water and sunlight. This competition can shape the appearance of the ecosystem. For example, the floor of a deciduous forest is not as full of plant life as might be thought. The taller trees shield the forest understory from sunlight, making it possible for the growth of mainly shade-tolerant plants. The life cycles of some plants are also impacted because many shorter plants flower and bear seeds before the leaves of the taller trees are fully developed, which makes it possible for shorter plants to receive sunlight.

Desert plants have developed shallow, far-reaching roots systems in order to successfully compete for valuable water resources, which is an example of how competition can affect the evolution of a species.

Evolutionary Specification

Competitive relationships are thought to be at least partially responsible for the evolutionary process. In natural selection, the individuals of a species that are best adapted to the environment around them survive to reproduce and pass on the genetics that make them well adapted. This can be seen in the development of the giraffe when the giraffe competes with other grazing herbivores such as zebras and antelope for food. Giraffes with longer necks are able to reach the leaves of high tree branches, giving them access to more food and a better chance of passing their genetics on to their offspring.

Exploitative competition, which is the use of resources that make it impossible for others to use them, can result in the extinction of a species or an evolution that allows that species to find another route of survival. This can include finding another food source or adapting nests to suit another type of shelter.

Ideas about how plant competition varies with productivity are rooted in classic theories that predict either increasing (Grime) or invariant (Tilman) competition with increasing productivity. Both predictions have received experimental support, although a decade-old meta-analysis supports neither. Attempts to reconcile the conflicting predictions and evidence
include: expanding the theory to include other conditions (e.g. stress gradient hypothesis), development of indices to differentiate either the ‘intensity’ or ‘importance’ of competition, a focus on resource supply and demand, and explicit recognition that both growth and survival may exhibit different relationships with productivity. To determine which of these theories accurately predict how competition varies with productivity within a native grassland site, competitive intensity and relative competitive importance using 22 species across the range of productivity naturally occurring within that site were estimated. Plant performance was measured as survival and size with and without neighbours and the local environment was quantified according to variability in standing crop, gross water supply, and net water supply. On average, neighbours weakly facilitated seedling survival, but strongly reduced seedling growth. For seedling survival and growth, relative competitive importance and competitive intensity declined with some measure of productivity; neighbour effects on survival declined with standing crop, while effects on growth declined with gross water supply. These results add to the growing evidence that plant-plant interactions vary among life history components with different life history components contingent upon separate environmental factors. Although the range of productivity measured in this study was not large, the results do not support the theories of Grime or Tilman. However, the results are consistent with the meta-analysis and parts of other theories, although no single theory is capable of explaining the entirety of these results. This suggests that, at least in moderately productive grasslands, new theory needs to be developed [Bennett and Cahill 2012].

Ecological model of competition

The ecological model of competition is a reassessment of the nature of competition in the economy. Traditional economics models the economy on the principles of physics (force, equilibrium, inertia, momentum, and linear relationships). This can be seen in the economics lexicon: terms like labour force, market equilibrium, capital flows, and price elasticity. This is probably due to historical coincidence. Classical Newtonian physics was the state of the art in science when Adam Smith was formulating the first principles of economics in the 18th century.

According to the ecological model, it is more appropriate to model the economy on biology (growth, change, death, evolution, survival of the fittest, complex inter-relationships, non-linear relationships). Businesses operate in a complex environment with interlinked sets of determinants. Companies co-evolve: they influence, and are influenced by, competitors, customers, governments, investors, suppliers, unions, distributors, banks, and others. We should look at this business environment as a business ecosystem that both sustains, and threatens the firm. A company that is not well matched to its environment might not survive. Companies that are able to develop a successful business model and turn a core competency into a sustainable competitive advantage will thrive and grow. Very successful firms may come to dominate their industry (referred to as category killers).

In a weed infested crop field it is possible to identify different components of the overall competitive effect:
- intraspecific competition between plants of the cultivated species;
- interspecific competition between plants of the cultivated species and weed species;
• interspecific competition between plants of the different weed species;
• intraspecific competition between plants of the same weed species.

Many empirical models have been developed to describe, and possibly predict, the effect of weeds in crops, many of which are based on the relationship between crop yield loss and weed density (Cousens, 1985b). In an attempt to solve the problems linked to predicting yield loss in relation to weed time of emergence, alternative models have been proposed based on the relative leaf area of the weeds and crop.

**Prediction of yield loss on the basis of weed density**

The model most widely used to describe the yield loss depending on the weed density is based on the rectangular hyperbola model (Cousens, 1985a):

\[ Y_L = \frac{iD}{1 + \frac{iD}{a}} \]

(1)

where \( Y_L \) is the relative yield loss, \( D \) is the weed density, \( i \) is a parameter that represents the initial slope of the curve and \( a \) represents the maximum yield loss found with a very high weed density (Fig 43).

Both parameters also vary with the crop-weed association as well as with crop density, time of emergence of the weed and crop and soil fertility. The values of \( i \) and \( a \) can therefore be used to compare various crop-weed associations in additive competition experiments (i.e. when the weed is added to a crop sown at a fixed density).

Equation (1) provides the relative yield loss, that cannot be measured directly, but only calculated starting from the yields observed with and without weeds. However, even the measurements taken in weed-free control plots can be affected by experimental error, so equation (1) can be adapted to include \( Y_{WF} \) among the equation parameters:
the third parameter $Y_{WF}$ represents the yield of the weed-free control, which can thus be estimated using all the observed data and not just those from the control plots.

Equations (1) and (2) assume that the weeds emerge contemporarily with the crop, but in practice this does not happen. Cousens et al. (1987) therefore introduced a modification to the above-described model to take into account contemporarily the weed density and relative time of emergence of the crop and weeds:

\[
Y_L = \frac{iD}{e^{c t_e} + \frac{iD}{a}}
\]

where $Y_L$, $D$, $i$ and $a$ have the same meaning as in (1), $t_e$ is the relative time of emergence of the crop and weeds and $c$ is the regression parameter that expresses the variation of the competitiveness of the weeds depending on the delay with which they emerge.

Model (3) is an improvement on (1) as it allows the experimental data to be better described when the emergence is not contemporary with that of the crop, but with very gradual emergences the determination of $t_e$ becomes difficult and time-consuming and the estimate of the parameters arguable. Moreover, the estimate of parameters $i$ and $a$, being dependent also on that of parameter $t_e$, generally show a higher variability over the years and with locations. This drawback can, at least partly, be obviated using the temperature sum instead of days as a ‘biological scale’.

Weed density is the variable most commonly used to explain the variations in crop yield loss. This has clear advantages, such as: a) simplicity of its control in experiments; b) determination in the field is relatively easy and fast. It also shows some disadvantages: a) in the field it is difficult to control the time of emergence of the weeds in relation to that of the crop, particularly when emergence occurs in flushes; b) the models based on it have weak eco-physiological bases.

For these reasons some authors have tried to identify another variable that would at the same time be easy to measure, take into account weed competitiveness determined by different times of emergence of crop and weeds, and be eco-physiologically sound.

Prediction of yield loss based on leaf area or relative weed cover

Kropff and Spitters (1991) proposed a relationship based on the relative leaf area ($L_w$) defined as the ratio between the leaf area index ($LAI$) of the weed and the total LAI of the crop plus weeds:

\[
L_w = \frac{LAI_w}{LAI_c + LAI_w}
\]

where LAI$_w$ and LAI$_c$ are the leaf area index of the weed and crop, respectively. $L_w$ can vary from 0 (absence of weeds) to 1 (leaf cover of the weed alone). The authors, starting with the processes that regulate crop growth and the results of many simulations done with an eco-
physiological competition model, demonstrate that the relative leaf area of the weeds compared to that of the crop at the moment of “row closure” could be a crucial measurement of the competitive process and very well correlated with the final yield loss.

The relationship between relative yield loss $Y_L$ and $L_w$ is expressed by:

$$Y_L = \frac{q L_w}{1 + (q - 1)L_w}$$  \hspace{1cm} (5)

where $q$ is an index of competitiveness typical of a given weed in a crop, called relative damage coefficient.

Kropff et al. (1995) modified equation (5) by inserting a parameter $m$ that represents the maximum damage caused by the weeds (asymptote of the hyperbole):

$$Y_L = \frac{q L_w}{1 + \left(\frac{q}{m} - 1\right)L_w}$$  \hspace{1cm} (6)

Model (6) is comparable to (1) with relative leaf area instead of density.

Considering $L_w$ instead of density takes into account, at least indirectly, that the damage caused by the weeds depends on the relative development of crop and weeds and therefore also their relative time of emergence. A certain value of $L_w$ can be given by a few early-emerging plants or by many late-emerging ones.

The major problem of this approach is the difficulty in measuring $L_w$ quickly and reliably. In fact, the precise measurement of leaf area is possible with destructive sampling of the vegetation (weeds and crop), but this method is neither rapid nor economical. An alternative is a visual survey, with the operator estimating the leaf area ratios between crop and weeds. With adequate training it is probably possible to obtain good results, but a level of subjectivity in the evaluations of $L_w$ cannot be eliminated.

In place of $L_w$, the competitiveness of an infestation can be evaluated on the basis of the partitioning of the upper layer of plant cover between crop and weeds (Relative Cover, RC). Observing the canopy vertically from above, the upper part of the plant cover will be formed by leaves of the crop and weeds: the ratio between the ground area covered by leaves of weeds and the total cover (i.e. weeds plus crop) represents the RC.

With $W$ and $C$ being the areas covered by weeds and crop, respectively, RC is given by:

$$RC = \frac{W}{W + C}$$  \hspace{1cm} (7)

The higher this value is, the greater the share of solar radiation intercepted by the weeds will be, and therefore the competition caused by them will be more intense. This method assumes that: 1) interference for light is a measure of interference by all mechanisms: the leaf canopy may serve as an ‘integrator’ of the combined effects of competition for light, water and nutrients, and possibly also allelopathic effects, since these all reduce height, shoot weight and therefore leaf area and radiation interception; 2) the competitive effect of weeds that are shorter than the crop at canopy closure is negligible; in other words, only the plants that are able to overgrow or, at least, reach a height similar to the crop can successfully compete. The use of this variable was proposed with crops of medium-low height (e.g. peas, soybean).
(Berti and Sattin, 1996): under these conditions, the use of the RC was shown to be valid. The applicability of this method still has to be evaluated with more widely spaced crops and on taller ones, such as maize and sunflower.

The ratio between RC and crop yield loss is similar to (6):

$$Y_L = \frac{a \cdot RC}{1 + \left( \frac{a}{m-1} \right) \cdot RC}$$

(8)

Both $L_w$ and RC proved to be good yield loss predictors at canopy closure stage (Kropff, 1988; Pike et al. 1990; Lutman, 1992; Berti and Sattin, 1996), which is far too late for any control treatment. The early estimation of these yield loss predictors involves estimating their evolution from the time of assessment to canopy closure. This represents a further source of variability that has to be determined by means of appropriate experiments.

The main advantage of RC is the easier measurement. While $L_w$ is based on LAI ratios and therefore requires all the leaf areas to be determined, RC requires the measurement of the ratios of cover between crop and weeds by observing the canopy vertically from above. This can either be done by means of a subjective visual estimate or, with greater precision, by measurements starting from photographs taken from 2-3 m above the crop. The possibility of using optical equipment that automatically take this measurement can also be foreseen.

It should be stressed that the basic data used for the determination of $L_w$ and RC do not give any indication on weed flora composition, information that is fundamental for a correct choice of type of control (e.g. herbicide).

**DAMAGE CAUSED BY MIXED INFESTATIONS**

Information on single crop-weed associations, although interesting, is of limited practical interest because infestations normally include various species and the control measures, in particular herbicides, have a well-defined spectrum of efficacy. The choices between control options (if and how to treat) must therefore be made, taking into account the damage that would be caused in the absence of control as well as the damage caused by the weeds that survive a given treatment. Both these evaluations require the competitive effect of a mixed infestation to be estimated.

In the case of the ratios between density and yield loss, the commonly used methods are based on the transformation of the observed densities into values that can be considered additive. It is obvious that two different weeds, even at the same density, will usually cause different yield losses: it is not therefore possible to directly sum up the observed density values to estimate the competitive effect of the infestation as a whole.

There are three main approaches: the first, proposed by Wilkerson et al. (1991) involves calculating the total competitive load (TCL). This method is used in the HERB program for the choice of post-emergence control options in maize and soybean. The second approach is based on the Density equivalent concept (Deq) (Berti and Zanin, 1994) and is the basis of a decision support system (GESTINF) adapted to Italian conditions and currently at the experimental stage at farm level. The third refers to relative cover and is still at the experimental stage.

**Total competitive load method**
The competitive ability of the various weed species is assigned through competition experiments by using an indexing method, i.e. assigning an arbitrary value $K$ to the most competitive species and ranking the others according to their relative competitiveness with the reference species. Indexing is based on linear relationships between crop yield or biomass and weed density, which, for low density values, represent a good approximation of the hyperbolic relationship that exists between these two variables.

For low values of weed density ($D$), the crop yield can be given by:

$$Y = a + bD \quad (9)$$

The ratio ‘$b/a$’ represents an index of the competitive ability of the considered species. A competitive index (CI) can therefore be defined for the $i_{th}$ species, obtained from the following:

$$CI_i = \frac{b_i}{b_r} \frac{a_i}{a_r} K \quad (10)$$

where $b_r$ and $a_r$ are the regression parameters of the reference species.

$K$ is a scale factor that can assume any value; the authors have chosen a value of 10. In this case, the weeds are ranked following a decimal scale with CI=10 for the reference species. CIs are the basic data used for the evaluation of the yield loss in a real field situation. Then, multiplying the density observed of the $i_{th}$ species by its CI, the competitive load (CL) for this species is obtained:

$$CL_i = CI_i D_i \quad (11)$$

The sum of these values for the various species present represents the TCL of that particular infestation:

$$TCL = \sum CI_i \quad (12)$$

Crop yield loss can be estimated on the basis of the TCL of the infestation. According to Wilkerson et al. (1991) the yield loss for low infestation levels can be calculated with a linear relationship. With the increase of the CL, the weeds start to interfere with one another as well as with the crop and the competitive effect caused by each single plant decreases. Under these conditions the crop yield loss follows a hyperbolic trend. In the case of soybean, Wilkerson et al. (1991) fixed the passing from the linear relationship to the hyperbolic one at a TCL of 50.

It is worth mentioning that this model was calibrated for the central-southern United States, where soybean was grown at wide interrow spacing.

The complete expression of the yield loss as a function of TCL will therefore be:

$$Y_L = \begin{cases} \frac{0.5TCL}{25 + \frac{55(TCL-50)}{TCL+60}} & \text{for } TCL \leq 50 \\ \frac{55(TCL-50)}{TCL+60} & \text{for } TCL > 50 \end{cases} \quad (13)$$

**Density equivalent method**

The Deq of a given weed species is defined as the density of a reference species that determines a yield loss equal to that caused by the studied species at the measured density.

The crop yield loss in competition with the reference species is:
While for the $i_{th}$ species present you have:

$$Y_L = \frac{i_i D}{1 + \frac{i_i D}{a_i}}$$  \hspace{1cm} (15)$$

From the above definition, the Deq of the $i_{th}$ species (Deq$_i$) is the value of the density of the reference species that makes the two preceding equations equal:

$$\frac{i_{ref} \ast \text{Deq}_i}{1 + \frac{i_{ref} \ast \text{Deq}_i}{a_{ref}}} = \frac{i_i \ast D_i}{1 + \frac{i_i \ast D_i}{a_i}}$$  \hspace{1cm} (16)$$

A series of algebraic steps leads to:

$$\text{Deq} = \frac{i_i \ast D_i}{i_{ref} + i_{ref} i_i D_i \left( \frac{1}{a_i} - \frac{1}{a_{ref}} \right)}$$  \hspace{1cm} (17)$$

The equation can be simplified choosing a hypothetical species as reference with the $i$ and $a$ parameters both equal to 1. This assumption gives:

$$\text{Deq} = \frac{i_i D_i}{1 + i_i D_i \left( \frac{1}{a_i} - 1 \right)}$$  \hspace{1cm} (18)$$

Adding up the Deq of the various species present gives a total Density equivalent (Deq$_t$):

$$\text{Deq}_t = \sum \text{Deq}$$  \hspace{1cm} (19)$$

The crop yield loss will then be obtained from:

$$Y_L = \frac{\text{Deq}_t}{1 + \text{Deq}_t}$$  \hspace{1cm} (20)$$

Knowing the indexes $i$ and $a$ of each weed species it is possible to calculate the damage that can be caused by any combination of these weeds.

Relative leaf area and relative weed cover methods.

If the competitiveness of the infestation is evaluated using the Lw instead of density, the equation that expresses the effect of a mixed population becomes simpler. The formula that is applied for a single species can in fact be developed in an additive way, giving the following:

$$Y_L = \frac{\sum q_i \text{Lw}_i}{1 + \sum \left( \frac{q_i}{m_i} - 1 \right) \text{Lw}_i}$$  \hspace{1cm} (21)$$
where \( q_i \), \( m_i \) and \( Lw_i \) indicate the relative damage coefficient, the asymptotic yield loss and observed value of \( Lw \) for the \( i \)th species, respectively. Where a maximum asymptotic value of yield loss is not considered, the value of \( m_i \) is equal to 1 for all the species.

When using RC instead of \( Lw \) as a descriptive variable for weed-crop competition, the extension to a multi-species situation is straightforward. RC \textit{per se} measures the ratio between the horizontal projections of crop and weed leaves, so integrating the effects of both leaf area and leaf posture of different weed species. This implies that RC is intrinsically a multi-species descriptor. Measurements taken in the field can therefore be directly used (see eq. 8) for estimating yield loss caused by a mixed weed infestation.

**Biological and agronomic basis of yield advantage under intercropping**

**Types of mixtures grown**

When it is believed that some favorable interaction occurs between the plants of certain crops, the crops are often cultured together for most of the period of growth. Thus, in Malaysia a cover of groundnuts is often maintained under rubber for the whole life of the trees (see photograph). Shorter-term mixtures which are sown and harvested together are the grass-legume hay combinations and the dredgecorn (oats and barley) grown in Britain. When there is space temporarily unused in a crop, another rapidly growing crop may be taken by interplanting. In India vegetables are planted between rows of young sugar cane, and in Malaysia tobacco is planted among young rubber. By interplanting vegetables in ripening paddy two weeks before the rice is harvested, Taiwan farmers are achieving up to five crops in one year.

Where the sunlight may be very intense, shade trees are planted over many crops. In a remarkable article on traditional mixed cropping methods in India, A. K. T. N. Aider has described how under one system up to three separate age-groups of shade trees are mixed within the same field with each planting of shade tree being followed by its own planting of crop areca. In the desert oases of the Sahara, a similarly three-layered canopy is sometimes produced by planting drought-tolerant date palms to protect the shorter fruit trees, which in turn shade a carpet of vegetables. Shade trees may also serve to support climbing plants such as peppers and betel. Some of the more complex mixtures described by Aiyer have many of the characteristics of natural plant communities; i.e.: stands of individuals of uneven age, and of a wide range of species and growth habit.

**Yields of crop mixtures in the absence of disease**

Mixed cropping is so widespread that it might be thought that a solid scientific basis for it would have already been discovered. This is not so. The question of how the yields of mixtures compare with yields of pure cultures has really only been answered for mixtures of rather similar components such as varieties of grain crops or species of grasses, and then only in relatively short-lived crops. In a series of experiments involving 139 50:50 two-component mixtures of varieties, 64% of the mixtures yielded more grain than the average yield of their components' pure cultures.3 Out of the dry-matter yields of over 300 mixtures of grasses or cereals again about 60% were greater than their average pure culture value.4 Perhaps more interesting, in 37% of the 344 comparisons the yield of the mixture exceeded that of the
better pure culture. This sort of advantage, termed "overyielding", is of great interest to agriculturalists, but unfortunately the margin by which the mixtures overyielded was usually not large enough for it to be due to anything but inevitable experimental error.

A few instances of apparently real overyielding by mixtures are however known: strong evidence of overyielding has been found in individual mixtures of rice varieties (overyielding by up to 20% on a series of occasions), barley varieties (by up to 24% in a series of treatments), grass varieties (by up to 15% in two treatments), and flax with linseed (up to 31% in a series of separate experiments). Mixtures of leguminous and non-leguminous species also sometimes overyield by up to about 10%, given the right conditions. With the exception of work on legume-nonlegume mixtures, surprisingly little has been done to follow up, understand and add to this list of cases of observed positive effects.

When advocates of mixed culture realize that the above results are quite exceptional, they often maintain instead that the real benefit from growing mixtures lies in the greater consistency of overall yield from season to season.

The observation that complex communities like tropical rain forests are more stable in their composition from year to year than simple arctic communities has led ecologists to suggest that the difference is due to the greater diversity of plant and animal species in the rain forest. Although the evidence presented by Sir Charles Elton and others appears compelling, experiment and theories suggest that greater diversity and complexity of themselves lead to less stability. The observed relationship in nature seems therefore likely to be due to some other factor, possibly differences in the stability of the physical environment or the time which has been available for the constituent species to convolve stabilizing characteristics.

Another argument for expecting that mixed cultures should produce more consistent yields is based on the differing responses of species to weather conditions. For example 'when maize is thriving, potatoes may look distressed (and vice versa)'. A combination of the two might be expected to produce at least some crop whether the season is sunny or dull. This sort of "insurance mixture of contrasting component might be recommended where the variation between seasons is so great, that no one species or crop variety performs well in all years. An analogous argument applied to space rather than time justifies the use of oats-barley mixtures in Denmark or problem land which has a mosaic or acid patches; oats thrive on the acid spots where barley fails, and barley dominates elsewhere.

Returning to results of experiments with mixtures of rather similar components, it seems that the stability (consistency) of mixture's yield is, like the yield itself, only rarely greater than that of the more stable component grown pure but usually greater than the average of the stability of the pure components. Some special conditions under which mixtures might be expected to yield more consistently than pure components will be considered later.

Another sort of stability, about which experimenters seem to know little, is long-term sustainability or production. Since individual specie make differing demands on the site and have differing requirements for soil nutrients and other resources continued occupancy of an area by the same species is likely to result in deficiencies (quite apart from; the build-up of pests and diseases). A carefully planned mixture of species is sometimes able to alleviate such deficiencies. Thus, the leguminous groundnut grown between rubber trees is able to control erosion and supply "fixed" nitrogen to the roots of the rubber; without some input of
nitrogen, rubber production fall steadily. Similarly, a shrubby Eupatorium species planted under cinchona and tee in Indonesia benefits the plantation crops by providing mulching material. This safeguards long-term production by controlling erosion and weeds, and by encouraging the turnover of nutrients by litter-decomposing organism.

**Interactions between mixture components**

In closely-planted agricultural crops, individual plants compete strongly for the supplies of plant growth factors (light, water and nutrients). When alternate plants of a pure culture of crop A are replaced by plants of crop B to make a 50:50 mixture, if plants of A compete more strongly than do plants of B for the growth factor in shortest supply, the plants will grow better in the mixture than they do in pure culture; the reverse will be true of plants of B. Uneven sharing of growth factors between the components of mixtures leads usually to roughly equal percentage increases and decreases in per-plant yield of the components as compared with their performances in pure culture. If the farmer is aiming at a particular proportion of the components' products in the yield, he will therefore need to know the likely effect of competition when deciding what proportions to plant. This type of interaction between components results in overall mixture yields lying somewhere between the yields of the pure cultures of the components (even if the mixture contains several components). The slight tendency for the higher yielding components to be stronger competitors may explain the tendency for the yield of a mixture to be greater than the average pure culture value.

The tendency for mixture yields to be better than might be expected may also be partly due to differences between the components in the way they exploit the site's growth factors. There are so many human examples of fruitful cooperation between unlike partners that well-chosen combinations of plant species could also be expected to perform better than either alone. One well-tried type of combination contains a leguminous species with one or more nonlegumes. Through the presence of symbiotic bacteria in their roots, plants of leguminous species are able to take in, "fix" and utilize nitrogen from the soil air. Because they draw on this usually unavailable source of nitrogen, leguminous species leave most of the soil's nitrogenous compounds available for use by associated species. Also, as the legume's roots die, the fixed nitrogen becomes available in the soil. Hence, on a soil where nitrate is in short supply, a mixture of clover (a legume) with a grass (non-legume) may overyield. Mixtures such as rubber and groundnut (Malaysia), sugarcane and soybean (India), and cereals and field beans (Greece) are expected to exploit this same principle. Importantly, where there is little nitrogen in the soil, the non-legume component in the mixture often has a much greater protein content than in pure culture under such conditions, a mixture of grass and clover will usually be preferred as fodder to pure grass (or to pure clover, which may cause "bloat").

If the components of a mixture differ in the times at which they make demands for soil nutrients or light, the mixture may use site resources more effectively. Experiments with mixtures of early and late season potatoes at Wageningen, Holland, have shown overyielding by more than half of 54 mixtures, sometimes by up to 50%. Mixtures of flax (early maturing) and linseed (late maturing) overyield for the same reason.

Another sort of difference which is expected to lead to an advantage for the mixture is the occupation of different layers of the soil by the roots of the components. Aiyer suggested that mixtures should be compounded to exploit the whole depth of soil. Although this point has
never been tested directly, in an experiment with mixtures of oat species, it was found that 5 out of 5 mixtures overyielded on deep soil whereas only 1 overyielded on shallow soil; the root systems of the components of the best yielding mixture were in fact later shown to occupy different depths in deep soil.

Tall vegetation often greatly alters the microenvironmental conditions below it and use may be made of this in compounding mixtures for use in harsh climates. The use of shade trees for protection from sun (and drying winds) has already been mentioned but trees may also have other effects. Thus, it has been observed that growth begins earlier in spring under trees in Salamanca probably because the soil there is not so cold at night. The removal of trees from groundnut plantations in Senegal (for the sake of "neatness") seems to have caused planting date to be much more critical than previously; the trees presumably used to moderate the microclimate under them. Taller growing components may act usefully as wind-breaks. Crop mixtures may also have advantages under certain unfavorable conditions such as frost, lodging and weed infestation. In mixtures of wheat varieties in Czechoslovakia, frost-hardy varieties have been found to protect less hardy ones. Similarly, cereal varieties which do not lodge (get beaten flat) in bad weather, may hold up weaker-stemmed components. In an experiment in Adelaide, Australia, a wheat variety which lodged in pure culture was prevented from lodging in all 5 of its mixtures with other varieties. Trials at IRRI in the Philippines have shown that if mung bean is grown mixed with maize, the weed-smothering effect of the mung protects the easily-infested maize.

There is growing interest at present among ecologists concerning the possible effects of chemicals released by plants of some species on neighbouring plants (allelopathy). Most of the well-studied examples involve substances which inhibit the growth of other plants of either the same sort (autotoxicity) or of other sorts (allotoxicity). In a mixture of individually autotoxic species, the plants of each component will to some extent escape the inhibitory influence of neighbors of its own species and so mixtures could overyield. Thus, it has been suggested that certain desirable forest trees which suffer badly from autotoxicity in Queensland ought perhaps to be cultivated in mixtures. Regular overyielding by a certain mixture of rice varieties in India suggests that one variety can sometimes actually stimulate the growth of another. In this case, it was shown that some growth-promoting substance traveled from plants of one component to those of the other. An observation that the presence of certain species of Eucalyptus tree can double the productivity of the pasture in which they stand may be explained by allelopathic stimulation, or, on the other hand by microenvironmental effects. The strongly depressive effects of other Eucalyptus species on pasture growth do not seem to be due to competition for resources but rather, to allotoxicity. Although the possibility has not been tested, a mixture of allotoxic components would probably yield below the poorer yielding pure culture.

Pests and diseases in crop mixture

A considerable body of traditional fore exists to recommend the "companion" planting of certain crops with other crops. The advantages claimed are usually that the companion plants reduce pest damage in the others. Occasional combinations conferring mutual advantage may be found, such as tomato and asparagus where the tomato will be protected from at least one species of parasitic nematode and the asparagus will be protected from asparagus beetle.
In the tropics where crop pests cause especially serious damage, foresters and planters have long since recognized that individuals of a species in pure culture are often more heavily damaged than individuals of the same species interspersed among individuals of other species. Accordingly, in Brazil the native rubber tree cannot be grown in pure culture although it can survive the level of pest attack suffered in the natural mixed forest. Agriculturalists are now belatedly coming to recognize the potentialities of mixed cropping as a powerful and non-polluting means of controlling pests and disease. For instance, recently at the National Institute of Agronomic Research, Paris, the incidence of foot rot in a susceptible wheat variety was found to be halved in a mixture with a resistant variety. Again, in Reconquista, Argentina, it was found that intersewing cotton with maize led to an 80% reduction of pest numbers on the cotton and a doubling of its yield.

To be able to choose combinations which are tolerant of pests and diseases, the grower needs to know something of how an attack in a mixture may differ from one in a pure culture. The presence of two or more kinds of crop has several effects:

1. Fly paper effect. Because many pest and disease organisms tend to be specialized to attack just one or a small group of host species, the individual of other plant species in a mixture constitute a potentially absorptive barrier to movement between those plants which can be attacked. Insect pests usually have a stage in their life cycles where they disperse from their host plants apparently to colonize new ones; at this stage they are often poor at recognizing suitable food plants and steering themselves towards them.

The spores of fungal diseases are passively transported by wind and rain-splash and so are even less likely to find a new host plant. Depending on the proportion of the species in the mixture a fraction of the dispersing individual will be intercepted by non-host plants. Where the dispersing insects or spores cannot "take off" again, they are lost from the population of their species. This loss onto an inert "fly-paper" reduces the rate of build-up of epidemics in mixtures of susceptible and resistant plants.

2. Compensation effects. Where a crop is attacked during vigorous growth, infected plants compete less strongly than healthy plants for growth factors. Plants surrounding a diseased individual therefore yield more than otherwise and compensate to some degree for the longer yields of the attacked plants. A mixture of crops which differ in their susceptibility to a series of diseases may thus produce total yields which are more consistent than those of any of the pure cultures if the various diseases are favored by different types of season.

3. Microenvironmental effects. The presence of companion plants creates a microenvironment for the susceptible crop which differs from that found in pure culture. This different environment may affect the host-parasite relationship in subtle ways:

(a) By acting on the potentially attacked component changing its susceptibility (from that in pure culture). For example, banana crops under shade trees in Malaysia are less attacked by the most damaging of a series of leaf-spot disease (although they are more susceptible to the less damaging ones); the leaves of coffee grown under shade trees in Indonesia provide a less suitable diet for woolly aphids and hence are less attacked.

(b) By acting directly on the attacking organism. For example, where broad-leafed trees grow within stands of spruce, the higher humidity (or possibly longer temperature) of the air is unfavorable to the growth of spruce-bud worm; cocoa under shade trees in Ghana is less
attacked by mistletoe because this parasite requires high light intensities for the establishment of its seedlings; the odour of shallots (more effective than onions) prevents the carrot root fly from finding inter-planted carrots; wheat without awns (sharp projections from the ear, as in barley) is protected from birds by being mixed with an awned variety.

(c) By influencing the populations of the natural enemies of the attacking organism. For instance, in the Philippines, the corn-stalk borer is less abundant in maize-groundnut mixtures because spiders which prey upon it are more numerous in such mixtures than in pure maize; citrus under shade has leaves with a thinner cuticle which allows leaf miners within them to be reached more easily by parasitic wasps; blackcurrant bushes planted in Californian vineyards support an alternate host for a parasite of a pest of the vines thus increasing its effectiveness in controlling the pest; buckwheat planted among broad beans is said to attract hover flies which prey on the bean aphids.

That most of the example available show improved control of attacking organisms may be the consequence partly of the greater interest in well-tried, successful mixtures, and partly of the lesser emphasis which negative results naturally receive in reports. Nevertheless, crop mixtures seem to have potential where crops are threatened by pest and diseases.

Multilines and disease

When a crop variety which has a new gene for resistance to some disease begins to be widely used, individual races of the disease organism appear which have a virulence gene which overcomes this resistance. Such races multiply rapidly on the variety. Sometimes, disease races with the necessary virulent gene are very rare at the time of introduction of the new resistance gene and so this resistance gene will protect the new variety for several years before the virulent races have built up to a destructive lever. Such effective resistance genes are called "strong". A resistance gene for which corresponding virulent races are already present in quantity at the time of its introduction will be ineffective and "weak".

Since mixed cropping often involves staggered plantings and selective harvesting it tends to be labour intensive. If it is soundly practiced it may require less pesticide, weedkiller and fertilizer, and so be a lowpolluting method of farming.

To appreciate the arguments in favour of multiline varieties (multilines), it is necessary to understand why some resistance genes appear strong and others weak: at the time of its introduction, a gene will seem strong if the disease races carrying the virulence gene to overcome it have been at a competitive disadvantage compared with the races not carrying the virulence gene, as they grew together on the old varieties. In simple terms, on the old varieties, this surplus virulence gene in a disease race conferred a disadvantage which kept it
rare. The greater this disadvantage, the stronger the corresponding resistance gene in the crop would appear to be.

