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PHOTOSYNTHESIS, CO_2 AND PLANT PRODUCTION

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INTRODUCTION

Agricultural production can be increased through better plant characteristics obtained either through breeding or through better growing conditions, both in the soil and above ground. In the chain of events necessary for plant growth, photosynthesis stands at the beginning as the primary conversion of light energy to chemical energy stored in organic substances. This paper deals with the influence of photosynthetic performance on the eventual dry matter production of plants. The approach used is mechanistic and quantitative, and, because the number of interacting factors is large, a simulation method is used. Our simulation model is essentially BACROS (de Wit et al., 1978), modified to the present (1983) version in a number of ways indicated below. We consider characteristics of C_3 plants only.

The main emphasis of this paper is on the effect of atmospheric CO_2 concentration on dry matter yield and water consumption. The results of our simulations indicate that this relation can be described by a simple response function, and we compare simulations with empirical results. The part of the effect of CO_2 concentration that is mediated by photosynthesis can be compared with the effects of internal changes in photosynthetic properties. Some reasons for differences will be discussed.

A potentially high rate of photosynthesis is not sufficient for a high plant growth rate. It is equally important that this rate is realised and that the photosynthetic products are used in the desired fashion. In the case of a sub-optimal nutrient supply, growth is impaired and then the rate of crop photosynthesis will inevitably fall. Although we consider only situations of optimum supply of nutrients and water, our results are relevant to poorer conditions because they define the potential demand for other growth factors.

PHOTOSYNTHESIS AT THE LEAF LEVEL

Photosynthesis

The properties of leaves that affect photosynthetic performance can be separated into those that describe the light reactions, and those that describe the dark reactions. We use a single parameter for the light reactions: the quantum use efficiency ε_o (mol CO_2 E^{-1} photosynthetically active radiation (PAR)). According to Farquhar and Von Caemmerer (1981), a minimum of 8.4 photons are required for the reduction of 1 molecule of CO_2. At the average spectral composition of solar radiation this can be converted into 25 x 10^{-9} kg CO_2 J^{-1} (PAR). However, measured maximum values of ε have rarely exceeded 17 x 10^{-9} kg CO_2 J^{-1} (12 Einstein per mole), probably because of absorption in non-chlorophyllic tissue and of some other energy-requiring processes. Therefore we set ε_o at 17 x 10^{-9} kg CO_2 J^{-1} bearing in mind that this efficiency is further reduced by photorespiration.

We use three parameters to describe the dark reactions.

The carboxylation conductance g_x (m s^{-1}). This parameter can be used directly to describe the maximum rate of assimilation, F_m, under low CO_2 levels and sufficient irradiance. Then the assimilation rate is proportional to the CO_2 level, and a resistance scheme can be used (Fig. 1). Between the outside air and the chloroplast, two resistances of a physical nature can be distinguished, the leaf boundary layer resistance, r_b, and the stomatal resistance, r_s, and one resistance of a chemical nature, the carboxylation resistance, r_x. Under optimum water supply, the stomatal resistance drops to about 130 s m^{-1} for H_2O, equivalent to about 200 s m^{-1} for CO_2. The carboxylation resistance is about 250 s m^{-1}. With a typical leaf boundary layer resistance of about 20 s m^{-1}, the CO_2 use efficiency is the conductance of the total resistance chain and equals about 1/470 m s^{-1}. With a CO_2 concentration difference of 500 mg CO_2 m^{-3} (about 270 ppmv) between ambient air and the chloroplast, the calculated maximum assimilation rate is 1.06 mg CO_2 m^{-2} s^{-1} (38 kg CO_2 ha^{-1} h^{-1}). In the BACROS model, r_s is computed from the water status of the the crop and r_b is computed on the basis of micrometeorological considerations (Goudriaan, 1977). The carboxylation conductance, g_x, is made dependent on temperature by a multiplication factor that increases linearly from zero to unity between temperatures 5 and

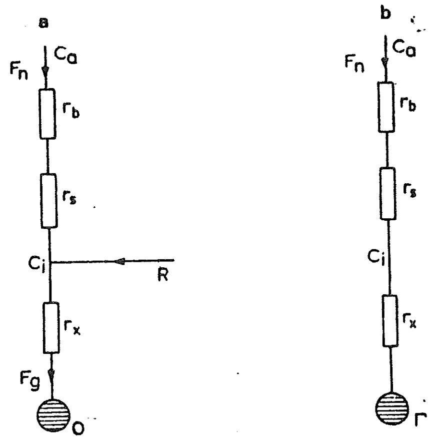

Fig. 1. Two equivalent resistance schemes for the CO_2 assimilation of a leaf under high radiation and low CO_2 concentration. The respiration rate, R, (left) can be taken into account by an apparent CO_2 concentration in the chloroplast at the compensation concentration, Γ (right). C_a is the ambient CO_2 concentration; r_b the boundary layer resistance; r_s the stomatal resistance, r_x the carboxylation resistance, C_i the sub-stomatal CO_2 concentration, F_g the rate of gross photosynthesis, and F_n the rate of net photosynthesis.

