

27 Photosynthetic Plant Productivity

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Feeding the world's population is considered to be one of the major challenges of the 21st century. The response to this challenge consists of several factors.

1. Policy makers and governments should make a major effort to alleviate hunger all over the world, particularly in developing countries where it is worst, by encouraging local production.

2. Economic and technological means should be used to maximize plant production in developing countries and to optimize it to resources in developed ones, without the distortions produced by subsidies and market protection.
3. Farmers should be provided with current knowledge about yield formation and how to increase efficiency of utilization of all the resources and technology, including use of

improved genotypes, fertilization, crop protection, and irrigation methods to preserve soil fertility and biodiversity, etc.

4. Scientists should enhance understanding of crop growth and development with special emphasis on the quantification of productive ideotypes for particular environments, with optimal efficiency in mineral nutrient use and dry matter allocation, and with resistance to various biotic and abiotic stresses.

This chapter does not deal with the first three aspects. Nevertheless, it is important to stress that science itself cannot solve the deplorable problem of food shortage. Scientists have to fulfill their duties to develop the understanding and techniques, enabling an environmentally friendly, and biologically effective, increase in crop production at all locations, not only those with optimal climate and soil conditions but also those with less favorable conditions.

This chapter deals with principles of photosynthetic productivity. It is evident that the scientific base of crop production involves many branches of science including pedology, chemistry, genetics, and plant physiology. Of all the aspects of plant processes contributing to production, photosynthesis has to be considered the most relevant. This is demonstrated by the following.

Crop biomass produced in the field consists of water and dry matter. Considering the energy and nutritional needs of people and other animal consumers, it is the dry mass which is important, particularly in the case of cereal and legume grains, the staple

food of humanity. Farmers harvest this biomass with various amounts of water simply because in many cases, it is not convenient or possible to leave the water on the field. Dry mass consists of organic substances (carbohydrates, proteins, lipids) and mineral elements (phosphorus, potassium, calcium, magnesium, etc.). These mineral constituents contribute only about 5% to the total dry mass. Hence, the majority of dry matter consists of assimilates synthesized in photosynthesis. This is not to say that both water and minerals in biomass are useless. But it is essential to emphasize that the amount (mass) of assimilate produced plays a decisive role in the formation of economic yield. Because assimilates are synthesized in photosynthesis, using energy derived from the sun and consuming carbon dioxide from the atmosphere, the amount of absorbed and fixed solar energy, as well as the amount of incorporated carbon dioxide, are the biological basis of crop production.

In this chapter, several features of photosynthetic productivity will be illustrated by considering cereals. This is because of their importance in nutrition (Figure 27.1) and because many principles of yield formation have been deduced from studies with cereal species, predominantly wheat, rice, and maize.

I. DRY MATTER PRODUCTION IN A CROP CANOPY

In most crops, economic yield is represented by only one structural part (grain, tubers, roots). The ratio of

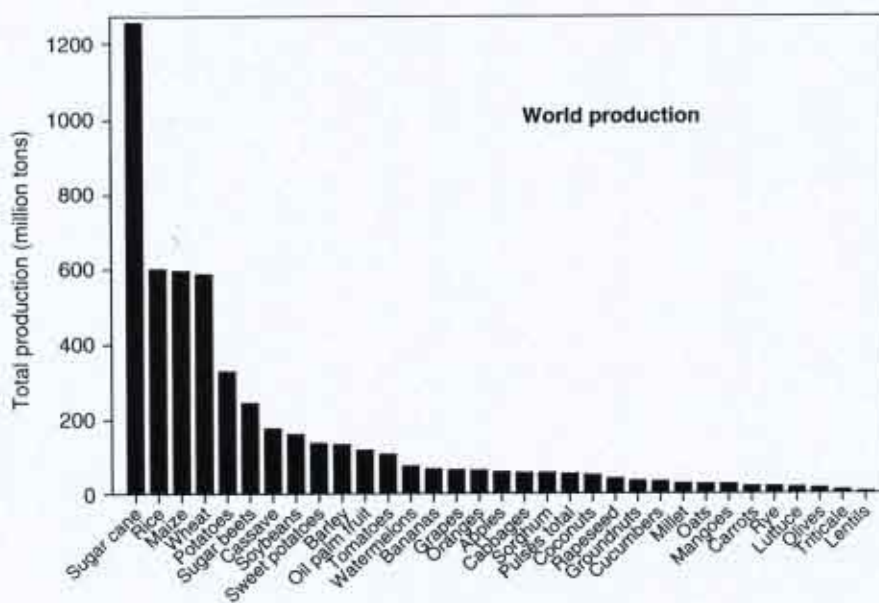


FIGURE 27.1 World production (10^6 tons) of the main crops. FAO data.

dry mass of the main economic yield (Y) to the total plant or canopy dry mass (W) is called the harvest index (HI). Hence,

$$Y = W \cdot HI$$

Instead of total plant dry mass (W), only shoot (above ground) dry mass is used because measuring root dry mass is often difficult.

It follows that yield could be increased either by increasing harvest index or total plant dry matter. Intuitively, HI cannot reach unity. This would be possible only for crops in which the main economic yield is represented by the total plant. In most crops, HI increases with selection of improved crop varieties and can be optimized for particular environmental conditions, so it is not a fixed value. However, it is assumed that HI has biological limits, the exact values of which are not known. For example, in cereals, HI ranges from about 0.4 to 0.6, indicating, that up to 60% of the total or above ground dry matter accumulates in grain.

The other possibility of increasing yield is by an enhancing total plant dry mass, which is determined by the length of the growing period (D), leaf area of the canopy (L), and rate of net photosynthesis per unit of leaf area (P). On the other hand, total plant dry mass (W) is reduced by losses due to respiration (R). Hence (Figure 27.2),

$$W = (D \cdot L \cdot P) - R$$

This expression is simplified, neglecting the variability of each of the components, but it clearly indicates the main factors determining both the absorption and utilization of solar radiation in a canopy. Next, the individual components are treated in more detail.

A. LENGTH OF THE GROWING PERIOD

There is no doubt that the longer the duration of active photosynthesis by a crop, the more the produc-

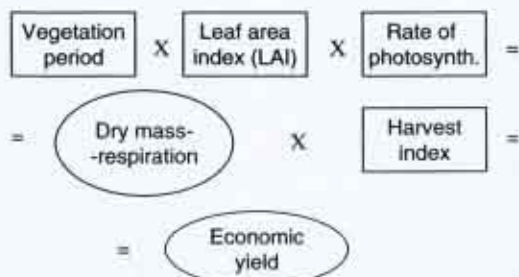


FIGURE 27.2 Schematic illustration of the participation of the main plant and canopy parameters in yield formation.

tion of assimilates. However, the period suitable for crop growth is mainly correlated with the genetically determined life-span of the crop and by the geographical location; the latter can hardly be altered although selective adaptation of wheat, for example, to grow at high latitudes with extended daylight in summer, is associated with increased yields. There are at least two other possibilities of how to extend the growing period:

1. The selection of genotypes (plant species or varieties) that have the capacity for growth and photosynthesis over longer periods, and are, for example, less sensitive to low temperature, could enhance the growing period in cold climates. Similarly, in climates where summer heat restricts the growing season, more drought and heat resistant genotypes could use more days of a year to capture solar radiation and use it for photosynthesis.
2. The use of all the days of a growing season by minimizing the time lag between the cultivation of successive crops. Bare soil, without a full green surface cover of growing plants, should be avoided as much as possible by suitable management practices.

Often, the final dry mass of crops depends on the length of their vegetation period (Figure 27.3) According to Monteith and Elston [1], the mean values of daily dry matter production of a canopy for the two plant groups are:

$$C_3 \text{ plants: } 13.0 \pm 1.6 \text{ g m}^{-2} \text{ day}^{-1}$$

$$C_4 \text{ plants: } 22.0 \pm 3.6 \text{ g m}^{-2} \text{ day}^{-1}$$

The values are realistic, obtained under conditions suitable for growth of the particular types and with no nutrient or water limitation. Similar values of the maximum rate of daily plant dry matter production have been given by de Wit in the 1960s (Table 27.1).

Obviously, in the term "vegetation period," solar radiation plays a decisive role as the amount of dry matter produced by a canopy, well supplied with water and nutrients, depends on the amount of solar radiation absorbed. Photosynthetic efficiency of a canopy is the amount of dry matter produced per unit of absorbed energy (Table 27.2). This efficiency is relatively constant during the period when the canopy is closed, and is mostly maintained by gradual replacement of old senescing leaves of lower insertion with newly developed leaves of higher insertion in the well-lit upper canopy.

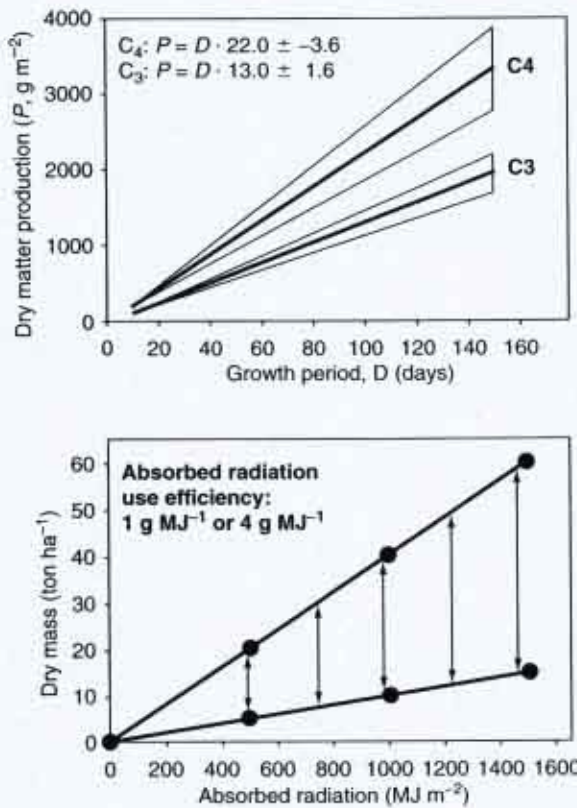


FIGURE 27.3 (Top) Dependence of canopy dry mass on the duration of growth of C_3 and C_4 plants. Equations (included in the graph) taken from Ref. [1]. (Bottom) The dependence of canopy dry mass on absorbed radiation, which is used with the efficiency of 1 or 4 g/MJ.