If we consider now a multiline made up of four lines where each carries one of a series of new resistance genes, A, B, C and D, each line will only be attacked by races which have acquired through mutation the virulence gene, a, b, c or d, corresponding to that line's resistance gene. Each of these races will face a strong fly-paper effect which will limit its multiplication and thus the harm it can do. If for some reason one race becomes relatively common, the damage it inflicts on the corresponding line will be to some extent compensated for by better growth of the other components. However, if further virulence genes are acquired through mutation, races such as ab, bc, ac, will appear. Being able to attack two components of the multiline instead of only one, the fly-paper effect on them will be weaker, the multiplication rates greater and the opportunity for further mutation greater. When a super-race, abcd, finally produced, all components of the multiline will be susceptible to it.

There are unfortunately some uncertainties in this attractive picture:

1. For some diseases, too few strong resistance genes are available in the crop for a multiline to be made (e.g. in potatoes against late blight). However, the production of new resistance genes by, say, irradiation, or the use of new techniques of hybridization may make more genes available.

2. High strength in the resistance genes is vital for the success of a multiline but unfortunately strength does not depend only on the resistance gene itself. Given a different set of "old varieties" in the explanation above, the same resistance gene might for example appear weak when introduced. Since the nature of the lines chosen to carry the various resistance genes will affect the apparent strengths of these genes in the multiline, the choice of ines could be crucial. At present the lines to be used are chosen for their agronomic performance; it seems important to select them also for their ability to maximize the apparent strengths of the resistance genes.

3. While it is known that the presence of non-virulent spores on a leaf can sometimes prevent infection by virulent ones ("cross-protection"), the presence of virulent spores can sometimes make non-virulent ones cause infections ("potentiation"). While cross-protection could increase the resistance of a multiline to attack, potentiation could decrease it. Too little is known about these phenomena to yet say which the commoner is.

4. Although experiments have measured disadvantages to races carrying many virulence genes (potential super-races) when mixed with races carrying few virulence genes, it is not clear yet whether this disadvantage is strong enough to balance the advantage to the former of their wider host range. Mathematical models now being developed may be able to show whether any equilibrium will be at a low enough level of infection for equilibrium is not wanted if it leaves our crops regularly devastated!

5. While a multiline can be reconstituted each year to meet shifts in the relative frequency of the attacking races, an optimized set of rules needs to be worked out to replace the rule of thumb used so far in Colombia and Iowa. There are opportunities for the application of control engineering techniques in disease and pest management.
Crop mixtures and the future
In a series of cases mixed cropping has biological advantages over the use of pure cultures; multilines may also have advantages. However, in real life, it usually is not biological but economic advantage which decides what farming and cropping systems are actually used. Since mixed cropping often involves staggered plantings and selective harvesting it tends to be labour intensive. If it is soundly practice, it may require less pesticide, weedkiller and fertilizer, and so be a lowpolluting method of farming. Where there is rural unemployment, where capital is in short supply and where production must be sustainable without expensive fossil fuels and pollution control, mixed cropping is a possible solution. Thus in Nigeria and Malaysia, rubber planters are being advised to interplant their rubber with cash crops to raise capital for replacing old stands. The jobs so created can help to slow or reverse the drift to the towns.

It has been emphasized already that for mixed cropping to be biologically advantageous, the mixture components need to be chosen with care. Unfortunately, the interactions among the plants, animals and microorganisms in a crop are so subtle and specific to particular locations that present knowledge only provides a rough guide as to what new combinations of crops and varieties should be tried. If then the possible advantages of mixed cropping are to be exploited, local experimentation will be needed, using a range of possible components and a series of seasons. In the search for "ecological combining ability", the traditional combinations should perhaps be evaluated first, as at the International Rice Research Institute in the Philippines. Better, more compatible components for mixtures are being actively sought in many research centres. Examples where ranges of types are under test include trials of shade trees for cocoa (Sarawak) and for tea (India), of intercrops for rubber (Malaysia), of grasses for hay mixtures, (UK, USA, USSR) and even of strains of nitrogen-fixing bacteria for introduction into the legume component of grass-legume mixtures (Australia). If the difficulties of managing diversity in the crop field can be overcome, diversity in this and other forms will help to safeguard our crops against pests and epidemic disease. Unless the Green Revolution changes course, much of the world's green could turn to rust-red almost overnight.

Producers and researchers carry out different cropping systems to increase productivity and sustainability by practicing crop rotations, relay cropping, and intercropping of annual cereals with legumes. Intercropping of cereals with legumes has been popular in tropics (Hauggaard-Nielsen et al., 2001; Tsubo et al., 2005) and rain-fed areas of the world (Banik et al., 2000; Ghosh, 2004; Agegnehu et al., 2006; Dhima et al., 2007) due to its advantages for soil conservation (Anil et al., 1998), weed control (Poggio, 2005; Banik et al., 2006), lodging resistance (Anil et al., 1998), yield increment (Anil et al., 1998; Chen et al., 2004), hay curing, forage preservation over pure legumes, high crude protein percentage and protein yield (Qamar et al., 1999; Karadag and Buyukburc, 2004), and legume root parasite infections control (Fenandez-Aparicio et al., 2007).

Different seeding ratios or planting patterns for cereal-legume intercropping have been practiced by many researchers (Tsubo et al., 2001; Karadag and Buyukburc, 2004; Banik et al., 2006; Dhima et al., 2007). Competition among mixtures is thought to be the major aspect affecting yield as compared with solitary cropping of cereals. Species or cultivar selections,
seeding ratios, and competition capability within mixtures may affect the growth of the species used in intercropping systems in rain-fed areas (Santalla et al., 2001; Karadag and Buyukburc, 2004; Carr et al., 2004; Agegnehu et al., 2006; Banik et al., 2006; Dhima et al., 2007). In Turkey, legumes, such as common vetch, common bean and cowpea are extensively used in intercropping with cereals (Kizilsimsek and Saglamtimur, 1996; Akman and Sencar, 1999).

A number of indices such as land equivalent ratio, relative crowding coefficient, competitive ratio, actual yield loss, monetary advantage, and intercropping advantage have been proposed to describe competition within and economic advantages of intercropping systems (Banik et al., 2000; Ghosh, 2004; Agegnehu et al., 2006; Banik et al., 2006; Dhima et al., 2007).

**Case Study**

Identification of Advantages of Maize-Legume Intercropping over Solitary Cropping through Competition Indices in the East Mediterranean Region (YILMAZ et al 2007)

**Crop management and experimental design**

The experiment was conducted during 2003-2004 growing periods (2 years) on a private farm in Elbistan, Kahramanmaraf province of Turkey (38°21’N, 37°21’E, and 1140 m above sea level). The treatments included sole maize (cv. P-2332) planted at the rate of 71,500 plants ha⁻¹, sole common bean (landrace “Horoz”) and a landrace cowpea planted at the rate of 285,750 plant ha⁻¹ each, and the 4 intercropping treatment mixtures of maize with common bean and cowpea were i) 1M:1B, 1M:1B, 1M:1B, ii) 2M:2B, 2M:2B, 2M:2B, iii) 1M:1C, 1M:1C, 1M:1C, and iv) 2M:2C, 2M:2C, 2M:2C (numbers represent row numbers, and M, B and C represent maize, common bean, and cowpea, respectively). As fixing the plant density of legumes, we modified the proportion of maize in the mixtures of each of 3 planting types in the proportions of 50:50, 67:50, and 100:50 maize-legume, respectively, where 50%, 67%, and 100% of sole maize plus 50% sole legumes were grown for each intercropping treatment. Row spacing of legumes were 70 x 10 cm while alternate row spacings for 50%, 67%, and 100% maize were 70 x 20 cm, 70 x 15 cm, and 70 x 10 cm, respectively. Common bean and cowpea were simultaneously planted with maize. Planting of the seed was done during the first week of May in each growing season.

**Competitions indices and monetary advantages**

The benefit of planting patterns and the effect of competition between the 3 species used were calculated using different competition indices.

The land equivalent ratio (LER) was used as the first criterion for mixed stand advantage for both legumes (common bean and cowpea) and cereal (maize) (Willey, 1979). In particular, LER verifies the effectiveness of intercropping for using the resources of the environment compared to sole cropping (Mead and Willey, 1980; Dhima et al., 2007). When LER is greater than 1, the intercropping favors the growth and yield of the species. In contrast, when LER is lower than 1, the intercropping negatively affects the growth and yield of plants grown in mixtures (Ofori and Stern, 1987; Caballero et al., 1995; Dhima et al., 2007). The LER values were calculated as:

\[
LER = (LER_{maize} + LER_{legume}),
\]

where \(LER_{maize} = \frac{Y_{ml}}{Y_m}\), and \(LER_{legume} = \frac{Y_{lm}}{Y_l}\).
where $Y_m$ and $Y_l$ are the yields of maize and legumes as sole crops, respectively, and $Y_{ml}$ and $Y_{lm}$ are the yields of maize and legumes as intercrops, respectively.

The second coefficient was the relative crowding coefficient (K) which is a measure of the relative dominance of one species over the other in a mixture (Banik et al., 2006). The K was calculated as:

$$K = (K_{maize} \times K_{legume}),$$

where $K_{maize} = Y_{ml} \times Z_{lm}/((Y_m - Y_{ml}) \times Z_{ml})$, and $K_{legume} = Y_{lm} \times Z_{ml}/((Y_l - Y_{lm}) \times Z_{lm})$

where $Z_{ml}$ and $Z_{lm}$ were the proportions of maize and legume in the mixture, respectively.

When the value of K is greater than 1, there is a yield advantage; when K is equal to 1, there is no yield advantage; and, when it is less than 1.00, there is a disadvantage (Dhima et al., 2007).

The third index was aggressivity (A) which is often used to determine the competitive relationship between 2 crops used in the mixed cropping (Willey, 1979). The aggressivity was formulated as follows:

$$A_{legume} = (Y_{lm} / Y_l \times Z_{lm}) - (Y_{ml} / Y_m \times Z_{ml}),$$

and

$$A_{cereal} = (Y_{ml} / Y_m \times Z_{ml}) - (Y_{lm} / Y_l \times Z_{lm})$$

(Dhima et al., 2007).

For cereal example; if $A_{cereal} = 0$, both crops are equally competitive, if $A_{cereal}$ is positive, then the cereal species is dominant, if $A_{cereal}$ is negative, then the cereal is weak.

Also, competitive ratio (CR) is another way to assess competition between different species. The CR gives more desirable competitive ability for the crops and is also advantageous as an index over K and AYL (Dhima et al., 2007). The CR represents simply the ratio of individual LERs of the 2 component crops and takes into account the proportion of the crops in which they are initially sown. Then, the CR index was calculated using the following formula:

$$CR_{maize} = (LER_{maize}/LER_{legume})(Z_{lm}/Z_{ml}),$$

and

$$CR_{legume} = (LER_{legume}/LER_{maize})(Z_{ml}/Z_{lm})$$

The next index was the actual yield loss (AYL) index, which provided more accurate information about the competition than the other indices between and within the component crops and the behaviour of each species in the intercropping system, as it is based on yield per plant (Banik et al., 2000). The AYL is the proportionate yield loss or gain of intercrops in comparison to the respective sole crop, i.e. it takes into account the actual sown proportion of the component crops with its sole stand. In addition, partial AYL$_{legumes}$ or AYL$_{cereal}$ represent the proportionate yield loss or gain of each species when grown as intercrops, relative to their yield in sole planting (Dhima et al., 2007). The AYL (Banik, 1996) was calculated as:

$$AYL = AYL_{maize} + AYL_{legume},$$

where

$$AYL_{maize} = ((Y_{ml}/X_{ml})/(Y_m/X_m)) - 1,$$

and

$$AYL_{legume} = ((Y_{lm}/X_{lm})/(Y_l/X_l)) - 1$$

where $X_{ml}$ and $X_{lm}$ represent the sown proportion of intercrop maize with legume, and legume with maize, respectively. The AYL can have positive or negative values indicating an advantage or disadvantage remained in intercrops when the main aim is to compare yield on a per plant basis.

Finally, the monetary advantage index (MAI) was calculated since none of the above competition indices provides any information on the economic advantage of the intercropping system. The calculation of MAI was as follows:
MAI = (value of combined intercrops)(LER-1)/LER; the higher the MAI value, the more profitable the cropping system is (Ghosh, 2004). Additionally, intercropping advantage (IA) was calculated using the following formula (Banik et al., 2000):

\[
IA_{\text{legume}} = \frac{AYL_{\text{legume}} P_{\text{legume}}}{P_{\text{legume}}}, \quad \text{and} \quad IA_{\text{maize}} = \frac{AYL_{\text{maize}} P_{\text{maize}}}{P_{\text{maize}}}
\]

where \( P_{\text{legume}} \) and \( P_{\text{maize}} \) are the commercial value of legumes (the price of common bean was 891.1 Euro and cowpea 912 Euro per Mg, respectively), and maize (190 Euro per Mg), respectively.

Data were analyzed using the SAS computer software program (SAS, 1998). A combined analysis of variance over 2 years was performed for the seed yield, partial LER, and total LER, as well as for all other indices using Bartlett’s test to check for homogeneity of variances of each parameter among years.

**Results**

The highest maize seed yield was obtained from 1-row 67 maize:50 cowpea mixture while the lowest one was from 2-row 100 maize:50 cowpea mixture. The highest legume seed yield was from sole planting and the lowest one was from 2-row 100 maize:50 cowpea mixture (Table 3.1). Intercropping of maize with common bean and cowpea at a mix-proportion of 50:50 or 67:50 under 2 planting patterns gave higher seed yield compared to sole planting. Such results may be misleading when one disregards the other external inputs as to be explained under several competition indices below.

**Land equivalent ratio and relative crowding coefficient**

In general, partial LER_{\text{legume}} was lower in maize:common bean mixture compared to cowpea:maize (Table 3.1). As expected, partial LER of common bean and cowpea decreased as the proportion of maize increased in mix-proportions. The partial LER_{\text{legume}} values were higher than 0.50 in the 1- or 2-row maize:cowpea mixtures in proportions of 50M:50C and 67M:50C; however, the partial LER_{\text{maize}} was higher than 0.50 in all cases while it decreased when the maize was more than 67%.

The intercropped common bean and cowpea had higher K_{\text{legume}} values than the intercropped maize in the cereal-legume mixtures of 50:50 and 67:50. When the maize was higher than 67%, the K_{\text{maize}} had larger values (Table 3.1). The total K was much higher than one in the case of 100M:50B and 100M:50C. On the other hand, in the maize-common bean and maize cowpea mixtures (mix proportions of 50:50 and 67:50), the total K values was close to one.

**Aggressivity, competitive ratio, and actual yield loss**

In all planting patterns, positive A_{\text{maize}} values showed that maize was the dominant species (Table 3.2). Intercropped maize had higher competitive ratios (CRs) in both mixtures and in all planting patterns; however, cowpea had higher CR values than those of common bean. In particular, AYL_{\text{maize}} had positive values in maize:common bean and maize:cowpea intercroppings when the maize proportion was less than 100% in all planting patterns and the highest AYL_{\text{maize}} value was obtained from 1- and 2-row 50 maize:50 common bean or 50 cowpea mixtures while the lowest was from 1-row 100 maize:50 cowpea. The highest AYL_{\text{legume}} value belonged to 1-row 50 maize:50 cowpea mixture while the lowest value was to 2-row 100 maize:50 common bean. Comparing 2 legumes, cowpea had the higher AYL_{\text{legume}} values than those of common bean.
Table 3.1. Seed yield, land equivalent ratio (LER) and relative crowding coefficient (K) for sole stands and mixture of maize with common bean and cowpea in 6 planting patterns (maize–legumes, common bean, and cowpea).

<table>
<thead>
<tr>
<th>Planting patterns*</th>
<th>Mix-proportions (%)</th>
<th>Seed yield (Mg ha⁻¹)</th>
<th>LER values</th>
<th>K</th>
<th>Kmaize</th>
<th>Klegume</th>
<th>Ktotal</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maize (M) (Sole)</td>
<td>100</td>
<td>11.02</td>
<td>11.02</td>
<td>1.00</td>
<td>1.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bean (B) (Sole)</td>
<td>100</td>
<td>2.01</td>
<td>2.01</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1 M:1 B 50:50</td>
<td>12.20 0.99</td>
<td>13.19</td>
<td>1.11 0.49</td>
<td>1.60</td>
<td>-10.34</td>
<td>0.97</td>
<td>-10.04</td>
</tr>
<tr>
<td>1 M:1 B 67:50</td>
<td>13.17 0.83</td>
<td>14.00</td>
<td>1.20 0.41</td>
<td>1.61</td>
<td>-4.60</td>
<td>0.93</td>
<td>-4.27</td>
</tr>
<tr>
<td>1 M:1 B 100:50</td>
<td>11.00 0.73</td>
<td>11.73</td>
<td>1.00 0.36</td>
<td>1.36</td>
<td>275.0</td>
<td>1.13</td>
<td>311.7</td>
</tr>
<tr>
<td>2 M:2 B 50:50</td>
<td>11.97 0.79</td>
<td>12.76</td>
<td>1.09 0.39</td>
<td>1.48</td>
<td>-12.6</td>
<td>0.65</td>
<td>-8.19</td>
</tr>
<tr>
<td>2 M:2 B 67:50</td>
<td>13.30 0.64</td>
<td>13.94</td>
<td>1.21 0.32</td>
<td>1.53</td>
<td>-4.38</td>
<td>0.63</td>
<td>-2.74</td>
</tr>
<tr>
<td>2 M:2 B 100:50</td>
<td>10.45 0.59</td>
<td>11.04</td>
<td>0.95 0.29</td>
<td>1.24</td>
<td>9.17</td>
<td>0.83</td>
<td>7.56</td>
</tr>
<tr>
<td>Cowpea (C) (Sole)</td>
<td>100 -</td>
<td>1.18</td>
<td>1.180</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1.00</td>
</tr>
<tr>
<td>1 M:1 C 50:50</td>
<td>12.15 0.68</td>
<td>12.83</td>
<td>1.10 0.58</td>
<td>1.68</td>
<td>-10.75</td>
<td>1.37</td>
<td>-14.78</td>
</tr>
<tr>
<td>1 M:1 C 67:50</td>
<td>10.68 0.54</td>
<td>11.22</td>
<td>0.97 0.46</td>
<td>1.43</td>
<td>15.71</td>
<td>1.71</td>
<td>26.78</td>
</tr>
<tr>
<td>1 M:1 C 100:50</td>
<td>12.27 0.57</td>
<td>12.84</td>
<td>1.11 0.48</td>
<td>1.59</td>
<td>-10.34</td>
<td>0.94</td>
<td>-9.73</td>
</tr>
<tr>
<td>2 M:2 C 50:50</td>
<td>12.28 0.51</td>
<td>13.29</td>
<td>1.18 0.43</td>
<td>1.61</td>
<td>-4.97</td>
<td>0.99</td>
<td>-4.96</td>
</tr>
<tr>
<td>2 M:2 C 67:50</td>
<td>9.86 0.49</td>
<td>10.35</td>
<td>0.89 0.42</td>
<td>1.31</td>
<td>-4.25</td>
<td>1.42</td>
<td>6.04</td>
</tr>
<tr>
<td>2 M:2 C 100:50</td>
<td>11.96 0.664</td>
<td>12.61</td>
<td>1.09 0.43</td>
<td>1.51</td>
<td>20.16</td>
<td>1.08</td>
<td>24.3</td>
</tr>
<tr>
<td>Mean</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>3.56</td>
<td>0.01</td>
<td>7.07</td>
</tr>
<tr>
<td>LSD (0.05)</td>
<td>0.43 0.05 0.52 0.56</td>
<td>0.12 0.15</td>
<td>3.56 0.01</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

*1M:1B, 2M:2B, represents planting pattern of maize-common bean, numbers represent number of rows. 1M:1C, 2M:2C, represents planting pattern of maize-cowpea, numbers represent number of rows.

Table 3.2. Aggressivity (A), competitive ratio (CR) and actual yield loss (AYL) for mixtures of maize with common bean and cowpea in 6 planting patterns (maize–legumes, common bean, and cowpea).

<table>
<thead>
<tr>
<th>Planting patterns*</th>
<th>Mix-proportions (%)</th>
<th>Amaize</th>
<th>Alegume</th>
<th>CRmaize</th>
<th>CRlegume</th>
<th>AYLmaize</th>
<th>AYLegume</th>
<th>AYLtotal</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 M:1 B 50:50</td>
<td>1.23</td>
<td>-1.23</td>
<td>2.25</td>
<td>0.45</td>
<td>1.21</td>
<td>-0.02</td>
<td>1.2</td>
<td></td>
</tr>
<tr>
<td>1 M:1 B 67:50</td>
<td>0.97</td>
<td>-0.97</td>
<td>2.19</td>
<td>0.46</td>
<td>0.79</td>
<td>-0.18</td>
<td>0.62</td>
<td></td>
</tr>
<tr>
<td>1 M:1 B 100:50</td>
<td>0.28</td>
<td>-0.28</td>
<td>1.38</td>
<td>0.73</td>
<td>-0.002</td>
<td>-0.28</td>
<td>-0.28</td>
<td></td>
</tr>
<tr>
<td>2 M:2 B 50:50</td>
<td>1.38</td>
<td>-1.38</td>
<td>2.76</td>
<td>0.36</td>
<td>1.17</td>
<td>-0.21</td>
<td>0.96</td>
<td></td>
</tr>
<tr>
<td>2 M:2 B 67:50</td>
<td>1.17</td>
<td>-1.17</td>
<td>2.84</td>
<td>0.35</td>
<td>0.81</td>
<td>-0.36</td>
<td>0.45</td>
<td></td>
</tr>
<tr>
<td>2 M:2 B 100:50</td>
<td>0.36</td>
<td>0.36</td>
<td>1.62</td>
<td>0.62</td>
<td>-0.05</td>
<td>-0.42</td>
<td>-0.47</td>
<td></td>
</tr>
<tr>
<td>1 M:1 C 50:50</td>
<td>1.05</td>
<td>1.05</td>
<td>1.91</td>
<td>0.53</td>
<td>1.21</td>
<td>0.16</td>
<td>1.36</td>
<td></td>
</tr>
<tr>
<td>1 M:1 C 67:50</td>
<td>0.81</td>
<td>0.81</td>
<td>1.80</td>
<td>0.56</td>
<td>0.83</td>
<td>0.01</td>
<td>0.84</td>
<td></td>
</tr>
<tr>
<td>1 M:1 C 100:50</td>
<td>0.05</td>
<td>-0.05</td>
<td>1.05</td>
<td>0.95</td>
<td>-0.03</td>
<td>-0.08</td>
<td>-0.11</td>
<td></td>
</tr>
<tr>
<td>2 M:2 C 50:50</td>
<td>1.25</td>
<td>-1.25</td>
<td>2.28</td>
<td>0.44</td>
<td>1.21</td>
<td>-0.03</td>
<td>1.18</td>
<td></td>
</tr>
<tr>
<td>2 M:2 C 67:50</td>
<td>0.91</td>
<td>-0.91</td>
<td>2.07</td>
<td>0.48</td>
<td>0.77</td>
<td>-0.14</td>
<td>0.62</td>
<td></td>
</tr>
<tr>
<td>2 M:2 C 100:50</td>
<td>0.06</td>
<td>-0.06</td>
<td>1.08</td>
<td>0.93</td>
<td>-0.11</td>
<td>-0.17</td>
<td>-0.28</td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>0.79</td>
<td>-0.79</td>
<td>1.94</td>
<td>0.57</td>
<td>0.65</td>
<td>-0.14</td>
<td>0.51</td>
<td></td>
</tr>
<tr>
<td>LSD (0.05)</td>
<td>0.12 0.12 0.14 0.05</td>
<td>0.03</td>
<td>0.04</td>
<td>0.03</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*1M:1B, 2M:2B, represents planting pattern of maize-common bean, numbers represent number of rows. 1M:1C, 2M:2C, represents planting pattern of maize-cowpea, numbers represent number of rows.

**Intercropping advantages and monetary advantage index**

The IA, which is an indicator of the economic feasibility of intercropping systems, affirmed that the most advantageous mixture was the maize-cowpea mixture at the mix-proportion of single-row 50M:50B plant density (mix proportion) with IA value of +372.75 (Table 3.3). The lowest IA value of -382.53 showed that 2-row 100M:50B lead to highest loss and there were fewer negative values for cowpea than for common bean (Table 3.3).
The values of MAI was higher in maize-cowpea intercropping than the maize-common bean intercropping and the highest MAI was observed for 1M:1C (mix proportion of 67M:50C) intercropping. The lowest MAI value belonged to 2-row 100 M:50 B. Compared to common bean, 1-row yielded better MAI values than did 2-row and cowpea had higher MAI values.

Table 3.3. Intercropping advantage (IA), Monetary advantage index (MAI) and actual yield loss (AYL) for mixtures of maize with common bean and cowpea in 6 planting patterns (maize–legumes, common bean, and cowpea).

<table>
<thead>
<tr>
<th>Planting patterns*</th>
<th>Mix- proportions (%)</th>
<th>IA&lt;sub&gt;Maize&lt;/sub&gt;</th>
<th>IA&lt;sub&gt;Legume&lt;/sub&gt;</th>
<th>CR&lt;sub&gt;total&lt;/sub&gt;</th>
<th>MAI</th>
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<td>230.69</td>
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<td>217.32</td>
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<td>-160.5</td>
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<td>8.01</td>
<td>5.49</td>
<td>9.57</td>
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*1M:1B, 2M:2B, represents planting pattern of maize-common bean, numbers represent number of rows. 1M:1C, 2M:2C, represents planting pattern of maize-cowpea, numbers represent number of rows.

Yield advantage in intercropping

Yield is taken as primary consideration in the assessment of the potential of intercropping practices. In legumes and non-legume intercropping, yield of non-legume increased in intercropping as compared with mono-cropping. It is found that by inter-cropping land was effectively utilized and yield was improved. The crops are grown together because of higher yields and greater biological and economic stability in the system. Land equivalent ration (LER) is the most common index adopted in intercropping to measure the land productivity. It is often used as an indicator to determine the efficacy of intercropping. LER>1 indicates greater efficiency of land utilization in the intercropping system. It is due to greater efficiency of resources utilization in intercropping or by increased plant density. LER shows advantage of cereal-legume intercropping. Tsubo et al (2005) stated legume-cereal intercropping generally more productive than monocrop. When two crops are grown together yield advantage occurs because of differences in their use of resources. Inter-cropping gives a greater stability of yield over monoculture and intercropping was more productive than the sole crop grown on the same area of land. LER value exceeding unity in radish vegetable + amaranth intercropping indicates yield advantages from inter-cropping compared to monocropping. Legume non-legume intercropping increases total grain and nitrogen yield. In intercropping higher yield and greater stability over mono-cropping was reported. Maize yield was affected by intercropping with soybeans. Maize + soybean intercropping gave LER of 1.18. Intercropping often provides higher cash returns than growing one crop alone. Intercropping occupies greater land use and thereby provides higher net returns.
Intercropping helps in increasing farm income on sustained basis. Intercropping commonly gave greater combined yields and monetary returns than obtained from either crop grown alone. Net return of radish and vegetable amaranth intercropping correlated with vegetable amarantes plant density. Intercropping capsicum and vegetable cowpea gave high net return compared to mono-cropping.

Maize based inter-cropping
Intercropping of legumes and cereals is an old practice in tropical agriculture that time back to ancient civilization. Legume – cereal is the most popular inter-cropping system in the tropics. Systems that intercrop maize with a legume are able to reduce the amount of nutrients taken from the soil as compared to a maize monocrop. During absence of nitrogen fertilizer, intercropped legume will fix nitrogen from the atmosphere and not compete with maize for nitrogen resources. The mixture of nitrogen fixing crop and non fixing crop give greater productivity than mono-cropping. Banik and Sharma (2009) reported that cereal-legume intercropping systems were superior to monocropping. Maize + French bean gave high maize equivalent yield over sole yield and kernel yield of maize was unaffected in maize + French bean intercropping. Akinnifesi et al (2006) revealed that without nitrogen fertilizer application, gliricidia + maize intercropping system gave high maize yield. West and Griffith (1992) observed maize yield was increased by 26% in maize + soybean strip inter-cropping. Sharma and Tiwari (1996) reported that tomato intercropped with maize increased the number and weight of fruit per plant and total yield. In maize-okra intercropping, yield and yield components of okra was increased. Maize-Kenaf-African yam bean intercropping gave highest value of LER compared to monocropping (Adeniyi et al 2007). Maize with pumpkins gave high LER (Cortes and Los 1997). Maize + potato intercropping performed better than sole potato (Begum et al 1999) and maize yield was not affected due to intercropping (Ifenkwe et al 1989).

Physiological principles of dry land crop production, constraints and remedial measures
Any environmental factor potentially unfavorable to plant is termed as stress. The effect of stress on plant condition is called strain. According to Newton's law of motion, a force is always accompanied by a counterforce, for an action there is always equal and opposite reaction. Stress is the action and whereas strain is the reaction. A body of a plant subjected to stress is in a state of strain.

Strain may be elastic or plastic strain.

Elastic strain
Up to a point, a strain may be completely reversible and when the stress is relieved, the plant becomes normal.

Plastic strain
Beyond the point of elastic strain, the strain may be partially reversible or partially irreversible, which is called plastic strain or permanent set.

The Environmental and Physiological Nature of Stress
Drought (and extreme temperature) is an environmental occurrence that can be defined and measured by indices derived from large historical databases on precipitation and other weather variables. Several drought indices are in use. Among these, the ‘Palmer Index’
seems to be widely adopted among climatologists.

**The development of plant water deficit**

Plant water deficit develops as its demand exceeds the supply of water. The supply is determined by the amount of water held in the soil to the depth of the crop root system. The demand for water is set by plant transpiration rate or crop evapotranspiration, which includes both plant transpiration and soil evaporation. Evapotranspiration is driven by the crop environment as well as major crop attributes such as plant architecture, leaf area and plant development. The plant functions within a physical system consisting of the soil-plant-atmosphere continuum. During the day the plant is under heavy energy load consisting mainly of the received solar radiation, ambient air temperature and humidity (VPD). While a fraction of this radiation energy is important for photosynthesis (photosynthetically active radiation), most of the total received radiation is not utilized and it must be dissipated. It is partly dissipated by radiation emitted from the plant in the form of heat, but most of it must be dissipated by transpiration. Henceforth the term "transpirational cooling" was coined. Transpiration causes leaves to cool relative to ambient temperature when the environmental energy load on the plant is high. If it were not for transpiration, leaves could be heated to killing temperatures.

Water is driven through the plant from the soil to the atmosphere by the difference in water potential between the atmosphere (very low potential) and the soil (relatively high potential when wet), analogous to the flow of electrical current under the differences in electric potentials (‘Ohm’s law’). Flow is also influenced by hydraulic resistances in the plant, such as the resistance regulated by stomata in the leaves or by the conductive system (root and stem xylem elements) of the plant, or by the resistance of cells and cell walls between soil and the root xylem vessel. Even cellular membranes can regulate the flow of water through the membrane by embedded proteins known as aquaporins.

As water transpires from the leaf, leaf water potential (LWP) is reduced (becoming more negative) (Fig.44). If water is available in the soil (at high soil water potential) then water will flow into the leaf to replenish the loss with only a small reduction in LWP. As soil water potential (SWP) is reduced LWP must be further reduced in order to create the necessary gradient differential ("pull"), which would drive the water up from the drying soil to the leaf.

![Fig 44. A schematic representation of the components of leaf water status during a soil drying cycle. SWP– soil water potential; LWP- leaf water potential ($\psi_w$); OP-s and OP-r represent two different cases of change in osmotic potential ($\psi_s$) with the reduction in LWP.](image)
The leaf cells contain various organic and inorganic solutes, which determine the leaf osmotic potential (OP). OP is lower (more negative) than LWP and the difference between the two is turgor potential. Turgor is lost (null value) when LWP=OP (in Fig.44, at about –3.0 or -4.0 MPa on days 8 and 16, respectively).

Leaf turgor is associated with cellular growth and function. When turgor becomes null cells collapse and the leaf wilts, though it is not dead. Stomata are responsive (among other factors) to turgor, and close to reduce transpiration. The reduction in stomatal conductance also causes a reduction in CO$_2$ fixation and photosynthetic assimilation and an increase in leaf temperature. The increased leaf temperature may reach a level causing heat damage to the leaf especially under hot conditions.

Turgor maintenance and transpiration are therefore crucial to plants under drought stress. Turgor can be sustained by keeping a high LWP through water uptake from the drying soil or by reducing OP through cellular solute accumulation (which is defined as “osmotic adjustment”). In Fig.44 OP-s represents a variety with little osmotic adjustment (OA), where turgor is lost at a LWP of –3.0 MPa on day 8, as compare with variety OP-r where due to its greater capacity for OA turgor is lost only on day 16 at LWP of -4.0 Mpa. Hence, OA delays turgor loss and wilting. Further details on OA are given in the Drought Mitigation/Drought Resistance section.

