CHAPTER 8

The Possible Effects of Increased CO_2 on Photosynthesis

J. GOUDRIAAN and G.L. AJTAY

ABSTRACT

Photosynthesis is considered in relation to CO_2 and other plant growth factors. It can be shown that plant production is more limited by shortages in water and nutrients than by atmospheric CO_2, except under optimal plant growth conditions, such as are achieved in greenhouses. It is of note, however, that CO_2 enrichment can directly increase plant production by an improved water use efficiency. The semi-annual variation in the atmospheric CO_2 content is not affected by its global rising trend, and thus independently confirms the secondary role of CO_2 in photosynthesis and plant production.

8.1 INTRODUCTION

In this contribution, we will consider the primary productivity in relation to the carbon cycle and to the increasing CO_2 concentration in the atmosphere. All animal and human life depends on the ability of plants to form organic material out of water, CO_2, nitrogen, and mineral nutrients by utilizing radiant energy. This process is called photosynthesis and constitutes the primary production. The organic matter produced is partly used for maintenance of life processes in the plants themselves (respiration). Figure 8.1 shows the main flows and states of carbon that occur in an ecosystem. The net primary production contributes to the living biomass, which is decreased by grazing, diseases, and harvesting, and by transition to dead organic matter. Most of the dead organic matter is decomposed in the course of time.

The questions to be dealt with concern the influence of increasing atmospheric CO_2 on the net primary productivity and, subsequently, on the amounts of living and dead biomass. It is useful to distinguish between natural and agricultural ecosystems. Agriculture is a human activity with the explicit goal of harvesting the produced organic matter. Therefore, no accumulation of organic matter may be expected in agricultural ecosystems, even if production increases. In natural ecosystems, accumulation depends on the rate of decomposition. We will restrict our attention to the net primary production.

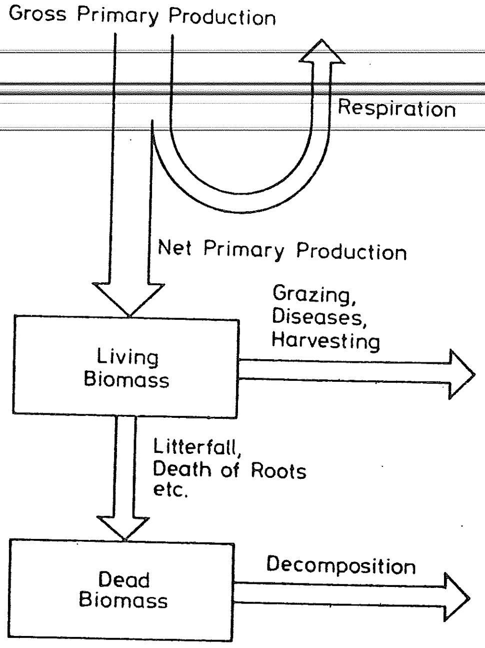

Figure 8.1 Scheme of the main flows (arrows) and states (rectangles) of carbon that occur in an ecosystem

For a more extensive and detailed review of the subject discussed here, the reader is referred to Larcher (1973) and to Cooper (1975).

8.2 THE BASIS OF NET PRIMARY PRODUCTIVITY

The production of organic plant material is based on the formation of glucose out of water and carbon dioxide under the action of light. In terrestrial plants, water vapour inevitably escapes when the plant takes up carbon dioxide from the air. When the plant loses too much water and is threatened by drought, it usually reacts by closing the stomatal openings, so that both water loss and CO_2 assimilation are reduced. Hence, water may be a limiting factor for net primary productivity (Figure 8.2).

The first product of photosynthesis, glucose, is converted to other plant material, such as starch, cellulose, lignin, fat, and proteins. Formation of proteins requires nutrients such as nitrogen, phosphate, and potassium. These plant nutrients are usually taken up from the soil by the roots. Lack of nutrients limits protein formation and, ultimately, the photosynthetic activity of the plants. Temperature influences all life processes and is, therefore, a major factor in plant production.