TABLE 27.1
Potential (Theoretical Maximum) Production of Assimilates ($\text{t ha}^{-1} \text{ month}^{-1}$). The Values in the Numerator and Denominator are for a Clear and a Cloudy Day, Respectively. Calculated with Data from [56]

Latitude	January	April	July
0°	12.8/6.8	12.8/6.8	12.8/6.8
40°	6.8/3.1	12.8/6.7	15.4/8.2
85°	0/0	10.0/4.0	19.6/9.2

B. LEAF AREA INDEX

Quanta of solar energy incident on a canopy must be absorbed as effectively as possible and then utilized with the maximum efficiency in photosynthetic processes for maximizing production (Figure 27.4). Photosynthesizing organs, mostly leaf blades but including leaf sheaths, stem, internodes, ears, etc., con-

TABLE 27.2
Efficiency with which Photosynthetically Active Radiation is Used to Form Dry Matter of Several Plant Species [100]. One Gram of Dry Matter Corresponds to About 17 kJ and so a 100% Use Efficiency would give Values of About 60 g Dry Matter per 1 MJ

Plant Species	g (dry matter) MJ^{-1}
Soybean (<i>Glycine max</i>)	1.3
Clover (<i>Trifolium subterraneum</i>)	1.6
Cotton (<i>Gossypium hirsutum</i>)	2.5
Sunflower (<i>Helianthus annuus</i>)	2.6
Maize (<i>Zea mays</i>)	3.4
Rice (<i>Oryza sativa</i>)	4.2

tribute to light absorption and photosynthesize to different extents. We should speak about the area of photosynthesizing or assimilating plant parts, but for simplicity and with respect to tradition, we shall call it leaf area. It has been shown that the size of individual leaves, or total leaf area per plant, is not so important as the total leaf area of a canopy per unit ground area, which is called the leaf area index (LAI), and is most often expressed as m^2 (leaf area) per m^2 (ground area). The concept of LAI proved to be extremely useful in assessing the most important parameter of the photosynthetic activity of a canopy [4,5].

It is interesting to recall that LAI is one of several parameters used in growth analysis, which was developed in England in the 1920s, and further elaborated and used, especially in the 1950s, by Watson and his coworkers [6,7]. At the same time, Ničiporovič represented a Soviet school [8,9], which also contributed substantially to our understanding of the importance of canopy leaf area.

Radiant energy incident on a canopy (Q) is either reflected (Q_R), absorbed (Q_A), or transmitted (Q_T). The coefficients of reflection (r), absorption (a), and transmission (t) are then given by Q_R/Q , Q_A/Q , and Q_T/Q , respectively. The mean values for these are 0.15, 0.75, and 0.1, respectively, for photosynthetically active radiation (PAR). However, it should be taken into account that the values of the coefficients also depend on the spectrum (wavelength) of the incoming radiation. Because leaves absorb blue and red wavelengths predominantly, in comparison with absorption of the green part of the spectrum, vegetation appears green to the human eye. In the ultraviolet part of the spectrum (wavelengths shorter than 380 nm), the absorption coefficient reaches nearly 1. On the other hand, in the near infrared part (750 to 1200 nm), absorption is rather low with values of the

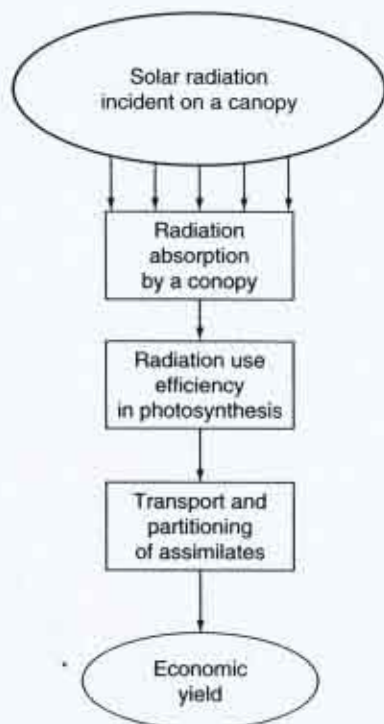


FIGURE 27.4 Consecutive steps in the use of solar radiation for production of crop yield.

absorption coefficient only 5% to 25%. And finally, long-wave radiation (above 4000 nm) is nearly completely absorbed by leaves.

C. PENETRATION OF SOLAR RADIATION INTO THE CANOPY

Leaf absorption characteristics are important photosynthetic features, but the penetration of radiation into the canopy is of more importance for photosynthesis of the whole stand. Japanese researchers Monsi and Saeki [10] quantitatively described penetration of radiation into the canopy. Irradiance at a particular positioning the canopy (I) is related to the cumulative LAI from the top of the canopy (L) by:

$$I = I_0 e^{-kL}$$

where I_0 is the solar radiation incident on the top of the canopy (Wm^{-2}), k is the extinction coefficient of the canopy, and L is the cumulative LAI from the top of the canopy down to the appropriate height.

According to a review [11], the extinction coefficients vary in canopies of different species (Table 27.3) from about 0.4 to 0.9. If the extinction coefficient equals 0.5, then the irradiance at the bottom of a canopy with LAI 3 equals $1 \times e^{-0.5 \cdot 3}$, i.e., 22%. Similarly for $L = 5$ irradiance at the bottom of the

TABLE 27.3
Extinction Coefficients of Radiation Penetration into the Canopy of Several Plant Species [11]

Plant Species	Coefficient
Reed (<i>Phragmites communis</i>)	0.51
Fescue (<i>Festuca arundinacea</i>)	0.57
Sugar cane (<i>Saccharum officinarum</i>)	0.59
Sorghum (<i>Sorghum vulgare</i>)	0.61
Clover (<i>Trifolium repens</i>)	0.76
Rape (<i>Brassica napus</i>)	0.84
Alfalfa (<i>Medicago sativa</i>)	0.88
Cowpea (<i>Vigna unguiculata</i>)	0.93

canopy corresponds to only 8.5% of the irradiance at the top (see Figure 27.5).

The extinction coefficient for canopies with vertically oriented leaves (monocots — cereals, grasses) is generally less than 0.6. On the other hand, canopies of dicots, with large leaves in a more horizontal orientation, have extinction coefficients larger than 0.7.

Knowing the proportion of reflected radiation, it is possible to calculate the amount of absorbed radiation by individual canopy layers on the basis of their cumulative LAI and extinction coefficients. The mean proportion of radiation reflected from a canopy is in the range of 15% to 25%. A canopy with predominantly vertical orientation of narrow leaf blades reflects less radiation, especially if the sun is high above the horizon. In this case, radiation penetrates deeper into the canopy. On the other hand, if the sun is low above the horizon, and particularly in canopies with large leaf blades, the reflection increases.

In order to determine the suitability of a canopy to maximize capture of the incident solar radiation, the static value of the LAI is not sufficient. The dynamics of the development of LAI during the whole growth period determines the total energy captured by the canopy.

D. DYNAMICS OF LEAF AREA INDEX

At sowing, the bare soil absorbs all of the incident radiation, thus increasing evaporation. After emergence, the leaves appear. If they are distributed horizontally, this enables a more rapid cover of the soil compared with the more vertical orientation. Hence, at this stage of canopy development, rapid growth of horizontally oriented leaves is required to achieve a highly productive canopy. When LAI reaches values of about 3 and higher, most of the incident radiation is absorbed by the leaves. At this stage, optimum LAI must be maintained as long as possible. It is evident

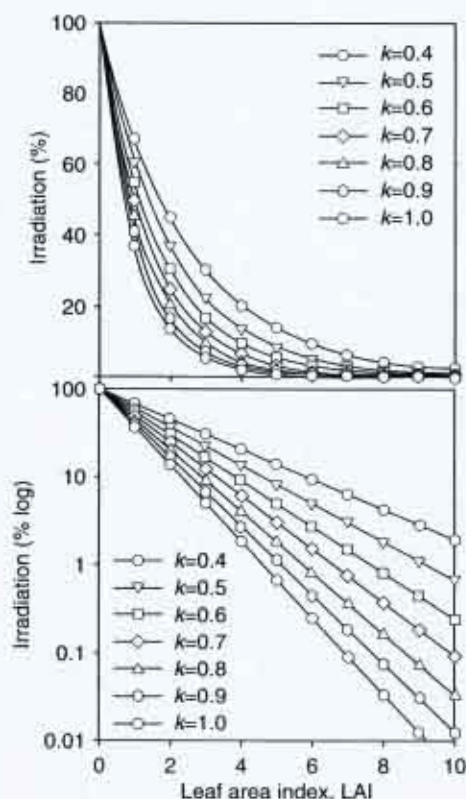


FIGURE 27.5 Radiation (I , % of the incident radiation I_0) within the canopy at a height expressed by cumulative leaf area index (L , from the canopy top) and its dependence on the canopy extinction coefficient (k) calculated as $I = I_0 e^{-Lk}$. For details, see text.

that in most crops, an optimum LAI is not maintained by the same leaves. The older leaves become senescent and die and must be regularly replaced by leaves of higher insertions. In cereals and other crops cultivated not for the whole shoot biomass but only for certain organs, the leaves should be active as long as possible. Theoretically, they should senesce just before harvest (Figure 27.6).

As seen from the description of the dynamics of LAI, there are three growth stages suitable for genetic or physiological manipulation. (1) The period from emergence to the time when optimum LAI is reached should be as short as possible. Otherwise, part of incident solar radiation is absorbed by the soil surface and lost for production. (2) The period of optimum LAI should last as long as possible. The question about the optimum value itself is dealt with in the next chapter. (3) Leaf senescence should be prevented, for as long as possible, in order to produce the maximum of carbohydrates. However, this statement should be taken with caution. In many crops, leaves

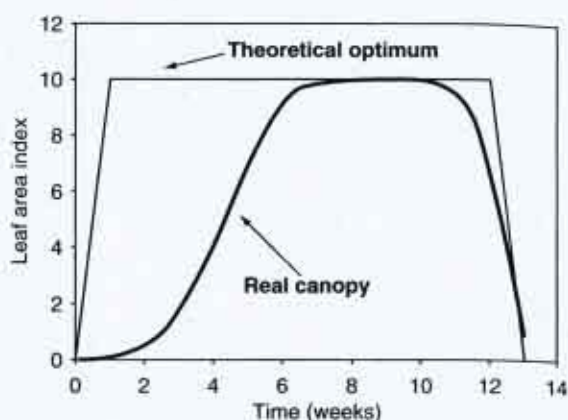


FIGURE 27.6 Schematic of the time course of development of the leaf area index in the real canopy (thick line) and theoretical optimum (thin line) for maximum absorption of incident solar radiation during the growing period.

contain a considerable amount of protein, which is broken down during senescence and the nitrogen compounds translocated into organs of economic importance (grain). Hence, this third stage represents a compromise between the need to prolong assimilate production in the leaves whilst allowing enough time for the break down of proteins and their transport out of senescent leaves.

E. RADIATION USE EFFICIENCY

According to many authors (see Ref. [12]), the radiation use efficiency of crops has not changed during the last century, a period over which yields increased considerably. The major contribution to this yield increase was modification of dry matter allocation, shown by an increase in HI of cereals from about 0.3 at the beginning of the last century up to the current values approaching about 0.6. However, the possibility of a further enhancement of HI is obviously limited because a plant cannot consist only of grains. Therefore, any further yield increase will depend on the increase in the efficiency with which the absorbed radiation is used in photosynthesis, to increase biomass production. However, this also requires that the capacity of the grain to accumulate dry matter must also increase.

Efficiency can be considered in the following way. For fixation of 1 mol CO_2 , some 8 to 10 mol of PAR quanta are needed, which approaches 20% of the utilization of the absorbed radiation energy at maximum efficiency. The global annual utilization of incident solar radiation corresponds to about 0.1% of total radiation, or 0.2% of the PAR. In canopies of

various crops, the utilization efficiency varies from about 0.5% to some 3%.

Depending on the CO₂ concentration and temperature, the amount of dry matter produced per unit of radiation ranges from 1 to 3 μg/J, corresponding to 3 g/MJ (Table 27.2; [13]). In legumes, the values are somewhat lower because of the higher content of proteins, the synthesis of which requires more energy. For example, Jeuffroy and Ney [14] found values in the range from 0.96 to 1.42 g dry mass per megajoule incident PAR.