Turgor can also be maintained by cell wall hardening during the development of water deficit. While cell wall hardening helps to sustain turgor, it impedes cell growth. This is only one of the many examples where the maintenance of plant water status under drought stress might partly be achieved at the cost of reduced growth.

Besides the factors controlling transpiration at the single leaf level, a most dominant factor in controlling whole plant and crop transpiration is total leaf area. When grown in a pot a large plant will require irrigation more frequently than a smaller one for the same pot volume. A major avenue by which plant evolution served to adapt plants to dry environments is by reduced plant size and growth rate, typical of many xerophytic plants. It is also a common observation that when severe water deficit develops, lower (older) leaves are desiccated and die first so as to reduce leaf area and water requirement, while upper (younger) leaves retain open stomata and carbon assimilation.

At the crop level plant size and the demand for water is mainly expressed by leaf area index (LAI), which is the total area of live leaves per unit ground surface (m$^2$ m$^{-2}$). Crop evapotranspiration (ET) increases with LAI until LAI reaches a maximum threshold beyond which ET does not increase. As the crop matures and leaves senesce, LAI is reduced and so does ET.

Cellular turgor is not the only important transducer of whole plant water stress. The growth regulating hormone abscisic acid (ABA) is produced in the shoot in response to desiccation, causing many of the known expressions and consequences of plant water deficit such as arrested growth, stomatal closure, and reproductive failure. ABA is also produced in the root in direct response to the drying soil and its hardness as it dries. ABA flows with the transpiration stream to the shoot. Since the soil may dry around only some of the roots (typically in the top-soil) while most roots are in wet soil, root ABA exported to the shoot may cause stomatal closure or arrested growth before any water deficit develops in the shoot.
This "hormonal or chemical root signal" may therefore serve as an "early warning system" to the plant. The function and value of this “root signal” in a crop plant subjected to drought stress has not yet been fully resolved. Without entering a long review and discussion it can be postulated that low ABA production or low shoot sensitivity to ABA might be beneficial in most cases of a crop in an agricultural ecosystem. The overall agronomic role of ABA is still under debate and unresolved. In the evolutionary sense it may well serve as a major signal to place the plant in a dormant and a life conserving state before it enters sever desiccation.

**Measuring plant water stress and water status**

Sensing and estimating plant stress at the whole crop level in the field is difficult mainly because of the need to integrate an estimate based on the whole canopy. Remote sensing technology enabled to develop the Crop Water Stress Index (CWSI). This index is developed mainly from measuring the canopy temperature with an infrared thermometer. Infrared remote measurement of leaf temperature is based on a relationship between leaf temperature and transpiration. Generally, as transpiration rate is reduced due to plant water deficit so does leaf temperature rises relative to air temperature. CWSI is mainly applied to irrigation scheduling, but can be applied to non-irrigated conditions. However, basic infrared thermometry in terms of canopy temperature differences among genotypes is used in phenotyping and selection work towards breeding for drought resistance.

Several direct measurements can be performed on single plants and leaves in order to assess their water status, stress status, the repercussions of water deficit and its physiological consequences. Here only the most essential and widely used measures of plant water status are mentioned.

**Leaf water potential** (LWP) can be measured in detached leaves or tissues by quickly sampling the leaves and putting the sample into the measuring instrument. Measurement can be done by the pressure chamber (Fig.45), which is suitable also for fieldwork. When a leaf (or a stem) is cut off a plant, the sap is sucked back into the xylem, since it is under tension. That tension is broadly equal to LWP. The detached leaf is therefore sealed in a steel chamber with only the cut end protruding out. Pressure is applied to the chamber (from a pressure source such as a compressed nitrogen gas).

When the sap meniscus appears at the xylem surface the pressure is recorded and taken as the xylem (leaf water) potential. Typical LWP of live transpiring leaves can range from about -0.3 MPa to –2.5 MPa.

![Fig.45. The pressure chamber; (A) pressurized gas cylinder; (B) the chamber pressurizing valve; (C) pressure gage; (D) the chamber; (E) magnifying glass. (A self made unit – not recommended to follow suit).]
The thermocouple psychrometer is a more elaborate method that is more suitable for lab conditions. The instrument was initially built by the scientists themselves until commercial systems were put on the market. With the basic design the tissue sample is sealed in a small chamber containing a thermocouple. After an equilibration period a cooling current is applied to the thermocouple in order to condense water on the junction. The amount of condensed water is proportional to the water potential of the tissue. That water is allowed to evaporate causing a change in the thermocouple output. That output is calibrated for water potential, using salt solutions. The method has been adapted also to measurement in situ by attaching a specially designed sensor to the leaf. The In situ psychrometric method did not receive wide adoption as compared with other methods.

The pressure probe for measuring turgor pressure is restricted to work with singular cells. With this method a small capillary tube filled with oil is used to puncture a cell. The oil is pushed back into the tube in proportion to the cellular turgor pressure. Applying and measuring a balancing pressure to the probe estimate pressure.

Relative water content (RWC) is a veteran method that has recently gained favour over LWP as a very relevant physiological measure of plant water deficit. Its advantage is that it accounts also for the effect of OA in affecting plant water status. Two plants with the same LWP can have different RWC if they differ for OA.

Osmotic potential (OP) is determined in freeze-thawed killed tissue, which serves to release all cellular solutes. The potential recorded in such a sample by the thermocouple psychrometer is OP. Alternatively if a drop of solute can be obtained by squeezing the killed tissue or by centrifugation then it can be measured for OP with a standard (micro) osmometer. Turgor is estimated as the difference between LWP and OP. Turgor is null when LWP=OP (Fig.44). When turgor estimates are required both LWP and OP should best be measured by the same technique, for example with the thermocouple psychrometer.

Osmotic adjustment (OA) is defined as the net accumulation of solutes after the plant has been exposed to a predetermined rate of water deficit. The reduction in OP during water deficit is not an estimate of OA because it is caused by both cellular water loss (a mere concentration effect) and real cellular solute accumulation (OA). OP is measured in the tissue of a tressed plant and OA is calculated as the difference between measured OP and OP estimated for a non-stressed fully turgid state. Alternatively, water deficit is applied to a predetermined level of stress (say 70% RWC) after which the plant is fully rehydrated (typically overnight). OP is then measured and compared with that of a fully hydrated non-stressed plant. It is crucial to remember that OA is proportional (non-linearly) to the rate of water deficit over time. When different genotypes are compared, careful application of drought stress must be applied to all for an extended period of time to a predetermined level of water deficit, best measured by RWC. The difference between the two measures of OP is OA, and the method is defined as the “rehydration method”. A more accurate but a resource demanding method involves the derivation of OA from the relationship between OP and RWC during a drying cycle. Typical OA values for crop plants can range from null to around 1.5 MPa.
Leaf pressure-volume curve
This is an elaborate laboratory method which can estimate various water status related attributes in a single detached leaf. These are: relative water content at zero turgor, osmotic potential at full turgor and at zero turgor, modulus of elasticity at full turgor, and relative and absolute capacitances at full turgor and at zero turgor. The method involves the development of a curve for each detached drying leaf sample between leaf water potential as measured by the pressure chamber and the respective mass of water loss from the leaf. It therefore involves repeated measurements over time of leaf water potential and leaf weight. The method is impractical for large scale phenotyping but is important in certain physiological studies.

Transpiration and stomatal conductance
There are numerous methods for measuring transpiration from single detached leaves, whole plants and whole canopies in the field. Methods vary in applicability, accuracy, cost and speed.
Field methods are often based on measuring the amount of water lost from the soil profile over time which represents evapotranspiration. An indirect estimate uses the crop energy balance which requires the measurements of certain given environmental and/or plant variables, depending on the model.
The classical gravimetric method is the oldest and in many cases the most real. It is based on the amount of water lost from a plant grown in a container or from a detached leaf, with known leaf area. Water loss from a pot represents transpiration if soil evaporation is accounted for or eliminated.
Leaf porometers were developed to measure transpiration from intact leaves in the field or the laboratory. The most common technical principle is the exposure of a humidity sensor to the transpiring leaves under standard cuvette conditions (the ‘diffusive resistance porometer’). Porometers vary in function and specifications, where some constitute only a part of a more elaborate system of monitoring total leaf gas exchange. The pressure-drop (or viscous flow) porometer was designed and used in the 1960’ to 1980’s. It is based on the relationship between stomatal conductance and the flow of pressurized air across the leaf. Judging by popularity it seems that this system was dropped in favour of the diffusive resistance porometer, which is also readily available commercially.
The sap-flow method is essential with trees, where transpiration is difficult to measure by other methods. It has been adapted also to certain crop plants such as maize or cotton. This method broadly estimates plant water use by the velocity of sap flow upward in the trunk/stem. A heat pulse applied to the trunk/stem at one point and then sensed above the point of application which allows to calculate sap velocity.

Measuring Soil Moisture
Soil moisture content (by volume) and status (by potential or tension) is a major variable affecting plant water status and crop water-use. Extractable soil moisture is the amount of water that a given crop can extract from the soil to a given soil water potential and soil depth.
Generally, different crops can use 50% to 80% of the extractable soil moisture before crop transpiration is reduced and plants present symptoms of water deficit. These values change with crop, soil and atmospheric conditions. The determination of soil moisture content or status is of major consideration regarding plant water relations.

Methods of testing soil moisture vary from feeling the soil by hand to remote sensing it from aerial or even space platforms. Methods vary in accuracy, cost, convenience and purpose. The basic method is the ‘gravimetric’ where soil samples are taken with an auger and their moisture content is determined by weighing before and after drying in an oven. This remains the benchmark for all other methods. More advanced methods are represented by the ‘Neutron scatter method’ and ‘Time-Domain Reflectometry’ (TDR) method. One popular method used in irrigation is the tensiometer. Regrettably tensiometers found their way into being used in studies under severe soil moisture stress. It should be remembered that the tensiometer is not functional around soil moisture potential below -0.05 to -0.1 MPa (ca. 0.5 to 1 bar) depending on the make.

The repercussions of plant water deficit

It is not quite clear which are the primary sensors of cellular dehydration and their order of importance or function, be it cellular water status, pressure, bound water, hormones, cellular membrane functions or other agents. It is not perfectly clear how cells perceive cellular water deficit and how cellular water deficit is transduced and transcribed into the various consequences of this stress, be it adaptation or mortality. Furthermore, it has not been clearly established which of these responses are stress adaptive and which are expressions of cellular degradation, shutdown or apoptosis. While certain researchers declared a consensus about a given issue, others did not agree. The working hypothesis underlying current research in this area (Fig. 46) recognizes multiple signal transduction pathways between stress perception and gene expression. Two major possible pathways transcribe the perception of this signal; one involving ABA production and the other is ABA independent. The ABA independent pathway is not fully resolved. In the ABA dependent pathway ABA induces novel protein synthesis, which regulates numerous "ABA responsive" genes. ABA may regulate stress responsive genes without novel protein synthesis. These gene products are either functional (e.g. water-channel proteins or key enzymes) or regulatory (e.g. protein kinases) and they are involved in mediating various cellular responses some of which are recognized as adaptive.

The interface between the molecular domain involving stress responsive gene expression and whole plant response and adaptation to drought stress is yet to be fully resolved. This
interface is critical for translating molecular genetics science into advances in crop production under stress conditions. At present there are thousands of recognized ‘drought stress responsive genes’ which are up-regulated or down-regulated under the effect of dehydration and the function of only a few has been firmly established with respect to plant adaptation in an agricultural ecosystem.

At the whole plant and the crop level, the important repercussions of water deficit are mediated by effects on growth, plant phenology, phasic development, carbon assimilation, assimilate partitioning and plant reproduction processes. These major effects account for most of the variation in crop yield caused by drought stress. Growth depends on cell expansion and cell division. Cell expansion is relatively more sensitive to water deficit. Cell expansion depends on the maintenance of turgor, cell wall extensibility and other factors possibly pertaining also to ABA signalling. Reduced cell expansion and growth as a primary response to water deficit serve to moderate plant water use but also lead to reduced plant productivity. If the reduction in total plant water use is not sufficient to sustain turgor, then transpiration is further reduced by stomatal closure. Initially, stomatal closure reduces transpiration more than it reduces CO\textsubscript{2} assimilation so that water-use efficiency appears to increase. At advanced stress both are reduced drastically. Wilting is an expression of turgor loss and it is expressed in a specific ways according to plant species, such as the case of leaf rolling in the cereals (Fig. 46).

Reduced cell expansion also carries a primary effect on meristem differentiation and growth such that size of various plant organs is reduced. In grain crops this directly lead to reduced yield components, such as inflorescence size or tillering in the cereals. This is an irreversible structural effect that is difficult to amend by re-watering. It can however be amended to some extent by inter-organ compensation following watering, such as renewed tillering in the cereals. The meristematic tissues are generally positioned within the plant in a relatively protected environment as compared with that of a fully expanded leaf and therefore it may take a severe stress for meristem to lose its turgor. However, ABA transported from stress-affected organs or roots in a drying soil can also arrest meristem development even at relatively high meristem water-status. Thus for example, ABA might affect reproductive failure via pollen dysfunction when water status is not very low.

Water deficit cause advanced or delayed flowering, depending on the species (for example, wheat and rice, respectively). ABA may have a role in this respect as it has been shown to delay flowering in tomato and maize. A delay of up to 50 days has been seen in rice subjected to pre-flowering drought stress. The effect of drought stress on phasic development has been shown to be crucial in affecting maize yield under stress. In maize stress cause a delay in female organ development while the male inflorescence is less affected. Hence, stress causes an increase in the time interval between silking and anthesis. A short anthesis-
to-silking interval (ASI) has been shown to be a main feature of drought resistance in maize. It is widely agreed that the reproductive growth stage is the most drought-sensitive stage. Water deficit can cause reproductive failure. Pollen or pollen mother cells are generally more sensitive to desiccation than the ovary so that male sterility is a common result of drought stress during flowering. Reduced grain set of wheat under drought stress has been ascribed to ABA accumulation in the shoot. An ABA responsive gene has been found in the floral parts of tomato. There are some interesting reports showing that grain set of maize subjected to drought stress could be partially improved by the experimental infusion of sugar solution into the stem, leading to conclude that sugar starvation could be an additional factor in affecting grain set and ovary abortion under stress. Short supply of carbohydrates could very well be a generally important factor in the abortion of fruit under drought stress. Shortage of assimilates and sometimes nitrogen availability is a major cause of arrested grain and fruit growth during drought stress. Drought stress during cereal grain development reduces the duration of grain filling. If the rate of grain filling is not adjusted upward, final grain weight is reduced. Increased grain growth rate under drought stress depends on the supply of assimilates. This supply is becoming short due to the inhibition of current photosynthesis during stress. An alternative source of stored stem reserves in the form of sugars, starch or fructans, depending on the species. These reserves can be readily utilized for grain filling and their availability may become a critical factor in sustaining grain filling and grain yield under drought stress. Root/shoot dry weight ratio increase as plant water stress develops. The increase is mostly due to a relative reduction in shoot dry weight. However there were rare cases where an absolute amount of root dry weight increase was observed under drought stress. ABA may have a role in promoting root growth under drought stress. Osmotic adjustment has also been found to improve deeper root growth under stress. Most certainly root distribution within the soil profile changes as stress develops, in a way that helps the plant to explore deep soil moisture. In the cereals, dry topsoil inhibits the formation and establishment of new roots in the topsoil while assimilates partitioned to the root are used in furthering the growth of existing roots into deeper soil. In the small grains and rice, tillering is associated with the development of new roots from tillers. Therefore, extensive tillering is generally associated with dense and shallow roots while limited tillering tends to associate with sparser and deeper roots. This is one of the reasons why most cereal crop cultivars developed in dry regions tend to have a limited tillering habit.

**MITIGATION OF DROUGHT STRESS BY CROP MANAGEMENT**

**Managing drought stress by supplemental irrigation**

Irrigation, where available, is the major means for combating drought conditions. It is a prime approach to the intensification of agriculture and the generation of stable income. The development of irrigation depends on various environmental, economical and social factors on both the macro and micro scales. There are hazards in irrigation if practiced indiscriminately, such as soil erosion, soil salination, soil leaching and soil disease infection.
General Crop Irrigation Guidelines
The key to planning irrigation system and scheduling is knowledge of the crop, the soil properties and the potential evapotranspiration (PET) of the specific crop. This information can also be used to estimate dryland crop water use and deficit at any given time during the crop cycle, which is actually an index of crop drought stress.

The Penman-Monteith potential evapotranspiration equation is recommended as the standard method for estimating reference and crop evapotranspiration. The new method has been proved to have a global validity as a standardized reference for grass evapotranspiration and it has been recognized by both the International Commission for Irrigation and Drainage and by the World Meteorological Organization.

The (FAO) Penman-Monteith method was developed by defining the reference crop as a hypothetical crop with an assumed height of 0.12 m having a surface resistance of 70 s m$^{-1}$ and an albedo of 0.23, closely resembling the evaporation of an extensive surface of green grass of uniform height, actively growing and adequately watered.

Irrigation to Control Drought in Various Crops
Deficit (or supplemental) irrigation is the more common irrigation practice for crops not designated \textit{a priori} for fully irrigated conditions and maximized yield. Supplementary irrigation is a practice dictated by constraints, which can be derived from the limited availability of water, irrigation equipment, the cost of water, or other economic and technical constraints. With supplemental irrigation the amount of water applied to the crop in irrigation is well below the full requirement of the crop. The water-use efficiency of supplemental irrigation is generally high if applied logically. It can be applied to save the crop in case of un-expected drought or as a planned practice to supplement the expected total seasonal rainfall. The practice may vary extensively with crop and region. In many environments, and especially the Mediterranean region, if only a single supplementary irrigation is given it is usually more effective if applied pre-planting. As such the crop enters the season with a stored supply, which can insure growth despite unexpected transient rainfall fluctuations.
Managing the Dryland Crop Environment

Modern dryland farming is a system of low inputs combined with soil and water conservation practices and risk reducing strategies. The system can be sustainable if practiced properly. Water shortage is the main limiting factor, but successful dryland systems also maintain reasonable practices to eliminate other limiting factors (poor nutrient status, weeds, biotic stresses, etc’), which can reduce the effectiveness by which the crop uses the limited moisture. However, as water shortage \emph{a priori} dictates a limit on yield, all other inputs must be carefully adjusted downwards to fit the expected low economic return.

The most advanced systems have been developed in the Great Plains of the USA, Canada and Australia, while traditional systems employed in Asia and the Middle East also offer important insights. In the USA, the lesson learned during the "dustbowl" years in the early 1930’s prompted extensive legislation and investments in developing sustainable dryland farming systems. These systems and the associated technological progress such as plant breeding, brought about an increase in mean winter wheat yield from \(0.5 \text{ t ha}^{-2}\) in 1930 to \(2 \text{ t ha}^{-2}\) in 1980. In Southern Australia the "ley farming" system was developed in the 1920’s and adopted widely in the late 1940’s. The system involves a rotation between a self-seeding legume grown for several years and wheat. The farmer grows wheat and raises sheep while the legume serves to sustain soil fertility (mainly nitrogen). This system has become less popular in recent years with the increase in economic pressures and other considerations.

The lesson learned from the American and Australian experience is that the development of a sustainable dryland farming system involves the following principles, not necessarily in their order of importance:

1. Improved soil and water conservation practices and the associated reduced tillage systems.
2. Optimization of the fit between crop growth cycle and the available moisture.
3. Weed control.
4. Soil fertility management.
5. Optimized plant population density and spatial arrangement of plants with respect to the expected soil moisture regime.
6. Control of soil biotic stress factors that reduce root development.
7. Improved forage/livestock/grains integration and rotation.
8. Avoidance of mono cropping and enhancement of crop diversification.
9. The increase of precipitation by cloud seeding, as an ongoing experiment.

Some of the above principles of the dryland farming system constitute general knowledge in agronomy. Here only several topics will be touched upon.

Soil and water conservation

Fallow and conservation tillage

The fallow system is designed to conserve soil moisture from one season to another or from one year to the other, depending on climate and crop. Increasing storage of soil moisture by the fallow system with or without conservation tillage is standard agricultural practice in dryland farming. The benefit of fallow and conservation tillage in terms of increasing available soil moisture to the crop depends on soil water-holding capacity, climate,
topography and management practices. Fallow efficiency, in terms of percent increase in soil moisture availability to the crop measured at planting date normally ranges from about 5% to 30%. While these amounts are not impressive, they can make a difference between crop failure and success. The fallow carries additional benefits such as improved soil nutrients availability and the eradication of certain soil-born pests, such as nematodes.

Conservation tillage is not a novel concept or practice, which has recently gained wider and sometimes an enthusiastic acceptance. It involves the principle of minimized tillage operations to conserve soil structure and to maintain ground cover by mulch, such as stubble. These practices reduce water runoff and increase soil infiltration. Conservation tillage has become the cornerstone of dryland systems (in the USA, Canada, Australia, and other regions). While the benefits of conservation tillage are well-documented, it has also been noted that crop residues under this system may promote certain crop diseases. Deep tillage is a system to overcome hardpan, very high bulk density and compacted soils. It can be performed by deep plowing or deep ripping. Deep plowing involves actual plowing to depth which is an expensive operation. It is uncommon in dryland farming. Deep ripping is less expensive and often used in crop production. The important consideration in deep ripping is to operate at the correct depth in order to break the hardpan, no less and no more.

**Furrow dikes and Soil pitting**

These techniques constitute a field surface tillage manipulation to minimize runoff away from the field. *Furrow dikes* are furrows, which are divided into short basins by small dikes (see right side photograph). This is achieved by special equipment. The system is very amenable to row crops such as cotton, corn, and sorghum and it can be integrated with or without furrow irrigation. It is generally considered effective for increasing rainfall capture and raising dryland yield where annual rainfall ranges between 500 and 800 mm. *Soil pitting* (left side photograph) involves the formation of small depressions at close proximity to reduce runoff from rainstorms. The crop is planted over this modified surface. Experiments performed with wheat in nine farmer demonstration plots in Southern Israel during 1988 showed that pitting increased yield by an average of 7.5% at a mean yield of 3.25 t/ha. Unlike furrow dikes, these systems are not limited to row crops.

**Water harvesting/spreading**

This is a broad term to describe various methods to collect runoff from large contributing areas and concentrate it for use in smaller crop area. This is an ancient practice. Presently, the basic water harvesting systems involve an external contributing area to induce runoff. This area is physically or chemically treated for maximizing runoff. The water is diverted into a receiving area comprising of cultivated plots, individual trees or small terraces. The contributing area may lie in the agricultural field (a system sometimes referred to as "conservation bench terrace") or outside the field in the natural watershed system. The size ratio between the contributing and the receiving areas is determined by the expected
rainfall events, crop water requirements, soil characteristics and topography. The resulting yield increase in the receiving (crop) area is proportional to the amount of water gained.

**Diversification of farming**

Diversification of farming is an ancient but an effective approach to reduce the risk associated with farming in unpredictable environments. Reduced diversification to the extent of mono-cropping is possible only with a high level of control over the crop environmental conditions. Such control method (irrigation, chemical pest control, etc’) are among the main reasons for the more recent environmental quality problems found to be associated with mono-cropping. Diversification of cropping to reduce risk is especially important under dryland conditions. It is achieved on several levels, as described by Pandey et al for the case of traditional rain-fed rice in Eastern India.

1. **Spatial diversification of fields.** The farmer’s land is divided into several fields or plots which may differ in their topography, soil and hydraulic properties. Some fields may be prone to flooding while others do not hold water. Certain fields may be on a warmer slope while others on a cooler one. The different field conditions allow to achieve a better fit between the crop and the environment and to reduce the general probability of stress affecting the farmer.

2. **Crop diversification** is an important feature of traditional farming. It takes an advantage of the generally low correlation between crops in performance when grown in a single stress environment. Crops differ in their response to a given environment and this difference is used to reduce the risk associated with growing one crop. “Mixed cropping” or “intercropping” is an example of a traditional and a successful approach to crop diversification on a single parcel of land, where two or more crops are grown together in various possible configurations. If for some reason only one crop is grown, a certain (though lower) level of risk reduction can be achieved by varietal diversification. Planting several crop varieties offer a better probability for reducing loss due to environmental stress, as compared with growing one variety only. For environmental stress conditions varietal diversification is based mainly on differential phenology, primarily flowering date. A typical example is a transient frost or heat wave that is likely to occur around flowering time of the specific crop. Damage reduction can be achieved when the crop is sown to several varieties of different flowering dates.

3. **Temporal diversification** may achieve the same result as varietal diversification, when phenology is concerned. The purpose of setting a distinct planting date is to optimize crop development with respect to seasonal climate, mainly rainfall in rain-fed agriculture. Ideally the crop is planted at the beginning of the rainy season, rainfall peaks when crop evapotranspiration peaks and it terminates just before harvest time. When such conditions are reasonable predictable, planting date can be set to optimize production. Where the timing of rainfall is very unpredictable, adopting more than one planting date for the given crop can reduce the risk involved with untimely rainfall and a given planting date.
Cloud seeding
Cloud seeding is a form of weather modification attempt. The process of cloud seeding involves deposition of cloud condensation nuclei (CCN) into a specific region of the cloud. Seeding may be achieved from above or through the clouds by aircraft, and from below where CCN are carried into the cloud by updrafts. With either method, the CCN must reach the super cooled cloud region, where water molecules remain unfrozen at temperatures below 0 °C. Experiments in cloud seeding have been performed for the last 60 years. The results and benefits of this practice are still under debate.

MITIGATION OF DROUGHT STRESS BY CROP PLANT BREEDING
The nature of drought resistance
Drought Resistance and Crop Yield

Crop plant breeding for drought resistance has long been part of the breeding process in most crops that are grown under dryland conditions. During the period of the pre-scientific agriculture the genetic improvement of plant adaptation to dry conditions was simply attained by repeatedly selecting plants that appeared to do well when drought stress occurred. As a result of many generations of selection by generations of farmers we now encounter such materials, which are defined as “landraces” of the crop. Such landraces were shown to possess distinct drought resistance traits. Later, as scientific agriculture developed and following the emergence of Mendelian genetics, elaborate biometrical and statistical methods for quantitative genetics analysis were developed to enable selection for yield and yield stability more effectively and efficiently. An important factor of yield stability is coping with drought and other abiotic plant stresses. As crop physiology emerged and developed, yield-based selection programs were augmented by observing plants under carefully managed stress environments, followed by the development of physiological selection criteria for stress resistance. More recently, molecular methods, such as marker-assisted selection are being adopted to facilitate more efficient selection for distinct components of abiotic stress resistance. Finally, biotechnology is experimenting with genetic transformation, open the way for additional genetic solutions to breeding for drought resistance.

Looking at crop drought resistance from a botanical perspective it must be realized at the onset that there is a vast difference between drought resistance in natural vegetation and in crop plants. Natural vegetation has evolved to conserve the species. Henceforth, plant survival and the capacity to produce at least one seed per life cycle despite stress is the most powerful component of natural selection. On the other hand, drought resistance in modern agriculture requires sustaining economically viable plant production despite stress. Crop
survival is of a lesser consequence to economical farming. On the other hand, plant survival can be a critical factor in subsistence agriculture, where the ability of a crop to survive drought and produce some yield at all may translate into a difference between famine and livelihood. Breeding for drought resistance is therefore very tightly linked to the target environment of the crop, not only with respect to its physical and chemical features but also its social grounds.

For a variety of reasons there is a general trade-off between a genetically high yield potential and drought resistance. At the same time there is a yield advantage under drought stress brought about by a high yield potential, to a limit. This is explained very briefly here through Fig.47.

Wheat cultivar C is different from A and B in that it has a lower yield potential (yield at high moisture conditions) but as moisture becoming deficient C turns out to be superior to A and B. In terms of yield, C may be defined as drought resistant while cultivars A and B are of high yield potential but are relatively drought susceptible. The “crossover” where the advantage of C over A and B under stress begins to be expressed is at about 300 mm or at a yield level of about 300 g m\(^{-2}\). Hence, drought resistance of C is expressed only when stress is severe (<300 mm). Still, it is extremely important to realize that the high yielding cultivars A and B are superior to the drought resistant C when drought stress is moderate (e.g. at 400 to 500 mm). A high yield potential therefore ascribes an advantage under moderate stress conditions. On the other hand Fig.47 indicates that by definition drought resistant cultivars have lower yield potential. Cases where drought resistance has been improved together with yield potential exist but they are very rare and exceptional and cannot be used to indicate a general rule. With the available evidence the rule seems to be with Fig.47, with exceptions. Fig.47 also implies that breeding for real drought resistance is not required if yield in the target environment is not reduced (schematically) to below 300-400 g m\(^{-2}\). On the other hand, real drought resistance cannot be field-tested or evaluated if yield level is above around 300-400 g m\(^{-2}\), schematically. Consider the principle not the actual numbers. The actual numbers were obtained for wheat and barley by several studies.

**The components of drought resistance**

Drought resistance in crop plants is conditioned by two major pathways: Dehydration avoidance and dehydration tolerance. Dehydration avoidance is the capacity to avoid plant tissues and cells dehydration under drought stress. Dehydration tolerance is the capacity to sustain function when the plant is dehydrated. Plant survival can be conditioned by either avoidance or tolerance.

Moisture stress signals the expression of certain stress responsive genes, which are responsible for a chain of events and gene “networking”, expressed at various levels of plant organization. It has been assumed almost axiomatically that stress responsive genes are involved in adaptation; henceforth that they are ‘stress adaptive’. It was later realized that not every stress responsive gene is necessarily adaptive in terms of drought resistance or survival or crop productivity under moisture stress.

Irrespective of the role and function of stress adaptive genes in plant drought resistance, it should be recognized that not only certain stress adaptive genes might determine plant performance under drought stress, genes that are expressed irrespective of the environment
also condition plant function and performance under stress. These genes are expressed constitutively and determine various plant traits irrespective of any stress. An example for a constitutive plant trait that may control drought resistance is potential root depth (maximum root length). Stress and soil conditions can affect root depth in several ways but potentially a deep rooted genotype will maintain its advantage over a potentially shallow rooted genotype under conditions of deep soil moisture. For this difference to be expressed plants do not have to be subjected to drought stress conditions. Therefore, drought resistance and plant production under drought stress is determined by constitutive and adaptive plant traits.

Dehydration Avoidance

Plant development and size

Plant size as expressed mainly in terms of single plant leaf area or leaf area index (LAI) has a major control over water-use, as explained earlier. Small plants and reduced leaf area are generally conducive to low potential productivity. Botanists have long recognized small plants bearing small leaves as typical ecotypes of xeric environments. While such plants withstand drought very well their growth rate and biomass are relatively low.

In the domain of plant breeding, cultivars developed for dryland conditions by selecting mainly for yield under such conditions often resulted in plants of moderate size and water-use. For example this can be seen in dryland temperate cereals as well as upland rice, which tend to have moderate tillering. On the other hand it has also been shown that early plant (and seedling) vigour are important traits for dry conditions. The reason is in the rapid ground cover achieved and the subsequent decrease in water loss by direct soil evaporation at this stage. However, other benefits for seedling vigor were also noted, such as the nitrogen status of the plant. Early flowering which determines ‘drought escape’ generally involves a reduction in adult plant size and leaf area leading to reduced water-use. Thus, small plant size and small leaf area are very often linked to improved dehydration avoidance and lower potential yield, a tradeoff discussed elsewhere.

The Root

The most important control of plant water status is with the root, whereas the roots is the main engine for meeting transpirational demand. Two major dimensions describe the root: root depth (or maximum length) and root-length density (Fig.48). The more practically and commonly important dimension for most breeding scenarios is root depth, which facilitate deep soil moisture extraction where such moisture is available. It is a primary component of drought resistance. The development of lateral roots at very shallow soil depth may have a role in capturing small amount of intermittent rainfall.

Root depth in the cereals is generally associated with a small number of main thick axes. Such fibrous root system is typically seen in upland
rice, which has a deeper root system, in contrast to lowland rice with the shallower roots. The control of root growth is not only in the root. In the cereals, tillering is associated with production of new crown roots from each developing tiller. Such profuse rooting can be at the expense of the growth of existing roots into deep soil. Hence, limited tillering in cereals and grasses has been repeatedly observed to be associated with relatively deeper root extension.

In certain soils a hardpan can limit deep root growth and the capacity for hardpan penetration by roots becomes a critical factor in drought resistance. The factors, which may support axial root force and hardpan penetration, are not known and most research in this area has been performed mostly with seedlings. In mature plants the penetration of hardpan by roots seems to be better in plants that constitutively develop fibrous and thick roots.

Many drought environments present a situation where rainfall is low and soil depth that contains moisture is permanently shallow. For example, in many of the drier Mediterranean wheat-growing regions the wetted soil depth of around 60-80 cm is shallower than the normal maximum root depth of wheat (≥100 cm). Under such conditions a deep root is not an issue. Other plant factors may then become far more important in the control and use of the limited soil moisture, such as shoot developmental characteristics (e.g. leaf area development or growth duration), osmotic adjustment, leaf surface properties, etc. Greater root length density within this limited soil horizon might allow extracting more moisture from a given soil volume which in certain cases should provide several more days before wilting.