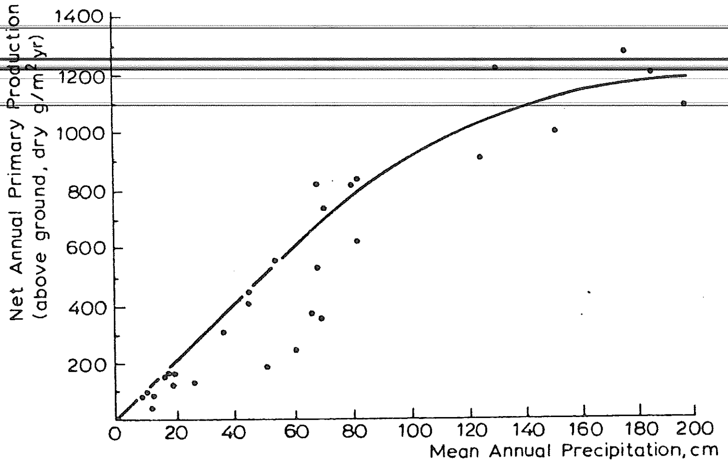

Figure 8.2 Annual NPP and annual precipitation. Data from various sources (Whittaker, 1970. Reproduced by permission of the Macmillan Publishing Co. Inc., New York)

The response of plants to their environment depends on internal factors and varies from species to species. Fortunately, most species are sufficiently alike, especially in agriculture, to allow general statements. For some purposes, grouping of species is necessary.

8.3 PLANT SPECIES

Two important groups of plants can be distinguished according to their photosynthetic performance, the C_3 and C_4 plants. The names derive from intermediate products in the biochemical pathway of carbon fixation. Some characteristics of C_3 and C_4 plants are given in Table 8.1. Details on the biochemical pathways can be found in Devlin and Barker (1971), but here the main interest concerns the differences in the net CO_2 assimilation rate. C_4 plants have a considerably higher optimum temperature than C_3 plants, so that it is not surprising to find them mainly in warm regions. Table 8.2 lists representative C_3 and

Table 8.1 Some characteristics of C_3 and C_4 plants

	C_3	C_4
CO_2 assimilation rate in high light	2–4 g $CO_2/m^2 h$	4–7 g $CO_2/m^2 h$
Temperature optimum	20–25 °C	30–35 °C
CO_2 compensation point in high light	50 ppm	10 ppm
Photorespiration	present	not present

Table 8.2 List of some C_3 and C_4 plants

C_3 plants	C_4 plants
Hordeae (wheat, barley, rye)	*Chlorideae* (Rhodes grass)
Aveneae (oats)	*Maydeae* (maize)
Agrostideae	*Andropogoneae* (sorghum)
Festuceae	*Eragrosteae*
Oryzoideae (rice)	*Saccarum* (sugar-cane)
Atriplex patula	*Spartina*
Beta (sugar-beet)	*Atriplex rosea*
All leguminous species	
Helianthus (sunflower)	
Gossypium (cotton)	
Solanum (potato, tomato)	

C_4 plants. Many tropical grasses are among the C_4 plants, while almost all plants from the temperate regions are C_3 plants. Other factors being optimal, the net CO_2 assimilation of a single leaf increases at first linearly with the intensity of the photosynthetically active radiation (PAR) which, for all practical purposes, coincides with the visible part of the spectrum. When light intensity is further increased, the CO_2 assimilation levels off because of saturation with light (Figure 8.3). In the dark, the net rate of CO_2 fixation is negative, due to respiration. At the so-called light compensation point, net CO_2 assimilation is zero. A similar curve can be found for the response of net assimilation to CO_2 concentration in the ambient air, provided light intensity is high enough. C_3 and C_4 plants show a marked

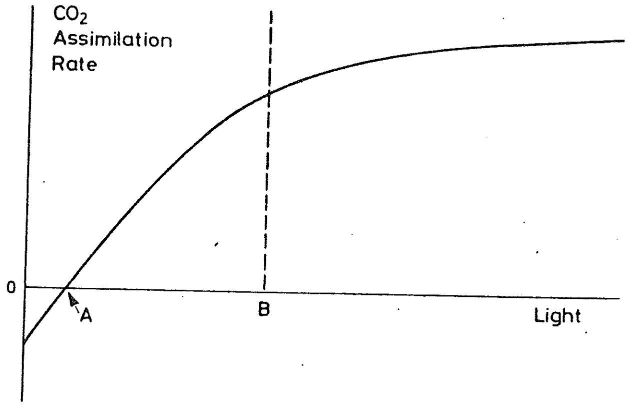

Figure 8.3 The usual dependence of the CO_2 assimilation per leaf area of an individual leaf on the absorbed photosynthetically active radiation. Point A denotes the light compensation point and B indicates, roughly, where saturation with light occurs