Theoretical analysis of radiation use efficiency in a closed canopy and its dependence on quantum requirement has been published [15]. The calculations show (Table 27.4) that a closed canopy could achieve radiation use efficiency from 4.2 to 5.8 g dry mass per megajoule PAR absorbed. There is no doubt that an increase in the radiation use efficiency achieved either by breeding or agronomic management is a major challenge to the plant sciences, and represents one of the most promising tools to obtain yield increase in the future.

F. EFFICIENCY OF SOLAR ENERGY UTILIZATION IN CANOPIES

Leaves absorb about 75% of the incident solar radiation. If we suppose that in a canopy, leaves with horizontal spatial arrangement are uniformly distributed, then with an LAI value of 3, nearly all incident radiation penetrating into the upper layers of a canopy would be absorbed. Hence, an LAI of 3 should be sufficient. Therefore, it is surprising that highly pro-

ductive canopies have been characterized by LAIs of 8 and more. The explanation becomes apparent, if we take into consideration not only maximization of solar energy capture, but also maximization of the use of absorbed energy in photosynthesis.

The rate of net photosynthesis per unit area of individual leaves increases with increasing irradiation, reaching saturation at about PAR 600 and 900 μmol m⁻² sec⁻¹ for C₃ and C₄ plants, respectively. In regions with moderate climate, the rate of canopy net photosynthesis is not saturated even at the highest summer irradiances. Leaves at the top of the canopy receive more light than can be efficiently used in photosynthesis. The amount of assimilate produced per unit leaf area increases progressively less with the increase in irradiance, so the radiation use efficiency per joule of absorbed radiation is highest at lowest irradiances and decreases with an increase in irradiation (Figure 27.7). This point explains the need to increase the LAI of highly productive canopies well above values that would assure the maximum physically possible absorption of the incident radiation.

It follows that in a productive canopy, not only the time course of the LAI but also optimization of the spatial distribution of leaves — mainly blades is of prime importance [16]. Varying spatial arrangement enables the absorption of energy by the individual leaves to be varied and optimized for photosynthesis.

Let us suppose that several types of canopies differ in the vertical inclination of their leaves. With an angle of 90° and uniform horizontal distribution, an LAI of

TABLE 27.4

Calculation of the Radiation use Efficiency (RUE, g(dry matter) MJ⁻¹) of a Closed Maize Canopy (C₄ plant) for Three Different Quantum Requirements (Quantum 15 is almost the Minimum for the Photosynthetic Fixation of 1 CO₂). Assumed Rate of Maintenance Respiration is 0.5 mmol (CH₂O) per g (Dry Mass) per Day, which is Equivalent to 0.015 g g⁻¹ Day⁻¹ of the 1400 g Canopy Dry Mass per m², and Incident Solar Radiation of 28 MJ m⁻² Day⁻¹. Growth Efficiency, i.e. Produced Plant Dry Mass per Unit Consumed Glucose, is 0.74, which Corresponds to Dry Matter Containing 43% Carbon and 1.1% Nitrogen. Assumptions: Intercepted Solar Radiation: 2.20 mol (1.00 MJ), Radiation Reflection from the Canopy: -0.13 mol, PhAR Quanta Absorbed by the Canopy: 2.07 mol [13]

Calculation of the RUE			
Quantum requirement	14	16	18
The amount of produced CH ₂ O (mmol)	148	129	115
CH ₂ O consumed for maintenance (mmol)	25	25	25
CH ₂ O available for growth (mmol/g)	123/3.69	104/3.12	90/2.70
RUE for intercepted solar radiation (g/MJ ⁻¹)	2.7	2.3	2.0
	RUE for PhAR		
g (dry matter) MJ ⁻¹ (incident/absorbed PhAR)	5.5/5.8	4.6/4.9	4.0/4.2

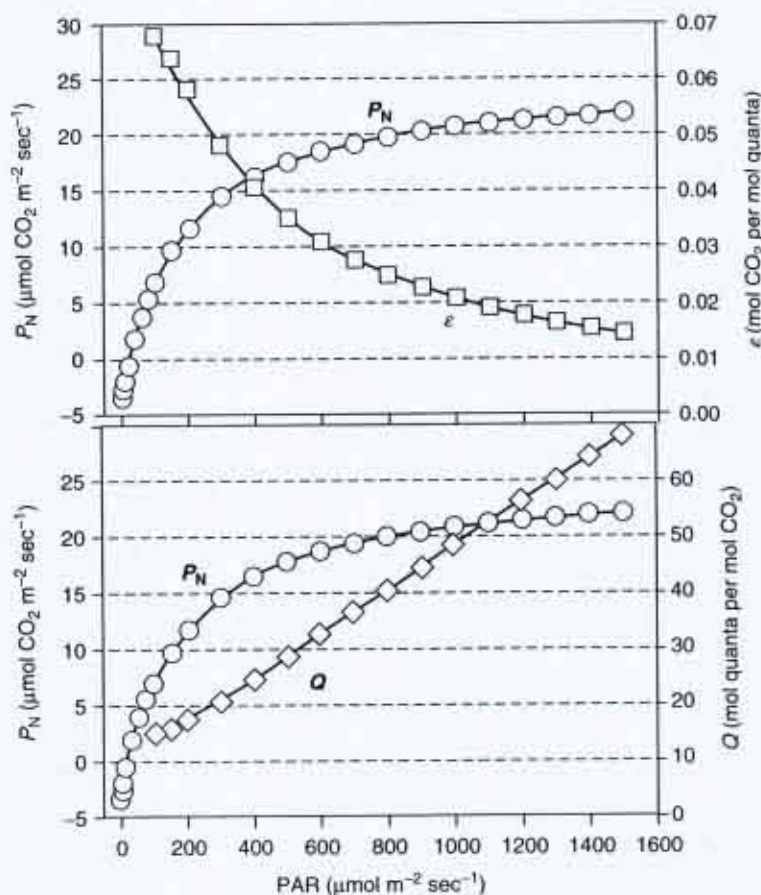


FIGURE 27.7 The effect of PAR flux on the rate of photosynthesis (P_N , $\mu\text{mol m}^{-2} \text{sec}^{-1}$) and quantum yield (ϵ , mol CO_2 per mol quanta) or (below) quantum requirement (mol quanta per mol CO_2).

unity is sufficient to cover the ground. All the leaves will be exposed to direct radiation of, for example, 1000 W m^{-2} from above (Figure 27.8). In this case, its leaves will be irradiated with 1000 W m^{-2} intensity (for simplicity neglecting reflectance), and their rate of photosynthesis will be high but their radiation use efficiency rather low. If the canopy is composed of plants with a uniform leaf angle of 20° , i.e., nearly vertical position, then its rate of photosynthesis will be only about $15 \mu\text{mol m}^{-2} \text{sec}^{-1}$, but its radiation use efficiency will be $0.05 \text{ mol CO}_2/\text{mol quanta}$ (Figure 27.9). Furthermore, in such a canopy, the LAI will be about 3 and the total photosynthetic absorption of CO_2 will reach $45 \mu\text{mol m}^{-2} \text{sec}^{-1}$. Figure 27.10 illustrates the effect of leaf angle on irradiation of individual leaves and on the rate of photosynthesis per unit leaf area and also per unit ground area. The relatively low rates of photosynthesis per leaf area of nearly vertical leaves is more than compensated by their potential maximum LAI (Figure 27.8) resulting in a large rate of photosynthesis per unit ground area (Figure 27.10). It is also important to stress that erect leaf blades are irradiated from both adaxial and abaxial surfaces, which further improves their radiation use efficiency [17].

As shown by Kuroiwa [18], using a theoretical model of canopy structure consisting of leaves with various inclinations, leaves of the highest insertion should be in a near vertical position, absorbing only a minor part of the incident radiation. The lower the insertion, the more horizontal the leaf position should be, with leaves of the lowest insertion being horizontal in order to absorb the remaining radiation penetrating deeply into the canopy.

Let us now recall the time course of the LAI during the vegetation. After sowing, rapid growth of horizontally oriented leaves is desirable in order to fully cover the whole ground surface. When this is achieved, leaves should take more vertical position in order to maximize not only energy absorption but also photosynthesis (see above).

Of course, leaves will not change their spatial orientation according to our theoretical consideration. But plant breeders have been successful in selecting genotypes, the first leaves of which are oriented horizontal, while the subsequent ones are much more vertical [19]. This is well demonstrated by the canopy structures of old and current cereal varieties. The old varieties were not only tall (and lodging prone), but also had large leaves, which

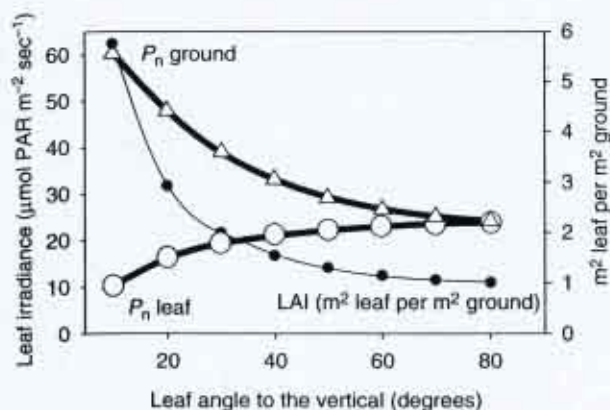


FIGURE 27.8 The effect on the rate of photosynthesis per unit leaf area (P_N leaf; $\mu\text{mol m}^{-2} \text{sec}^{-1}$) and per unit ground area (P_N ground; $\mu\text{mol m}^{-2} \text{sec}^{-1}$) of the angle between the leaf and the vertical, and the maximum leaf area index (m^2 leaf per m^2 ground) that would uniformly cover the ground by one leaf layer of the appropriate inclination. For details, see text.

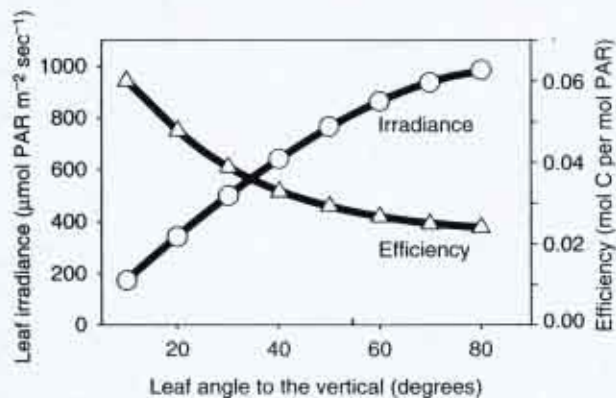


FIGURE 27.9 The effect of leaf angle, on the radiation incident on the leaf and on the leaf's radiation use efficiency.

were unable to maintain a vertical orientation. In contrast, modern wheat or barley varieties are not only much shorter (in order to prevent lodging) but also their leaf blades are small and practically vertical. The optimum spatial arrangement of leaves of cereal varieties has been supported by fact that their leaf sheaths and internodes are vertical and also contribute substantially to total assimilate production. In this way, the LAI, including the total assimilating area, of these crops reaches values well above 6.