Another scenario of seasonal soil moisture status is where the crop is grown on stored soil moisture and there is little effective rainfall during the growing season. Under such conditions the main consideration is to manage seasonal soil moisture use such that sufficient moisture will remain for carrying the crop to maturity. It is to be expected that with the available moisture the crop might grow luxuriously leading to a large leaf area and an even greater water requirement towards the latter part of the season. Hence, short growth duration, small leaf area and perhaps a higher root hydraulic resistance can achieve the control of seasonal water use. The last option has been researched at the CSIRO Australia and an increase wheat root hydraulic resistance was effectively attained by selection for smaller root xylem element diameter. It is not known whether this approach has found its way into actual application in wheat breeding or whether such a cultivar was released.

Whatever may be the constitutive form and function of roots, the environment can modify the root in a pronounced way. Of course, soil conditions in terms of topsoil moisture and deep soil hardness alter root growth and depth. Drought stress generally inhibit total root mass (while it can modify its distribution). Root-length density may locally increase in wet regions in the soil while it might decrease in the drying parts. As soil moisture deficit develop throughout the profile, the proportion of dry to wet soil increase so that the proportion of dead to live roots increase. There is hardly evidence to show that total root mass increase with drought stress. The shoot/root mass ratios consistently decrease under drought stress, which is a universal expression of adaptation. The ratio changes mainly due to the reduction in shoot mass.
The root system is highly dynamic and as long as it is not senesced or diseased it is capable of regrowth from meristems in the root axes and meristems in the root crown (in cereals and grasses). The renewal of root branching into wet soil immediately after rainfall is considered as an important factor in plant recovery from drought stress. Root hairs are considered an important component of root length density and the capacity for soil moisture extraction via improved contact with the soil.

Roots are a major target and a candidate for marker assisted selection (MAS) for the apparent reason that phenotypic selection for root traits is a slow and impractical in large populations. Still, practical results from MAS for root traits are limited.

**Plant Surface**

Plant surface structure, form and composition carry a major impact on the plant interaction with the environment. Plant surface absorbs solar energy part of which is used for photosynthesis and most of which must be dissipated. Energy is dissipated by reflection, emission and the dissipation of latent energy by transpiration. Plant surface structure determines the reflective properties of the leaves and their resistance to transpiration. Leaf resistance to transpiration is off course largely determined by stomatal activity. However, plant surface structure determines the hydraulics of leaf surface, which affect the rate of water removal from the leaf surface, upon transpiration. Therefore plant surface help to avoid dehydration by two channels: improved reflectance of incoming radiation (i.e. decreasing net radiation) and by improved cuticular hydraulic resistance.

After the stomata, the secondary site for water loss by transpiration is the cuticle. The hydraulic permeability of the cuticle is determined by the wax embedded in the cuticle matrix as well as by the wax deposited over the cuticle. High cuticular permeability not only affects non-stomatal transpiration pathway but it may also directly affect water loss from guard cells and therefore their water status and stomatal aperture. Fig. 49 presents an example of a difference in epicuticular wax load between two sorghum genotypes. The lower wax (bm) genotype had far greater total leaf transpiration than the Bm genotype.

Epicuticular wax is deposited in different forms and structures, mostly as a function of its composition. The environment also affects the density of epicuticular wax. Conditions of water stress, high temperature, and high radiation increase its density. The full genetic potential for wax deposition is therefore best evaluated in plants subjected to stress.

In practical terms, the quantitative effect of wax on transpiration is finite, and for a given plant, the increase in epicuticular wax load beyond a given threshold would not reduce...
transpiration. Sorghum typically represents relatively high potential epicuticular wax deposition while rice represents species that lack in this respect, as estimated by quantifying epicuticular wax and by rate of cuticular transpiration. Hence, there is a potential for improving drought resistance in rice by genetically increasing epicuticular wax load. The shape and angles of the cuticular wax deposits may affect the spectral properties of the leaf. Thus, for example, the glaucous appearance of some wheat genotypes is determined by the structural properties of the wax deposits. Increased glaucousness was found to result in an increase in leaf reflectance of wheat and sorghum within the spectrum range of at least 400 to 700 nm and possibly also at the UV-B. This increase in reflectance may result in a reduction in net radiation and leaf temperatures in glaucous genotypes.

Leaf pubescence is a common feature in xerophytic plants (Fig. 50) as well as in some crop plants, such as soybean. Generally it increases reflectance from the leaf within the range of 400 to 700 nm and sometimes up to 900 nm, resulting in lower leaf temperatures under high irradiance. It is sometimes argued that the increased reflectance in the photosynthetically active spectrum would reduce photosynthesis under non-stress conditions. Under conditions of stress, there is a trade-off between the effect of pubescence towards the reduced stress load and its possible effect on photosynthesis. Increased leaf pubescence may increase the leaf boundary-layer resistance by up to 50%. However, it has been argued that this should carry a relatively small effect on water and CO₂ exchange, as compared with the effect of pubescence on the radiative properties of the leaf.

Leaf color can affect the thermal properties of the leaf. In both wheat and barley there are ‘yellow leaf’ cultivars, which have about a third less chlorophyll than the ‘normal’ ones. The ‘yellow’ cultivars tend to perform relatively better under drought stress as compared with the normal green. Yellow leaves are more reflective and their temperature is relatively lower than that of green ones. Beyond this difference in reflective properties, the low chlorophyll lines seem to sustain lower injury to the photosystem under conditions of high irradiance and water deficit.

**Osmotic adjustment (OA)**

When water deficit develop various solutes accumulate in cells and subsequently tissue osmotic potential is reduced. OA is derived from the net increase in cellular osmolality caused by the accumulation of solutes such as various ions (mainly potassium), sugars, poly-sugars (e.g. fructan), amino acids (e.g. proline), glycinebetaine, etc.’ OA occurs when cellular water deficit exceeds a certain threshold, which is not universally determined. Nor has the exact signaling for OA been resolved. OA is a slow process requiring time, and very rapid desiccation in experiments or even in the field may not allow for OA. Ideally the rate of plant dehydration should not be faster than about 0.1 MPa day⁻¹. Practically, it should take about 2 weeks from fully hydrated state to wilting on order for the full capacity and impact of OA to be expressed in whole plant, depending on species and the growth history of the specific
The rate of OA varies greatly among species and cultivars. A minimal rate of OA, which can be considered as effective, is about 0.3 MPa and rates of up to 1.5 to 2.0 MPa were observed in certain cereal cultivars. Some crop plants generally tend to be better at OA than others with cowpea, japonica rice and maize generally having lower rates while indica rice, sorghum and wheat tend to express higher rates.

OA is probably one of the most crucial components of dehydration avoidance and drought resistance in general. It helps maintain cellular turgor at a given leaf water potential and thus delay wilting (Fig. 51). OA enables to sustain growth and productivity at lower plant water status. Irrespective of the effect on turgor maintenance, the accumulated solutes can protect cellular proteins, various enzymes, cellular organelles, and cellular membranes against desiccation injury. Hence, cells and tissues may continue to function despite the progressing desiccation. This is why the accumulated osmotic solutes are sometimes defined as “protectants”. One consequence of OA at the whole plant level is the continued growth of roots and the extraction of deeper soil moisture. Finally, OA is crucial for the conservation of meristem viability under desiccation towards the recovery of function upon dehydration. OA in different cultivars of wheat, sorghum, various pulses and brassicas has been shown to be positively associated with biomass and/or yield under drought stress.

Upon rehydration the various solutes are recycled and metabolized to the extent that the accumulated sugars, for example, are considered as an important energy resource for recovery growth.

Extensive genetic engineering efforts are being made to use the phenomenon of OA in the design of stress resistant plants. Most experiments involve transgenic model plants that were modified to constitutively express the accumulation of osmolytes. Such transgenics that accumulate glycinebetaine, D-ononitol, mannitol, and trehalose gave positive or inconclusive results with respect to stress resistance, and work in this area is developing rapidly.

**Non-senescence (delayed senescence or ‘staygreen’ -SG)**

Plant senescence is a genetically programmed process, accelerated by environmental stress such as drought, heat, and nitrogen deficiency. The primary expression of leaf senescence is the breakdown of chlorophyll and the subsequent collapse of photosynthesis. Leaf greenness as measured by chlorophyll content or by leaf reflectance properties is becoming an acceptable estimate of senescence (and leaf nitrogen status). In various crops certain genotypes were identified as expressing delayed senescence or non-senescence or stay-green phenotype (Fig. 52). These genotypes generally sustain leaf greenness and photosynthesis for a longer time and consequently tend to yield more. Since drought stress accelerates senescence, SG genotypes are important in sustaining green leaf area under stress.

SG does not present a uniform expression across different crop plants. In sorghum for example SG can be associated with high stem soluble carbohydrate content and greater...
resistance to lodging caused by stem ‘charcoal rot’. In sorghum and millet at least, SG genotypes sustain higher RWC under stress as compared with normal ones. This is why SG is discussed under ‘dehydration avoidance’. Maintenance of RWC is not necessarily an expected result of delayed chlorophyll loss or delayed leaf protein breakdown. Furthermore, certain SG genotypes of sorghum are expressed better when exposed to drought stress. Hence, the phenotypic selection of SG in sorghum (and perhaps other crops) is more effective under post-flowering drought stress.

SG is at least partly regulated by endogenous plant hormones, whereas in certain cases an increase in kinetin in leaves promoted SG. In other cases SG was associated with decrease in plant ethylene content. Such hormonal regulation can involve both nitrogen and water status of leaves.

The expression of SG and plant senescence in general can be markedly influenced by intraplant interactions which involve assimilate partitioning and endogenous hormonal balance. A simple exercise to obtain a SG phenotype in grain producing crops is by detaching the inflorescence at flowering. Grain set and grain growth generally enhance leaf senescence by enhancing carbohydrate and nitrogen export from leaves into the grain.

Very low yielding or partially sterile plants may present some delay in senescence when subjected to drought stress during grain filling. There are ongoing attempts to achieve genetic transformation of SG trait by either promotion of endogenous kinetin or by antisense suppression of ethylene. QTLs for SG are being identified in several crops and marker assisted selection for the trait is becoming possible in sorghum and probably other crops in the future.

### Dehydration Tolerance

<table>
<thead>
<tr>
<th>Stress Phenotyping</th>
<th>Stress kinetics</th>
<th>% genes responding</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stress in a large pot</td>
<td>Rapid (5 days)</td>
<td>27</td>
</tr>
<tr>
<td>Stress in the field</td>
<td>Slow (4 weeks)</td>
<td>2</td>
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</tbody>
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Cellular and molecular adaptive processes in response to water deficit do not occur until a certain level of water deficit has been reached. Cellular and molecular adaptive responses serve one or more of the following major functions: (a) reduce whole plant growth in order to reduce plant water-use; (b) reduce the rate of cellular water loss and retain cellular hydration; and (c) protect various cellular structures and functions as cells desiccate.

With modern genomic tools it becomes fairly straightforward to reveal hundreds of genes that are up regulated or down regulated in response to plant tissue water loss. However, research into the function of most of these genes is not as developed. Subsequently the exact function at the whole plant level of the found gene responses to cellular water deficit is not well understood.
to the extent that they can be used in plant breeding. In terms of application to plant breeding dehydration tolerance is the capacity to function in a dehydrated state which often (but not always) means the involvement of stress responsive and adaptive genes. Most of the information that is relevant for application to breeding is derived from whole plant physiological studies while some rudimental information comes from genomics. Plant physiology always cautioned that the evaluation of plant response to drought stress and the evaluation of plant adaptation require sufficient time under stress. Adaptive plant responses to drought stress do not only depend on the level of tissue desiccation but also on its rate. It was well established that fast or slow desiccation may have totally different impact on results in terms of adaptation. Very rapid desiccation often exercised in laboratory experiments is totally irrelevant even though statistically significant results can be obtained. Tissue desiccation under natural conditions is slow. Confirmation of this axiom is now received from a gene expression study in maize as presented in Table 3.4, which speaks for itself.

**Stem Reserve Utilization**

The current source of carbon for **grain filling** is assimilation by the light intercepting viable green leaf area. This source is normally diminishing due to natural senescence and the effect of various stresses. At the same time the demand by the growing kernel is increasing, in addition to the demand posed by maintenance respiration of the live plant biomass. When the demand by the grain is not fully supplied by the source of current assimilation, then plant reserves can provide the balance. Small grains and cereal stems as well as several other crops store carbohydrates in the form of glucose, fructose, sucrose, fructans or starch. Type of storage depends on the species. Total storage in cereal plant roots or leaves is relatively small to that in the stem (including leaf sheaths). This storage is commonly analyzed as total non-structural carbohydrates (TNC) or water-soluble carbohydrates (WSC) and it is available for translocation to the grain.

Usage of stem reserves depends on the available storage and the rate and duration of mobilization of storage to the grain. The size of the storage strongly depends on favourable growing conditions before anthesis and genotype. Developmentally, potential stem storage as a sink will also be determined by stem length and stem weight density (stem dry weight per unit stem length). Stem length, as affected by the height genes is important in affecting stem reserve storage, as demonstrated in sorghum. The Rht1 and Rht2 dwarfing genes of wheat were also found to limit the reserve storage by about one third as a consequence of a reduction in stem length. This may be one of the reasons for the general greater drought susceptibility of the dwarf high yielding wheat cultivars.

Stem reserve mobilization or the percentage of stem reserves in total grain mass is affected by sink size, by the environment and by cultivar. It is not surprising therefore those different estimates of the percentage of grain yield that is accounted by stem reserves range from 9 to 100%.

The demand by the grain yield sink is a primary factor in determining stem reserve mobilization. When manual de-graining reduced sink size, more reserves were stored in the stem, as compared with intact ears. The availability of storage at grain filling does not necessarily assure mobilization. There are cases on record where despite stress conditions the
available storage was not utilized. This may be traced to problems in enzymatic conversion
of storage to transportable constituents or sometimes inhibition of sink processes. For
example, under heat stress starch synthesis in the wheat grain might be inhibited by a
thermolabile enzyme (such as soluble starch synthase) and available stem reserves would not
be in demand. Heat tolerant starch synthase is therefore also essential for grain filling under
heat stress. Hormonal signaling might also be involved in reserve mobilization.

The reduction in current assimilation during
grain filling, under different stresses, will
induce greater stem reserve mobilization to the
grain. What is important is the reduction in
assimilation and not the nature of stress causing
the reduction. Thus, stem reserve mobilization
is a solid source of carbon for grain filling under
any stress (such as heat stress also), which
would inhibit current photosynthesis, including
biotic stresses such as late developed leaf
diseases. Tolerance to Septoria leaf blotch in
wheat was expressed in sustained grain filling
under severe epiphytotic. It has been
demonstrated that mobilized stem reserve is a
major component of Septoria tolerance in
wheat.

The full potential for stem reserve utilization of
a cereal cultivar can be experimentally assessed by growing plants under favourable
conditions and then detaching all leaf blades and shading the inflorescence at the onset of
grain filling. Grain weights per inflorescence in such treated plants as compared with
controls provide a reliable estimate. It appears that wheat genotypes differ in their capacity to
store stem reserves (Fig. 53). Cultivars that have this high capacity must also possess
relatively long grain filling period in order to allow sufficient time for reserves to be
mobilized into the grain.

A possible “penalty” for high stem reserve utilization capacity is accelerated shoot
senescence, due to the export of C and N storage into the grain. Thus, it seems that the two
factors may not be recombined and the breeder will probably have to opt for either stem
reserve mobilization or delayed senescence trait as mechanisms supporting grain filling
under stress.

**Cellular membranes stability**
The fluid mosaic model of the cellular membranes (CM) describes the membrane as a bi-
layer of phospholipids and glycolipids studded and spanned by proteins partially or fully
solvated by the lipid matrix. CM is central site for various cellular functions; especially those
associated with membrane bound enzymes and transport of water and solutes. The function
and role of the CM under extreme temperature stress is somewhat clearer than with drought
stress.
The phospholipids in terms of their quantity and composition are generally considered as the more crucial components of cellular membrane stability under drought stress. The most notable factor in cellular membrane function under desiccation and heat stress is that plant previous exposure to moderate stress signal a hardening (“acclimation”) effect that is expressed in increased membrane stability under stress. Cellular membrane stability under stress has been shown to be positively correlated with yield advantage under stress, more often for heat than for drought stress. The simplest way to assess membrane stability is by measuring the leakage of cellular electrolytes under stress.

Water passage through both the plasma membrane and the tonoplast is crucial to cell life and specific proteins inserted in the membrane largely regulate it. These ‘water-channel’ proteins, also termed aquaporins respond to various signals and “molecular switches”. These pores are highly selective to water and they play an important role in cellular water relations in response to plant water deficit and osmotic stress. For example, maize root aquaporins were found to be stimulated by water deficit, resulting in improved water transport. The study of aquaporins and their function is now at the forefront of research on cell water relations.

**Antioxidation**

Oxidative Stress is a general term used to describe a state of damage caused by reactive oxygen species (ROS). ROS, such as free radicals and peroxides, represent a class of molecules that are derived from the metabolism of oxygen. There are many different sources of ROS that can cause oxidative damage to an organism. Most come from endogenous sources as by-products of normal and essential reactions, such as energy generation from mitochondria or the detoxification reactions. Free radicals are unstable because they have unpaired electrons in their molecular structure. This causes them to react almost instantly with any substance in their vicinity. Free radicals destroy cellular membranes, enzymes and DNA.

Antioxidants are active substances naturally occurring in all organisms which detoxify free radicals. These are for example superoxide dismutase (SOD), catalase, glutathione reductase or ascorbate peroxidase. SOD, for example, converts the $O_2$ to $H_2O_2$ and Catalase converts $H_2O_2$ to molecular oxygen.

Drought, as well as other stresses cause oxidative stress in plants and antioxidant abundance and activity is important for the protection of metabolism under stress. When various studies are reviewed it is unclear whether the genetic enhancement of antioxidant production in plants beyond the natural level is indeed required to alleviate drought stress at the whole plant level and whether the naturally occurring active antioxidants are not sufficient to protect the plant. It has been shown that drought induced oxidative stress related genes and that this was associated with increased levels of various antioxidants in plants. The most important information in this respect is coming from the developing work with transgenic plants, which over-express antioxidant production. When these studies are taken as a whole, no clear conclusions can be made yet with respect to the possible importance of breeding for overproduction of antioxidants towards the improvement of plant production under drought stress.
Stress proteins and Chaperons

Stress proteins is a large group of different proteins induced by different environmental and biotic stress in various organisms ranging from prokaryotes to man. A group of relatively small molecular weight proteins is developmentally regulated in growing seed such as that of barley. Their accumulation during embryo development has a role in protecting the embryo as the seed matures and desiccates during maturation (typically to about 10% water content). These are defined as ‘late embryogenesis abundant’ (LEA) proteins. Further research found that LEA proteins consist of a family, including several similar proteins such as dehydrins. These are not limited to seed embryo and they can be induced by drought stress in various plant tissues. Some are ABA responsive while others are not. Additional information especially on LEA protein and desiccation tolerance in seed is available online.

Work with transgenic plants indicated that the LEA family of stress protein might have a role in drought and osmotic stress resistance. Their exact function is not clear but it may involve osmotic adjustment or protection of cellular membranes or organelles during desiccation. They may also act as molecular chaperons and in that respect they are very similar to low molecular weight heat shock proteins (HSP). In this role they may conserve protein structure during stress. The LEA family of proteins may carry an important potential for enhancing stress resistance (Fig.54).

Abscisic acid (ABA) accumulation and its consequences
ABA accumulates in various plant parts subjected to desiccation. ABA responsive genes are often assumed to be stress adaptive. The rational is that if plants under stress consistently respond by producing ABA in leaves and root, then ABA must be important for coping with stress. The most prominent effect of ABA accumulation in the plant is stomatal closure and reduced transpiration. Thus, when transgenic model plants such as Arabidopsis or tobacco are engineered to over-produce ABA they maintain turgor when grown in pots subjected to dehydration. Thus it is often concluded that ABA promotes drought resistance. Turgor maintenance by stomatal closure is important for survival but not for plant production under drought stress. ABA has numerous critical negative effects on plants especially when crop productivity is considered (Table 3.5).

| Table 3.5. Effects of ABA on plant processes involved with growth and reproduction |
|----------------------------------|------------------|
| **Growth** |                   |
| General growth | Inhibition |
| Cell division | Decrease |
| Cell expansion | Decrease |
| Leaf initiation | Inhibition |
| Germination | Decrease |
| Root growth | Increase |
| Tillering | Decrease |
| Dormancy | Improved |
| **Reproduction** |                   |
| Flowering (annuals) | Advance |
| Flower induction | Inhibition |
| Flower abscission | Increase |
| Pollen viability | Decrease |
| Seed set | Decrease |
Genotypes of wheat that were selected for a high ABA accumulation under drought stress were found to be no better or even worse than the normal ones in terms of function and yield under drought stress. Selection for low leaf ABA content in maize was correlated with reduced yield under conditions of limited water supply. On the other hand ABA may have an important role in regulating an orderly shutdown of plant functions towards a state of dormancy, as the case is for the maturing seed. Dormancy is essential for surviving extreme plant desiccation (Fig.55). ABA mediated dormancy is crucial for attaining freezing tolerance, which involves cellular desiccation. The value of plant survival under severe desiccation depends on the agricultural ecosystem concerned. It can be important in subsistence agricultural where plant recovery from severe drought stress can provide some growth and production. Plant survival is of lesser consequence to commercial crop production as practiced in developed countries. Even the ability of seedling survival and recovery after a prolonged drought in commercial wheat production does not carry great impact when re-seeding the crop is a viable option. A commercial crop based on recovered seedlings is likely to be inferior to that grown from newly planted seed. The present knowledge on ABA and its role in plant adaptation to drought stress as well as in general plant production capacity does not allow yet to formulate a breeding strategy with respect to ABA.

**Drought escape and plant phenology**

Short growth duration (generally defined by early flowering) constitutes an important attribute of ‘drought escape’, especially for conditions of a late-season drought stress (Fig.56). On the other hand, longer growth duration is often associated with high yield potential. Consequently, using drought escape as a solution may involve a cost in terms of reduced yield potential. This is serious, especially when the moisture environment is absolutely unpredictable and may vary to a large extent between years. The more predictable the environment is, the easier it is to optimize phenology. The unpredictability of the environment may reach a state where short growth duration is a drawback, especially in indeterminate plants that offer a potential for regrowth and productivity upon recovery. Longer growth duration in both determinate and indeterminate plants would improve the probability for regrowth upon
recovery simply because, on the same calendar day, late-maturing genotypes are younger than early ones and younger plants recover better. The final decision on the optimum growth duration has, of course, to consider additional factors, such as late-season disease and insect pressure or periods of frost. Early maturity leads to reduced, total seasonal evapotranspiration simply because of the shorter time in the field. However, as growth duration is genetically linked with leaf number, early genotypes tend to have a small transpiring leaf-area index. Thus, early genotypes show reduced evapotranspiration during most growth stages, up to the point where a full ground cover is achieved. At most growth stages, root-length density and total root length per plant is generally greater in a late than in an early cultivar. This should be reflected in an advantage for the late genotype under conditions where extensive rooting is required.

A phenological feature specific to maize is the timing of anthesis with respect to silking, defined as anthesis-to-silking interval (ASI). Evidently a short interval is desirable whereas a large interval results in poor pollination. The maize program at CIMMYT dedicated many years of work to research the trait and explore its significance in tropical maize breeding for stress environments. Maize germplasm can vary for ASI irrespective of the effect of stress; a short ASI is a universally important trait for maize production. However, stress, and especially drought during the reproductive stage may extend ASI and thus reduce yield. Maize genotypes may vary in ASI under drought stress from few days up to a month or more. The effect on yield of change in ASI between null and 10 days is exponential. Selection for short ASI under drought stress proved to be an effective approach to improve drought resistance of tropical maize. QTLs (quantitative trait loci) controlling ASI were located and marker-assisted selection is possible.

Different crop plants may advance (e.g. wheat) or delay (e.g. rice) their flowering when stress occurs before flowering. The rate of delay is a function of plant water deficit and probably also ABA signaling. The rate of change in flowering time under stress can be taken as an index of genotypic rate of stress in the field.

**Water-use efficiency (WUE)**

WUE is not a component of drought resistance but the term implies greater production for a given amount of limited water. Namely “more crop per drop”. This is not necessarily the case. High WUE result (in most cases) from “less drop per crop”.

WUE was originally developed by agriculture engineers as a ratio between yield and irrigation water in order to assess returns for irrigation input and cost. WUE is an important yardstick to measure irrigation efficiency. The WUE term was later adopted by soil scientists and agronomists for a wider use in agronomy, including dryland-rainfed crop production. Physiologists found the term useful also at the leaf level in studies of gas exchange where WUE (i.e. “transpiration ratio”) is defined as the ratio of carbon fixation to transpiration. WUE can therefore be used at various levels of the crop, from the single leaf to the field. Studies of water use efficiency at the whole plant and field level were cumbersome due to the work load and costs involved in assessing whole plant or crop water use, especially when large plant populations in plant breeding were considered. The breakthrough came with the development of better understanding of stomatal dynamics, gas exchange and photosystem function, leading to the carbon isotope discrimination (delta) assay as a heritable marker for
WUE at the whole plant level (Farquhar et al. 1989; Hall et al. 1994). In the majority of cases low carbon isotope discrimination (low delta) as measured in the grain or the leaves was found to be well correlated with high WUE across variable genetic materials and vice versa, with few exceptions where delta was not associated with WUE. An important contribution of the carbon isotope discrimination method was that it enhanced research on WUE and provided extensive data on the subject especially in the context of breeding and genetic diversity. At the same time the large volume of published information on delta, WUE and their implications towards selection for water limited environments created some confusion in the plant breeding community. Confusion was largely created by the fact that the relations between delta (WUE) and yield were sometimes positive and sometimes negative, depending on the crop growing conditions. Plant breeders discussing carbon isotope discrimination and WUE expressed confusion on two primary questions: (1) under what environmental conditions selection for carbon isotope discrimination is expected to result in yield gain, and (2) which direction should selection be made, high (low delta) or low (high delta) WUE.

Beyond these questions the real issue is whether selection for high WUE is universally associated with drought resistance and improved plant production under drought stress. WUE is often equated in a simplistic manner with drought resistance without considering the fact that it is a ratio between two physiological (photosynthesis and transpiration) or agronomic (yield and crop water use) variables. This ratio it is often susceptible to misinterpretation, especially when the dynamics of the nominator and the denominator are ignored. When all studies of carbon isotope discrimination in breeding population are taken together it can be seen that higher WUE is derived from a reduction in water use rather than from an increase in production. Reduced water-use under dryland conditions is contradictory to productivity. Thus genotypes of high WUE under drought stress tend to be less productive under stress – with few specific exceptions. However, the target of plant breeding for water limited environments is effective use of water (EUW) rather than WUE (Blum 2009).

**Photosynthetic systems and plant production under stress**

Plant science is still seeking ways to genetically increase productivity for a given unit of water-use under drought stress. The key is in photosynthesis. The C_4 photosynthetic metabolism as compared with the more widely common C_3 type photosynthetic metabolism is intimately associated with superior productivity at given water-use. The C_4 pathway of photosynthesis as found in maize, sorghum, pearl millet, and various other crops is often referred to as a "water-use efficient" system because it is able to maintain high photosynthesis rates at lower water-use levels compared to C_3 crops. This is largely due to the fact that C_4 plants are able to limit water loss through stomata, which are the pores in the leaf surface that allow gas exchange. The stomata in C_4 plants are kept closed for most of the day, which reduces water loss and enhances photosynthesis efficiency. This system is particularly advantageous in water-limited environments.

**Conclusion about nature of drought resistance in crop plants**

It is not uncommon to come across opinions that drought resistance is “very complex” or “confusing” or “difficult” (Blum 2011). However, while drought resistance is not perfectly simple in terms of its physiological nature, it is conceptually simple with regard to breeding if one accounts for the following main considerations.

Firstly, besides adaptive traits drought resistance is strongly dependent on plant constitutive traits that are not necessarily induced by stress and do not require stress for their expression and are often easily manipulated genetically. Secondly, plant survival under extreme desiccation and its capacity to recover may depend on both dehydration avoidance and dehydration tolerance. In the extreme case we find resurrection plants as a model for extreme tolerance. However, survival is rarely an important feature in crop drought resistance. Thirdly, the most important factor of drought resistance towards crop production and very possibly also in natural vegetation is dehydration avoidance, namely the ability of the plant to maintain high water status or high turgidity. This would allow sustaining function better as environmental stress increases. Plants rarely function at zero turgor. Lastly, various plant traits, constitutive or adaptive, affect the capacity to maintain high plant water status and turgor. Depending on the drought stress profile and intensity, the most effective traits in terms of agronomic value are growth duration, plant size, root depth, osmotic adjustment, and plant surface properties. Stem reserve utilization for grain filling is an exception as it functions when plants are dehydrated to the extent that photosynthesis is inhibited.
forage grasses is essentially a pumping mechanism that moves CO$_2$ from the mesophyll cells and causes high CO$_2$ concentrations in the specific biochemically active vascular-bundle sheath cells. This mechanism goes hand in hand with certain anatomical and morphological features of the C$_4$ plant ("Kranz leaf anatomy") that are inseparable from the system as a whole. The CO$_2$-concentrating mechanism results in a high utilization efficiency of low intercellular CO$_2$ concentrations. This is due to the PEP carboxylase enzyme in the C$_4$ plant, which unlike RuBP carboxylase is insensitive to atmospheric O$_2$ concentrations. Atmospheric O$_2$ concentrations are strongly inhibitive to CO$_2$ uptake in C$_3$ plants where CO$_2$ is fixed directly by RuBP carboxylase. In C$_4$ plants CO$_2$ fixation is carried out in the bundle-sheath cells using CO$_2$ from decarboxylated C$_4$ acids in the mesophyll cells. This sequence results in sufficiently high CO$_2$ concentration maintained at the bundle sheath cell. The efficiency of the CO$_2$ fixation pathway in the C$_4$ plant bears significance toward its transpiration-ratio. For a given rate of transpiration, photosynthesis is greater in C$_4$ than in C$_3$ plants. This advantage is also translated into a greater plant or crop WUE, which is not always necessarily related to drought resistance and a relatively better yield under stress. For reasons other than the biochemistry of photosynthesis (say, deep roots or OA) a certain C$_3$ crop might produce better than a C$_4$ one under drought stress. However, under well-watered conditions the greater WUE of the C$_4$ plant is most likely translated into better economic returns on the cost of irrigation. The normal WUE (for grain yield) of supplemental irrigation in grain sorghum (C$_4$) is about 20 kg mm$^{-1}$ ha$^{-1}$, as compared with 10 kg mm$^{-1}$ ha$^{-1}$ in wheat (C$_3$).

Whereas WUE is often confused with drought resistance it is very important to take note of a comparative study of C$_4$ and C$_3$ Panicoid grasses. It concluded that declining C$_4$ photosynthesis with water deficit was mainly a consequence of metabolic limitations to CO$_2$ assimilation, whereas, in the C$_3$ species, stomatal limitations had a prevailing role in the drought-induced decrease in photosynthesis. The drought-sensitive metabolism of the C$_4$ plants could explain the observed slower recovery of photosynthesis upon re-watering, in comparison with C$_3$ plants which recovered a greater proportion of photosynthesis through increased stomatal conductance. Therefore, within the Panicoid grasses, the high WUE C$_4$ species are metabolically more sensitive to drought than the lower WUE C$_3$ species and recover more slowly from drought.

Plant science is attempting to improve yield of C$_3$ plants such as rice by converting their biochemistry to C$_4$. Less ambitious but probably more closely at hand is the improvement of C$_3$ leaf internal, or mesophyll, conductance to CO$_2$, leading to greater leaf productivity per unit transpiration.

**BREEDING FOR DROUGHT RESISTANCE**

**Some Principles**

The primary difficulty and the most important task in planning a breeding program for the improvement of drought resistance is the formulation of the drought resistant ideotype with respect to the target of the breeding program. This involves an educated logical integration of most of the information as discussed. The primary issue is the decision on the important phenological, developmental and adaptive traits that would be most effective in supporting
production or survival under drought stress, depending on the agro-ecological, social and economic conditions of the target environment.

Conventional breeding for general yield improvement relies very strongly on selection for yield and its components as a main approach. Modern conventional breeding for drought resistance supplements selection for yield with selection for developmental and physiological attributes, that may require physiological measurements in breeding populations. Physiological methodology is generally slow and meticulous and it does not allow to measure and screen large plant populations. In most cases, indirect or rapid methods were developed as screening aids to replace the slow physiological methods. While this resulted in reduced accuracy of the measurement, it still allows partitioning the population into the desirable subpopulations. This is sufficient in the eye of the breeder who is not interested in utmost accuracy of measurements but rather in being able to reduce the population by excluding the least appropriate phenotypes.