difference in CO_2 compensation point. The higher values in C_3 plants are caused by photorespiration: an additional respiratory process induced by the combined action of light and oxygen. At low O_2 concentrations, the photorespiration disappears and the C_3 plants have the same CO_2 compensation point as C_4 plants. Apparently in C_3 plants, O_2 and CO_2 have a competitive behaviour towards the carboxylating enzyme system. In C_4 plants, oxygen does not have such an effect.

There exists a third group of plants with the so-called Crassulacean acid metabolism (CAM plants). These plants are able to absorb CO_2 during the night and to fix it to organic acids. During daytime, the stored carbon dioxide is reduced photosynthetically. The stomata are open during the night and can be closed in daytime, so that water loss is very low in relation to dry matter production. A large storage capacity of carbon dioxide requires fleshy leaves. Therefore, this type of metabolism is limited to succulent plants such as *Crassulaceae*. The ecological advantage of CAM in dry regions is obvious, but in terms of dry matter production the quantitative importance is negligible. The pineapple is the only CAM plant used in agriculture.

8.4 POTENTIAL NET PRIMARY PRODUCTIVITY

The potential net primary productivity depends on which variables are assumed to be optimal. Man's ability to change climatic conditions is very limited. Therefore, it is standard procedure to take the climatic conditions for given external parameters and only to assume an optimal water and nutrient supply. Under such conditions, crop production is still limited by incoming radiation, by suboptimal temperatures, and by the length of the vegetation period. Under high light conditions, the leaves become saturated at a higher level in C_4 plants than in C_3 plants. De Wit (1965) calculated a potential gross rate of dry matter production of 37.5 g per m^2 ground per day for a sunny day in June in the northern hemisphere. This calculation was made for a C_3 plant. For C_4 plants the result would probably be 30–50% higher. If respiratory losses are taken into account, the potential net dry matter production per m^2 ground per day is 20 g for C_3 and about 28 g for C_4 plants. The effective growing period in northwestern Europe is about 100 days, so that the potential annual net primary production is about 2000 g/m^2. In the tropics, the growing season covers the whole year. Due to higher temperatures respiratory losses are larger, so that C_4 plants there produce about 20 g/m^2 day at most, the same level as for C^3 plants in temperate regions. Potential net annual primary productivity in the tropics, therefore, amounts to 7000 g dry matter/m^2. These potential yields have been experimentally achieved (Loomis and Gerakis, 1975), with water and nutrients optimally available and in disease-free cultures.

Under farming conditions, and especially in natural vegetations, the circumstances are not as favourable, since one or more factors are suboptimal. Although interactions between different factors must sometimes be taken into account, the

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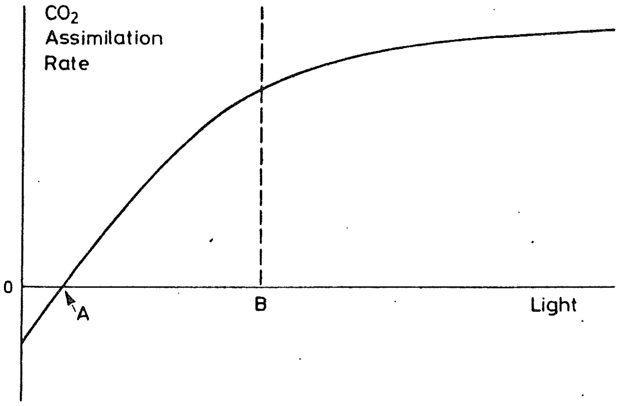

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Under farming conditions, and especially in natural vegetations, the circumstances are not as favourable, since one or more factors are suboptimal. Although interactions between different factors must sometimes be taken into account, the most fruitful way to analyse deviations from the potential productivity is to consider only one factor as limiting. After this particular factor has been improved, another one may become limiting. Some possible limiting factors will be discussed in some detail.