A remarkable confirmation of the advantage of vertical orientation of the leaves in the canopy was provided by Blackmann [20]. Under the climatic conditions of Oxford, U.K., dry matter production of several plant species cultivated for 101 days was com-

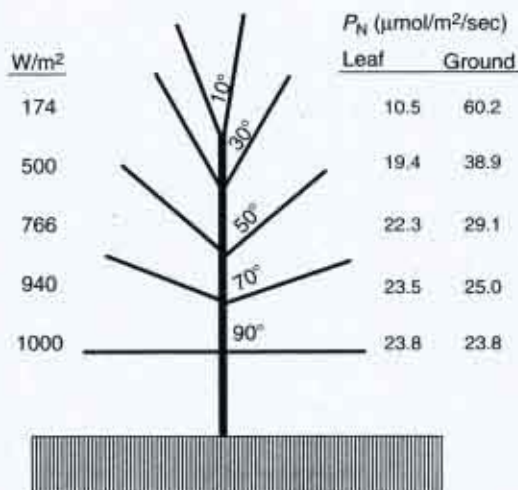


FIGURE 27.10 Schematic of the effect of leaf inclinations, from 10° to 90° , on PAR fluxes received ($W \text{ m}^{-2}$) and on P_N (the rate of photosynthesis per unit leaf area, $\mu\text{mol m}^{-2} \text{sec}^{-1}$). The rate per unit ground area was calculated on the assumption that the ground is uniformly covered by one leaf layer of the appropriate inclination.

pared. Surprisingly, the maximum dry matter production corresponding to 30 ton ha^{-1} was reached by Gladiolus, the canopy of which consisted of vertical leaves and reached an LAI above 20.

The great increases in production and efficiency that may result from the growing conditions is shown by Polonskij and Lisovskij [21]. Wheat plants were cultivated in environmentally controlled chambers at 20°C to 21°C , relative air humidity 50 to 60%, 0.4 to 0.9% of CO_2 concentration, and irradiance up to 1300 W m^{-2} PAR. There were $2000 \text{ plants m}^{-2}$ and the vegetation period was 63 to 65 days. At highest irradiance, the LAI reached 33.2, the total plant biomass 8 kg m^{-2} , and grain yield 3.3 kg m^{-2} . These correspond to 80 and 33 ton ha^{-1} . Their experiments clearly demonstrate the importance of high values of LAI. Furthermore, the authors also document that even the current varieties are able to produce unexpected high yields, if cultivated at optimum conditions. In a similar way, Angus et al. [22] confirmed that modern varieties of barley, with more or less vertical spatial arrangement of their leaves, have to be cultivated at very high densities, either by high sowing rate or by producing a large number of tillers.

In fact, the LAI of canopies with prevailing vertical orientation of leaves cannot be too high. From this point of view, the optimum LAI represents an equilibrium between two contrasting processes:

1. In a theoretical canopy with vertical leaves, the LAI could be so high that the irradiation of

leaves would approach irradiance compensation point. In this case, the energy utilization efficiency and canopy production would be the highest although the rate of photosynthesis per unit leaf area would be very low.

- Increase in LAI increases the construction costs (e.g., for carbon, nitrogen, and energy) of leaf formation. Such an increase is desirable only if the subsequent production of the constructed leaves is high enough to ensure high economic yield [23].

The fact that the daily course of irradiance varies must also be taken into consideration. The LAI cannot be too large, because at lower irradiance (cloudy days, during the early morning and late afternoon) the leaves of lower insertion could not be sufficiently irradiated and their loss of assimilate due to respiration could be higher than their gain in photosynthesis. Thus, the optimization must take into account the dynamics of plant growth and environmental conditions.

Finally, leaves of different insertion differ in their physiological properties [24]. The leaves adapt to their immediate environment. The adaptation irradiance, which is defined as an irradiance at which the radiation use efficiency of the leaf reaches its maximum, was calculated [25]. The adaptation irradiance of the upper leaves should be higher than that of the lower ones because of the light environment. In this case, an optimum canopy structure should ensure that irradiance of the leaves at various depths in the canopy would correspond to their appropriate adaptation irradiance. This concept extends the features of an optimum structure from one of light absorption and includes the physiological considerations.

G. THE ROLE OF RESPIRATION

Mitochondrial respiration decreases the amount of accumulated dry matter. However, this physiological

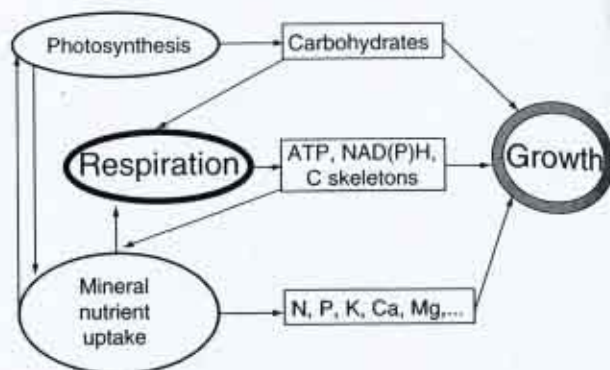


FIGURE 27.11 Schematic of the role of respiration in the provision of chemical energy (ATP), reducing equivalents (NAD(P)H), and carbon skeletons for both growth and nutrient uptake. The mutual interdependence of photosynthesis and nutrient uptake is also shown.

process cannot be considered negative for yield formation. Respiration is needed for the production of both various metabolites in the whole plant and of energy for growth and maintenance (Figure 27.11). There is no longer the tendency to suggest minimization of respiration in order to maximize production of plant organic matter. Growth efficiency is used to assess the efficiency with which the primary photosynthetic products are transformed into plant structures. Its value (ϵ) is calculated as the ratio between plant dry mass (W) and the total assimilates (P), i.e., $\epsilon = W/P$.

Growth efficiency is often expressed in percent. The value of growth efficiency varies from about 50% to 70% (Figure 27.12), meaning that about 30% to 50% of assimilates are respired in the processes of plant growth. Because of the higher energy demand for protein and lipid synthesis, it is not surprising that growth efficiency is negatively related to the content of these substances (Figure 27.13).

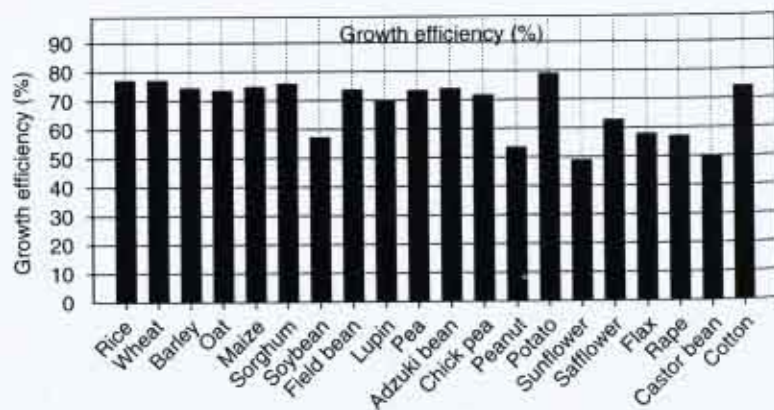


FIGURE 27.12 Growth efficiency expressed as the ratio of plant dry mass to plant dry mass + plant dry mass respired, in 20 crop species. Data from Ref. [26].

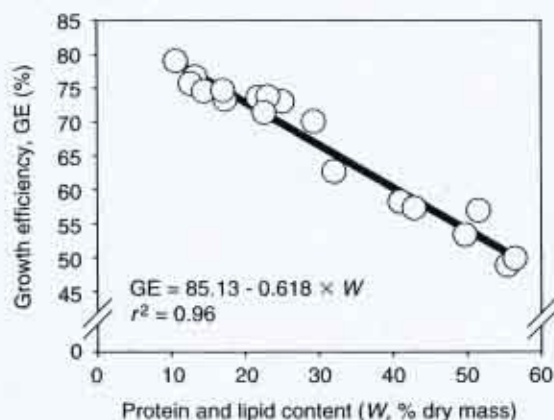


FIGURE 27.13 The effect of the protein and lipid content in plant dry matter (%) on the growth efficiency expressed as described in Figure 27.12. Data from Ref. [26].

In a more detailed analysis, it is useful to distinguish several components of respiration. Often the most important components are [27]:

1. Respiration for synthesis of new structures of a growing plant.
2. Maintenance respiration, which produces necessary energy and turnover of metabolites for a nongrowing plant, i.e., when no substance for growth is available or required.
3. Respiration involved in the active processes of mineral nutrition, especially nitrogen metabolism, and active uptake of ions by plant roots.
4. Respiration providing carbon skeletons, ATP and NAD(P)H for the assimilation of mineral nutrients, predominantly nitrate, into organic components.
5. Respiration needed for the active loading and unloading of carbohydrates and amino acids into the phloem.

It is possible to quantify the individual components of respiration in model situations, but more research is needed in order to understand energy costs of the individual metabolic processes enabling a plant to grow.

The relationships between photosynthesis and respiration in the formation of plant dry matter are illustrated in Figure 27.14. Increasing the quantum requirement for CO_2 fixation decreases dry matter production and increases the ratio between the rates of respiration and photosynthesis. Because of the relatively constant maintenance respiration, a decrease in radiation use efficiency decreases final plant dry matter production.

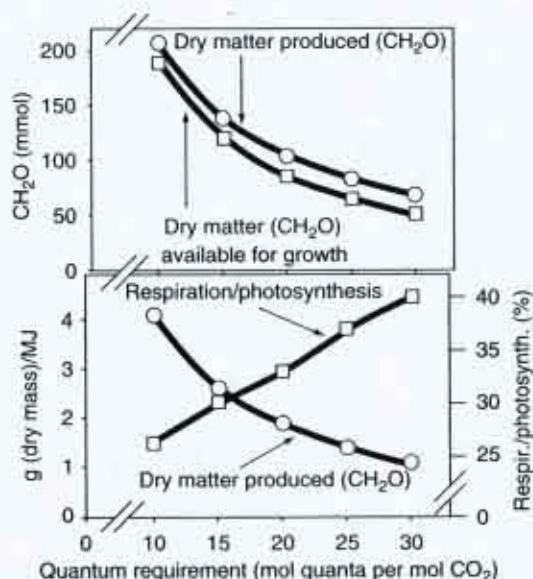


FIGURE 27.14 The effect of quantum requirement (top) on the amount (mmol) of assimilate produced and on the amount of assimilate (mmol) available for growth assuming that maintenance respiration consumes 18 mmol assimilate and (bottom) on the amount of plant dry mass produced per megajoule solar radiation and on the ratio of the rate of total respiration to the rate of gross respiration. Data from Ref. [12].

II. TRANSPORT AND DISTRIBUTION OF ASSIMILATES

Not only the economic yield but also the total dry matter production could be modified substantially by the allocation of assimilate. Simply, if a plant invests most of its new assimilates into leaf growth, then it enhances the growth of the whole much more than if the majority of assimilates were allocated to roots. Optimization of this distribution depends on the environment; where water or nutrients are scarce, the investment in roots will be of greater benefit. The importance of assimilate distribution was identified in the 1970s and the 1980s. Previously, it was believed that yields could be enhanced if photosynthetic production was increased by any means (e.g., Refs. [28,29]). However, in the 1970s the concept of the sink emerged [30,31]. Finally, it was recognized that, depending on the genotype and external conditions, the yield is determined by the interplay between the source and the sink. Most recently, the importance of translocation capacity has been identified.