The flaw in conventional breeding is that the breeder can identify the genotype only by measuring the phenotype. The efficiency of this approach depends on many factors, including inheritance of traits, environmental effects, measurement error and more. For certain traits, such as root depth, phenotypic measurements in very large breeding populations are technically impractical. Marker assisted selection (MAS) allows to select the desirable genotype without actually measuring the phenotype.

**The Managed Stress Environment**

While the field in the target stress environment is the primary goal of the breeding program, paradoxically, it is often inappropriate for selection work. Besides the amplified spatial field variability when water is limited, stress is/can also be variable from year to year. The water regime can be too severe in one year, causing complete loss of breeding materials on one hand or too favorable to constitute any stress pressure in another year. Drought stress in different seasons can also occur in different growth stages. Stress in the target field environment is typically inconsistent, causing reduced efficiency in the overall selection program. It may be argued that this variability is an inherent problem to be addressed in breeding. While this may be true, selection becomes very ineffective if it is practice under such a variable protocol. For example, if drought resistance is to be improved at two different growth stages, it must be logically addressed separately for each different stage, followed by recombination. It follows therefore that the field-screening environment must be managed for stress intensity and timing to a level that can result in a consistent selection pressure from one cycle to the next. Thus, controlled drought stress in the selection process is essential, quite analogous to the use of controlled disease infection or the use of consistent natural “hot spots” in the selection for disease resistance.

Controlled drought stress implies the appropriate duration and severity of stress at the appropriate plant growth stage. Controlling drought stress in the greenhouse or the growth chamber is relatively straightforward. In the field, however various means are required to achieve control by eliminating rainfall on one hand and by providing irrigation on the other. The ideal field selection site for drought resistance would be in a desert environment with a minimal amount of rainfall, where almost any crop water regime can be designed by irrigation. While this may not always be possible it is the conceptual basis of the managed
stress environment. It follows that most breeding programs which have a component for drought resistance must develop a special phenotyping site where stress can be managed to a reasonable extent. Alternatively, certain natural drought stress conditions may be quite repeatable from year to year or very easy to manage by irrigation. This is the case for crops grown exclusively on stored soil moisture from previous season precipitation. This stress scenario is found for example in the Mediterranean summer crops or the ‘rabi’ season in parts of India.

When terminal stress (stress at the final reproductive growth stages) is considered, a delay in planting in most cases would put this stage in a dry season. Another possibility is to grow the population during a dry off-season if climate and biotic factors allow it. This approach was very successful with upland rice breeding at IRRI in the Philippines. Since growing plants in the dry offseason might expose them to somewhat different climatic conditions, an off-season nursery should be used mainly for recording results on drought resistance responses but actual selection should be performed with the same (duplicate) materials during the normal season. Exceptions are noted where selection for yield under stress in an off-season stress nursery was effective in gaining progress for drought resistance. The corollary is to understand the climatic and biotic factors which might affect plant growth and yield in the off-season nursery, besides drought.

When a managed field site is impossible to achieve, the next option is the rainout shelter.

Where rainfall is limited in the natural field selection environment, such as dry season in the tropics or the summer season in the Mediterranean, managed stress environments can be designed by irrigation scheduling. Options range from having a stress and non-stress environments side by side to the ‘line-source’ irrigation system (Fig.57). This system is based on the fact that any sprinkler irrigation system spreads water in a gradient where the maximum amount is discharged at the source with a diminishing amount away from the source. Hence the amount of water available to the plants decreases perpendicular to the sprinkler irrigation line. Breeding materials can be planted in long plots or rows perpendicular to the line and be subjected to an increasing drought stress away from the line. Observations on plant response along a water supply gradient within each genotype can be very effective for revealing resistant materials.

**Variability of the field environment**

The field is variable in terms of topography and soil characteristics. Soil characteristics vary in all dimensions. This variability is amplified when the water regime is concerned and especially when water is lacking. Fig.58 demonstrates field variability for soil moisture seen in a sorghum breeding nursery subjected to drought stress. Plots that are generally above the drawn line on the photograph are situated on wetter soil and therefore appear more colour saturated (having higher leaf water status) as compared with the more desiccated plots below.
the line. An experiment laid out across this line is practically useless, whatever statistics are deployed. It is therefore crucial not to find yourself in this situation to begin with.

Whichever methods and precautions are used to handle field variability as a generator of experimental error, these become especially critical in experiments involving water deficit. While suitable field topography (flat with a slight homogenous slope) can be identified, it is extremely difficult to estimate spatial variability of the site with respect to its soil moisture characteristics. It is therefore highly recommended to perform a field homogeneity test by growing a homogenous commercial crop in the candidate field before choosing it for screening work. The crop should be water stressed and then observed for variability in plant development. Photogrammetric methods can also be applied for this purpose. Machinery that surveys the field by measuring soil electro-conductivity is becoming a popular method after its use in precision agriculture application. In certain cases (typically rice in Asia) a field may be situated above a high water table. Whatever might be the rainfall regime or irrigation the crop in such a field can never be water stressed for experimental purpose. Monitoring ground water level before using such a field for drought phenotyping is essential.

Yield as a Selection Criterion for Drought Resistance

The issue of selection for yield and the impact of the environment on genetic gains from selection and selection efficiency are under continuous debate as a central issue in conventional plant breeding. The comparative yield performance of two genotypes with respect to one another can vary from one environment to the other and this is basically defined as genotype by environment interaction (GxE) for yield. Generally, the ideotype preferred by most breeders is one that expresses minimal GxE and its yield is “stable” across all environments. The question is the spectrum of environmental diversity across which one variety can be stable. When environmental variation is extreme a GxE (crossover or other) is unavoidable. The classical solution is then to adapt different varieties to the very different environments, such as varieties A and B for one environment and C for the other.

However, while yield under stress is the target of the breeding program, selection for yield under stress is generally inefficient. Yield is a complex trait that is basically not directly inherited. It is the various developmental and physiological processes which make up yield that are inherited. Therefore the heritability of yield is generally not high and it becomes especially low under stress. It has been the general and repeatable observation of breeders that using yield as a selection index under stress to improve drought resistance is generally not efficient. To compensate for the low efficiency breeders screen very large populations with the expectation that the “numbers game” will allow to identify the desirable genotype. While this approach has been successful, it is expensive. The use of molecular markers to tag and select for certain yield related quantitative trait loci (QTLs) can increase the efficiency of
selection for yield, but again, less effectively under stress. Again, QTL by environment interaction seems to be the rule.

However, when the breeding population contains effective genes for drought resistance (say, segregation for deep roots in upland rice population) the efficiency of selection for yield under drought stress can be increased, provided all precautions are taken to minimize spatial variability at the selection site (see above).

If selection for yield under stress is practiced, a positive GxE for the specific drought stress conditions is a strong indicator of resistance. There are many statistical models and methods that estimate GxE in different contexts and accuracies. In most cases of a planned breeding program for drought resistance the evaluation of GxE simply requires a comparison of yield performance under stress and non-stress (fully irrigated) conditions. The comparison of genotypic performance between the two environments can be simply evaluated in yield under stress as percent of yield under non-stress. Alternatively, the ‘Fischer and Maurer’ stress resistance index’ (RI) can be computed as:

\[RI=\frac{(Gs/Gn)}{(Ms/Mn)}\]

where genotype yield under stress (Gs) and non-stress (Gn) is normalized for mean yield of all genotypes under stress (Ms) and non-stress (Mn). Values above 1 indicate a relative resistance as compared with the mean of the population. It has been argued that this index is flawed because it is affected by yield potential. This is true and as we have seen above indeed genotypes of high yield potential tend to be more susceptible to drought stress. This is a reality not a mathematical flaw.

A major impediment in comparing genotypic response to a managed water stress environment is the variation among genotypes in their phenology. With such variation, different genotypes may be water-stressed at different growth stages. This has been a major pitfall in many drought resistance mapping exercises using populations such as recombinant inbred lines. The solution is to divide the population into several phenology sub-populations and compare the effect of stress only within sub-populations of similar phenology. Alternatively, staggered planting dates can be attempted where the earlier materials are planted later as compared with the late flowering materials. However, in most breeding programs, when tests for drought resistance are performed in the field at more advanced generations (e.g. =>F4), the population of lines does not express large variability for phenology.

**Selection for Drought Resistance by Developmental Traits**

Selection for most plant developmental traits involving drought resistance are conducive to general breeding principles, such as the case for phenology, anthesis to silking interval (ASI) in maize, tillering, plant size, etc’. Two unique developmental features are discussed here: roots and stem reserve utilization.

**Roots**

Root size and development is a crucial parameter in most selection programs for drought resistance. Detailed measurements of roots or even rough screening techniques for roots are generally laborious. Probably the most practical way to select for deep and effective roots is to judge their performance by observing the shoot performance under drought stress.
Very detailed root measurements can be performed with special growing containers and installations where roots can be observed in situ through a glass panel. These installations are defined as rhizotrons and they may take various forms such as individual glass-paneled soil-filled root boxes set in the ground (Fig. 59). By weighing these root boxes it is also possible to estimate plant transpiration and relate it to shoot and root development. Rhizotrons and lysimeters are important tools for root research and for studying a few cultivars but they are not amenable to large scale screening work.

The simplest method for a direct selection for root length involves growing single plants in vertical soil filled disposable polyethylene tubes (used in polyethylene bags production) and then washing the root out of the soil at the time of measurement (usually at flowering). Alternatively plants can be grown in re-useable soil filled PVC tubes (~10 cm in diameter) (Fig. 60). Tubes can be sawed into two halves and then taped together before planting so that they can be opened at any time and destructive measurements can be taken on roots in situ or after washing away the soil. The two methods (Fig. 59 and 60) can be combined into one, where PVC tubes are set in a trench and weighed for water-use measurements while being lifted periodically.

Root penetration capacity through a hardpan is phenotyped by challenging the root to penetrate a hard layer of paraffin-wax at depth. The number of roots penetrating the wax layer is an estimate of root penetration capacity. While some criticism was expressed about the predictive power of the method, it has still gained popularity with breeders.

**Stem reserve utilization for grain filling**
The capacity for stem reserve utilization for grain filling when the photosynthetic source is completely inhibited by stress can be estimated in selection work by destroying the photosynthetic source at the onset of grain filling and measuring grain filling with no current photosynthesis in comparison with normal plants. Spraying the plants with an oxidizing chemical desiccant such as magnesium chlorate or with potassium iodide (KI) destroys chlorophyll and the photosynthetic source (Fig. 61). The chemical is applied by spraying the whole plant or just the leaf canopy. The treatment is applied at the onset of the exponential stage of grain filling, which is about two weeks after anthesis in the small grains. Too early application of the chemical can kill florets and drastically reduce kernel number – which may undermine the test. Spray is therefore scheduled according to the different dates of anthesis of the different genotypes. Non-treated control plots are required. Since the capacity for stem reserve support of grain filling is measured by the difference in final kernel weight between treated and control plots of any given genotype, the control must be totally free of stress, especially drought or disease. It should be understated that the method does not simulate drought, it only simulate the effect of drought in terms of leaf killing and destruction of the photosynthetic source. The method has been thoroughly tested and applied in wheat breeding.

Selection for Drought Resistance by Assessing Plant Water Status

Methods can vary from purely physiological to indirect assessments that are useful mainly for selection purposes. Most of the physiological methods were reviewed in previous pages. Here only methods for applied selection work in large populations are indicated. Certainly for a limited number of genotypes such as in pre-breeding work, direct measurement of leaf water potential by the pressure chamber and leaf RWC are consensus estimates of plant water status. RWC is considered here as a preferred estimate in breeding work since it accounts also for the effect of OA of leaf hydration.

Stress Symptoms

When plants reduce their water status and lose turgor under stress they display very distinct symptoms. Symptoms progress in proportion to plant water deficit and they can be visually scored and used in selection. The most notable symptom is off course leaf wilting. Leaf Rolling is an expression of wilting in the cereals and it is being widely used in field selection work. It is visually scored (typically on a 0 to 5 scale) and used in selection for drought resistance in various crops such as rice, wheat, barley, maize, millet and sorghum. Other leaf stress symptoms include leaf desiccation (“firing”), leaf tip “burning”, leaf “drooping” and leaf drop. General scores of plot appearance under stress are also used by experienced breeders who are well acquainted with the various responses of their crop to drought stress. Genotypes of delayed wilting or leaf rolling are preferred off course, indicating sustained turgor under stress.

Stress symptoms are also expressed in flowering time if stress occurs before normal flowering time. A delay in inflorescence appearance or exertion is typical of rice or sorghum.
An advance in flowering is seen in wheat. Assessing the rate of delay or advance requires a comparison between stress and non-stress plots. The rule of thumb regarding stress symptoms and phenotypic variation for drought resistance is simple: “if you can’t see it – it is not there”.

**Canopy Temperature**

Selection methods were developed and applied to plant breeding following principles and techniques used in Remote Sensing in Agriculture. Most methods are based on the spectral response of leaves and its modification with plant response to the environment.

Canopy temperature is a function of transpirational cooling. As water deficit develops, canopy temperature differences among genotypes increase and plant water status becomes the main source of this variation. Canopy temperature was used to develop a crop water stress index as a tool for crop management. Canopy temperature measured under drought stress has become a most popular, fast and significant field screening method for plant water status under drought stress. Since dehydration avoidance is the major drought resistance mechanism in crop plants, canopy temperature is a most relevant screen for drought resistance. Relatively lower canopy temperatures under stress indicate a relatively better plant water status, ongoing transpiration and carbon fixation and an effective use of water. Lower canopy temperatures were generally found to be correlated with relatively higher yield under stress across diverse genetic materials. Canopy temperature can be measured remotely with the infrared thermometer, provided the correct protocol is strictly followed. Since its initial development as a screening method for dehydration avoidance by Blum et al. (1982), infrared thermometry of plant canopies under drought stress has become a popular method in breeding and phenotyping drought resistance. Twenty five years later and in tune with some 30 reports since then which verified the utility of the method in different crops, Olivares-Villegas et al. (2007) summarized their exhaustive study with wheat as follows: “Field trials under different water regimes were conducted over 3 years in Mexico and under rainfed conditions in Australia. Under drought, canopy temperature was the single-most drought-adaptive trait contributing to a higher performance, highly heritable and consistently associated with yield phenotypically and genetically. Canopy temperature epitomizes a mechanism of dehydration avoidance expressed throughout the cycle and across latitudes, which can be utilized … as an important predictor of yield performance under drought”.

Leaf canopy temperature can be sensed and recorded by infrared digital cameras which present an image of the target in different colors according to temperature. With the lightweight and portable camera available today the resolution of the image is not very high but useful images can still be obtained. The instrument and its application is finding its way into agronomic research and some preliminary breeding work. The infrared camera has not replaced the infrared thermometer in large scale actual ground level screening work. Still the infrared camera has some potential uses in pre-breeding work and possibly when viewing breeding plots from aerial platforms, depending on its resolution and cost.

The measurement of the spectral reflectance of leaf canopies viewed from various platforms as done very early by NASA and associates, brought about the development of various spectral indices which are correlated with plant water status, leaf greenness or sometimes even yield.
Selection for Drought Resistance by Assessing Plant Function

As discussed previously the comparative assessment of plant function in different genotypes under drought stress (dehydration tolerance) must be normalized for plant water status. Else, differences in function among genotypes can be ascribed to differences in water status and not necessarily to real difference in function at a given plant stress. This is a difficult requirement in selection work especially under field conditions.

An effective approach for normalizing measurements of function against plant water status is to measure plant water status at the time of function measurement. Then develop a regression of the specific function on water status across all genotypes. Genotypes that deviate positively from the regression are more resistant while those that deviate negatively are more susceptible in terms of the specific function. Of course, these measurements cannot be performed on large breeding populations and they might be useful for pre-breeding work with potential parents or certain germplasm.

Published attempts to attain control of plant water status in laboratory studies are almost always seen to be flawed. One flawed example is to achieve a given set level of a stress low soil moisture content by frequently irrigating potted plants with small amounts of water to a given volumetric soil moisture content. This is an abnormal water regime with respect to a stressed plant, even though the accounting of soil moisture content is correct. A normally stressed plant is subjected for days to a given (or a receding) soil moisture status while these potted plants are subjected to a frequent cycle of moisture supply which is taken up mainly by the dry top soil.

One method which has gained some popularity is by growing plants in polyethylene (PEG) fortified nutrient solution. With this method (pending some limitations) plants are at least subjected to standard root medium water potential. It is most amenable for measuring juvenile plant growth rate under a given root medium moisture stress, taking into consideration all the precautions mentioned in the described protocol.

Two examples of the more popular selection methods for function are given here, namely cell membrane stability (CMS) and chlorophyll fluorescence.

Cell Membrane Stability (CMS)

This method is based on the fact that stress cause injury to cellular membranes (see above). This injury is expressed in leakage of various cellular solutes, including electrolytes. Electrolyte leakage can be easily measured by the electro-conductivity of the medium in which the affected leaf sample is placed. The method is being used mostly for assessing thermotolerance in heated leaf samples. Basically the method compares leakage from stress-affected leaf samples with leakage from control samples, calculating the relative injury or stability (the inverse of injury).

When CMS is used as a dehydration tolerance trait it is estimated in leaves subjected to advanced stress, typical to a set RWC of around 50-70% depending on species. Samples are taken from stressed and non-stressed (control) leaves. Samples are also taken for estimating RWC as a measure of water status. The first case of such a study was in rice where QTLs for CMS under drought stress were identified. Another way to subject leaf tissues to drought stress under this CMS protocol is to incubate leaf samples (e.g. leaf discs) in polyethylene glycol (PEG) solution as compared to non-treated well hydrated leaf samples. This method
provides nice and consistent genotypic differences in drought CMS, but its relations to field performance under drought stress requires further validation.

**Chlorophyll Fluorescence**

The phenomenon of chlorophyll fluorescence and its value as a marker of photosystem-II function has been discussed above. A number of instruments and imaging systems were developed for analyzing chlorophyll fluorescence. There are different levels of analysis, depending on the purpose of the study. A unique and detailed analytical probe defines as the JIP test has been developed by Prof. Strasser in Geneva. It allows a very comprehensive dissection and interpretation of the fluorescence phenomenon. This is mainly a research rather than a selection tool.

However, fast portable and simple instruments are needed for selection work. Chlorophyll fluorescence is even entering the domain of remote sensing where vegetation function might be monitored from above ground and even aerial platforms in the near future. It must be realized however that the measurement and interpretation of chlorophyll fluorescence signal, even with simple instrumentation require a complete understanding of the phenomenon. Furthermore, it cannot be over-emphasized again that comparison of genotypes for chlorophyll fluorescence must be normalized for leaf water status.

**Using Growing Degree Days and Crop Heat Units**

In the absence of extreme conditions such as unseasonal drought or disease, plants grow in a cumulative stepwise manner which is strongly influenced by the ambient temperature. Growing degree days take aspects of local weather into account and predict the plants’ pace toward maturity.

Unless stressed by other environmental factors like moisture, the development rate from emergence to maturity for many plants depends upon the daily air temperature. Because many developmental events of plants and insects depend on the accumulation of specific quantities of heat, it is possible to predict when these events should occur during a growing season regardless of differences in temperatures from year to year. Growing degrees (GDs) is defined as the number of temperature degrees above a certain threshold base temperature, which varies among crop species. The base temperature is that temperature below which plant growth is zero. GDs are calculated each day as maximum temperature plus the minimum temperature divided by 2 (or the mean temperature), minus the base temperature. GDUs are accumulated by adding each day’s GDs contribution as the season progresses.

GDUs can be used to: assess the suitability of a region for production of a particular crop; estimate the growth-stages of crops, weeds or even life stages of insects; predict maturity and cutting dates of forage crops; predict best timing of fertilizer or pesticide application; estimate the heat stress on crops; plan spacing of planting dates to produce separate harvest dates. Crop specific indices that employ separate equations for the influence of the daily minimum (nighttime) and the maximum (daytime) temperatures on growth are called crop heat units (CHUs).
Growth and development of corn are strongly dependent on temperature. Corn develops faster when temperatures are warmer and more slowly when temperatures are cooler. For example, a string of warmer than normal days in late spring will encourage faster leaf development than normal. Another example is that a cooler than normal grain filling period will delay the calendar date of grain maturity.

The phrases “string of warmer than normal days” and “cooler than normal grain filling period” can be converted mathematically into measures of thermal time by calculating the daily accumulations of heat. Commonly used terms for thermal time are Growing Degree Days (GDDs), Growing Degree Units (GDUs), or heat units (HUs). Different methods exist for calculating heat units depending on a) the crop or biological organism of interest and b) the whim or personal preference of the researcher. The calculation method most commonly used for determining heat unit accumulation relative to corn phenology is the formula first suggested by the National Oceanic and Atmospheric Administration in 1969 and labeled as the ‘Modified Growing Degree Day’ formula in 1971.

This method calculates daily accumulation of GDDs as the average daily temperature (°F) minus 50. The “modification” refers to the limits imposed on the daily maximum and minimum temperatures allowed in the calculation. Daily maximums greater than 86 degrees F are set equal to 86 in the calculation of the daily average temperature. Similarly, daily minimums less than 50 °F are set equal to 50 in the calculation.

Baselines

10 °C is the most common base for GDD calculations, however, the optimal base is often determined experimentally based on the lifecycle of the plant or insect in question.

- 5.5 °C wheat, barley, rye, oats, flaxseed, lettuce, asparagus
- 6 °C Stalk Borer
- 7 °C Corn rootworm
- 8 °C sunflower, potato
- 9 °C Alfalfa weevil
- 10 °C maize (including sweet corn), sorghum, rice, soybeans, tomato, Black cutworm, European Corn Borer, Coffee (Jaramillo-Robledo & Guzman-Martinez published by Cenicafé), standard baseline for insect and mite pests of woody plants
- 11 °C Green Cloverworm
- 12 °C many other crop calculations
- 30 °C the USDA measure heat zones in GDD above 30 °C; for many plants this is significant for seed maturation, e.g. reed (*Phragmites*) requires at least some days reaching this temperature to mature viable seeds

GDDs may be calculated using either Celsius or Fahrenheit, though they must be converted appropriately; 5 GDD°C = 9 GDD°F

**Growing Degree Days**

Growing degree days (GDDs) are used to estimate the growth and development of plants and insects during the growing season. Insect and plant development are very dependent on temperature and the daily accumulation of heat. The amount of heat required to move a plant
or pest to the next development stage remains constant from year to year. However, the actual amount of time (days) can vary considerably from year to year because of weather conditions.

Each organism has a minimum base temperature or threshold below which development does not occur. These base temperatures have been determined experimentally and are different for each organism. GDD information can be very useful for predicting crop and insect development. Field crops that still use the GDD system are cereals (Base: 0), alfalfa (Base: 5) and canola (Base: 5).

To calculate GDD, first determine the mean temperature for the day. This is usually done by taking the maximum and minimum temperatures for the day, adding them together and dividing by 2. The base temperature is then subtracted from the mean temperature to give a daily GDD. If the daily GDD calculates to a negative number it is made equal to zero. Each daily GDD is then added up (accumulated) over the growing season.

Growing degree days are sometimes referred to as "degree days" or the "degree days averaging method." Some jurisdictions also use the term "heat units" interchangeably with "degree days". However, the terms "growing degree days" (GDD) and "crop heat units" (CHUs) are used independently since they represent two very different, temperature-dependent, development models.

**Growing Degree Day Equation**

The GDD equation is as follows:

\[
\text{Daily GDD} = \left(\frac{T_{\text{max}} + T_{\text{min}}}{2}\right) - T_{\text{base}}
\]

- \(T_{\text{max}}\) = the daily maximum air temperature
- \(T_{\text{min}}\) = the daily minimum air temperature
- \(T_{\text{base}}\) = the GDD base temperature for the organism being monitored

**Example**

Maximum Temperature: 28°C
Minimum Temperature: 15°C
Pest: European corn borer (ECB)
Base Temperature for ECB: 10°C

**Calculation**

Daily GDD = \((28 + 15) ÷ 2\) - 10 = 11.5

Therefore: 11.5 growing degree days were accumulated for that day for the European corn borer GDD model.

There are four factors to consider when comparing GDD accumulations from various sources or regions.

1. **Are the base temperatures used in the equations the same?**
   Different organisms have different base temperatures used to calculate GDDs: 150 GDD at base 10 does not equal 150 GDD at base 0.

2. **Are the start dates for the accumulations the same?**
   Generally, GDD accumulations start on April 1 each year, but some insect GDD models start at the emergence of a specific life stage. This is referred to as a biofix.
3. Are the equations used to calculate the daily GDD the same? Many modifications to the simple GDD calculation have been developed over the years and may be referred to generally as degree days.

4. Are the temperatures used in degrees Celsius or Fahrenheit? GDD accumulations will vary significantly, depending on whether they are being tracked in Celsius or Fahrenheit. GDD models have been designed specifically for use in one or the other and cannot be interchanged without making conversions. The ECB GDD model was based on measurements in Celsius.

Table 3.6. Daily Crop Heat Unit Accumulations (Based on Maximum and Minimum Temperatures)

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Table 3.6. Daily Crop Heat Unit Accumulations (Based on Maximum and Minimum Temperatures)

<table>
<thead>
<tr>
<th>Daily CHU Values for °C Temperature Recordings</th>
<th>Daily Recorded Minimum Temperature</th>
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<td>(°C)</td>
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Crop Heat Units (CHUs)

Crop heat units (CHU) are based on a similar principle to growing degree days. CHUs are calculated on a daily basis, using the maximum and minimum temperatures; however, the equation that is used is quite different. The CHU model uses separate calculations for maximum and minimum temperatures. The maximum or daytime relationship uses 10°C as the base temperature and 30°C as the ceiling, because warm-season crops do not develop at all when daytime temperatures fall below 10°C, and develop fastest at about 30°C. The minimum or nighttime relationship uses 4.4°C as the base temperature and does not specify an optimum temperature, because nighttime minimum temperatures very seldom exceed 25°C. The nighttime relationship is considered a linear relationship, while the daytime relationship is considered non-linear because crop development peaks at 30°C and begins to decline at higher temperatures. Daily crop heat units are calculated by using the average of the two daily values from the equations below or can be read from the matrix in Table 3.6, Daily Crop Heat Unit Accumulations Based on Maximum and Minimum Temperatures.

Producers who record high and low temperatures can use Table 3.6, Daily Crop Heat Unit Accumulations Based on Maximum and Minimum Temperatures, to calculate CHUs for their own farm. As of 2009, CHUs accumulate from May 1st at all locations and end with the first occurrence of -2°C in the fall. Corn development is driven primarily by temperature, and this is especially true during the planting-to-silking period. Unlike soybeans, day length has little effect on the rate at which corn develops. The Crop Heat Unit System has been developed to calculate the impact of temperature on crop development.

Calculating Daily CHU

The following equation is used to calculate a daily CHU for a site:

\[
\text{Daily CHU} = (\text{Ymax} + \text{Ymin}) \div 2
\]

where:

\[\text{Ymax} = (3.33 \times (T_{\text{max}} - 10)) - (0.084 \times (T_{\text{max}} - 10.0)) \]  
(If values are negative, set to 0)

Heat unit efficiency (HUE) or thermal time use efficiency (TTUE) – amount of dry matter produced per unit of thermal time or growing degree day. It is expressed in gm² day⁻¹ °C.

\[
\text{HUE} = \frac{\text{Dry matter production (g/m²)}}{\text{Growing degree day base temperature of cotton}}
\]
## Unit – IV

<table>
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<td>Growth hormones</td>
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Plant Ideotypes

In recent years due to all round efforts of agricultural scientists it has been possible to cultivate HYVs of cereal crops which are often been termed as “NEW PLANT TYPES”.

IDEOTYPE: refers to plant type in which morphological and physiological characteristics are ideally suited to achieve high production potential and yield reliability. The concept of ideotype was given by Donald in 1968. He illustrated that there should be minimum competition between the crops and crop must be competent to compete with weeds. The single plant would give the better result in a group when the crop has at least competition with the same type of the crop. Ideotype is the model type which may also be defined as “a biological model which is expected to perform or behave in a predictable manner within a defined environment”. On the basis of environment Donald and Hamblin (1976) identified two forms of ideotypes i.e. isolation ideotypes and competition ideotypes. Competition ideotypes are suitable for mixed cultivation.

Plant breeders have developed an impressive range of techniques in their search for increased yield and better quality in crops. Mutation breeding, polyploidy, the exploitation of hybrid vigour, embryo culture and advanced statistical design and analysis are among the many procedures which have enabled more effective breeding programmes. Yet if we examine the philosophies behind these programmes, we see that they are of but two kinds. In the first group, the purpose is to remedy some known defect in the crop, and this we may call “defect elimination”. In the second group, the basic procedure is “selection for yield”.

“Defect elimination” is adopted when disease resistance is bred into a susceptible genotype or when earliness is incorporated into a variety prone to water stress late in the season. It may involve the correction of physical imperfections such as weak straw in cereals, or deficiencies within man-made circumstances, such as a fragile skin in tomatoes which are to be mechanically harvested. In yet other projects attention is given to defects in quality, such as weak malting performance in barley or poor flavor in potatoes. These programmes of “defect elimination” have given substantially increased crop yield and quality in a great array of circumstances.

In plant breeding programmes based on “selection for yield”, there is no incorporation of a designated physiological or morphological character, but only an intent to improve yield, without consideration of the why or wherefore of that greater yield. In simplest form, such a programme involves hybridization among “promising parents”, (they are defined as “promising” either because they are themselves high yielding or because they have already shown good combining ability for yield), the production of segregating populations, and the selection of high yielding material from among the segregates. This type of breeding has also been highly productive; success has especially depended on the availability of a wide range of material in the programme, the choice of the crosses to be made and the skilful evaluation of the emergent genotypes - together with one’s share of good fortune.
When a new variety is produced in this way, the plant breeder may not know why it yields better than its predecessors. A wheat breeder who recently produced a high yielding variety of wheat, was asked what attributes gave it such capacity for yield; he replied, “I do not know... but I will list the characteristics of the variety, and it is for the physiologist to judge whether these may be the reasons for the high yield.” Many cereal breeders selecting for yield give a like reply, or state that the new variety has “better adaptation” to the environment. BELL and KIRBY (1966) cite the extension of wheat and barley cultivation into high latitudes in Europe as illustrative of the breeding of cereals for a new environment by selection for yield.

The current remarkable advance in maize yields in the United States is due to higher soil fertility levels, denser plant populations and the use of hybrids able to yield well in these heavily fertilised, crowded communities. In these conditions some hybrids show a substantial proportion of sterility, while others maintain a satisfactory cob on all plants. How are the successful hybrids developed? They are basically developed by the production of inbred parents of likely value, hybridization and the selection of hybrids for high yield in dense, heavily fertilized communities. STRINGFIELD (1964) suggests that breeding for tolerance to crowding at high fertility is potentially the greatest contribution that maize breeders can make in this decade. Little is known of the characters which govern such “tolerance”, but hybrids derived from “prolific” inbreds (STRINGFIELD, 1964) or which are themselves ‘prolific’ (LANG et al., 1956) seem more likely to be successful. (“Prolific” here means a capacity to produce a second ear at wide spacing). Shade tolerance by the whole plant is also a feature of successful hybrids (STINSON AND Moss, 1960), while HAGEMAN et al. (1967) suggest that the levels of activity of enzymes such as nitrate reductase may ultimately provide breeding criteria. These are as yet but faint and uncertain indices of the attributes of success, and the maize breeding programmes, other than those aimed at “defect elimination”, continue to be based principally on inbreeding, hybridization, and the selection of F,’s for yield performance.

THE DEVELOPMENT OF MODELS
The bases of crop breeding programmes can be usefully extended by a third philosophy, namely “the breeding of model plants or ideotypes”. Man has long used models in his approach to a great range of problems; indeed the process of invention comprises the development of theoretical models based on knowledge, experience and imagination, the construction of the models, their testing and their use. It is the familiar approach in aircraft production, building construction and instrument design, and its validity for these physical purposes is generally accepted. Can this principle be applied to biological needs? We must pose a further question: Is it possible in any defined environmental situation to design a plant which is (i) theoretically capable of greater production than the genotype it is to replace and (ii) of such design as to offer reasonable prospect that it can be bred from the material available? The satisfaction of these criteria lies in the availability of three resources, namely sufficient knowledge, adequate genetic diversity and suitable techniques.
We may not yet have enough understanding of the anatomy and physiology of some crop species to permit the design of new cultivars, but in others, notably the cereals, we may now be able to conceive models of superior productivity. Admittedly, there can be no immediate certainty of success; all agree that models must be tested for performance. But if we can sensibly postulate a model, albeit a crude attempt at perfection, then we have the opportunity to devise and examine a combination of characters which otherwise may not occur in breeders’ plots for centuries. Further, even though the early models produce no immediately useful commercial material, they will provide new bases for the understanding of crop ecology and for the design of progressively more effective models. In contrast, “selection for yield” is unlikely ever to approach the asymptote of yield, since the appropriate combination of plant characters, never being sought, can be attained only by attrition or chance. Selection for yield has all the immediate advantages and all the longer term limitations of a wholly pragmatic procedure.