8.5 LIMITING FACTORS

8.5.1 Shortage of Nutrients

If man does not harvest the produced organic material, it will return to the soil as fallen leaves, seeds, etc. During microbial decomposition, part of the nutrients will again become available to the plants. They are added to the quantities released by weathering of soil minerals and to those supplied by rain and microbial nitrogen fixation. Therefore, in mature ecosystems the net primary productivity may sometimes approach the potential NPP. However, nothing should then be harvested by man. In primitive agricultural systems, such as shifting cultivation, the stock of nutrients built up in the past is made available to a crop by forest burning. For the first few years, the crop is reasonably well supplied with nutrients, but the level soon declines through uptake and leaching. Without fertilizer application, the annual yield will reach a rather low equilibrium level, determined by the natural sources of nutrients.

The most important plant nutrients are nitrogen, phosphorus, and potassium (N, P, K), but other elements such as Ca, Mg, Fe, Cu, Mn are also required, the latter in smaller amounts. Deficiency of an element not only shows up in a characteristic symptom (Hambridge, 1949; Nátr, 1975), but it invariably reduces the net primary production. Each of the nutrients plays a role in specific processes. We will consider only nitrogen, because it is often limiting and the most suitable for calculations.

In rye grass, the minimum nitrogen content of living tissue is 1.6% (Alberda, 1965). In small grains, the minimum nitrogen content of straw is $\simeq$0.4% and of kernels $\simeq$ 1% (van Keulen, 1977), resulting in a minimum requirement of 14 g N per 1000 g grain (grain : straw = 1 : 1). The annual natural nitrogen supply (rain + microbial activity) is about 3 g N/m^2 year so that, without additional fertilizer application, grain productions greater than 200 g/m^2 year are seldom recorded. However, nitrogen fixation by leguminous species or by blue-green algae in paddy fields can increase this level by a factor 2 or 3. Without such additional fixation, nitrogen is the main limiting factor for natural production, even under semi-arid conditions (van Keulen, 1975).

8.5.2 Some Climatic Factors

Mean annual temperature and mean annual precipitation can be considered as factors that determine the type of natural vegetation (Etherington, 1975). The

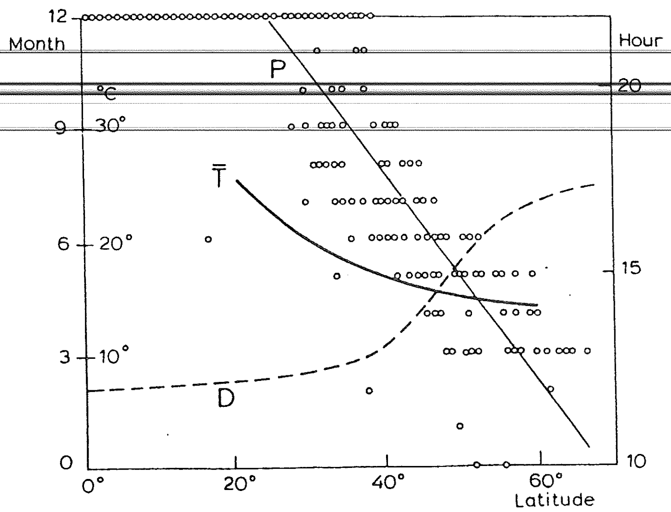


Figure 8.4 The length of the growing season (*P*) in months, the average temperature (*T*) during the growing season in °C, and the day length *D* in hours as a function of latitude (Larcher, 1973. Reproduced by permission of Eugen Ulmer GmbH and Co., Stuttgart)

decline in NPP with decreasing mean annual temperature is mainly due to a decrease in length of the growing season (Figure 8.4). The influence of temperature on the performance of a single species may not be taken as representative for its influence on net primary productivity as a whole. With changing climatic conditions, the species composition changes to such an extent that the net primary productivity is not limited by mean temperature, as long as its value is higher than 10 °C. Because of water shortage, the actual growing period of the vegetation may be shorter than the period permitted by temperature. The potential evapotranspiration during the summer months in the Netherlands is about 500 mm, whereas the average rainfall in this period is 300 mm. To permit unrestricted growth, 200 mm of water should, therefore, be stored in the soil from excess precipitation in winter. A clay or loam soil can retain this amount of water in the potential rooting zone, but not so sandy soils, where water shortage may occur in summer. Sometimes the water cannot be taken up, because growth and functioning of roots are prevented by anaerobic conditions. Paradoxically, such conditions occur in poorly drained soils, suffering from water surplus. Drainage of soils and a good supply of water are, therefore, extremely important for good agricultural production.