A. PHOTOSYNTHESIS AND SINKS

Sinks could be defined as places within a plant (tissue, organ) where assimilates are consumed (growing

young leaves, tillers, buds) or accumulated (grains, bulbs, tubers). While the principles of the capacity to produce assimilates in the source (mostly leaves) have been fully understood (e.g., Ref. [32]), the mechanisms underlying sink attraction capacity or sink strength are still unknown. But it is well documented that sufficient sink size, expressed as number of growing or accumulating organs, is a necessary prerequisite for high yields. It has also been recognized that sinks are not only able to attract assimilates, but also alter the rate of photosynthesis [30,31] by mechanisms that are still poorly understood. For example, King et al. [30] found a decrease in the rate of photosynthesis of the main source (flag leaf blade), when the main sink (ear) was removed: experiments [33] confirmed this. On the other hand, a close relationship between sink size and rate of photosynthesis is not always observed (e.g., Ref. [34]). Mokronosov [31,35] explained the dependence of the rate of photosynthesis on the "need" of the plants. Relatively early, the effect of sink on the regulation of photosynthesis was ascribed to phytohormones [36,37].

At present, photosynthesis remains the center of attempts to enhance crop production. However, it is not just a problem of optimization of the external conditions or photosynthetic properties of the genotype. It is evident that understanding of the mechanisms of growth, morphogenesis, and organogenesis are decisive, not only because these processes are strongly dependent on production of assimilates but also because they regulate photosynthetic properties of the plant. Hence, photosynthesis, allocation, and accumulation of assimilates must be considered as integrated activities of the whole plant which determine the growth and productivity. From this point of view, the rate of photosynthesis under certain conditions could be better understood and subsequently regulated by manipulating seemingly independent processes of leaf growth, reproductive organ initiation, plant hormone regulation, etc.

B. ASSIMILATE DISTRIBUTION AND DRY MATTER PRODUCTION

In most crops, economic yield results from assimilate allocation into particular, mostly reproductive or storage, organs. It is obvious that the translocation capacity could alter the total amount of assimilate moving into the organs providing the economic yield (see next chapter). However, the model of assimilate allocation within a plant is also decisive for the total plant production. This is illustrated with a theoretical example as presented by Good and Bell [38].

Plant dry mass (W) may be separated into dry matter of assimilating organs (W_p) and the remaining

organs (W_s). The rate of production of the new biomass is expressed by the relative growth rate (RGR), which calculates the dry mass increase per unit plant dry mass and unit of time (t), i.e.

$$\text{RGR} = \frac{dW}{dt} \frac{1}{W}$$

Let us also define α as that ratio of the newly synthesized assimilate, which is used for the construction of photosynthesizing organs (W_p). Then the rate of dry mass increase in photosynthesizing organs is:

$$\frac{dW_p}{dt} = \alpha \cdot \text{RGR} \cdot W_p$$

By integrating this equation, an expression describing dry mass of the photosynthesizing organs (W_p) at any time (t) is obtained, i.e.,

$$W_p(t) = W_{p0} \cdot e^{\alpha t \cdot \text{RGR}}$$

where W_{p0} is the dry mass of the photosynthesizing organs at time $t = 0$.

Let us suppose that the total plant dry matter increase is distributed both into the production of new assimilating structures (W_p) and into the other (supporting, accumulating, etc.) organs and tissues (W_s). Then the ratio W_p/W_s is proportional to the ratio $\alpha/(1 - \alpha)$. It can be shown that:

$$W_p + W_s = \frac{1}{\alpha} W_{p0} e^{\alpha t \cdot \text{RGR}} - \frac{1 - \alpha}{\alpha} W_{p0}$$

Figure 27.15 illustrates this relationship. It is evident that the total plant dry mass depends not only on the rate of photosynthesis, in this example represented by RGR, but also on the dry matter allocation (α). Any factor decreasing the investment of newly synthesized assimilates into photosynthetic organs also decreases the potential increase in the total plant dry matter although the rate of photosynthesis remains constant. The importance of dry matter partitioning increases with the increase in the assimilate production, as illustrated by the curves in the right-hand part of Figure 27.15.

Under nonlimiting conditions, the source production of assimilate corresponds to the sink capacity of the plant. This equilibrium is determined by unknown mechanisms, with which the sink endogenously regulates the longevity, size or activity of the source organs. Alterations of this equilibrium by both abiotic and biotic stresses could result in changes in importance of either source (nitrogen or water limitation, premature senescence, attack of pathogens) or sink

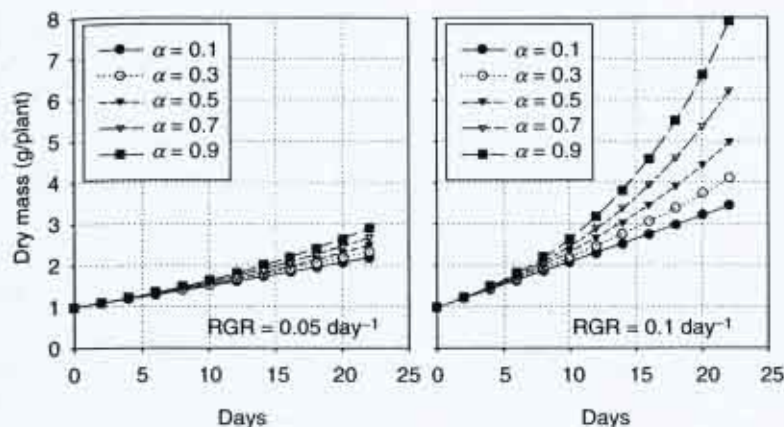


FIGURE 27.15 The effect on total plant dry mass of the way in which assimilates are partitioned between photosynthetic and non-photosynthetic organs. Relative growth rate (RGR) equals 0.05 day^{-1} (left) or 0.1 day^{-1} (right). See text for details.

(disturbance of flowering, embryo or tuber development). From the agronomic point of view, it is important to identify whether yield has been limited by source or sink limitation. In the former case, management should improve leaf development and activity, while in the latter case, stimulation of branching, tillering, and flower initiation could help.

C. ASSIMILATE TRANSLOCATION

In most crops, economic yield is represented by particular organs (grains, tubers), the dry matter of which has been accumulated via translocation from other organs. With increases in productivity, both source production and sink accumulation are enhanced to such a degree that translocation capacity between the source and sink could become limiting. This translocation capacity is determined by both size (cross-sectional area) of the phloem tissue and the speed of the translocation.

There is some evidence that the amount of translocated assimilates could be correlated with the cross-sectional area of the phloem. Using three wheat genotypes with potentially very high grain dry mass per ear has shown [39] (Figure 27.16) that grain dry mass per ear closely correlates with the number of sheath bundles, their cross-sectional area and cross-sectional area of phloem. Subsequently, using 26 winter wheat varieties, it was shown [40] (Figure 27.17) that the cross-sectional area of phloem of the last internode (the one below the ear) is a very useful indicator of the maximum translocation capacity of the genotypes. As illustrated in Figure 27.17, the values for some genotypes strongly deviate from the general regression, for all the data, of grain dry mass per ear on phloem cross-sectional area. If the limiting lines of all but one value have been calculated, a maximum translocation capacity was obtained which was not surpassed by any variety (with one exception). It is concluded that in varieties approaching the limiting

regression value, further yield enhancement is limited by the translocation capacity.

Obviously, cross-sectional area of translocation tissue need not be the best expression of the translocation capacity. However, it is a first attempt to quantify this plant characteristic. More sophisticated measurements are needed, which would characterize not only the size but also the actual ability to translocate assimilates. The main difficulty arises from the fact that the basic mechanism of phloem movement, as described long ago by Münch [41], is still poorly understood [42]. An understanding of the mechanism of phloem translocation is of prime importance, as is the establishment of quantitative parameters suitable for the assessment of the translocation ability [43].

D. HARVEST INDEX

The final result of dry matter production, translocation, distribution, and allocation is manifested in the HI. It may be determined at the end of the growing season and, in a certain way, it integrates the whole of the preceding period. This is its major advantage — it sums up the whole growing period — but also its disadvantage — it cannot identify changes during plant growth.

It is generally accepted that the increase in HI has been the main reason for the enormous increase in economic yields in developed agriculture in the last century. This increase has been mainly due to the reduction in crop height, which simultaneously increased lodging resistance and allowed an increase in the use of fertilizers [44]. For example [45], an old variety (Nürnberg from the year 1832) was compared with newly released spring barley varieties. Total dry matter production was comparable, but the HI of the modern varieties increased considerably. As shown by Wacker et al. [46], the dry matter distribution among leaves, stems, and roots did not change during the domestication of wheat and barley varieties.

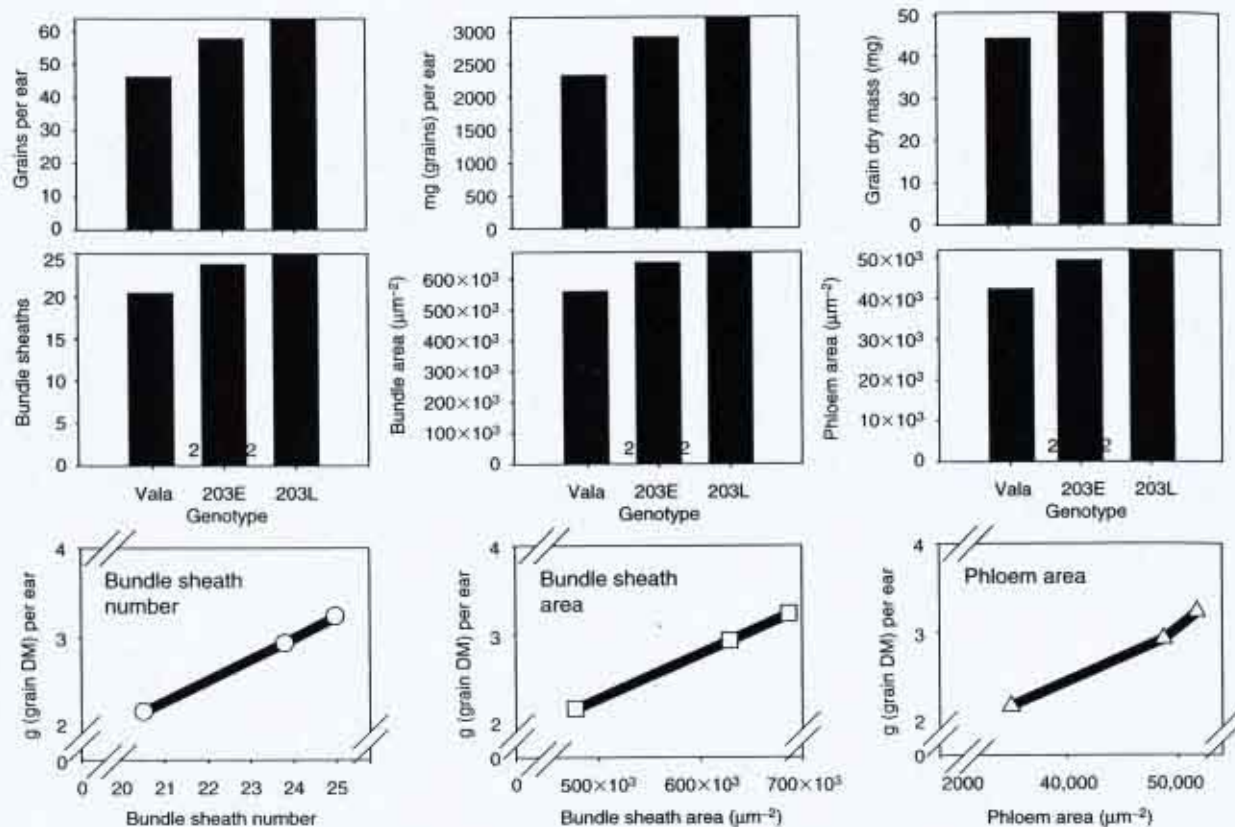


FIGURE 27.16 (Top) Productivity characteristics of three winter wheat genotypes: grain number per ear, grain dry mass per ear, and dry mass per grain. (Middle) Characteristics of the conducting tissue in the last internode (below the ear): number of bundle sheaths, cross-sectional area of the bundle sheaths and of the phloem. (Bottom) The dependence of the grain dry mass per ear on characteristics of the conducting tissue as given above. Data from Ref. [39].