Those who question the usefulness of designing or breeding model plants do so on a number of grounds. Firstly, they affirm that we do not have sufficient physiological knowledge to devise a model with confidence. In any breeder’s plots, high yielding material of diverse growth form may be seen. How, they ask, can one nominate a particular plant form when there seems to be such a wide array of compensating mechanisms or routes towards high yield. Secondly, the definition of a model is potentially hazardous, in that it will narrow the spectrum of a breeding programme, rather than permit the emergence of the highest yielding segregates without prejudice by the breeder as to the most desirable plant form. And thirdly, they add, even if the model plant were to prove high yielding, the unique character of the model would not be established. Any other model could perhaps lead to equally high yields. Only if we breed and test many different models, or a series of models with varying degrees of model-character input, can we determine the advantage, if any, of the preferred model.

LANGER (1967) questions whether the plant breeder can be expected to react to the multiplicity of suggestions currently offered by the physiologist, but he envisages considerable impact on plant breeding objectives as the physiology of yield is further elucidated. MAC KEY (1966) while contributing to the design of models, believes that they cannot be directly applied in practical plant breeding; he considers that their value will lie in providing concepts which permit appropriate decisions within breeding programmes. While the weight of these arguments and reservations is recognized, they are believed not to invalidate the proposition that cereal models of likely value can be designed and bred at the present time. The very diversity of form among currently successful cultivars may indeed suggest that each variety is deficient in one or several characteristics. The narrower array of material to be used in the breeding of models is implicit in the concepts behind such a programme, just as the aircraft designer chooses materials appropriate to his model.

THORNE (1966) and TANAKA et al. (1966) contribute to thought on models by discussing and evaluating a number of attributes which are believed to influence the grain yield of wheat, barley
and rice. Others have taken a further step and have advocated cereal breeding programmes incorporating individual model characters or have actively undertaken such projects (DONALD, 1962; ASANA, 1965; BEACHELL and JENNINGS, 1965; MAC KEY, 1966; TANNER et al., 1966).

Several examples can be given of the use of model characters. Cereal breeders have long laid emphasis on **resistance to lodging**, based both on the maintenance of grain yield and on the difficulty of harvesting lodged crops. The crop physiologist has established the influence of lodging in terms of its interference with light relationships and photosynthesis. Here then, in a stout stem, is a “model character”, a character currently receiving increased recognition because of the extreme resistance to lodging at high fertility of the semi-dwarf wheat of Japan, used so successfully in breeding programmes in Washington State and Mexico.

A second model character of proven value, defined both from physiological studies and through breeders’ observations, is the **awn on the floret of wheat and barley**. But though this character makes a positive contribution to photosynthesis and yield, and is easily incorporated into breeding programmes, there are still many new varieties which do not have this valuable attribute.

A third model character, now gaining recognition by a few cereal breeders, is **erect foliage**. There is theoretical advantage to be gained in the photosynthesis of various cereals if they have upright leaves (e.g. MONSI and SAEKI, 1953; DUNCAN et al., 1967); it is significant that the modern high yielding rice varieties of Japan and Taiwan, both japonica and indica types, which yield so much more than do the rice varieties of the tropics, all have this feature in common, together with relatively dwarf stature.

TSUNODA (1959a, 1959b, 1960, 1962) has shown that the kinds of rice responsive to high fertility and high density are those with short, sturdy erect stems and short erect dark green leaves. Workers at the IRRI in The Philippines have further examined and elaborated the importance of these characters in growth and grain yield (TANAKA et al., 1966; BEACHELL and JENNINGS, 1965; JENNINGS, 1964) and by hybridizing a productive Taiwanese variety (**Dee-geo-woo-gen**) of short stature and erect leaf habit with a tall, lax, locally adapted variety (Peta), they have produced a short, erect variety which has given excellent performance under a heavy fertiliser regime both in The Philippines and elsewhere in tropical Asia (I.R.R.I., 1966). Thus we see growing evidence that “model characters”, especially those emerging from physiological studies, are now influencing the approach by a few plant breeders.

Perhaps model plants will in fact develop in this way, by the progressive adoption of individual model characters until, in the aggregate, these characters constitute a total model in the mind of breeders. If this were so, then the development of models might evolve from “defect elimination” but in the positive sense of “character incorporation”.

Whether there has been an incorporation of one or many “model characters”, there will remain other attributes which, according to local circumstances, must be incorporated into the new variety, such as disease resistance and maturity. Because of this, and also because of the unpredictability with which “model-character genes” may affect other characters, any intended
cultivars produced to model specifications must finally be subjected to rigorous selection for yield. Further this testing must include examination of the adaptability of the cultivar and its capacity for yield over a sufficient range of environmental situations. Yet if the model is successful, the whole level of testing will be at higher yields than those of existing cultivars.
The term “ideotype”, literally “a form denoting an idea”, is here proposed for biological models. In its broadest sense, an ideotype is a biological model which is expected to perform or behave in a predictable manner within a defined environment. More specifically, a crop ideotype is a plant model which is expected to yield a greater quantity or quality of grain, oil or other useful product when developed as a cultivar.

**Principles of design of cereal ideotypes**

Concepts of cereal plants with high yield based on more culms, more ears, spikelets or grains are derived from considerations of the isolated plant. Here such criteria are valid. But the performance of a plant growing in isolation may have little relationship to its potential for yield as a community. The principles of plant design here enunciated are based on experimental findings and theoretical concepts related specifically to capacity for high grain yield when grown as a crop.

In a field crop each plant suffers intense competition from its neighbours, with its yield reduced to 20% or 10% or less of the yield of an isolated plant, and it is in this crowded community that any ideotype has to succeed. This capacity of a genotype to yield well in a community can be analysed in terms of two parameters, namely
(a) the yield per plant in the absence of competition from neighbours, and
(b) its response to crowding among other plants of like genotype.

The response by wheat cultivars to crowding is almost unexplored. In no wheat environment do we know how much of the success of leading cultivars is due to their capacity to yield well at wide spacing and to maintain that margin over other cultivars when sown as a dense crop, or alternatively the degree to which a successful cultivar may be a low producer under very wide spacing, but with a capacity to maintain its yield per plant relatively well within a crop. In rice it is the latter attribute which gives success under crop conditions (TANAKA et al., 1964), and a similar situation may be indicated for wheat (WIEBE et al., 1963). It is because of these relationships that much of the work on the physiology and yield of the isolated plant may have but limited relevance to the crop situation.

Clearly the individual plant within the community will express its potential for yield most fully if it suffers minimum interference from its neighbours. Thus its neighbours should be weak competitors. And since, for the purpose of this discussion, all plants in the crop are of like genotype, then the ideotype itself must be of low competitive ability.

This may seem a paradox - that a successful crop plant should be other than an aggressive competitor for those factors needed for growth. But this seems to be so. While strong competitive ability is advantageous against other species such as weeds, it will lead in a monoculture to intensified competition and heavy mutual depression among the crowded plants.
For example, a genotype which shows effective interception of light through expansive leaf display by the isolated plant, may show less efficient utilization of light within a community of that genotype, because of mutual shading by neighbours.

The efficient production of dry matter by a monotypic community will depend on the ability of the individual plant to make maximum use of the resources of the limited environment in which it grows, and to encroach to a minimum degree on the environment of its like neighbours. For example, if an erect leaf can photosynthesize effectively within a less horizontal area than a drooping leaf of like size, it is operating with a less demand on the light resources. Similarly a genotype of high net assimilation rate or with a particular pattern of deployment of photosynthates may be efficient in terms of its demand on resources within the community. But some of these same attributes may be disadvantageous among widely spaced plants.

Though the individual plant in a crop should have a low demand on resources relative to its production, the community as a whole must press on total resources to a maximum degree, for only then can full production be envisaged. The means towards this end does not lie in the aggressiveness of the individual plant but in a high density of plants resistant to crowding (i.e. of low competitive ability against each other), each making efficient use of its limited environment, yet each ultimately in intense competition with its neighbours because of dense planting.

It is submitted that the successful crop plant will be of low competitive ability relative to its mass and of high efficiency relative to its environmental resources.

This low competitive ability of the successful crop plant means that as well as the negative relationship already indicated (performance at low and high density respectively), there may be a second negative relationship; this is the relationship of (a) the competitive ability of a particular cultivar within a mixture of different cultivars with (b) the yield of that same cultivar in pure culture. This has been demonstrated with barley (SUNESON, 1949), and dramatically for rice (JENNINGS and DE JESUS, 1968), where it has been shown that high yielding cultivars are suppressed and even totally eliminated in mixtures.

Because of these relationships, selection for yield in heterozygous communities may be an erratic means of advance. WIEBE et al. (1963), studying mixtures of parental and heterozygous barley to simulate successive filial generations, concluded that because of competitive effects between genotypes, “where high yield is the criterion selected for, say in the F, and the selection is intended for use in pure stands, the instructions from the present study are that one should save the poorest plants from the F, rather than the good ones”. JENNINGS and AQLJINO (1968) advocates the hand rogueing of F, populations of rice to eliminate tall, leafy and spreading types, which would otherwise shade and depress the potentially more productive segregates.

Thus the successful crop ideotype, despite its potential for high yield as a monotypic community, may not emerge from mixed or segregating populations. The development of ideotypes must depend on the active recognition of their attributes and not on their ability to compete with other genotypes.
The foregoing relationships will apply especially to total dry matter production. However NICHIPOROVIC (1954) and many others have emphasized that total production (biological yield) is an insufficient criterion of crop yield when the economic yield comprises only a part of the plant, such as its grain, fibre or oil. Assuming that the model is capable of heavy dry matter production (net photosynthesis), a further feature must be its capacity to render a maximum part of that yield as the useful product. Nichiporovic terms this ratio of ‘economic yield’ to ‘biological yield’, the ‘coefficient of effectiveness of formation of the economic part of the total yield’; DONALD (1962) has suggested the term ‘harvest index’. The translation of a ‘high harvest index’ into meaningful morphological and physiological plant characteristics is a specific and major need in the design of any model. It is not enough that a model plant have many large ears or bolls, but that the weight of these organs be high relative to its dry matter production. This is a critical aspect of plant design.

In some species the ‘economic part’ clearly forms a sink for photosynthates during the later part of the plant’s growth. The cereal grain and the potato tuber are such organs; thus ear production and ear characteristics in cereals will have high relevance to grain yields. Here lies further opportunity to define characteristics of an effective ideotype.

The design of a cereal ideotype will thus depend heavily on theoretical knowledge and experimental evidence in three areas, namely photosynthesis in cereal communities, the role of the cereal ear as an available or limiting sink for photosynthates and the operation of plant competition in crop communities.

The question arises whether any of these principles of design can have substantial constancy of expression over a wide range of environments. Though the principles be valid, their application may conceivably lead to such a range of models as to make plant design both difficult and profitless.

It is suggested that two considerations should influence the approach to plant ideotypes in relation to environments. Firstly, it seems reasonable that the designer should initially seek to cater for the simplest environmental situation, and, further, one which can readily be defined. In general this will be the situation in which the factors needed for growth and development approach maximal needs. In particular, water and nutrients should be in non-limiting supply, with emphasis centred on the efficiency of the crop community as a photosynthesizing system. Here then will be a basic ideotype designed to give maximum production in a highly favourable or idealized environment. If such an ideotype is developed, then the effect of any curtailment of resources, as by a decrease in nutrient or water supply, can be examined in terms of the progressive modification of the basic ideotype. This approach promises a more rational array of variants than could be achieved by a series of ideotypes independently conceived for each major environmental situation.

The second point pertaining to environment is that the production of a crop ideotype may call for the concurrent creation of a new environment. HUTCHINSON et al. (1947) wrote, “Successful evolutionary change depends on a fortunate coincidence of the emergence of a new character with the occurrence of an environmental change which makes it advantageous.” Similarly the
conscious development of an ideotype may need to be accompanied by conscious change of the environment. Though we are concerned in this instance with a potential to yield well as a pure culture rather than with a potential to compete successfully with other genotypes, the concept of the relationship to the environment is basically the same. Model building need not, therefore, be exclusively associated with existing environments, but may involve the concurrent design of new environments, including such man-made components of the plant environment as the crop density, planting arrangement and nutrient level.

A WHEAT IDEOTYPE

The feasibility of designing a wheat ideotype is best examined by attempting such a design. In accordance with the foregoing discussion, the ideotype here presented is conceived as potentially capable of high grain yield when grown as a crop community in an environment favourably endowed for water and nutrient supply, though most of the characters are believed also to be of ubiquitous value. This basic ideotype is submitted therefore as suited to well-fertilized, well-watered lands.

All the attributes of the ideotype are morphological characters, but all are based on physiological considerations. It is believed that the model may offer levels of yield appreciably greater than those available from genotypes of currently prevalent plant form. The features of the model are:

1. A short, strong stem. As already discussed, the advantage of a short stout stem in reducing the likelihood of lodging, is well established. The need for a strong stem increases as fertility is raised, since the modulus due to wind becomes greater as the weight of the ear increases. A secondary effect of height will be to change leaf disposition, in particular the vertical interval between successive leaves on the stem. If the leaves are very closely spaced, as on an extremely short stem, there may be serious shading of all but the top leaves, especially because of the two-ranked arrangement of grass leaves. This seems to be a possible explanation for the lack of sorghum cultivars with all four of the known dwarf genes, and it suggests a disability of excessive dwarfness. (This relates also to the ‘leaf area density’ (KASANAGA and MONSI, 1954), discussed under leaf size). It is possible that shortness of stem may make a small contribution by reducing the investment of photosynthates into stem production, but this proposition is doubtful.
in wheat because the stem is itself covered with photosynthesizing tissues. If we weigh these points it seems that a relatively short stout stem, though not excessively so, is essential as a safeguard against lodging, while still providing a sufficient dispersal of leaves in the canopy.

2. Erect leaves. Reference has been made to this aspect of plant form in rice breeding programmes. It is based on the concept that in a dense community, near-vertical leaves will permit adequate illumination of a greater area of leaf surface than will occur in a canopy of long, horizontal or drooping leaves, in which the upper leaves will be overlit and the lower leaves harmfully shaded. This relationship will apply to any species in which the leaf is nearly saturated for photosynthesis at a light intensity substantially below that of the ambient light. Such is the case for rice (e.g. MURATA, 1961) and wheat (e.g. WARDLAW, 1967).

A direct demonstration of the effect of leaf angle in rice was made by MATSUSHIMA et al. in 1964. They grew an erect-leaved rice variety at wide and at close spacing; half the plants were treated by dropping the leaf angle with paper fasteners attached at the leaf tips. Carbon assimilation was unaffected in the widely spaced plants, but was depressed by 35% in plants at close spacing. HAYASHI and ITO (1962) similarly showed in a collection of rice varieties that the steeper the leaf angle the greater was the light penetration (lower coefficient of extinction), and the greater the crop growth rate.

GARDENER (1966), working at Guelph, Canada, compared three barleys known to be high yielding for grain with three known low-yielding barleys. The high yielders had narrow, upright leaves and showed deep light penetration into the leaf canopy, while the low yielders characteristically had long wide drooping leaves and showed strong light interception by the upper leaves of the canopy. TANNER et al. (1966) classified 300 varieties of wheat, oats and barley at Guelph into high, medium and lowyielders purely on the basis of their leaf angle and leaf width. They found that they had correctly selected all but two of the 50 high yielding varieties, and they consider leaf habit to be a valuable criterion in selecting for cereal yield in Ontario.

Vertical foliage accords with the concept of greater production per unit of environmental factor and with low competitive ability. Plants (or culms) with vertical leaves can be crowded with less mutual competition than would occur among crowded plants with floppy leaves, and this potentially permits a greater population of ears per unit area. (Varieties of rice with large floppy leaves give low production, but become dominant in mixtures; they are characteristic of much tropical village agriculture because of their ability to suppress both weeds and other rice genotypes (JENNINGS, 1966).

3. Few small leaves. The postulated advantage of small leaves is mainly based on theoretical considerations. KASANAGA and MONSI (1954) showed that a scattered leaf arrangement (a low leaf area within each ‘leaf plane’ of the canopy) is potentially advantageous in plant communities under high illumination, i.e. in crops, in contrast to shade communities. WILSON (1960) similarly calculated that the more uniform the dispersion of leaves in each leaf layer, the
greater will be the crop growth rate. Each of these theoretical considerations indicates an advantage of many small leaves over a few larger leaves. In support of this hypothesis, TSUNODA (1959b) reported that in both rice and soybean the varieties adapted to heavy fertilizer application (we may regard this as applicable also to high density situations) tend to have smaller-sized leaves. In wheat, small leaves and more especially shorter leaves, tend also to be erect leaves, while longer leaves are more likely to be floppy and downward curving.

The number of leaves on the main shoot of wheat ranges from 7 to 20 or more. The axils of the lower leaves are the sites of origin of the primary tillers, but in a uniculm plant (see below) this role disappears, and we are concerned with leaves mainly as photosynthetic, respiring and evaporating surfaces. If we assume that each leaf produces net photosynthates exceeding the sum of its own dry weight and the contribution it makes to later leaves, stems and roots, then the greater the number of leaves, the greater will be the culm’s potential to produce a large ear. But this will be true only as long as each additional leaf permits a more complete exploitation of the environment. If, for example, the leaves in the crop are already sufficient to intercept all light then there can be no advantage in more leaves (DONALD, 1963; PUCKRIDGE and DONALD, 1967). The same general considerations would be true if water or nitrogen were limiting. Though our understanding of the significance of leaf number is very incomplete, it seems that a high density of culms offers better prospects of a heavy grain yield than does a high number of leaves per culm; for any given leaf area index it permits greater potential sink size relative to vegetative growth.

4. A large ear. (Many florets per unit of dry matter). There is much circumstantial evidence that the wheat ear is normally a limiting sink for photosynthates. In brief, this evidence is of two kinds. Firstly, when various individual parts of the photosynthetic surface responsible for grain filling (flag leaf, upper stem, ear) are removed or shaded, the remaining parts can partially compensate for the loss of the part that has been removed or shaded (e.g. BUTTROSE and MAY, 1959; THORNE, 1963). Thus none of these organs normally operates at full capacity. Secondly when the grain number in a wheat ear is reduced from the full complement, the weight per grain may show no increase (BUTTROSE, 1962). This indicates that in the control ear, the number and potential size of the grains, rather than the supply of assimilates, may govern the total weight of grain produced.

Thus at least up to the time of fertilization, the wheat plant may be said to re-act ‘conservatively’, in the sense that its number of tillers, its number of surviving spikelets per ear or its number of fertilized florets show such reduction, relative to past and current environmental conditions, as to offer high probability that the load of developing grain will lie within the photosynthetic capacity of the plant to bring it to maturity. This means that a limitation to yield may occur in existing cultivars in the pre-anthesis period simply because of the genotype-environment interaction. (There is probably survival value in ‘conservative’ grain production by
annual grasses in natural communities. In very adverse seasons a smaller number of fully formed seeds is advantageous over a greater number of seeds which are imperfectly formed).

THORNE (1966) points out that any limitation to yield imposed by the capacity of the ear is at present supported only by indirect evidence. Nevertheless the reasonable deduction from a considerable array of data is that the receptive capacity of the grains of the wheat ear is usually less than the post-anthesis photosynthetic capacity of the shoot that bears them.

If the proposition of sink limitation be accepted, then clearly the model wheat plant must have large ears. We have yet to learn whether the spikelet number or the floret number per spikelet is per se of the greater consequence, but by ‘large ears’ we certainly mean ears with many fertile florets. In particular the attribute of high floret number, relative to that of other genotypes, must be expressed under the acute competitive stress of a crop community.

It may be thought that all this is but a truism - that the number of fertile florets in the cereal ear is not only related to yield but is indeed synonymous with it. But this is not necessarily so. The wheat breeder has long been familiar with argument on the relative advantage of a large number of ears on the one hand or of many grains per ear on the other. The rice breeders of Japan are similarly divided into devotees of ‘panicle number’ and ‘panicle weight’. Further, it is recognized that these attributes are usually negatively correlated, and that pursuit of size of ears commonly leads to a decline in ear number.

The proposition that the ideotype should have a ‘large ear’ is therefore interdependent with other points. ‘Large ears’ must specifically mean a large number of florets per unit of dry matter of the whole of the plant tops. (If one uses weight of grain instead of florets, the ratio to total dry matter is then the ‘harvest index’). It is of interest that the increased grain yield by the varieties of oats currently in use in Australia is associated with a higher harvest index, without increase in the total dry matter production (SIMS, 1963). Compared with earlier varieties the index has risen from about 0.32 to about 0.40. The meaning of ‘large ears’ in a wheat crop is thus a sufficient number of florets per unit of total dry matter to ensure that their aggregate capacity will impose no sink limitation for photosynthates. No cereal breeding programme can be wholly effective without measurement of the total yield of dry matter as well as of grain.

A further model character critically related to the ear size of the model plant is a single-culm habit of growth, discussed below.

5. An erect ear. This is adopted in the belief that the best mean illumination of all sides of all ears will be attained in a community of erect ears. This is the common ear disposition in wheat, though drooping ears are to be seen in some commercial varieties.

6. The presence of awns. There is evidence dating back to 1920 (HARLAN and ANTHONY, 1920) that the additional surface provided by awns will contribute significantly to photosynthesis by the cereal ear. GRUNDBACHER (1963), who has reviewed the literature on this topic, considers that as assimilating organs they may contribute more than ten percent of the total grain dry weight. The contribution seems to be greater under semi-arid conditions, supposedly because
of the xeromorphic structure of awns compared to that of cereal leaves. This contribution to yield by the awns has been recognized in many plant breeding programmes (e.g. VOGEL et al., 1963). Perhaps there is a limitation to the advantage of awns, in that very heavy awns or branched awns may shade the photosynthetic surface of the glumes to a significant degree. But of the value of simple awns there can be no doubt.

7. A single culm. It is important to appreciate that the number of culms per plant (main stem plus tillers) in any cereal community is not characteristic of the species, but is a consequence of the selection of a genotype to fit the local climate and more particularly the local agronomic practices. For example under crop conditions, rice in Japan has more than 20 fertile culms, while wheat in the United Kingdom has 2 or 3.

This is no indication of any inter-specific difference between rice and wheat in respect to tillering. Rice plants in Japan are normally spaced at about 24 cm x 24 cm. Any closer spacing would intensify the enormous annual task of hand planting some six hundred thousand million individual rice seedlings. And so a genotype has been selected which will occupy the 24 cm x 24 cm environment - one which tillers freely.

The number of tillers on wheat in England is similarly a consequence of agronomic practice - of the selection of a seeding rate in the days of hand broadcasting on unfertilised fields and of the subsequent transfer of that seed rate to 18 cm rows. No new variety is accepted into the system unless it produces well when sown at the usual rate in these rows, and this includes having the appropriate number of fertile tillers per plant.

If this viewpoint is accepted, then the desirability of a low or high tillering capacity in any cereal can be re-considered without prejudice invoked by past or current practice. In this context it is now proposed that a community of wheat plants with a single culm - that is, with a main stem and no tillers - will give greater production per unit area than is given by a variety which tillers freely or even sparsely.

The wheat plant is potentially capable of indefinite perennation through culms successively developed from buds on the primary, secondary, tertiary and succeeding orders of tillers - a sustained production of ‘daughter’ vegetative organs. But at a later stage, because of competition between the ears and the younger tillers for nutrients, and because of the suppression of tiller buds through the apical dominance of the ear bearing tillers, the younger tillers produce no ears and die, or are even totally suppressed (ASPINALL with barley, 1961, 1963; RAWSON with wheat, 1967).

The growth of the wheat plant can thus be regarded as beginning with a period of perennation, followed by a period of active competition between perennial and annual attributes, and finally by a period in which the annual habit prevails. Seed is produced and the plant dies. To the extent that ‘unsuccessful’ sterile tillers are produced, wheat has not yet evolved to become a fully efficient annual plant.
On the other hand, a wheat plant comprising only a main stem and no tillers will have no remnant of perenniality. There can be no internal competition between developing ears and young tillers, but only a uni-directional organization towards ear and grain formation. Though the sterile tillers in wheat crops are considerably smaller than those which produce an ear, they nevertheless use a part of the environment. Some of these environmental resources, notably part of the nitrogen and minerals, are passed to the fertile tillers as the sterile tillers senesce, but there is a net ‘loss’ in the sterile tillers even of these nutrients. When we turn to water and light, the competition by the sterile tillers is essentially irreversible. The loss of water through sterile tillers may be particularly significant in the drier environments where most of the wheat of the world is grown.

Reference has been made to the inverse relationship between the number of ears per plant and the size of the ear in multi-culm plants, either in comparisons of genotypes or due to environmental or density differences. As a result there is no control of ear number per plant or per unit area when the density of multi-culm plants is varied. On the other hand if a uni-culm plant is used, the ear number per plant will be constant at unity (except at excessively high densities), and the numbers of ears per unit area will be controllable; it will be feasible to achieve an optimum density/ear size relationship.

Similarly, in plant breeding programmes with uniculm material, there can be positive pursuit of ear size as a character of the ideotype, because of the non-plasticity of the culm number. If the seed rate of a normally multi-culm wheat variety is heavily increased, then eventually a density is attained at which all plants will have a single culm. At such a seed rate, the plants will be extremely depauperate, and the yield per unit area will be less than at a lower seed rate (PUCKRIDGE and DONALD, 1967). This single culm community attained by crowding multi-culm plants is thus not comparable with a crop of genetically single-culm plants. The latter will of course be plastic as density rises, at first in ear size, then by total ear failure and finally by plant mortality. But the uniculm habit will prevail at the optimum density for grain yield and not only at excessive densities.

We can examine as a separate point the question of whether the main stem, as a single culm, has any advantage over any other tiller, also as a single culm. The greater grain production by the main stem than by any tiller of a wheat plant in a crop is not proof that a community wholly of main stems will produce more grain than a community made up of both main stems and tillers. If the main stem in the latter situation uses environmental resources proportional to its greater production, then obviously its yield may be correspondingly depressed when it competes only with other main stems. Nevertheless the main stem may truly have a greater potential for production within a defined and finite environment than has any other single tiller. In the first place it has the principal benefit of the early water and nutrient uptake by the seminal root system (KRASSOVSKY, 1926). Secondly the early development of the main stem gives a much longer interval for the development of ears than in later culms. It has a far longer period to double ridge formation (RAWSON, 1967) and this may be the factor leading to its greater number of spikelets. Similarly it has a longer period in which to initiate florets. This time factor
could give additional advantage to a community of main stems compared with a mixed community of main stems and tillers.

It may be noted that the non-tillering character has appeared in barley (e.g. as a mutant cv. Kindred, and also as chemical mutants, SWAMINATHAN et al., 1962). Meanwhile there is already a trend in wheat varieties in N.W. Europe towards decreased tillering, larger heads and larger seeds (MAC KEY, 1966).

8. Other characters. The ideotype here formulated does not permit the nomination of particular parents solely because of their strong display of desired characters. There may be various routes towards a variety conforming to the general pattern of the model; further it has already been emphasized that the ideotype must meet local requirements for disease resistance and so on. Thus the parental material must include high yielding, locally adapted cultivars, and indeed the extent to which this is needed is an index of the limit to our knowledge of the desirable attributes of our ideotype.

The features of the ideotype here described do not, for example, designate any specific maturity nor do they show the pattern of leaf area duration after anthesis. In general, early flowering, relative to the environment, may be indicated as a means of gaining a maximum number of florets per unit of dry matter at flowering and a lengthened period of grain filling. And similarly the finding by WELBANK et al. (1966) that leaf area duration (area of green leaf integrated with time) above the flag leaf node after anthesis is related to grain yield, suggests the desirability of strong persistence of the uppermost photosynthetic tissue. (May it be however that the persistence of these green surfaces is in part an effect rather than a cause of high yield? If an ear fills quickly because it is small, may the leaves then die early?)

Another character that could perhaps be developed to advantage is the heavy accumulation of sugar in the stem, followed by a maximum transfer to the growing grain; the transfer of these substances may again depend on ears of such capacity as to be non-limiting sinks (BUNTING and DRENNAN, 1966). Residual carbohydrates in the base of the cereal stem at maturity may, like tillering, be an undesirable vestige of perenniiality, corresponding to the swollen lower internodes which serve as inter-seasonal survival organs in many perennial grasses.

Brief reference has been made to the influence of the single culm habit on the root system. In a community of uniculm plants the seminal root system will retain far greater importance relative to the adventitious roots, and because the seminal roots are the oldest they will potentially be more deeply penetrating. Beyond this, no model characters of the root system are here specified. The extent to which the ideotype is defined will be a matter of judgement by the designer. Those characters which are left unspecified must be cared for in the final selection for yield.

9. In summary the wheat ideotype will be of such form that it is a weak competitor relative to its mass, and thus will be less affected by crowding among like neighbours. It will make a minimum demand on resources per unit of dry matter produced, but each unit of dry matter will include a sufficient number of florets. The ear is to have a capacity to accept all photosynthates either from
its own green surfaces or from other parts of the plant. These criteria are to be satisfied especially at high fertility, and when the total pressure by the community on the environmental resources is intensified by high density of population.

AGRONOMIC CONSIDERATIONS
The wheat ideotype here described calls for a number of modifications in the environment or in the agronomic practices relating to the crop; we can also consider some of the possible variants from the basic ideotype which may be needed in less favourable situations than those for which the ideotype is primarily designed.

I. Density of planting. Since each plant will produce only one ear, the rate of planting must be increased by a factor about equal to the mean number of ears per plant in existing varieties. The factor will however need to be greater than this, because the ideotype is specifically intended to ‘tolerate’ a high density of ears per unit area. (Here we see certain disabilities of the model, associated with its single culm habit. First, its yield as a crop must more than compensate the heavier seed rate. Secondly any partial failure of establishment or any winter killing will not be compensated by an increased rate of tillering by the surviving plants.)

2. Rate of fertilizer application. The whole philosophy behind the ideotype and especially its strong stem and small erect leaves is that it will produce well at high density and high fertility, with maximum utilization of light, minimum lodging and minimum sterility. A heavy nutrient supply is a cardinal feature of the environment of the proposed ideotype. When the fertility level is lower, small erect leaves or a ‘large ear’ becomes progressively less advantageous.

3. Plant spacing. When wheat is sown in narrower rows instead of the standard 18-20 cm rows, it commonly gives a slightly increased yield (HOLLIDAY, 1963) an effect almost certainly due to the closer approximation to square planting, and thus to improved illumination of the foliage and more efficient soil exploration by the roots. The small and erratic nature of the increases so gained in wheat is presumably due in part to the multi-culm units involved, and the consequent ‘aggregation’ of the culms, particularly in the earlier growth stages, irrespective of the planting arrangement.

If a uni-culm plant is used, the benefits of square planting can be realized to the fullest degree, with a uniform spacing of all culms. Depending on the appropriate seed rate, (say 250 kg seed/ha) the drilling of uni-culm plants in 18 cm rows would give ordinates for each plant of about 18 cm x 1 cm (a rectilinearity of 18 : 1), while the ordinates for square planting would be about 4.2 cm x 4.2 cm. Square planting at this density, or its approximation by sowing in say 5 cm rows, would present mechanical problems, though probably not of insuperable kind.

It should be noted that the advantages discussed earlier for single culm plants are independent of planting arrangement and would be expressed in 18 cm rows. Regular spacing is potentially a further source of increased yield.
4. Competition with weeds. A disability of cereal varieties with erect leaves is their weaker capacity to suppress weeds by shading. TANNER et al. (1966) have recorded that a wheat variety with erect leaves, unable to suppress weeds effectively, gave the lowest yield in a variety trial in a weedy situation; on the other hand it gave the highest yield on a site which was weed free; and conversely for varieties with floppy leaves. Thus the use of varieties with erect foliage will involve greater attention to weed control by methods other than by competition from the crop.

5. Water supply. The basic ideotype, being unable to tiller, will attain its full potential as a photosynthesizing community only if the water supply and seed rate are constant in all seasons—a situation approached only under irrigation or in favoured wheat growing regions. Here a constant seed rate will give the optimal population density of culms and ears in all seasons. But in regions of fluctuating rainfall, the optimal density of ears will vary between seasons. In present-day tillering cultivars of wheat, the principal adaptation to ample or deficient water supply within the season is a variation in the number of tillers and ears per plant. Thus a constant rate of sowing in all seasons is acceptable, even though imperfect. This will not be so with a uniculm cultivar. KASPER (1929) has well illustrated this relationship among older cultivars of grain sorghum; the free-tilling cultivar, Milo, gave maximum yields at the same spacing (60 cm rows) in both dry (ca. 230 mm rainfall) and wet (ca. 740 mm rainfall) seasons. On the other hand the sparse tillering variety, Kafir, gave its highest yield in 90 cm rows in dry years and in 7.6 cm rows in wet years.

A uniculm wheat thus seems to have prospective limitations in an environment of erratic seasonal rainfall. It would presumably offer satisfactory yields (relative to other cultivars) if the rainfall were predictably and reliably low, and a low seed rate were chosen accordingly, but it cannot show phenotypic adaptation to more favourable seasons by tillering. In areas of erratic rainfall a limited capacity to produce tillers in favourable seasons thus seems desirable. Probably a range of one to three culms per plant according to conditions would suffice for the full array of seasons likely to be experienced in such regions.