Water shortage builds up gradually, while it becomes more and more difficult for the plant to withdraw water from the soil. Some plants react by closing their stomata, but others do not. There is an important ecological difference between these two groups. Those that close their stomata are savers that wait for better times. The others are spenders that use the water as fast as they can, and hope that it will start raining in time or that they will have completed their life cycle by the time the water is finished. Still, there is no marked difference in the ratio of transpired water and dry matter formed between these types of plants. This ratio does decline with fertilization (Lof, 1976), because nitrogen increases dry matter production but not the transpiration rate.

Since water shortage often limits production, the relation between crop transpiration and crop production is a classical problem of agricultural science (Briggs and Shantz, 1913; de Wit, 1958). In northwestern Europe the transpiration and net production rates are approximately proportional to radiation (Figure 8.5). In semi-arid regions, were bright sunshine prevails, photosynthesis is saturated with light for a large part of the growing season. A unique relation between production and water use is obtained when the latter is divided by the free water evaporation (Figure 8.6). Different species use water with varying degrees of efficiency, in particular C_4 plants use water twice as efficiently as C_3 plants (de Wit and Alberda, 1961; Troughton, 1975). Typical ratios for the amount of transpired water per unit

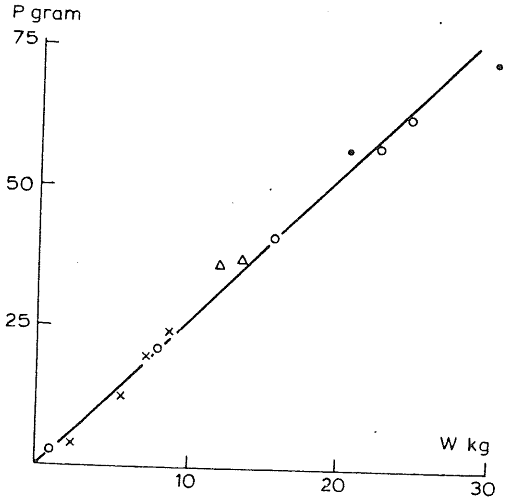


Figure 8.5 Measured relation between dry matter production (*P*) and total transpiration (*W*) of oats grown in containers. The experiments were made by various researchers in different years, but all in the Netherlands (from De Wit, 1958. Reproduced by permission of Pudoc, Center for Agricultural Publishing and Documentation, Wageningen, Netherlands)