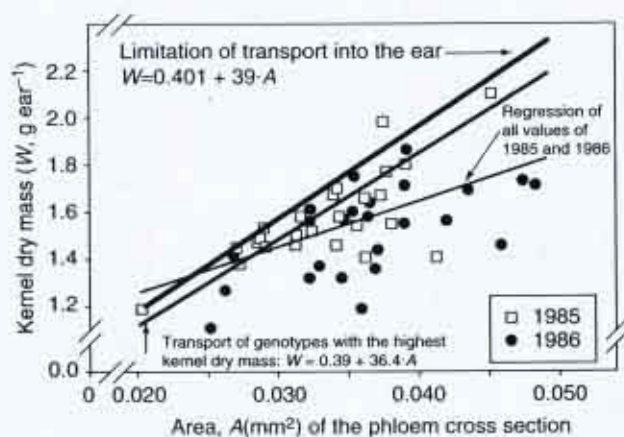


FIGURE 27.17 Dependence of the grain dry mass per ear on the cross-sectional area of the phloem in all bundle sheaths in the last internode of 26 winter wheat varieties cultivated in 1985 and 1986. For details see text. Data from Ref. [40].

Characteristic values of HI of various crops are given in Table 27.5. In some crops, more than 50% of the total plant dry matter is accumulated in the eco-

nomous yield. There is an upper limit for HI. In most cases, there are no useless organs present on a plant even if we take economic yield as the main criterion of usefulness. We could think of the possible reduction of all the unfertile tillers or florets in cereals. However, a plant has to produce roots, stem and leaves in order to be able to produce sufficient assimilates to be accumulated in the organs with most important economic yield. In cereals, the upper limit for HI could be in the range of about 0.6 to 0.65. In the individual varieties, its value will also depend on the longevity and photosynthetic activity of the assimilating tissue.

III. PLANT PHOTOSYNTHETIC CHARACTERISTICS AND YIELD IMPROVEMENT

Before agriculture was developed, natural food resources were able to support only several million people globally. At present, modern agriculture can support, reasonably well, the current 6 billion people, if economic and political conditions are suitable. And

TABLE 27.5
Characteristic Values of Harvests Index of Several
Crop Species Cultivated in the 1980s (simplified
from a review [44])

Plant Species	Harvest Index
Wheat (<i>Triticum aestivum</i>)	0.31–0.54
Barley (<i>Hordeum vulgare</i>)	0.33–0.63
Triticale	0.45–0.47
Rice (<i>Oriza sativa</i>)	0.35–0.62
Maize (<i>Zea mays</i>)	0.36–0.57
Soybean (<i>Glycine max</i>)	0.35–0.53
Chickpea (<i>Cicer arietinum</i>)	0.28–0.36
Cowpea (<i>Vigna unguiculata</i>)	0.15–0.64
Rape (<i>Brassica napus</i>)	0.22–0.38
Cassava (<i>Manihot esculenta</i>)	0.30–0.65
Potato (<i>Solanum tuberosum</i>)	0.47–0.62

in the future, agriculture must produce food for 8 to 12 billion humans.

Photosynthesis is no doubt the very basis of any economic yield. In the past, yields have been mainly increased by the change of assimilate allocation favoring the accumulation in the organs of prime economic importance. This increase in HI has been achieved predominantly by: (1) breeding and (2) fertilizer use. By emphasizing these two factors it is not the intention to negate the importance of other factors, such as plant protection, irrigation, soil management, etc. But it seems that the former two played a decisive role. Furthermore, they could be of prime importance in future yield improvement, which will be achieved by the enhancement of photosynthetic production and not only by the assimilate allocation.

A. HIGHLY PRODUCTIVE VARIETIES

The discovery of the basic genetic laws by Mendel in the middle of the 19th century [47] enabled their application in crop selection in the first half of the last century. In the 1950s and the 1960s, the role of photosynthesis in yield formation was elucidated and parameters of the optimum leaf area size and spatial distribution formulated. This enabled the unexpected rise of yields in the second half of the 20th century.

One of the most important achievements was the Green Revolution, with the use of new, short stem, and photoperiodically neutral wheat varieties selected by Borlaug (awarded the Nobel Prize in 1970), which subsequently increased yields in Mexico, India, Bangladesh, Pakistan, and other developing countries [48].

An important milestone reached by the tremendous yield increase in the 20th century was the selec-

tion of new rice varieties in the International Rice Research Institute in the Philippines. Their success is attested by the fact that in Asia, since 1962, the population increased from 1.6 to 3.7 billion and rice production increased by 170% [17,49].

Another achievement, which however, has not yet been fully exploited in breeding was the concept of ideotype described by Donald [50]. According to him, selection aimed only at removing defects in existing varieties or simply at yield improvement by any means. Donald emphasizes that it is time to adopt a new strategy, namely selection on the basis of an ideotype, i.e., "a form denoting an idea." Now, some 35 years after the Donald's definition of an ideotype, the time is here to use it both in research in the photosynthetic basis of yield formation, as well as in practical breeding. The concept required adaptation to include the interaction of plant with environment, and indeed the development of an ideotype has been achieved in several complex dynamic mathematical models, which could well be used as a starting point for the research into the quantitative parameters for breeding.

Donald [50] also described his idea of an ideotype of spring wheat, which was characterized as a single shoot (uniculum) plant. His idea has been criticized as unrealistic, because tillering is considered a necessity to fill in gaps in a canopy, caused, for example, by plant death. However, the time to appreciate Donald's unicum plant is approaching and modern wheats have very limited tillering, with production of yield mainly from the main stem ear. Combining such a variety with methods of precision agriculture could be very promising [51].

As regards the future possibilities for improvement of photosynthetic characteristics of more productive varieties, there are many, some that could be considered as ready for practical breeding or at least highly desirable for applied research are mentioned here.

1. Plant Morphology

Plants are characterized by their morphology, which includes number and size of individual organs, their longevity, activity, and spatial arrangement. Compared with varieties from some 50 years ago, current varieties are shorter, with smaller leaf blades, which are more vertically oriented. This trend will continue. More information is needed about optimum stature of the plant and the whole canopy best adapted to current local climate and soil conditions. Knowledge about canopy LAI and its time course should be better exploited with the aim of maximizing solar energy absorption by the leaves and increasing efficiency in photosynthesis.

Using the example of rice, the yield potential of the modern high-yielding varieties, cultivated under optimum conditions, is 10 ton ha⁻¹, which corresponds to about 20 ton dry matter ha⁻¹ with an HI of 0.5. The need to further increase food availability has stimulated researchers at the International Rice Research Institute (IRRI) to attempt to develop a new plant type, which would further increase total plant dry matter production by enhancing the rate of photosynthesis and which would have an HI of 0.6. Such varieties would have a yield potential of about 13 ton ha⁻¹. It is also expected that the use of these new plant type varieties could be used to produce hybrid rice, exceeding the best of its parents by about 25% and thus reaching a yield potential of 15 ton/ha. It is important to mention that among the most important attributes of the new plant type, the following have been included: lower tillering capacity with no unproductive tillers, short growth duration which is needed in order to get high values of HI, and dark green, thick, erect leaves [17,49,52].

2. Rate of Photosynthesis

Current techniques enable measurement of the rate of photosynthesis, its individual processes or spectral characteristics even under field conditions, and on hundreds of plants [53,54]. Varietal differences in the rate of photosynthesis have been known for a long time [28,55]. Although this parameter depends on external conditions (irradiation, temperature, nutrient and water availability), selection could stimulate progress in total plant dry matter production [56].

3. Dependence of the Rate of Photosynthesis on CO₂ Concentration

The current CO₂ concentration (370 μmol mol⁻¹) exceeds that of the 19th century by about one third and the rise will continue. Remarkable variety differences have been found in the effect of enhanced CO₂ concentration on the rate of photosynthesis and especially on the plant dry matter production. As far as we are aware, no attempt has been described in the literature about the practical use of these differences.

4. Mathematical Modeling

Mathematical modeling has not been restricted to photosynthetic aspects of crop production, but has proved to be extremely useful in explaining photosynthesis at the organ, plant, and canopy level by incorporating biophysical and biochemical principles of energy and CO₂ absorption and assimilation.

Since the 1970s, mathematical modeling has been used both as a tool for integrating knowledge across several hierarchical levels of plant functioning and as a heuristic means to stimulate formulation, as well as testing, of new scientific hypothesis [2,57,58]. Mathematical modeling is the only means for the objective integration of the steadily growing knowledge of plant growth. Furthermore, only by combining scientific knowledge with management practices, will further progress in crop productivity be achieved. In a stimulating review [59], two major goals for extending modeling activity in the future were identified:

1. Heuristic role supporting further scientific activity aimed at facilitating decision making by farmers as well as education of students. The authors also emphasize that modeling will be needed in order to integrate crop and landscape management.
2. Simulation to enhance understanding of the genetic regulation of plant growth and crop improvement.

5. Introduction of C₄ Photosynthesis into C₃ Plants

The most productive and efficient crops — maize and sugar cane — have C₄ photosynthesis. With the advances in molecular genetics [60], attempts have been made to introduce C₄ photosynthesis into the less efficient C₃ plants (rice, wheat, etc.). The C₄ carboxylating enzyme phosphoenolpyruvate carboxylase has been successfully expressed in the C₃ plants [61–63], and in some plants not only higher rate of photosynthesis but also increased yield has been found [64,65]. Until recently, it has been argued that such an introduction of the C₄ photosynthesis into C₃ plants will be extremely difficult because of the special leaf anatomy ("Kranz" type) of C₄ plants. However, in CAM plants, practically the C₄ type of photosynthesis occurs in the same cells in which the two carboxylating reactions take place at different times — C₄ fixation at night and C₃ during the day. Furthermore, it has recently been found that some other species — not of the CAM type — exist, in which the typical C₄ photosynthesis takes place in the same cells [66,67]. Understanding of this type of one-cell-C₄ photosynthesis will further facilitate the possibility of genetically introducing the C₄ type of photosynthesis into C₃ plants of economic value [68].