In the longer term, tillering may become redundant and undesirable even in areas of erratic rainfall. If the ear were of adequate capacity and plasticity relative to the culm and its environment, then it could carry the present role of the tiller number in adapting to a range of seasonal conditions. Such is the case for the modern, non-tilling or weak-tilling cultivars of sorghum. The same cultivars are grown under irrigation and under low rainfall, except where length of season is a restricting factor; the sorghum head varies in size according to the favourability of the environment. The same adaptability to season holds for uniculm maize and its ear. Such a relationship may also be attainable in wheat once ear size is divorced from its reciprocal relationship with ear number and if the ear has an adequate range of capacity for photosynthates. Meanwhile it is proposed that the uniculm habit may first prove of value under irrigation or high rainfall conditions.
6. Alternative uses. The wheat ideotype here proposed is intended specifically for high grain production. In situations where yield of straw or recovery from grazing or any other attribute is important, considerable modification of the basic ideotype would doubtless be needed.

THE PRODUCTION OF AN IDEOTYPE

It will be clear that the wheat ideotype here depicted is unlikely ever to be developed in breeding programmes based on selection for yield under prevailing agronomic practices. It has a low yield per plant; it is susceptible to competition by other genotypes or by weeds; it is unsuited by current seed rates; and it may need novel sowing machinery. All newly wrought ideotypes may similarly involve changed practices, and it seems that advantageous combinations of radical ideotypes and radical practices will be attained only by hypothesis and test.

The ideotype here formulated may prove an imperfect image. Yet the design, breeding, testing and exploitation of plant ideotypes is a logical step towards new levels of yield and should be pursued with imagination. Eventually most plant breeding may be based on ideotypes.

A rice ideotype

World rice production must increase by approximately 1% annually to meet the growing demand for food that will result from population growth and economic development (Rosegrant et al., 1993). Yield potential is defined as the yield of a variety when grown in environments to which it is adapted; with nutrients and water non-limiting; and with pests, diseases, weeds, lodging, and other stresses effectively controlled (Evans, 1993).

Yield potential of irrigated rice has experienced two quantum leaps (Chen et al., 2002a). The first one was brought about by the development of semi-dwarf varieties in the late 1950s in China and early 1960s at the International Rice Research Institute (IRRI). Dwarf breeding began in China in 1956 using the Sd-1 gene from Ai-zi-zhan (Huang, 2001). In 1959, the first dwarf variety, Guang-chang-ai, was developed in China. In 1962, plant breeders at IRRI made crosses to introduce dwarfing genes from Taiwanese varieties such as Dee-geo-woo-gen, Taichung Native 1, and I-geo-tse to tropical tall land races. In 1966, IR8, the first semi-dwarf, high-yielding modern rice variety, was released for the tropical irrigated lowlands (Khush et al., 2001). The birth of IR8 increased the yield potential of the irrigated rice crop from 6 to 10 t ha⁻¹ in the tropics (Chandler, 1982). The second leap in yield potential was brought about by the development of hybrid rice in 1976 in China (Yuan et al., 1994). Standard heterosis of indica/indica hybrids was reported to range from 15% to 25% in China, but no information is available about the actual increase in yield potential of hybrid rice in temperate and subtropical areas. In the tropics, Peng et
al. (1999) reported that indica/indica hybrid rice has increased yield potential by 9% compared with the best inbred cultivars in irrigated lowlands. Improving rice yield potential has been the main breeding objective in many countries for several decades. Tongil-type rice varieties were developed in Korea in 1971 from a japonica/indica cross (Chung and Heu, 1980). These varieties showed a 30% yield increase compared with japonica varieties. Morphologically, Tongil varieties were characterized by medium–long and erect leaves, thick leaf sheaths and culms, short plant height but relatively long panicles, open plant shape, and lodging resistance. In 1982, the Japanese government started a super-high-yielding rice breeding program (Kushibuchi, 1997). The target was to increase rice yield by 50% in 15 years by crossing indica with japonica. Several promising super-high-yielding cultivars such as Akenohoshi and Akichikara have been developed at several breeding stations in Japan. These varieties are panicle-weight type with a large number of spikelets per panicle (Wang et al., 1997).

However, stagnant yield potential of semi-dwarf indica inbred rice varieties has been observed in the tropics since the release of IR8 (Peng et al., 1999), although a genetic gain in yield per day has been achieved due to a reduction in total growth duration. It was postulated that this stagnation might be the result of the plant type of these varieties. They produce a large number of unproductive tillers and have excessive leaf area that may cause mutual shading and a reduction in canopy photosynthesis and sink size, especially when grown under direct-seeded conditions (Dingkuhn et al., 1991). Most of these varieties have high tillering capacity and small panicles. A large number of unproductive tillers, limited sink size, and lodging susceptibility were identified as the major constraints to yield improvement in these varieties.

Donald (1968) proposed the ideotype approach to plant breeding in contrast to the empirical breeding approach of defect elimination and selection for yield per se. He defined “crop ideotype” as an idealized plant type with a specific combination of characteristics favorable for photosynthesis, growth, and grain production based on knowledge of plant and crop physiology and morphology. He argued that it would be more efficient to define a plant type that was theoretically efficient and then breed for this (Hamblin, 1993). In rice, Tsunoda (1962) compared yield potential and yield response to nitrogen (N) fertilizer in relation to the plant type of rice genotypes. Varieties with high yield potential and greater responsiveness to applied N had short sturdy stems and leaves that were erect, short, narrow, thick, and dark green. The close association between certain morphological traits and yielding ability in response to N led to the “plant type concept” as a guide for breeding
improved varieties (Yoshida, 1972).

Simulation models predicted that a 25% increase in yield potential was possible by modification of the following traits of the current plant type (Dingkuhn et al., 1991): (1) enhanced leaf growth combined with reduced tillering during early vegetative growth, (2) reduced leaf growth and greater foliar N concentration during late vegetative and reproductive growth, (3) a steeper slope of the vertical N concentration gradient in the leaf canopy with a greater proportion of total leaf N in the upper leaves, (4) increased carbohydrate storage capacity in stems, and (5) a greater reproductive sink capacity and an extended grain-filling period. These traits are both physiological and morphological. To break the yield potential barrier, IRRI scientists proposed modifications to the high-yielding indica plant type in the late 1980s and early 1990s (Khush, 1995). The newly designed plant type was mainly based on the results of simulation modelling and new traits were mostly morphological since they are relatively easy to select for compared with physiological traits in a breeding program. The proposed new plant type (NPT) has low tillering capacity (3–4 tillers when direct seeded); few unproductive tillers; 200–250 grains per panicle; a plant height of 90–100 cm; thick and sturdy stems; leaves that are thick, dark green, and erect; a vigorous root system; 100–130 days’ growth duration; and increased harvest index (Peng et al., 1994).

Breeding of first-generation NPT

Breeding work began in 1989 when about 2000 entries from the IRRI germplasm bank were grown during the dry and wet seasons to identify donors for the desired traits (Khush, 1995). Donors for low-tillering trait, large panicles, thick stems, vigorous root system, and short stature were identified in the “bulu” or javanica germplasm mainly from Indonesia. This germplasm is now referred to as tropical japonica (Khush, 1995). Hybridization began in the 1990 dry season. The F$_1$ progenies were grown in the 1990 wet season, F$_2$ progenies in the 1991 dry season, and the first pedigree nursery in the 1991 wet season. Since then, more than 2000 crosses have been made, 100,000 pedigree lines have been produced, breeding lines with the desired morphological ideotype traits have been selected, and about 500 NPT lines have been evaluated in observational yield trials. The first-generation NPT lines based on tropical japonicas were developed in less than 5 years. They were grown in a replicated observational trial for the first time in late 1993.

As intended, the NPT lines had large panicles, few unproductive tillers, and lodging resistance. Grain yield was disappointing, however, because of low biomass production and poor grain filling. Reduced tillering capacity might
contribute to low biomass production because the crop growth rate during the vegetative stage of NPT lines was lower than that of indica varieties. Less biomass production was also associated with poor grain filling, but a cause-and-effect relationship has not been established. The poor grain filling of NPT lines was probably due to a lack of apical dominance within a panicle (Yamagishi et al., 1996), the compact arrangement of spikelets on the panicle (Khush and Peng, 1996), a limited number of large vascular bundles for assimilate transport, and source limitation due to early leaf senescence (Ladha et al., 1998). The first-generation NPT lines are also susceptible to diseases and insects and have poor grain quality. Therefore, they could not be released for rice production in farmers’ fields. However, the first-generation NPT lines have been distributed through the International Network for Genetic Evaluation of Rice (INGER) to more than 90 countries for evaluation. This valuable germplasm has been used as genetic materials in rice breeding programs worldwide.

Breeding of second-generation NPT

In 1995, development of second-generation NPT lines began by crossing first-generation tropical japonica NPT lines with elite indica parents. Multiple site-year comparisons of first-generation NPT lines with the highest-yielding indica varieties have shown that the original NPT design did not have sufficient tillering capacity. An increase in tillering capacity is needed to increase biomass production and to improve compensation when tillers are lost to insect damage or other causes during the vegetative stage. A slightly smaller panicle size without a change in panicle length also appeared to be advantageous to reduce the compact arrangement of spikelets. Genes from indica parents have effectively reduced panicle size and increased tillering capacity in second-generation NPT lines. Indica germplasm also helped improve other NPT attributes such as grain quality and disease and insect resistance. Some second-generation NPT lines (F5 generation) with these refinements were then selected and were planted in a replicated observation trial for the first time in the 1998 wet season. Agronomic trials on the second-generation NPT lines started in the 2002 dry season. One second-generation NPT line, IR77186-122-2-2-3, was released under the name of NSIC Rc158 in the Philippines in 2007.

Performance of second-generation NPT

Laza et al. (2003) reported that yield improvement was achieved in the second-generation NPT lines as compared with the first-generation NPT lines. This yield increase was attributed to increased panicle number per m² and
improved grain-filling percentage through the introduction of genes from elite indica parents to the first-generation NPT lines. The poor yield of the first-generation NPT lines was attributed to low harvest index, which was the result of small sink size (i.e., few spikelets per m$^2$), low grain-filling percentage, and poor translocation of biomass accumulated before flowering to the grains during grain filling (Laza et al., 2003; Peng et al., 2004). A few second-generation NPT lines produced significantly higher yield than the indica check variety, IR72, in several seasons (Peng et al., 2004). This increase was due to improved aboveground total biomass production or improved harvest index. Spikelet number per panicle of these second-generation NPT lines was 45–75% greater than that of IR72. The difference between these NPT lines and the check variety in other yield components was not consistent. In the 2003 dry season, a second-generation NPT line (IR72967-12-2-3) produced 10.16 t ha$^{-1}$, which was significantly higher than the yield of the indica check variety, PSBRc52 (Peng et al., 2004). Its higher yield was associated with its higher aboveground total biomass production and greater grain weight.

If the check varieties were newly developed indica varieties and lines instead of IR72 or PSBRc52, the advantage of second-generation NPT lines over indica checks in grain yield became smaller and even disappeared because yield progress had also been achieved in indica inbred breeding programs (Peng et al., 2004; Yang et al., 2007). If a comparison was made between two groups of varieties, there was no significant difference in grain yield between the second-generation NPT lines and indica check varieties. These results suggest that second-generation NPT lines have not increased the yield potential of irrigated lowland rice in the dry season of the tropics.

In order to achieve a 10% increase in the yield potential of irrigated lowland rice in the dry season of the tropics with second-generation NPT lines, the following are the target traits: 330 panicles per m$^2$, 150 spikelets per panicle, 80% grain filling, 25 mg grain weight (oven-dry), 22 t ha$^{-1}$ aboveground total biomass (at 14% moisture content), and 50% harvest index (Peng and Khush, 2003). Among these traits, the key is to develop more second-generation NPT lines with a panicle size of 150 spikelets per panicle. Then, the best line with the required panicle number, grain-filling percentage, and harvest index can be selected among these large-panicle materials.

China’s “super” rice breeding

Since the development of the first improved semi-dwarf variety in Guangdong, China, in 1959 (Huang, 2001) and three-line indica F$_1$ hybrid rice in 1976 (Yuan et al., 1994), breeding for high-yielding rice varieties has never
stopped in China. Huang (2001) developed bushy-type varieties with early vigour such as Guichao and Teqing in 1980s. These varieties are tolerant of shading and high plant density and were widely grown in southern China. Yang et al. (1996) stated that a further increase in rice yield potential has to come from a combination of improvement in plant type and use of growth vigor. They proposed an erect panicle plant type and developed Shennong265 with this trait, which was grown in Liaoning Province. Zhou (1995) developed three-line intersubspecific F1 hybrid rice between indica and japonica with a heavy-panicle plant type, which is suitable for rice-growing areas such as Sichuan with high humidity, high temperature, and limited solar radiation. Although progress has been achieved in increasing rice grain yield through crop improvement, China’s rice breeding activities for increasing yield potential using an ideotype approach were not organized at the national level until 1996.

Stimulated by IRRI’s NPT breeding program, China established a nationwide mega project on the development of “super” rice in 1996 (Cheng et al., 1998, 2007). The “super” rice varieties can be developed by breeding inbred and/or hybrid varieties. A “super” hybrid rice breeding program was started in 1998 by Prof. Longping Yuan. In this program, the strategy was to combine an ideotype approach with the use of intersubspecific heterosis (Yuan, 2001). The ideotype was reflected in the following morphological traits:

a. Moderate tillering capacity (270–300 panicles m$^{-2}$).
b. Heavy (5 g per panicle) and drooping panicles at maturity.
c. Plant height of at least 100 cm (from soil surface to unbent plant tip) and panicle height of 60 cm (from soil surface to the top of panicles with panicles in natural position) at maturity.
d. Top three leaves: Flag-leaf length of 50 and 55 cm for the 2nd and 3rd leaves. All three leaves are above panicle height. Should remain erect until maturity. Leaf angles of the flag, 2nd, and 3rd leaf are around 5°, 10°, and 20°, respectively. Narrow and V-shape leaves (2 cm leaf width when flattened).

Thick leaves (specific leaf weight of top three leaves = 55 g m$^{-2}$).

Leaf area index (LAI) of top three leaves is about 6.0 and Harvest index of about 0.55.

**Success of “super” rice breeding**

Up to 2001, 7 inbred and 44 hybrid varieties that met the “super” rice criteria were released by provincial or national seed boards (Min et al., 2002). In 1998–2005, 34 commercially released “super” hybrid rice varieties were grown on a total area of 13.5 million ha and produced an additional 6.7 million tonnes of
rough rice in China (Cheng et al., 2007). These “super” rice varieties such as Xieyou9308 and Liangyoupeijiu became popular because they produce high yield and have good grain quality. Xieyou9308 is an intersubspecific hybrid rice developed by the China National Rice Research Institute with Xieqingzao-A as the female parent and Zhonghui9308 as the male parent using a three-line method (Mao et al., 2003). The restorer line, Zhonghui9308, is an intermediate type with canopy morphology close to a japonica type and panicle morphology close to an indica type. It was estimated that there are 25% japonica genetic components in Zhonghui9308 (Cheng et al., 2007). Xieyou9308 was released in Zhejiang Province in 1999. It was grown in Zhejiang, Fujian, and Anhui with accumulated planting area of 1 million ha until 2005 (Cheng et al., 2007). Maximum grain yield of Xieyou9308 reached 12.23 t ha\(^{-1}\) (Min et al., 2002). Xieyou9308 outyielded the hybrid check variety (Xieyou63) by 17.5% while their crop growth duration was not significantly different (Zhu et al., 2002). The morphological traits of Xieyou9308 are (1) 120–135 cm plant height; (2) 45, 55, and 60 cm leaf length and less than 10\(^\circ\), 20\(^\circ\), and 30\(^\circ\) leaf angles for flag, 2nd, and 3rd leaf, respectively; (3) 2.5, 2.1, and 2.1 cm leaf width and 15%, 10%, and 10% leaf curling for flag, 2nd, and 3rd leaf, respectively; (4) 26–28 cm panicle length; (5) 170–190 spikelets per panicle; (6) 250 panicles m\(^{-2}\); (7) 90% grain filling; (8) 28 g 1000-grain weight; and (9) 4 g panicle weight.

Lin et al. (2002) compared leaf area development between Xieyou9308 and Shanyou63 (an indica hybrid variety used as a check) and found that Xieyou9308 had slower leaf area growth from transplanting to 20 days after transplanting than Shanyou63. However, leaf area development of Xieyou9308 from stem elongation to booting was greater than that of Shanyou63. Consequently, Xieyou9308 maintained higher LAI than Shanyou63 during the ripening phase. Light measurement at 25 days after flowering suggested that light penetration inside the canopy was greater in Xieyou9308 than in Shanyou63 because of the small leaf angles of the top four leaves. In an on-farm demonstration experiment, Xieyou9308 produced 11.53 t ha\(^{-1}\) while the hybrid check variety (Xieyou63) yielded 9.82 t ha\(^{-1}\) (Zhu et al., 2002). Zhu et al. (2002) attributed the high yield of Xieyou9308 to its large panicle size. More importantly, the large panicles of Xieyou9308 were achieved not at the expense of panicle number and grain-filling percentage. Xieyou9308 had 52% greater spikelet number per panicle than Xieyou63, but panicle number per m\(^{2}\) of Xieyou9308 was less than 5% lower than Xieyou63 and grain-filling percentage was similar between the two hybrid varieties. In another study, Xieyou9038 yielded 11.7 t ha\(^{-1}\), which was 20% higher than the yield of
Xieyou63 (Wang et al., 2002). Wang et al. (2002) reported that productive tiller percentage of Xieyou9308 was 68.6%, and 57.7% for Xieyou63. Aboveground biomass of Xieyou9308 was 22% and 43% greater than that of Xieyou63 at heading and maturity, respectively. Grain-filling percentage of superior spikelets was 89.6% for Xieyou9308 and 84.6% for Xieyou63. Grain-filling percentage of inferior spikelets was 80.0% for Xieyou9308 and 65.7% for Xieyou63. The high grain-filling percentage of Xieyou9308 despite its large panicle size was associated with a high rate of flag-leaf photosynthesis, slow leaf senescence, efficient remobilization, and great root activity (Wang et al., 2002; Zhai et al., 2002).

Liangyoupeijiu is an intersubspecific hybrid rice developed by the Jiangsu Academy of Agricultural Sciences and China National Hybrid Rice R&D Center with Pei’ai64S as the female parent and 9311 as the male parent using the two-line method (Yuan, 2001). Pei’ai64S is a thermosensitive genetic male sterile line and belongs to the intermediate type with indica, temperate, and tropical japonica ancestries (Cheng et al., 2007). It is unknown whether Pei’ai64S was developed using IRRI’s first-generation NPT line, an improved tropical japonica as one of the parents. The restorer line 9311 is a typical indica type. Liangyoupeijiu was released in Jiangsu Province in 1999. It has been widely grown in 13 provinces in China, with accumulated planting area of 2.23 million ha until 2002. Maximum grain yield of Liangyoupeijiu reached 12.11 t ha\(^{-1}\) with crop growth duration of 135 days, which was measured from on-farm demonstration fields in Hunan in 2000 (Yu and Lei, 2001). Liangyoupeijiu outyielded the hybrid check variety (Shanyou63) by 8–15% in farmers’ fields (Zong et al., 2000). The crop growth duration of Liangyoupeijiu was slightly longer than that of Shanyou63 (5–7 days). The morphological traits of Liangyoupeijiu are (1) 115–125 cm plant height, (2) 35–45 cm flag-leaf length, (3) 24–26 cm panicle length, (4) 190–210 spikelets per panicle, (5) 200–250 panicles m\(^{-2}\), (6) 85% grain filling, and (7) 26–27 g 1000-grain weight (Yu and Lei, 2001).

In an experimental plot, Liangyoupeijiu produced 11.3 t ha\(^{-1}\), 28.6% greater than that of the hybrid check variety, Shanyou63 (Zong et al., 2000). Liangyoupeijiu had 12.1% higher aboveground total biomass than Shanyou63. The high biomass was associated with high LAI, large leaf area duration (LAD), thick leaf, high chlorophyll content, and high photosynthetic rate. Maximum LAI was 9.10 for Liangyoupeijiu and 8.42 for Shanyou63. Daily rate of LAI decline after heading was 0.8% for Liangyoupeijiu and 1.4% for Shanyou63. Consequently, Liangyoupeijiu had 17.1% higher LAD than Shanyou63. Liangyoupeijiu also had higher specific leaf weight (12.1%), higher chlorophyll content per unit leaf area (8.4%), and higher photosynthetic rate at heading (6.9%) than Shanyou63. At heading, the extinction coefficient of canopy was 0.318 for Liangyoupeijiu and 0.423 for
Shanyou63, suggesting that Liangyoupeijiu had more erect leaf canopy than Shanyou63. The high yield of Liangyoupeijiu was also attributed to higher harvest index (56% versus 49% for Shanyou63). From heading to maturity, remobilization from straw to grain was 25.9% for Liangyoupeijiu and 20.2% for Shanyou63. Net assimilation rate from tillering to heading was 9.6% higher in Liangyoupeijiu than in Shanyou63. However, the grain-filling percentage of Liangyoupeijiu was lower than Shanyou63 (81–87% for Liangyoupeijiu and 88–94% for Shanyou63).

Katsura et al. (2007) compared the grain yield and crop physiological traits of Liangyoupeijiu with those of Takanari and Nipponbare in Kyoto, Japan. Liangyoupeijiu produced significantly higher grain yield than Nipponbare. Although the difference in grain yield between Liangyoupeijiu and Takanari was statistically insignificant, Liangyoupeijiu achieved a yield of 11.8 t ha\(^{-1}\), which is the highest yield observed under the environmental conditions of Kyoto. The high yield of Liangyoupeijiu was associated with larger LAD before heading, greater biomass accumulation before heading, larger number of grains, and more translocation of carbohydrates from the vegetative organ to the panicle during the grain-filling period. Radiation-use efficiency of the whole growth period did not explain the yield superiority of Liangyoupeijiu.

In another study, Yao et al. (2000) reported that specific leaf weight of the top three leaves in Liangyoupeijiu was 30% greater than in Shanyou63, but area of these leaves was not significantly different between the two hybrids. The average leaf angle of the top three leaves was 9.48 for Liangyoupeijiu and 16.18 for Shanyou63. It was also observed that Liangyoupeijiu had slower leaf senescence and higher LAD than Shanyou63.

Photosynthetic characteristics and photoinhibition were compared between Liangyoupeijiu and Shanyou63 (Chen et al., 2002b; Ou et al., 2003; Wang et al., 2005, 2006). At heading, the light-saturated photosynthetic rate of flag leaf in Liangyoupeijiu was 13% higher than in Shanyou63 (Chen et al., 2002b). Liangyoupeijiu also exhibited a higher photosynthetic rate than Shanyou63 over a wide range of light intensity (200–1200 mmol m\(^{-2}\) s\(^{-1}\)). Wang et al. (2006) reported that Liangyoupeijiu had significantly higher activities of the C\(_4\) pathway enzymes in both flag leaves and lemmas than did Shanyou63. From heading to 40 days after heading, chlorophyll content declined by 48.2% in Liangyoupeijiu and by 85% in Shanyou63. This supports previous conclusions that Liangyoupeijiu had slower leaf senescence than Shanyou63 during the ripening phase. Chen et al. (2002b) observed that Liangyoupeijiu was more tolerant of photooxidative stress than Shanyou63 because the reduction in primary photochemical efficiency (F\(_{v}/\) F\(_{m}\)) and increase in superoxide anion generation rate and malondialdehyde content under photooxidative stress...
were less in Liangyoupeijiu than in Shanyou63. Wang et al. (2005) reported that Liangyoupeijiu had higher resistance to photoinhibition induced by strong light and higher capacity of non-radiative energy dissipation associated with the xanthophyll cycle than Shanyou63. Therefore, high photosynthetic rate, slow leaf senescence, and tolerance of photoinhibition are thought to be the physiological basis for the high grain yield of Liangyoupeijiu.

Remarks on ideotype breeding approaches
It is clear that the plant type of China’s ‘‘super’’ hybrid rice has many similarities with IRRI’s NPT design. Both emphasize large and heavy panicles with reduced tillering capacity and improved lodging resistance. It was expected that harvest index could be improved with increased sink size and few unproductive tillers. Other common traits are erect-leaf canopy and slightly increased plant height in order to increase biomass production. In the plant type of ‘‘super’’ hybrid rice, however, panicles are kept inside the leaf canopy by increasing the distance between panicle height and plant height. This trait was not clearly defined in IRRI’s original NPT design because an IRRI physiologist discovered the benefit of reducing panicle height for improving canopy photosynthesis and yield potential only in the mid-1990s (Setter et al., 1995, 1996). The distance between panicle height and plant height can be increased by either reducing panicle height or increasing plant height. The latter approach was used in developing ‘‘super’’ hybrid rice in China and appears to be more effective than the former in improving rice yield. Another improvement in plant type design of ‘‘super’’ hybrid rice over IRRI’s original NPT design was the great emphasis on the top three leaves. Length, angle, shape, thickness, and area of the top three leaves were quantitatively defined in detail in the ‘‘super’’ hybrid rice design.

The initial breeding strategy for the NPT at IRRI was to use genes for large panicles and sturdy stems from tropical japonica germplasm. The second step was to cross the improved tropical japonica with elite indica varieties to produce an intermediate rice type. In breeding for ‘‘super’’ hybrid rice in China, the two-line or three-line method was used to develop F1 hybrid combinations by crossing an intermediate type between indica and japonica with an indica parent in order to use intersubspecific heterosis.

The success of ‘‘super’’ hybrid rice breeding in China and progress in NPT breeding at IRRI suggest that the ideotype approach is effective for breaking the yield ceiling of the irrigated rice crop. The following lessons should be remembered when the ideotype breeding approach is used in other crops:

a. The genetic background of an inferior donor parent for desirable traits may have a negative effect on the performance of progenies (Marshall, 1991).
It is necessary to select donor parents without severe defects in agronomic fitness.
b. The targeted morphological traits should be related to the physiological processes that determine the ultimate performance of the plant.
c. Extremes in plant type traits should be avoided (Belford and Sedgley, 1991). For example, the initial design of IRRI’s NPT aimed at 200–250 grains per panicle, which resulted in poor grain filling. This was modified to 150 spikelets per panicle.
d. Interrelationships among the traits and compensation among plant parts should be considered (Marshall, 1991). For example, there is a negative relationship between panicle size and panicle number per m². Only an increase in overall biomass production can break this negative relationship and result in an improvement in yield potential (Ying et al., 1998).
e. The ideotype breeding approach is not an alternative but a supplement to empirical breeding approaches because selection for yield is still needed in ideotype breeding.
f. A new rice ideotype may require concurrent modification of crop management such as seedling age, planting geometry, fertilization, irrigation regime, and weed control in order to fully express its yield potential (Abuelgasim, 1991).

At last it may be inferred that IRRI’s breeding of first-generation NPT lines using tropical japonica did not produce rice varieties that reached the expected yield performance. The introduction of indica genes to a tropical japonica background to develop intermediate-type varieties between indica and japonica has resulted in several promising second-generation NPT lines. Great progress has been achieved in China’s ‘‘super’’ hybrid rice breeding project by combining an ideotype approach with the use of intersubspecific heterosis. The success of China’s ‘‘super’’ hybrid rice was partially the result of assembling the good components of IRRI’s NPT design. More importantly, improvement in plant type design was achieved in China ‘‘super’’ hybrid rice by emphasizing more on the top three leaves and panicle position within the canopy. Both designs focused on large panicle size, but source–sink relations were well balanced in China’s ‘‘super’’ hybrid rice breeding project by improving photosynthesis and delaying leaf senescence of the top three leaves during the ripening phase. These morpho-physiological traits related to the top three leaves will be incorporated into IRRI’s second-generation NPT lines in order to provide sufficient assimilates for grain filling of large panicles with 150 spikelets per panicle. Future research should focus on (1) understanding the physiological function of the
A Maize ideotype

Ideotype root architecture for efficient nitrogen acquisition

The use of nitrogen (N) fertilizers has contributed to the production of a food supply sufficient for both animals and humans despite some negative environmental impact. Sustaining food production by increasing N use efficiency in intensive cropping systems has become a major concern for scientists, environmental groups, and agricultural policymakers worldwide. In high-yielding maize systems the major method of N loss is nitrate leaching. In this review paper, the characteristic of nitrate movement in the soil, N uptake by maize as well as the regulation of root growth by soil N availability are discussed. We suggest that an ideotype root architecture for efficient N acquisition in maize should include (i) deeper roots with high activity that are able to uptake nitrate before it moves downward into deep soil; (ii) vigorous lateral root growth under high N input conditions so as to increase spatial N availability in the soil; and (iii) strong response of lateral root growth to localized nitrogen supply so as to utilize unevenly distributed nitrate especially under limited N conditions.

Maize Seedlings Predict Drought Tolerance

Scientists have developed a new method for measuring drought tolerance in maize. By comparing the shoot-to-root ratio in seedlings stressed by low water, scientists can predict whether a plant has the right mix of genes for adapting to drought conditions.

The ideal drought-resistant maize should have a higher ratio of root surface area compared to leaves and stems. Developing enough adult plants to determine this feature is a costly investment. The research, conducted by Nathinee Ruta at the Swiss Federal Institute of Technology, tested whether the root to shoot ratio in seedlings subjected to water stress would provide the basic genetic information about the general pattern of root system architecture leading to drought avoidance.

The findings were reported in the July/August 2010 edition of Crop Science, published by the Crop Science Society of America. The study was conducted at Peter Stamp’s laboratory at the Swiss Federal Institute of Technology (ETH) in Zurich, using maize populations developed by the breeding program of the International Maize and Wheat Improvement Center (CIMMYT), headquartered in Mexico.
These maize lines were developed to increase yield in drought-prone environments such as Sub-Saharan Africa. Therefore, the data on seedling roots could be compared with yield trials in drought environments that had been generated throughout several years.

The roots of these seedlings grew on filter paper in growth pouches and were measured non-destructively using digital image analysis. The system was kept simple to allow for a handling of 200 plants per day. This was a sufficient amount of data to allow researchers to locate the positions of the genes that control root growth, and link them to other genes in the maize genome.

Most genetic studies of water stress of maize tend to focus on the above ground portion of the plant, with the roots not easily accessible, particularly under drought conditions. With little known about the correlation between root structure and drought tolerance, this research offers promising prospects for using root traits in predicting maize yield under water stress.

“There is probably an optimal maize ideotype for each combination of soil type and climate condition,” stated Andreas Hund, the senior scientist leading the project. “We aim to define these ideotypes for contrasting environments and identify key loci allowing us to select for more efficient root systems.”

Research is ongoing at ETH to improve techniques to measure genetic relationships between leaf and root surface area as they respond to environmental conditions. A strong focus will be on how these factors change over time or with respect to environmental stresses, such as extreme temperatures or drought.

**Crop modelling to determine ideotypes to design plants for target environments**

An example of an improved plant type design that had a major impact on agricultural production is the short stature design for cereals that was developed in the 1960s. These early breeding efforts had their focus on wide adaptation. Although the wide adaptation concept worked for some systems like the homogeneous irrigated rice systems in the tropics and sub-tropics and wheat in South Asia, it has been recognized that strong genotype environment management interactions in most agricultural systems make it necessary to use genotypes that are adapted to the specific agro-environments. To meet the challenges to increase food production, ways have to be found to improve the productivity and profitability of agricultural production systems. That can only be done by using a systems approach that helps to optimize local agricultural production systems. That will require not only improved crop management systems, but also new crop types for different agro-environments.

Hammer et al. (1999) proposed that crop models have the potential to interpret and predict performance of individual genotypes in different management and environments. They also concluded that crop models based on physiologically sound mechanisms, can quantify and integrate crop responses to genetic, environmental, and management factors, and therefore, can be used as a tool to study genotype by environment interactions and genotypes suited for particular climatic zones.
To analyze the need for different plant types for different environments, Kropff et al. (1995) determined the opportunities for using models to optimize the performance of specific genotypes in target environments with rice and potato as case studies. Differences in the requirements for rice varieties for the different seasons became clear in the simulations for the tropical wet season and the dry season. However, the basic traits were similar. Model analyses showed that the key to the optimization of potential yield in potato was the proper timing of the moment of tuber initiation. If that moment is too late for a particular environment, too much foliar tissue is formed and the tuber growth period can be too short. If tuber initiation is too early, not enough foliar tissue is formed to sustain growth until the end of the growing season. LINTUL-POTATO was used to determine the cultivar characteristics with respect to temperature and daylength response that give the highest yield in a particular environment. This means that for each environment the optimal moment of tuber initiation can be calculated and only genotypes with such desired earliness have to be evaluated in this environment.