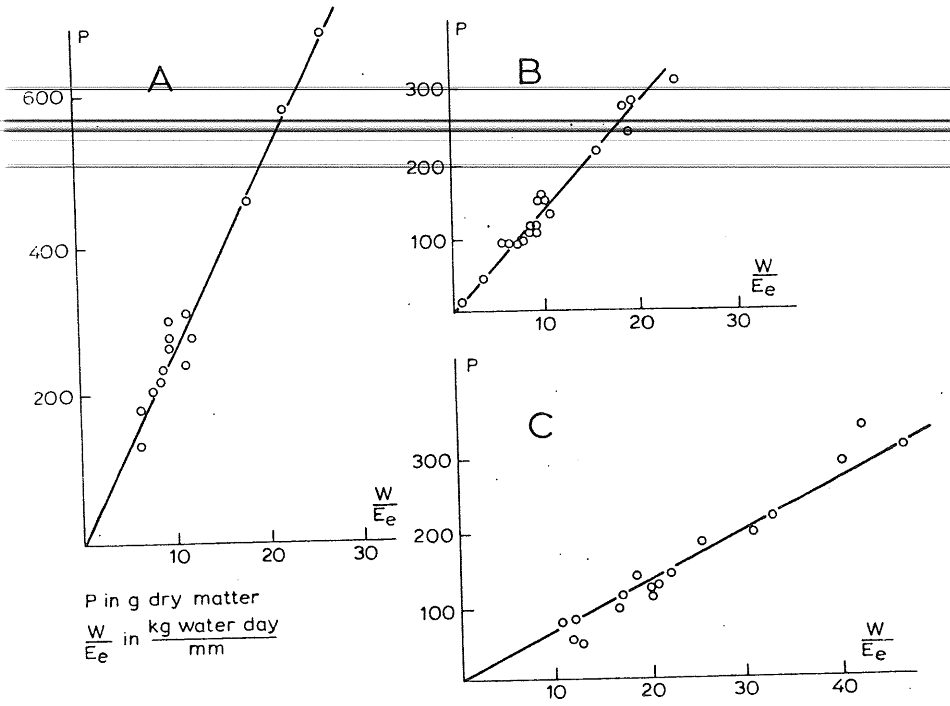


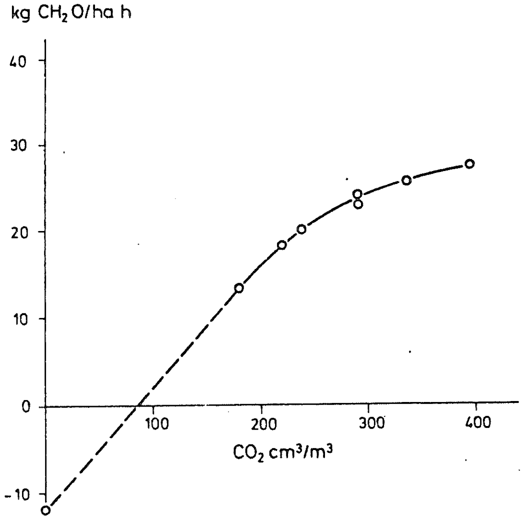
Figure 8.6 Measured relation between dry matter production (P) and the ratio of transpiration (W) and pan evaporation (E_e). The experiments were made by various researchers in different years, but all in dry and hot regions (the Great Plains) of the United States (from De Wit, 1958. Reproduced by permission of Pudoc, Center for Agricultural Publishing and Documentation, Wageningen, Netherlands.)

dry matter produced are 200 for C_4 plants and 400 for C_3 plants. Therefore, in regions with limited irrigation facilities, such as South America, Australia, and Africa, C_4 plants are more productive (Buringh *et al.*, 1975).

8.5.3 Carbon Dioxide

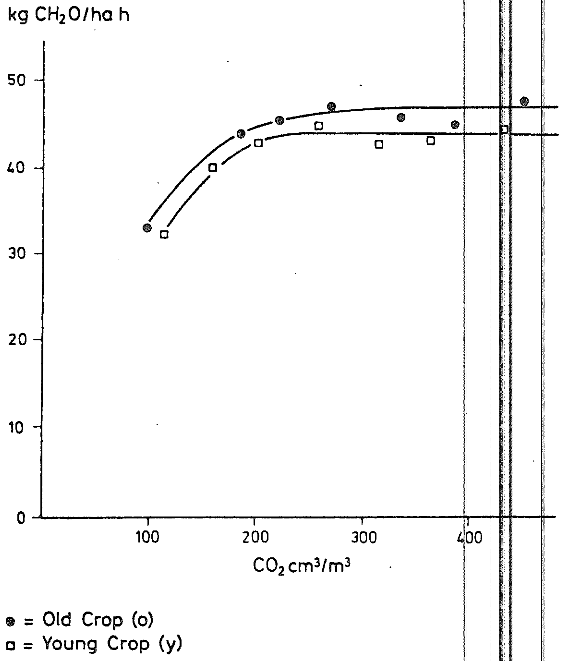
Measurements on individual leaves show that, in many cases, a CO_2 enrichment of the ambient external air increases the net assimilation rate at light saturation. In other circumstances, saturation with CO_2 occurs at 300 ppm, even under light saturation (Goudriaan and Van Laar, 1978; Gifford and Musgrave, 1970).

Measurements by an enclosure method (Louwerse and Eikhoudt, 1975) over a crop surface show for rye grass that CO_2 enrichment enhances the assimilation rate over the whole range of light intensities, but that for maize the assimilation is constant above 200 ppm (Figure 8.7, Alberda, 1977).



(a)

Figure 8.7 (a) The measured dependence of the CO_2 assimilation rate of a grass sward in the field on the CO_2 concentration of the ambient air under high light conditions (from Alberda, 1977. Reproduced by permission of Pudoc, Center for Agricultural Publishing and Documentation, Wageningen, Netherlands.)