13°C. Moreover, if the plant does not have sufficient sinks, a reserve level rising above 20% on a dry weight basis will gradually diminish the carboxylation conductance to zero when reserves reach 25%. The justification for this procedure is that reserve levels higher than 25% on a dry matter basis are hardly ever found. An alternative possibility would be for additional respiration to remove surplus assimilates (Lambers, 1982); we do not include such respiration.

The CO_2 compensation point Γ ($mg\ m^{-3}$). This is the CO_2 concentration at the bottom of the resistance chain (Fig. 1). The maximum assimilation rate, F_m, is linearly related to the ambient CO_2 concentration, C_a, with an intercept at C_a = Γ. It appears that the value of Γ is almost entirely determined by photorespiration, and is equal to about 100 mg CO_2 m^{-3} at 20°C. Measurements show a strong rise with temperature (Bykov et al., 1981) and with water stress (Lawlor and Pearlman, 1981).

Dark respiration rate R_d($mg\ m^{-2}\ s^{-1}$). The dissimilation rate in the dark, R_d, per unit leaf area is estimated as the maintenance respiration of the whole crop multiplied by the leaf weight ratio and divided by the leaf area, to give a value of about 1 kg CO_2 ha^{-1} h^{-1}

at 20°C. Theoretically, this process may contribute to the value of the CO_2 compensation point by an amount equal to R_d times r_x (about 5 mg CO_2 m^{-3} or 3 ppmv). According to Peisker et al. (1983) this respiration is largely superseded in the light by direct ATP consumption, but this conclusion is disputed by Azcon-Bieto and Osmond (1983). The difference between these two possibilities is equivalent to a difference of 3 ppmv in value of the CO_2 compensation point. In view of the conflicting evidence we have chosen the simplest assumption and neglected the influence of R_d on Γ.

Photorespiration

In an atmosphere of ambient oxygen concentration, and at a constant leaf temperature, the photorespiration rate, R_f, is equal to the gross assimilation rate, F_g, multiplied by Γ/C_i (Laing et al., 1974):

$$R_f = \frac{\Gamma F_g}{C_i}, \tag{1}$$

where C_i is the CO_2 concentration in the substomatal cavities. This simple equation is valid over the full range of combinations of light and CO_2 concentration.

In conditions of high light and low CO_2, the dark respiration, R_d, has vanished and the net assimilation rate, F_n, is equal to $F_g - R_f$. Because the gross assimilation rate, F_g, is given by C_i/r_x and the photorespiration rate is then equal to Γ/r_s, the net assimilation rate, F_n, is:

$$F_{n,c} = (C_i - \Gamma)/r_x. \tag{2}$$

The subscript c indicates that this is CO_2 limited F_n. In BACROS, Equation (2) is used to compute the carboxylation resistance, r_x, from a measured light-saturated assimilation rate. A fundamental assumption is that r_x itself is independent of the CO_2 concentration.

In conditions of high CO_2 and low light it is important to consider the energy requirement of photorespiration as well. According to data of Peisker and Apel (1981) twice as many photons are required to regenerate PGA in the photorespiratory cycle as in the reducing cycle of photosynthesis, where both are expressed per mole of CO_2:

$$2\ R_f + F_g = \varepsilon_o H, \tag{3}$$

where H is absorbed radiation (PAR) per unit leaf area. In low light, dark respiration is not suppressed and the net assimilation,

F_n, is equal to $F_g - R_f - R_d$. When this is combined with Equation (3) we find that:

$$F_{n,l} = \varepsilon H - R_d, \tag{4}$$

where subscript l indicates light-limited F_n, and ε contains the photorespiratory losses,

$$\varepsilon = \frac{(C_a - \Gamma)}{(C_a + 2\Gamma)} \varepsilon_o. \tag{5}$$

The CO_2 concentration in this equation should be the internal CO_2 concentration, C_i, but since the equation applies close to the light compensation point, C_i has about the same value as the ambient concentration, C_a.

The fraction of assimilate lost via photorespiration is usually more under low light than under high light conditions, because of the energy requirement of photorespiration. Equation (5) calculates the loss at about 35% under low light, whereas according to Equation (2) the loss is only about 25% under high light conditions.

Interaction of light and CO_2

The transition between the light- and the CO_2-limited region of the photosynthesis-light response curve can be either sharp, or more smooth (Fig. 2). A broad transition zone ("shoulder") can be caused by spatial heterogeneity in the leaf. In addition the extinction of radiation inside the leaf leads to a broadening of the response. From biochemical considerations, the degree of coupling between NADPH supply and PGA regeneration is expressed in the sharpness of the transition. Another explanation for a sharp shoulder would be a high transport resistance in the mesophyll in combination with a low carboxylation resistance (Prioul and Chartier, 1977). However, this possibility must be discarded in view of biochemical evidence, and of data on discrimination between C^{13} and C^{14} (Björkman, 1981).