This procedure has been hailed as the most promising breakthrough in enhancing the rate of dry matter production in the most important crops — rice and wheat. However, confirmation of such work is required. Also, even if achievable, an increase in the potential rate of photosynthesis need not be automat-

ically coupled with an increase in grain yield. C_4 photosynthesis is more energy demanding and its temperature optimum is higher than that of C_3 photosynthesis. Furthermore, with future increase in the atmospheric CO_2 concentration the photosynthetic predominance of the C_4 photosynthesis over C_3 type will decrease [69]. However, introduction of C_4 photosynthesis into C_3 plants would greatly increase the potential for selection of important crops with improved production.

6. Plant Biotechnology Potential

Modern plant biotechnology has provided new transgenic varieties grown on millions of hectares. They are mostly improved in their resistance to pathogens or herbicides. Some of the biotechnology achievements represent varieties with improved nutritional properties, as the well-known "golden rice" with enhanced content of provitamin A and several other [70–72]. However, the value of this is contested because of the large amounts of the grain that would be needed to provide for daily need. It is believed that the use of plants for pharmaceutical purposes will rise and could be a considerable part of agriculture activities in the next decades [73].

Considerable enhancement of yield from biotechnology alone is not to be expected in the near future [74]. Yield represents a very complex phenomenon, involving many metabolic processes in the source and sink organs as well as translocation of large amounts of sugars and amino acids over long distance. Plant metabolic engineering is far less understood than the genetic manipulation of only one or few genes, e.g., of herbicide resistance. It is extremely difficult to predict the effects of alteration of appropriate metabolic route in cells with thousands of metabolites, if only the concentration of one enzyme is modified by changing gene expression [75]. In the case of yield, not only thousands of metabolites in one cell, but also billions of cells within the organism have to be taken into account. This is not to negate the present and future role of biotechnologies [76,77]. But we fully agree with the statement of Morandini and Salamini [75] that classical "plant breeding will not be substituted in a few years by plant biotechnology, rather the two different approaches are — and will be — cooperating for years to come." And in this connection, the following quotation concerning the role of mathematical modeling in connecting plant breeding and functional genomics from Ref. [59] is of special importance: "This frontier provides a unique opportunity for crop modeling to play a significant role in enhancing the integration of molecular genetics with crop improvement whilst offering new intellectual

challenges to those who assemble logically constructed frameworks of how plant systems work." Present knowledge represents a very good starting point for such constructions [78,79].

7. Other Possibilities for Future Plant Use

There is a shortage of food in large parts of the globe (particularly with extreme environmental conditions) with many millions of people lacking adequate nutrition for growth and energy (and this becomes particularly acute in times of civil unrest). However, crop production will continue to be oriented not only toward producing food, but also toward production of animal feed, raw materials, and biomass for energy [80]. In any orientation of crop production, high rate of photosynthesis will always be a desirable trait [81]. The main differences will consist of dry matter allocation between individual organs. Maximizing solar energy utilization in photosynthetic CO_2 fixation will remain the ultimate goal.

This chapter was devoted to crop photosynthetic production, but it is worth mentioning the role of photosynthesis of algae, cultivation of which is very efficient and could play an important role in the production of food and feed as well as a non- CO_2 producing source of energy [82–84].

B. MINERAL NUTRIENTS

Mineral nutrients, and especially nitrogen, play an important role both in plant growth and crop productivity (Figure 27.18).

1. About half of the soluble nitrogen in the leaf is present in the main carboxylating enzyme — Rubisco, the content of which may reach 8 g m^{-2} [32,79]. There is much evidence that the rate of net photosynthesis is directly proportional to the content of N in the leaf [85] over a broad range of N content, with an upper limit. C_4 plants, which are more efficient in photosynthetic CO_2 assimilation than C_3 plants, also use N with higher efficiency, expressed as the amount of produced dry matter per unit nitrogen in the photosynthetic tissue [32].
2. In cereals, grains contain some 2% to 3% N per unit dry mass. Hence, removing a yield of about 5 tons grain per hectare each year means removal of some 100 to 150 kg nitrogen. There is no evidence that in the long term, high yields can be achieved without the use of the appropriate applications of fertilizers [86]. Although the Green Revolution was achieved predominantly by the use of new short-stem

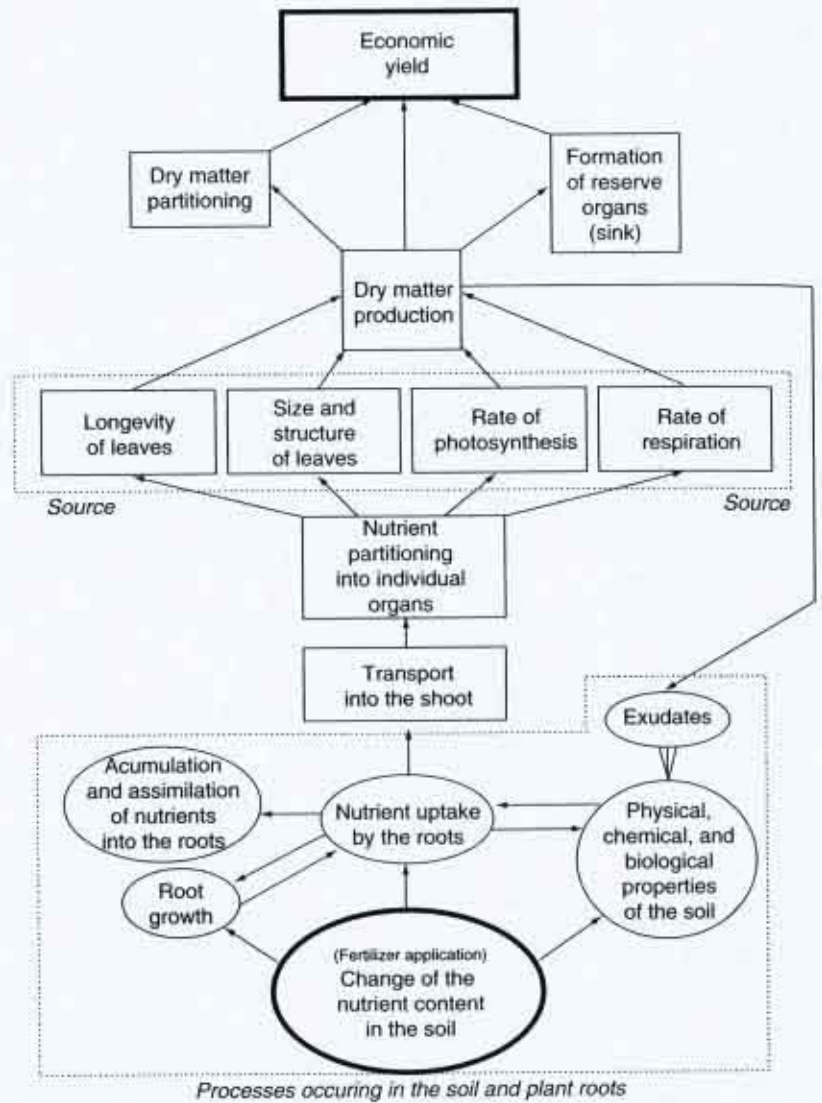


FIGURE 27.18 Schematic of the changes induced by the alteration of mineral nutrients in the soil (addition of fertilizers), leading to a sequence of structural and metabolic changes in the roots and shoots, resulting finally in changes to economic yield.

varieties, their successful cultivation was only possible by use of higher fertilization applications [87,88]. The content of N in the plant dry matter steadily decreases during growth period and this general course has been also successfully modeled (Figure 27.19). Such a decrease is well explained by the continuous accumulation of both structural (cellulose in cell walls) and nonstructural carbohydrates (starch).

1. Mineral Nutrients and Yield

Mineral nutrients do not affect yield directly (Figure 27.18). They may alter, directly (Figure 27.20):

1. duration of the vegetation period by delaying or accelerating senescence,
2. LAI by modifying the rate of appearance of individual leaves and by modifying their size,

3. rate of photosynthesis predominantly by an adequate supply of nitrogen and phosphorus,
4. allocation of assimilates by encouraging translocation into shoot and reproductive organs, if mineral nutrient and water supply is adequate.

An interplay of the four factors leads to the final plant dry matter, a proportion of which is the economic yield.

Uptake of mineral nutrients depends not only on nutrient availability in the soil, but also on their rate of absorption by the roots, which may be limited by assimilate availability (see Figure 27.11). Assimilates are needed as a source of energy (ATP) and reducing equivalents (NAD(P)H) for active ion uptake. Furthermore, carbon skeletons, produced mainly in the processes of plant respiration, are needed for the incorporation — assimilation — of the mineral nutrients into organic substances. Again,

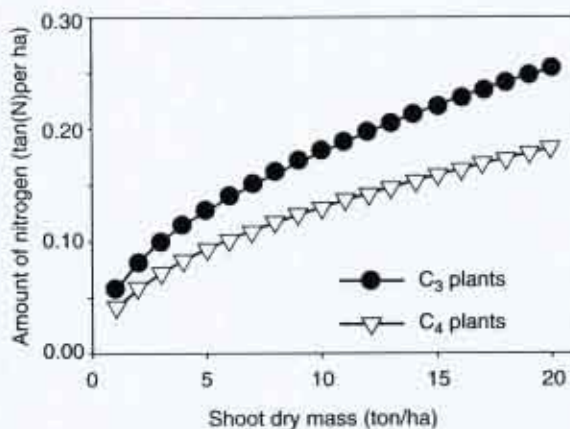
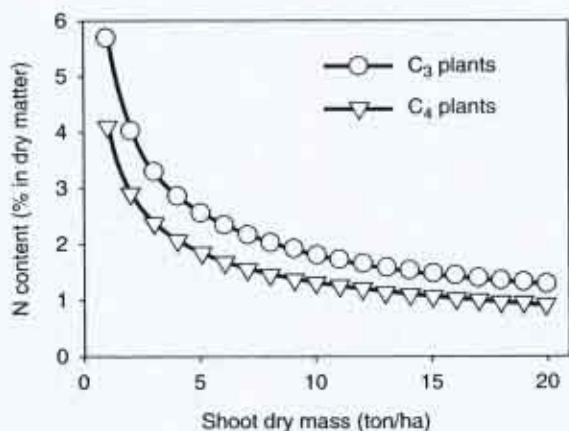


FIGURE 27.19 Dependence of the nitrogen content (left) and nitrogen amount (right) in dry matter on shoot dry mass during growth in C_3 and C_4 plants. Figures constructed with the use of equations from Ref. [89].