(b)

(b) The measured dependence of the CO_2 assimilation rate of a maize crop in the field on the CO_2 concentration of the ambient air under high light conditions for an old and a young crop (from Alberda, 1977. Reproduced by permission of Pudoc, Center for Agricultural Publishing and Documentation, Wageningen, Netherlands.)

This saturation effect is probably caused by CO_2-induced stomatal closure. In a number of plant species, stomatal conductance is regulated in such a way that the CO_2 concentration in the substomatal cavity is approximately constant. When the CO_2 assimilation rate rises with increasing radiation intensity, the stomata open up further to compensate the CO_2 depletion in the cavity below them. The level at which the CO_2 concentration inside the substomatal cavity is maintained is about 120 ppm in C_4 plants and about 220 ppm in some C_3 plants. Hence, the C_4 plants maintain a CO_2 concentration gradient across the stomata that is twice as large as in C_3 plants. The ratio between CO_2 uptake and water vapour loss or the efficiency of water use is, therefore, twice as large in C_4 plants than in C_3 plants.

Sometimes plants simply keep their stomata wide open and do not react to increasing CO_2 with closure. Goudriaan and Van Laar (1978) recorded such behaviour for the sunflower. Absence of this CO_2-steered regulation of stomatal resistance results in higher transpiration coefficients (than with regulation), but also in increased CO_2 assimilation rates at high light intensities. According to Raschke (1975), CO_2 regulation of stomatal resistance may be induced by waterstress. Therefore, it may well be that the same species of sunflower does show regulation under field conditions where waterstress is almost inevitable. Considering the success of CO_2 enrichment in the production of crops such as cucumber and lettuce in glasshouses, it is likely that such crops do not close their stomata (water and nutrient supply is optimal in glasshouses). Moreover, the experience with CO_2 enrichment in glasshouses may not be extrapolated to field conditions because in glasshouses without CO_2 fertilization, the CO_2 concentration in the air may drop to values as low as 100 ppm. As mainly C_3 plants are grown in glasshouses, it is not surprising that such low values limit production. In the field, CO_2 is usually not depleted to less than 250 ppm, because of the much better turbulent exchange with the atmosphere.

Carbon dioxide uptake is not the same as photosynthesis. We have already seen that in CAM plants these processes are separated in time. Under the influence of light, the energy-carrying substance ATP is formed. ATP can also be used for the reduction of nitrate instead of CO_2. Nitrate must be reduced for the formation of proteins. Normally plants obtain the energy for this reaction by burning glucose (= respiration) both during the day and the night. When CO_2 diffusion is limiting assimilation, the surplus of light energy can be used for nitrate reduction, thus diminishing future respiration. Penning de Vries (1973) estimated that in terms of energy, photosynthetic nitrate reduction may amount to 20% of the photosynthetic CO_2 assimilation. Therefore, the daily total of dry matter formation is less limited by CO_2 than suggested by the CO_2 assimilation response.

8.6 CONCLUSION

Shortage of nutrients, unfavourable climatic factors, or shortage of CO_2 may all limit NPP. Mostly the nutrients, especially nitrogen and water, are exhausted before the end of the growing season, both in farming conditions and in natural ecosystems. Since the total amount of available nutrients and water is not raised by increased CO_2, the total seasonal NPP is not increased either, even if a higher rate might temporarily be obtained. Only in highly developed agriculture is nutrient shortage prevented throughout the growing season, and might CO_2 increase have a beneficial effect. Therefore, on a global scale, CO_2 increase will not appreciably affect the net CO_2 assimilation. An independent confirmation of this conclusion is provided by the measurement of semi-annual variation of the atmospheric CO_2 content. Hall *et al.* (1975) showed that there is no evidence for changes in the basic pattern of net CO_2 assimilation in the northern hemisphere.

When water shortage, rather than nutrient shortage, limits agricultural production, CO_2 increase may have an indirect beneficial effect through a more efficient use of water. Other indirect, but almost unpredictable, effects may be exerted through CO_2-induced climatic changes, such as increase in temperature and changes in rainfall patterns. Such effects are, however, rather speculative. On the whole, CO_2 is a secondary factor for NPP, and only highly developed agriculture may be able to benefit from its increase. In natural terrestrial ecosystems, nutrients and water remain the limiting factors for NPP.

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