Kropff et al. (1995) and in more detail, Aggarwal et al. (1997) determined the importance of various traits for maximum yield potential in the tropical dry season and the wet season using ORYZA1 (Kropff et al., 1994) which is based on the Wageningen models SUCROS (Spitters et al., 1989) and MACROS (Penning de Vries et al., 1989). Crop characteristics of IR72 and weather data of Los Banos for 1992 were used. The critical model parameter values were varied with respect to those of IR72 to simulate the effect of a change in specific leaf area, spikelet growth factor, potential grain weight, maximum leaf N concentration, and crop development rates during juvenile phase and grain filling period. The study was conducted at three levels of N management: normal practice in breeders plots, recommended N for high yield potential and growth-rate driven N management. Results showed that no trait individually or in combination could provide more than 5% yield increase in the normal N management practice. These genotypes were not able to express these traits in these somewhat limited-N environments. With improved N management, yield potential was predicted to be significantly increased (>30%) by an increased sink capacity, maintenance of high leaf N content and a longer grain filling duration (Aggarwal et al., 1997).

Differential drought patterns are a major cause for reported genotype by environment interactions. Chapman et al. (2000) used a sorghum simulation model for environmental characterization of long-term historical weather data for different regions. They classified several different drought patterns that led to different growth and yield patterns. Cultivar selection under these different environments could lead to selection of different cultivar types. Even more important is that the occurrence of a given drought pattern from one year to the next, relative to variety trials conducted over a 3-year span (of good or of poor weather) could lead to selection of a variety that will not be the best over the long term. So one valuable role of crop models is to evaluate optimum cultivar types over long-term weather, rather than the short-term 1–3 year duration typical prior to release of a new cultivar.

Using crop models as tools, Bindraban (1997) showed that at optimum planting dates and optimum management conditions in a highly productive site (Obregon, north-west Mexico) the photosynthesis capacity of the canopy exceeded the actual yield. Residual reserves in the stem were higher in crops grown under these optimal conditions than in low-yielding crops grown with insufficient nitrogen. Optimally managed crops that were sown later, and therefore experienced higher temperatures, gave lower yields as the
rapidly declining post-anthesis leaf area strongly reduced photosynthesis capacity. Bindraban (1997) concluded that the sink rather than the source limits yield potential in highly productive sites, while the reverse is true for crops at lower yielding levels. Yield potential under optimum managed conditions in productive sites should therefore be improved by increasing sink capacity, either through increasing kernel number or kernel weight. With the aid of crop modelling it was shown that different crop characteristics ought to be adjusted depending on environmental conditions. Under the optimum planting conditions of Obregon, kernel number could be increased by increasing crop growth rate during the period between early booting and final anthesis. For late planted crops in Obregon, an elongation of this period appeared more appropriate (Bindraban et al., 1998).

While solving for genetic coefficients and site characteristics (soil water holding traits and fertility) from soybean variety trials across differing environments (described previously in this paper), we found that the crop model successfully reproduced part of the observed G × E interaction for different simulated cultivar pairs. The observed steeper slope of Thomas (lower yield in poor environments and higher yield in good environments) compared with Colquitt was substantially captured by the model after solving cultivar traits (slopes of Thomas and Colquitt differed significantly, both in observed and simulated pair comparisons). We believe that some of the G × E in yield is related to different phenologies which the optimizer solves quite efficiently. In addition, G × E for yield also is influenced by soil fertility and soil water availability (solved for sites), as well as genetic traits influencing yield through photosynthesis and seed HI. Other reasons for G × E for yield include effects of excess water and pests, which most models do not presently account for, but could address in the future. It is encouraging that G × E interactions noted here resulted naturally from the process of solving for genotypic traits across many environments, rather than the need to explicitly ‘hard-code’ such G × E features as genetic coefficients.

Analyses using crop models can improve our insight into the quantitative impact of crop characteristics on yield potential. With this information, plant breeders can concentrate their efforts on the quantitatively most important traits that need to be considered for improving yields, while modellers can enhance their crop models to better mimic such genetic differences.

**Optimization of source–sink dynamics in plant growth for ideotype breeding**

There are two main strategies to investigate ideotype breeding: experimental based and plant model based approaches. The critical drawback of experimental based approach is that the time consumed for experiments is long (10 years needed by Dencic, 1994 and by Lauri and Costes, 2004, and 20 years by Peng et al., 2008) and it consumes resources that are limited (field, water, labor) due to the cultivation of thousands of plants (Dencic, 1994). Moreover, the performance of the improved plant might prove disappointing in terms of grain yield compared with the original variety when the environmental conditions vary (Peng et al., 2008). Nowadays, it becomes widely accepted that plant growth models may provide efficient tools to study plant growth behavior (Tardieu, 2003; Herndl et al., 2007; Letort et al., 2008a), since they can not only complement field
experiments, but also save time and resources. Therefore, researchers dedicated themselves to study ideotype breeding based on plant models (Yin et al., 2003; Cilas et al., 2006). Even though Cilas et al. (2006) investigated ideotype breeding from the architectural point of view, and Yin et al. (2003) from the physiological point of view using a process-based plant growth model, they all agree that there exist critical relationships between plant architectures and physiological processes during plant growth, with other researchers like Rasmusson (1987), Kaitaniemi et al. (2000), Sievänen et al. (2000), Luquet et al. (2006), and Fourcaud et al. (2008). The design of ideotypes should thus take into account both architectural and physiological aspects. In parallel, functional–structural plant growth models were developed (see Sievänen et al., 2000 or de Reffye et al., 2008 for reviews), combining the description of organogenesis (plant development), photosynthesis and biomass partitioning. They offer interesting perspectives to improve plant breeding.

**GreenLab plant growth model (Cournède et al., 2008)**

GreenLab is a functional–structural plant growth model combining the descriptions of plant architecture and physiological processes of plant growth at organ level, in interaction with the environment (light, water, temperature and density). The dynamic mechanisms to generate plant architecture (organogenesis) and to calculate plant biomass production and partitioning to organs are introduced in detail in de Reffye et al. (2008). It describes plant growth, both from ecophysiological and architectural points of view, at the individual organ scale. Breeders can get information about physiological characteristics in determining yield.

In plant breeding, the criteria for segregating or introducing accessions are mostly based on intuition or convention, but also increasingly on mechanistic knowledge of how traits contribute to the performance of interest. There is a recent agreement among plant breeders and physiologists that plant growth models based on ecophysiological knowledge can be applied to improve ideotype breeding efficiency (Yin et al., 2003; Hammer et al., 2006). They can help to provide quantitative answers to “what if…” questions for alternative plant types (Dingkuhn et al., 1993). Dingkuhn et al. (1993) and Yin et al. (2003) also pointed out that the model properties required for ideotype design are (1) to quantify feedback between physiological processes and environmental variables and (2) to have the ability of yield prediction without restricting to the environment in which the model parameters are derived. Ma et al. (2007, 2008) studied the stability of GreenLab parameters to different environmental conditions, e.g. seasonal variation and planting density. Most parameters revealed stable. Dong et al. (2008) also studied the stability of GreenLab parameters for
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To characterize organ sink strengths and governing light interception were shown to be environment-dependent. These two studies lead us to consider a possible genotypic determination of GreenLab parameters and yet enhance the necessity to build up more sophisticated model versions, in order to fully unravel the genetic and environmental effects. It implies a better modelling of the effects of the environmental stresses. Preliminary results were introduced in Wu et al. (2005) and Le Chevalier et al. (2007) regarding water. Taking into account the current time step in GreenLab, which is equal to 2 or 3 days corresponding to thermal time interval for successive phytomer appearance for maize cultivar ND108 in this study, it may be long for the simulation of environmental stresses. However, the time step in GreenLab can be changed to calendar time, e.g. 1 day or 1 h (Li et al., to appear). In this way, the environmental stresses can be well simulated.

In quantitative genetics, many methods have been developed to identify particular loci in plant chromosomes that contribute to phenotypic traits (de Vienne, 1998), by establishing statistical correlations between quantitative traits that can be measured on plant (e.g. plant height, yield) and the values of particular genes, known as quantitative trait loci (QTL) analysis. Many researchers have raised the potential benefits and possibilities of coupling these genetic models to plant models, for genetic improvement (Tardieu, 2003; Yin et al., 2004; Hammer et al., 2006). A simulation study of linking the GreenLab model to a genetic model is presented by Letort et al. (2008b). The theoretical study illustrated how QTL analysis should give better results when performed on model parameters than on phenotypic traits, the latter being the results of complex interacting phenomenon difficult to statically assess with QTL analysis.

The parameters that we optimized are oriented to those related to the cob sink variation function, whereas the others are fixed to be the estimated values. However, there might be some correlation between parameters that we were not able to estimate. Such correlations could only be assessed if the model parameters were available on a large number of genotypes. Therefore, in this context, even if the link of GreenLab model parameters to genetics has not been proved yet and the information of correlations between all the parameters are missing, at least optimal parameters should provide some useful information for ideotype design, by unravelling the source–sink complex interactions.

Rui (2010) working with the above mentioned model found that the ideotype of maize can be deduced from the optimal results. It provides a reference to improve breeding strategies. From a physiological point of view, the cob begins to absorb biomass from about the 20th growth cycle when the leaf area saturates. And then, it should absorb biomass smoothly or significantly, depending on the breeding objective. If the objective is to have a maximal cob weight, the maize
should have a bigger reproductive capacity, and the cob should grow with post-
expansion (i.e. a long delay for expansion) and fast growth rate (i.e. expand
within a short period). From an architectural point of view, the leaf size is
reduced during the last vegetative and reproductive stages of growth. The
harvest index is above 50%. It is coincident with the ideotype of maize proposed
by Mock and Pearce (1975) by analyzing the research results of other people with
an experimental based approach. The Pareto front of the multi- objective
optimization problem presents all the different optimal strategies, and the
decision-maker could choose his optimal strategy according to market prices or
the application purposes for example.
Particle Swarm Optimization (PSO), which is a population-based heuristic
optimization algorithm, is used to solve the single and multi-objective
optimization problems. As it does not require the differentiation of the
objective functions, and it returns several solutions at the same time, we can
benefit from it to solve non- convex, single objective or multi-objective
optimization problems, with potentially non-unique solutions. Theoretically
speaking, it obtains global optimal solutions of optimization problems. Com-
pared to other population-based heuristic optimization algorithms, such as
Genetic Algorithm, the PSO has a high convergence rate for some problems
and a better accuracy (Kennedy and Eberhart, 2001). Moreover, it has few
parameters to adjust and is easy to implement due to its simple single operator,
contrary to Genetic Algorithm that has evolutionary operators such as crossover
and mutation. It is computationally inexpensive in terms of both memory and
speed. Even though the optimal solutions found by the PSO cannot be proved to
be global, it is generally good enough to practically guide genetic selection.
The maize that we optimized is assumed to have only one cob like the
experimental data used for parameter estimation. However, the methodology
that we used in this work is not restricted by the number of cobs on the stem.
For the objective of the optimization problem, which is the maximization of cob
weight, the crucial factor is not the number of cobs, but the optimal trade-offs
between sources and sinks. However, in order to have more realistic optimal
values, more constraints should be concerned. Since the cob growth requires
pollen from the tassel and since there exists a strong interaction between cob
and tassel (Borrás et al., 2002; Uribelarrea et al., 2002), we integrate the tassel
weight into the multi-objective optimization problem as a constraint. A
threshold is set for tassel weight (not less than 10 g referred from experimental
data). However, for all optimal solutions this constraint is not active (tassel
weights strictly above 10 g). One reason is that so far we do not know the
relationship between cob and tassel quantitatively. Hence, it is difficult to set
the threshold value. Another reason is that tassel sink variation is fixed and it
does not change according to the cob sink variation, in this work. The understanding of the interaction between cob and tassel should be improved in our future works. Finally, in cobs, only kernels give the food for human beings or for livestock. The number of kernels is a critical factor that affects the final kernel weight (Borrás and Otegui, 2001). Therefore, taking into account the number of kernels per cob could be an interesting complement to this study. So far, we do not have the information about the proportion of the kernel weight to the cob weight, which raises the difficulty to estimate the corresponding model parameters. Experiments are conducted in 2009 for this purpose.

A Gram ideotype

Pande and Saxena (1973) proposed the ideotype for gram having following features-

1. The vegetative growth must be stopped before the starting of reproductive stage.
2. The plant should have erect branching. (In the prevalent varieties of gram, the spreading and branching of its canopy is just like umbrella which interfere to penetrate the sunshine into its canopy causing humid conditions favourable for insect-pest and diseases).
3. To harness the long photoperiod and favourable temperature at the time of flowering, there should be 2-3 longer pods in the leaf axis and 2-3 seeds in each pod.

A Arhar ideotype

The growth of arhar varieties in the beginning is too less i.e. in the first two months only one or two branches are come out. Therefore, arhar is unable to harness the solar energy properly in the first two months. The flower’s drop is also a major problem. The filling of pods according to Hydro-dynamic model sets up the competition between vegetative and reproductive phases. considering all the views Pande and Saxena suggested ideotypes having following features-

1. The fast growth of plant’s canopy at least in the beginning.
2. The reproductive phase starts after the closure of vegetative growth.
3. Long floral axis having 2-3 flowers in each trifoliate axis.
4. Synchronized flowering.
5. Active root nodules for the long time.

A Ideotype for Dryland Farming

1. Short growth duration.
2. Effective root system.
3. Drought tolerance.
4. High yield potential with altered morphology viz.
a. Plant with few leaves just sufficient to maintain photosynthetic output and growth (to minimize the use of water).

b. Leaves horizontally disposed for better light interception contrary to vertically disposed under irrigated conditions.

Growth hormones

Plant growth and development involves the integration of many environmental and endogenous signals that, together with the intrinsic genetic program, determine plant form. Fundamental to this process are several growth regulators collectively called the plant hormones or phytohormones. This group includes auxin, the gibberellins (GAs), cytokinin, abscisic acid (ABA), ethylene, the brassinosteroids (BRs), and jasmonic acid (JA), each of which acts at low concentrations to regulate many aspects of plant growth and development.

![Chemical Structures of the Plant Hormones](image)

A partial list of the responses elicited by each hormone is provided below. Ethylene gas promotes fruit ripening, senescence, and responses to pathogens and abiotic stresses. IAA (an auxin) regulates cell division and expansion, vascular differentiation, lateral root development, and apical dominance. Cytokinins are adenine derivatives first identified by their ability to promote cytokinesis. JA is a volatile signal that modulates pollen development and responses to pathogen infection. The BRs regulate cell expansion and photomorphogenesis (light-regulated development). GAs are diterpenoid compounds that promote germination, stem elongation, and the induction of flowering. ABA promotes seed dormancy and is involved in several stress signaling pathways.

With the notable exception of the steroidal hormones of the BR group, plant hormones bear little resemblance to their animal counterparts (Fig 63). Rather, they are relatively simple, small molecules such as ethylene gas and indole-3-acetic acid (IAA), the primary auxin in the majority of plant species. The concept of plant hormones originates from a classical experiment on phototropism, the bending of plants toward light, carried out by Charles Darwin and his son Francis in 1880. The Darwins were able to demonstrate that when oat seedlings were exposed to...
a lateral light source, a transported signal originating from the plant apex promoted differential cell elongation in the lower parts of the seedling that resulted in it bending toward the light source. This signal was subsequently shown to be IAA, the first known plant hormone.

**What Do They Do?**

Virtually every aspect of plant growth and development is under hormonal control to some degree. A single hormone can regulate an amazingly diverse array of cellular and developmental processes, while at the same time multiple hormones often influence a single process. Well-studied examples include the promotion of fruit ripening by ethylene, regulation of the cell cycle by auxin and cytokinin, induction of seed germination and stem elongation by GA, and the maintenance of seed dormancy by ABA. Historically, the effects of each hormone have been defined largely by the application of exogenous hormone. More recently, the isolation of hormone biosynthetic and response mutants has provided powerful new tools for painting a clearer picture of the roles of the various phytohormones in plant growth and development.

**How Do They Work?**

Plant biologists have been fascinated by the regulatory capacity of phytohormones since the time of their discovery, and the notion that hormone levels or responses could be manipulated to improve desired plant traits has long been an area of intense interest. Perhaps the best-known example of this is the isolation of dwarf varieties of wheat and rice that led to the “green revolution” in the second half of the 20th century, which is credited with saving millions of people around the globe from starvation. These dwarf varieties have shorter stems than wild-type, making these plants less susceptible to damage by wind and rain. The molecular isolation of these “dwarfing genes” has revealed that they encode components of the GA biosynthesis and response pathways (Peng et al. 1999; Sasaki et al. 2002).

To elucidate the molecular mechanisms underlying phytohormone action, several researchers have utilized the genetically facile model plant *Arabidopsis thaliana* to isolate mutations that confer altered response to applied hormone. Molecular and biochemical analysis of the gene products defined by these mutations, coupled with expression studies aimed at identifying the downstream target genes that mediate hormonal changes in growth and development, has begun to unlock some of the mysteries behind phytohormone action. While no hormone transduction pathway is completely understood, we now have a rudimentary understanding of many of the molecular events underlying hormone action.

**Common Themes**

Regulation by proteolysis has emerged as a resounding theme in plant hormone signaling. The ubiquitin-mediated degradation of key regulatory proteins has been demonstrated, or is at least likely, for all of the phytohormone response pathways (Smalle and Vierstra 2004). In the case of auxin, the response pathway is normally subject to repression by a large family of transcriptional regulators called the Aux/IAA proteins (Fig 64). These proteins dimerize with members of the auxin response factor (ARF) family of transcription factors, thus preventing ARFs from activating auxin-responsive genes (Tiwari et al. 2004). Upon an auxin stimulus, an SCF (SKP1/Cullin/F-box protein) ubiquitin ligase (Deshaies 1999) containing the TIR1 F-box protein...
ubiquitinates the Aux/IAA proteins, marking them for degradation by the 26S proteasome thereby de-repressing the response pathway (Gray et al. 2001). The hormone promotes the Aux/IAA–TIR1 interaction; however, the molecular mechanisms behind this regulation are unclear. Most yeast and animal SCF substrates must be post-translationally modified, usually by phosphorylation, before they are recognized by their cognate F-box protein. Despite numerous efforts to identify auxin-induced modification of Aux/IAA proteins, no such signal has been discovered, raising the distinct possibility that auxin uses a novel mechanism to regulate SCF–substrate interactions.

Fig 64. The Ubiquitin-Mediated Proteolysis of Aux/IAA Proteins Regulates Auxin Response
(A) Wild-type Arabidopsis thaliana and the axr2-1 mutant. axr2-1 is a dominant gain-of-function mutation in an Aux/IAA gene that confers reduced auxin response. The mutant axr2-1 protein constitutively represses auxin response because it cannot be targeted for proteolysis by the SCF$_{TIR1}$ ubiquitin ligase. The effect of the mutation on AXR2 stability is shown in a pulse-chase experiment (inset). Wild-type and axr2-1 seedlings were labeled with $^{35}$S-methionine and AXR2/axr2-1 protein was immunoprecipitated either immediately after the labeling period (t = 0) or following a 15-minute chase with unlabeled methionine (t = 15).

(B) A simplified model for auxin response. In the absence of an auxin stimulus, Aux/IAA proteins inhibit ARF transcriptional activity by forming heterodimers. Auxin perception (by an unknown receptor) targets the Aux/IAA proteins to the SCF$_{TIR1}$ complex, resulting in their ubiquitination and degradation, thereby de-repressing the ARF transcription factors. Among the ARF targets are the Aux/IAA genes themselves, which produce nascent Aux/IAA proteins that restore repression upon the pathway in a negative feedback loop.

Ethylene and cytokinin are both perceived by receptors sharing similarity to bacterial two-component regulators. Common in prokaryotes, but apparently restricted to plants and fungi in eukaryotes, these modular signaling systems involve a membrane-bound receptor containing an intracellular histidine kinase (HK) domain (Wolanin et al. 2002). Ligand binding activates the kinase, resulting in autophosphorylation and initiation of a series of phosphotransfer reactions.
that culminates with the activation of a response regulator protein that functions as the effector component of the pathway. Cytokinin signaling appears to largely follow this paradigm (Kakimoto 2003). Ethylene response, however, appears more complex (Guo and Ecker 2004).

Ethylene is perceived by a family of five receptors. ETR1 and ERS1 contain a consensus HK domain, however, the HK domains of ETR2, ERS2, and EIN4 are degenerate and lack elements necessary for catalytic activity. This fact, together with studies of “kinase-dead” mutants of ETR1, suggests that HK activity is not required for ethylene response. Mutations that abolish ethylene binding in any of the five receptor genes are dominant and confer ethylene insensitivity, indicating that the receptors function as negative regulators of the ethylene pathway.

Genetic and molecular studies have positioned these receptors upstream of the Raf-like MAP kinase kinase kinase, CTR1, which interacts with the receptors and also acts as a negative regulator (Fig 65). The integral membrane protein, EIN2, and the transcription factors EIN3 and EIL1 are positive regulators of ethylene signaling downstream of CTR1. Current models propose that hormone binding inactivates the receptors, thus resulting in down-regulation of CTR1 activity. Since the identification of CTR1, biologists have speculated that a MAP kinase cascade may be involved. Only recently, however, have putative MAP kinase kinase and MAP kinase components of the ethylene pathway been identified (Chang 2003). Interestingly, these kinases appear to positively regulate ethylene response, suggesting that CTR1 must inhibit their function. If so, this would represent a novel twist on the traditional MAP kinase signaling paradigm. Precisely how the ethylene signal is transduced to the EIN3 and EIL1 transcription factors remains unclear. However, the recent finding that ethylene stabilizes these transcription factors, which are targeted for degradation by an SCF complex in the absence of ethylene, clearly indicates a role for the ubiquitin pathway (Guo and Ecker 2003; Potuschak et al. 2003). One of the known targets for EIN3 is the ERF1 transcription factor, which activates several genes involved in a subset of ethylene responses.

**Signal Integration and Combinatorial Control**

Long ago, plant physiologists noted the apparent antagonistic interactions between some of the phytohormones, such as between auxin and cytokinin in the regulation of root–shoot differentiation and between GA and ABA in germination. Other processes are synergistically regulated by multiple hormones. While it has long been obvious that hormones do not function in discrete pathways, but rather exhibit extensive cross-talk and signal integration with each other and with environmental and developmental signaling pathways, the molecular basis for such coordinated regulation has been unclear. Several recent findings have begun to elucidate the molecular details of some of these events.
Fig 65. A Model for the *Arabidopsis* Ethylene Response Pathway
Ethylene is perceived by a family of two-component receptors containing a consensus (unshaded) or degenerate (shaded) HK domain (H). Three of the receptors also contain a C-terminal receiver domain (R). The receptors negatively regulate ethylene response together with CTR1 in a complex on the endoplasmic reticulum membrane. Perception results in reduced receptor and CTR1 activities and activation of a MAP kinase kinase, which transmits the signal through the EIN2 membrane protein, ultimately resulting in the activation of a transcriptional cascade in the nucleus. The EIN3 and EIL1 transcription factors regulate primary response genes including *ERF1*, which activates a subset of secondary ethylene-induced genes involved in defense responses. EIN3/EIL1 abundance is regulated in an ethylene-dependent manner by SCF complexes containing F-box proteins encoded by the ethylene-induced genes *EBF1* and *EBF2*. Positive- and negative-acting components of the pathway are indicated in green and red, respectively. Solid lines indicate regulation that is likely to be through direct interactions. Dotted lines indicate speculative interactions based on genetic studies.
One example of such signal integration was recently described for the ethylene and JA pathways (Lorenzo et al. 2003). Genetic studies had previously implicated both hormones as important regulators of pathogen defense responses, as well as of the wounding response and other stress-related pathways. Additionally, microarray analysis has identified a large number of genes that are responsive to both hormones. The ERF1 transcription factor was recently found to be an intersection point for these two signaling pathways (Lorenzo et al. 2003). Like ethylene, JA rapidly induces \textit{ERF1} expression, and treatment with both hormones synergistically activates \textit{ERF1}. Induction of \textit{ERF1} by both hormones alone or in combination is dependent upon both signaling pathways, and constitutive overexpression of \textit{ERF1} rescues the defense-response defects of both ethylene- and JA-insensitive mutants. These findings suggest that \textit{ERF1} represents one of the first signaling nodes identified in the complex web of hormonal cross-talk.

The auxin and BR pathways also appear to converge and mutually regulate some developmental processes. Both hormones promote cell expansion, and microarray studies have revealed that as many as 40% of all BR-induced genes are also up-regulated by auxin (Goda et al. 2004; Nemhauser et al. 2004). BR is perceived by the cell surface receptor kinase BRI1 (Wang and He 2004). The SHAGGY/GSK3-type kinase BIN2 acts as a negative regulator of the pathway downstream of the receptor. In the absence of a BR signal, BIN2 phosphorylates the transcription factors BES1 and BZR1, targeting them for proteolysis by the 26S proteasome. Upon a BR stimulus, BIN2 is inactivated, allowing BES1 and BZR1 to accumulate in the nucleus, where they are presumably involved in regulating BR-responsive genes.

Using combined genetic, physiological, and genomic approaches, Nemhauser et al (2004) were able to demonstrate that auxin and BR regulate \textit{Arabidopsis} hypocotyl (embryonic stem) elongation in a synergistic and interdependent fashion. Elevating endogenous auxin levels rendered plants more sensitive to BR application in hypocotyl elongation assays, and this response was dependent upon both the auxin and BR signaling pathways. Genetic studies suggest that the convergence of these two pathways occurs at a late point in hormone signaling, perhaps at the promoters of the many genes responsive to both hormones. In support of this notion, bioinformatic analysis identified distinct sequence elements that were enriched specifically in the promoters of auxin-induced, BR-induced, and auxin/BR-induced genes.

Many Unanswered Questions

While great strides have been made in recent years in understanding the molecular basis of phytohormone action, many fundamental questions remain. Receptors and other upstream signaling components remain to be identified for the majority of the phytohormones. Equally important are the elucidation of hormonal networks and the integration of these networks with the morphogenetic program, such that our understanding of hormone action can be placed in a developmental context.

Role of growth hormones in field crop production and efficient use of resources

Plant hormones have been extensively studied for their importance in innate immunity particularly in the dicotyledonous model plant \textit{Arabidopsis} thaliana. However, only in the last decade, plant hormones were demonstrated to play conserved and divergent roles in fine-tuning
immune in rice (Oryza sativa L.), a monocotyledonous model crop plant. Emerging evidence showed that salicylic acid (SA) plays a role in rice basal defense but is differentially required by rice pattern recognition receptor (PRR) and resistance (R) protein-mediated immunity, and its function is likely dependent on the signaling pathway rather than the change of endogenous levels. Jasmonate (JA) plays an important role in rice basal defense against bacterial and fungal infection and may be involved in the SA-mediated resistance. Ethylene (ET) can act as a positive or negative modulator of disease resistance, depending on the pathogen type and environmental conditions. Brassinosteroid (BR) signaling and abscisic acid (ABA) either promote or defend against infection of pathogens with distinct infection/colonization strategies. Auxin and gibberellin (GA) are generally thought of as negative regulators of innate immunity in rice. Moreover, GA interacts antagonistically with JA signaling in rice development and immunity through the DELLA protein as a master regulator of the two hormone pathways.

Plant growth and response to environmental cues are largely governed by phytohormones. The plant hormones ethylene, jasmonic acid, and salicylic acid (SA) play a central role in the regulation of plant immune responses. In addition, other plant hormones, such as auxins, abscisic acid (ABA), cytokinins, gibberellins, and brassinosteroids, that have been thoroughly described to regulate plant development and growth, have recently emerged as key regulators of plant immunity. Plant hormones interact in complex networks to balance the response to developmental and environmental cues and thus limiting defense-associated fitness costs. The molecular mechanisms that govern these hormonal networks are largely unknown. Moreover, hormone signaling pathways are targeted by pathogens to disturb and evade plant defense responses. Plant growth and response to environmental cues are largely governed by phytohormones. The plant hormones ethylene, jasmonic acid, and salicylic acid (SA) play a central role in the regulation of plant immune responses. In addition, other plant hormones, such as auxins, abscisic acid (ABA), cytokinins, gibberellins, and brassinosteroids, that have been thoroughly described to regulate plant development and growth, have recently emerged as key regulators of plant immunity. Plant hormones interact in complex networks to balance the response to developmental and environmental cues and thus limiting defense-associated fitness costs. The molecular mechanisms that govern these hormonal networks are largely unknown. Moreover, hormone signaling pathways are targeted by pathogens to disturb and evade plant defense responses.

Synthetic as well as natural hormones are extensively used in the propagation of various horticultural, silvicultural plants through tissue culture techniques.

**Auxins**

a) Auxins are effectively used in rooting of difficult to root plants. This has a wide application in vegetative propagation of plants. IBA at 250 ppm and NAA (1-Naphthalene Acetic Acid) were found to increase root development in the propagation of stem cuttings.

b) Some of the synthetic auxins can be used in removing weeds growing in the farms and agricultural fields. Certain hormones specifically weed out
monocots, like grasses and some destroy dicots, for ex. 2.2. Dichloro propionic acid removes grasses, while 2, 4-Dichlorophenoxy acetic acid (2, 4-D) & (2, 4, 5 Trichloro phenoxy acetic acid) 2, 4, 5-T) are employed in weeding out the dicots. 2,4-D stimulates excessive uncontrolled growth in broad-leaf plants for which it is used as a herbicide.

c) Application of NAA reduces flower and fruit drop in Mango.

d) Auxins like Naphthalene acetic acid (NAA) are used in prolonging the dormancy period, thus the storage and shelf life of food in potatoes, corms, bulbs, etc., is prolonged. NAA application brings uniform flowering and fruit set by inducing ethylene formation in pineapple.

e) NAA application at 10-100 ppm during fruit setting period controls boll shedding in cotton.

f) Auxins and Gibberellins are used in inducing parthenocarpity. Parthenocarpic fruits are seedless, at the same time they are larger and sweetish. These qualities of fruits have greater commercial value.

g) Spraying of auxins to fruit plants like orange, lemon apple etc prevents the premature falling of the fruits by formation of abscission layers premature falling cause greater economic loss to cultivators. This can be prevented by the use of auxins.

**Gibberellins**

a) GA is used extensively on seedless grape varieties to increase the size and quality of the fruit. Pre-bloom spray of 20 ppm induces rachis of the fruit cluster to elongate. This creates looser clusters that are less susceptible to disease during the growing season.

b) GA is used to increase the yield of barley malt and to decrease the time required for this process to occur. Application of GA to germinating barley supplements the endogenous content of this hormone and accelerates the production and release of hydrolytic enzymes. they can easily degrade the stored carbohydrates.

c) Foliar spray of GA$_3$ at 100 ppm during panicle initiation stage enhances the panicle exertion and increases seed weight and yield in hybrid rice.

d) GA has also been used to control flower sex expression in cucumbers and squash. GA application tends to promote maleness in these plants.

e) GA is also applied to citrus crops, through the actual use depends on the particular crop. For example GA$_3$ is sprayed onto oranges and tangerines to delay or prevent or prevent rind-aging, so that fruit can be harvested later without adverse effects on rind quality and appearance. For lemons and limes, GA$_3$ synchronizes ripening and enhances fruit size.

f) GA is used extensively to increase the sucrose yield of sugarcane. Sugarcane, a normally fast growing C$_4$ member of the Poaceae is sensitive to cooler winter temperatures, which
reduce internode elongation and subsequent sucrose yield. The adverse effects of cooler temperature can be counteracted by the application of GA$_3$.

**Ethylene**

a) Ethylene is most widely used plant hormone in agriculture because it regulates so many physiological processes. Auxins and ACC can trigger the natural biosynthesis of ethylene and in several cases are used in agricultural practice.

b) Ethylene is very difficult to apply in the field as a gas. This limitation can be overcome if an ethylene compound is used. The most widely used such compound is ethephon or 2-chloro ethyl phosphonic acid (CEPA) (trade name ethrel).

c) Ethrel at 100-250 ppm sprayed at 2-3 leaf stage induce femaleness in cucumber and melons.

d) Ethylene can be used for quick ripening of fruits for marketing. It helps in degreening of citrus and banana which increases its market acceptability.

e) Storage facilities developed to inhibit the ethylene production and promote preservation of fruits have a controlled atmosphere of low O$_2$ concentration and low temperature that inhibits ethylene biosynthesis. A relatively low concentration of CO$_2$ (3-5%) prevents ethylene action as a ripening promoter.

**Other growth regulators**

- Abscissic acid can be used to obtain uniform harvesting of citrus fruits and cotton bolls.
- AMO 1618 (a quaternary ammonium salt) is used in the cultivation of ornamental plants and causes a bushy shape and a study growth of the treated plants.
- Paclobutrazol: Reduces the problem of biennial bearing in mango.
- Mapiquat chloride, cloromequat chloride (cycocel): used in ornamental plants for shorter internodes and thicker stems (used in poinsettias). It also prevents lodging and increases tillering in cereals.
- Malichydrazide (MH) prevents premature sprouting of onion and potato.
- 2,3,5-T or Triiodo benzoic acid (TIBA): Increases flowering in chrysanthemum.