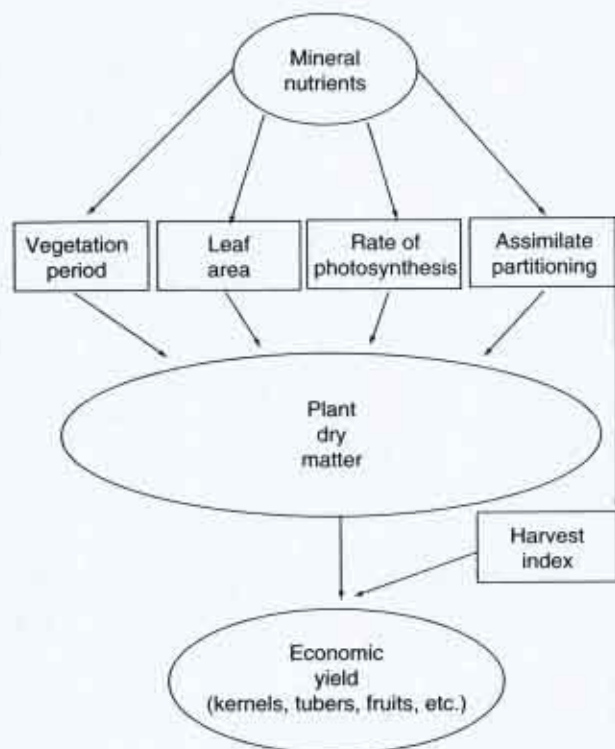


FIGURE 27.20 Schematic of the effect of mineral nutrients on parameters determining plant dry matter production and subsequently the economic yield.

nitrogen, which is taken up predominantly in the form of nitrate ions, requires large amount of energy for its reduction and subsequent incorporation into amino acids.

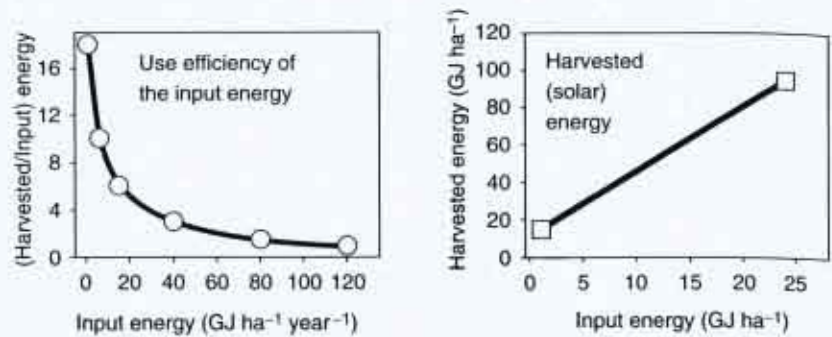
Unfortunately, fertilizer production requires huge amount of energy. In this respect, nitrogen fertilizers are of special importance. Generally, fertilizers repre-

sent the major part of the input energy, which is needed to support crop growth. This energy is provided by fossil fuel burning. The highest efficiency of input energy use is obtained at very low levels of this input energy, i.e., in primitive, extensive agriculture (Figure 27.21). However, high yields need considerable support in various forms (fertilizers, mechanization, soil management, pesticides) all of which require energy, although their efficiency of use decreases steadily with increasing input. This is another important reason why agriculture should shift from “oil assisted” to “solar powered” forms. In another words, future increase in crop yields should rely mostly on an enhanced rate of photosynthesis. To increase the photosynthetic rate without increasing capacity (more biochemical component of the photosynthetic system per unit leaf area) is essential if nutrient requirements are not to increase. This means that the components and the system as a whole must work more efficiently. This is a major challenge to the plant sciences, breeders, and genetic engineers.

2. Nitrogen and Photosynthesis

There is a general relationship between the rate of photosynthesis (yield, dry matter accumulation) and the content of mineral nutrients in the plant [90]. An increase in nutrient content in the region where it is deficient increases the rate of photosynthesis considerably [91]. Photosynthesis reaches a plateau with final decline when the nutrients reach such concentrations at which they become toxic. Because of the difficulty in determining the beginning of the saturating content of the nutrient, the so-called critical content or critical concentration is often taken as the value at which 90% of the maximum rate is reached [92].

FIGURE 27.21 The effect of input energy on the ratio of solar to input energy (left) and on the amount of harvested energy (right). Data for graph construction taken from Ref. [4].



Although the value of the optimum nutrient content in the crops is of prime importance for crop management [93], physiologically it is not a constant value, as it depends on radiation, CO₂ concentration, temperature, etc. Furthermore, it has been shown that the mineral nutrient content varies considerably, even in different tissue of a leaf [94]. Sufficient data and understanding of the biochemical system are available for making an attempt to construct a generally valid model, although many aspects, including the most important external and internal (age, leaf insertion) factors modifying the optimum content of nitrogen and other biogenic elements in leaves, plants, or canopies are poorly understood.

3. Nitrogen Allocation

Shoot and root growth are colimited by the availability of assimilate provided by the shoot and availability of nutrients and water supplied by the roots. Primarily, local carbon and nitrogen availability control dry matter distribution between the shoot and the leaf. A relative surplus of nitrogen within the plant will enhance dry matter allocation into the shoot because this organ is able to restore the balance between C and N. In contrast, with N limitation, roots assume priority as assimilate sinks because they can decrease the N/C imbalance. However, knowledge of how these imbalances are sensed and of the mechanisms regulating assimilate partitioning is required [95] within a framework allowing for interpretation.

Leaves represent the basic unit of photosynthesis of the whole plant or canopy. Leaf structure and heterogeneity of chemical components have been often studied in order to establish the optimum for maximizing the rate of CO₂ assimilation. Although the rate of photosynthesis is most often expressed per unit leaf area surface, it is also related to dry matter or leaf volume. Each of these relationships has some advantages and shortcomings. Leaf surface area is the most natural because it determines the amount of absorbed solar radiation as well as the diffusion of CO₂. On the other hand, leaf volume may better

express the internal (intercellular) leaf surface, which reflects the final diffusion step for the CO₂. Dry matter may reflect the amount of enzymes available for photosynthetic CO₂ fixation. For example, Garnier et al. [96] demonstrated that rate of photosynthesis per unit leaf area was positively correlated with leaf thickness and with the amount of mesophyll tissue. On the other hand, rate of photosynthesis per unit leaf volume negatively correlated with leaf thickness, but positively with leaf organic nitrogen. A positive correlation occurred between the rate of photosynthesis per unit leaf mass and the relative growth rate in several *Poa* species [97]. Such aspects should not be an impediment to developing effective models of crop photosynthesis.

Rubisco and other enzymes of CO₂ assimilation and carbohydrate metabolism, each containing nitrogen, have to be distributed within the leaf to make most effective use of the captured light energy. Considerable differences in irradiance occur over a leaf and the chloroplasts are spread along the mesophyll cell surface exposed to intercellular airspaces [98]. A high ratio of the mesophyll cell surface to volume thus facilitates diffusion of CO₂ to the carboxylation sites in the chloroplast stroma. Figure 27.22 demonstrates that high diffusion conductance for CO₂ does not necessarily correlate with large amounts of Rubisco (potentially large rates of CO₂ assimilation), and with large nitrogen allocation that is required. There is an optimum "cooperation" between nitrogen and carbon metabolism and light energy capture and use. At the top of the canopy, bright light and availability of CO₂ require photosynthetic systems of large capacity, whereas at the bottom, light and capacity are much smaller. This is the reason, as Sheehy et al. [99] concluded, that radiation absorption within a leaf declines exponentially with cumulative chlorophyll content measured from the irradiated surface. Hence, the light absorption profile is dominated by the distribution of pigments. Similarly, the distribution of nitrogen within the canopy is of comparable importance. More knowledge on the carbon and nitrogen metabolism and their relationships is needed [32]. In the near

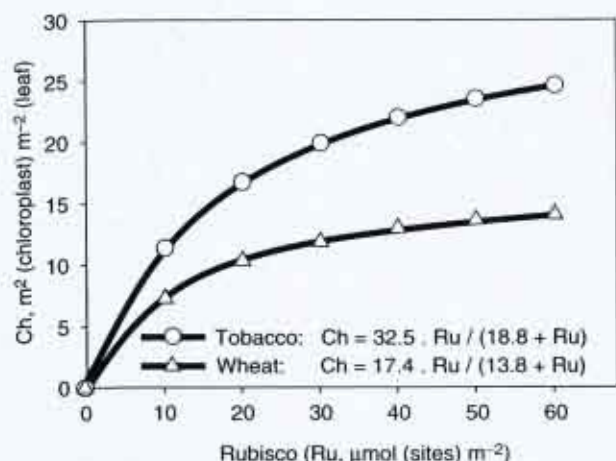


FIGURE 27.22 The relationships between chloroplast surface area exposed to intercellular air spaces per unit leaf area (Ch) and the amount of rubisco per unit leaf area (Ru) in tobacco and wheat. Graphs constructed with the use of equations taken from Ref. [98].

future, current use of empirical correlations between yield and mineral nutrient content in the plant needs to be replaced by the quantitative description of events starting with ion uptake by root cells, leading up to the appropriate modification of photosynthesis with subsequent assimilate partitioning.

IV. CONCLUSION

Innumerable experiments have been carried out for analyzing the effect of increasing amount of fertilizer on yield. Figure 27.23 illustrates the well-known concept of Mitscherlich. These types of experiment were needed in the early stages of fertilizer use between 1850 and 1950 and offered valuable advice to farmers, and stimulation to research. It was soon realized, however, that considerable differences could exist between the amount of nutrients in the soil and in the plant itself. Hence, by the middle of the 20th century, much attention was paid toward establishing suitable criteria for the assessment of nutritional status to achieve an appropriate crop canopy [100]. At the same time, considerable progress has been made in the elucidation of both photosynthetic carbon fixation and nutrient assimilation. Biophysical, biochemical, and physiological principles of photosynthesis have already enabled agricultural scientists to construct mechanistic models describing the effects of the main climatic factors on canopy photosynthesis. However, similar progress has not been made in understanding the mechanisms of absorption and assimilation of mineral nutrients. This field of plant biology is just beginning to be studied in detail.

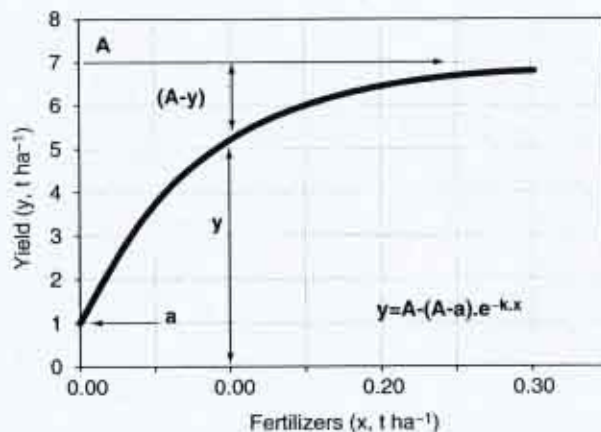


FIGURE 27.23 Illustration of the Mitscherlich equation (in the figure) expressing the dependence of yield on applied fertilizers. Explanation of symbols is given in the figure.

However, taking the formation of economic yield into consideration, even good knowledge of both carbon and nitrogen metabolism will not be sufficient to replace — within a realistic time frame — Mitscherlich's equation with a mechanistic model of crop growth and yield. Individual yield components (e.g., ear number, grains per year, grain dry mass) are established at various times during crop development (tillering and tiller death, flowering, grain set, and filling). Each of these components depends on both genetic determination and on environmental factors, including weather and soil conditions, determining nutrient and water supply. The interplay between carbon and nitrogen metabolism represents the fundamental process of dry matter production. Its understanding will enhance not only our ability to describe plant growth, but also offer valuable hints for crop management. Nevertheless, mechanisms controlling dry matter partitioning within plants, as well as all the processes of morphogenesis and developmental regulation, also await improved understanding. In summary, we repeat from Ref. [32]: "The processes involved in crop production are very complex and multilayered, ranging from the molecular to the whole organism, and environmental factors affect all levels of organization."

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