For our purpose all the factors influencing the shape of the shoulder are contained in an empirical relationship that gives a reasonable description of photosynthesis, such as the asymptotic exponential:

$$F_n = (F_{n,c} + R_d)\ (1 - \exp\ (-\varepsilon H/(F_{n,c} + R_d)) - R_d) \tag{6}$$

with ε given by Equation (5).

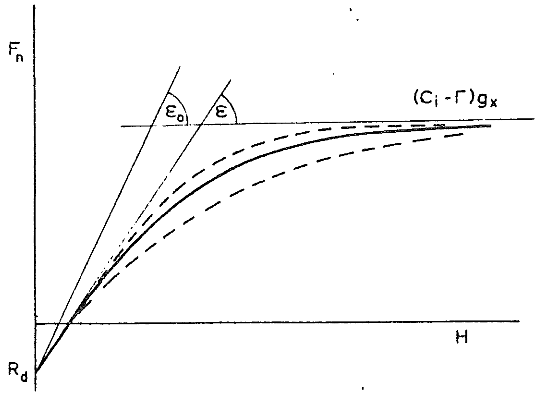

Fig. 2. Typical relationship between net CO_2 assimilation rate, F_n, and absorbed photosynthetically active radiation, H, both expressed per unit leaf area. The dashed lines indicate alternative relations which have the same asymptotes but differ in the 'shoulder' region.

STOMATAL REGULATION

Variability in stomatal conductance between leaves under the same irradiance is much larger than variability in photosynthesis. Even so, there is ample experimental evidence to indicate a linear relationship between stomatal conductance and assimilation rate at least when light is varied (Louwerse, 1980; Bell, 1982; Wong, 1979; Goudriaan and van Laar, 1978). When ambient CO_2 concentration is raised the ratio of conductance to assimilation is decreased. The difference in CO_2 concentration across the leaf boundary layer and stomatal resistances is proportional to the ambient CO_2 level, and can be described by:

$$C_i = f\ (C_a - \Gamma) + \Gamma. \tag{7}$$

The value of f is between 0.7 and 0.8 for C_3 plants. Equation (7) is a key equation for computing $F_{n,c}$ (Equation (2)), net assimilation F_n (Equation (6)) and the associated stomatal conductance. It not only generates the internal CO_2 concentration as a supply level for assimilation, but also the difference $C_a - C_i$. The magnitude of this difference, in combination with the assimilation rate, determines the value of the stomatal conductance. This description assumes that stomatal conductance follows assimilation rate. This may not be a direct cause-and-effect relationship, but an intricate simultaneous reaction to irradiance and CO_2. Such stomatal behaviour results in increasing CO_2 assimilation and decreasing transpiration per unit leaf area with rising ambient CO_2 levels.

It is well-known that this relationship between stomatal conductance and assimilation can be reversed by water shortage. The water status of the crop may put an upper limit to stomatal conductance that is lower than the value computed above. In this case we assume that the effect of water shortage becomes dominant and assimilation is calculated for the new value of r_s. Effects of water shortage on the carboxylation resistance or CO_2 compensation point have been ignored in the present model.

There are situations in which the observed stomatal conductance considerably exceeds the value needed for the realised assimilation rate. Usually this happens under ample water supply, and in that situation there is virtually no response of stomata to CO_2 concentration. It is probable that this non-regulated behaviour is more characteristic of phytotron-grown plants than of field-grown plants, and is therefore not simulated here.

PUTTING THE MODEL TOGETHER IN SPACE AND TIME

For the transition from leaf level to crop level and from seconds to a growing season, a quantitative synthesis of the constituent processes is necessary. This integration in space and in time requires careful consideration of numerous interactions.

Integration in Space

The contribution of various leaves to crop assimilation and respiration must be integrated. Leaves partly shade each other, and are at different angles with respect to incoming light, so that their radiation environment must be modelled (Goudriaan, 1977). In addition, the leaves modify their aerial environment by the release of heat and moisture. A detailed evaluation of these micrometeorological effects requires the solution of a complicated scheme of resistances and fluxes, but a great simplification is possible by neglecting the profiles of temperature and moisture inside the leaf canopy. For the computation of the fluxes of transpiration and assimilation, it is sufficient to lump the ventilation by turbulence into just one resistance connecting canopy space and crop atmosphere (Goudriaan et al., 1983).

Integration in Time

Because the time span covered by the present model is a growing season, the amounts of dry matter in the organs are important state variables. Although the most natural time step of integration is one day, we have chosen much smaller time steps, one hour, to allow for diurnal courses. The non-linearity of the photosynthesis-light response curve, and a possible afternoon depression in assimilation resulting from water stress can then be taken into account. Moreover, the reserve level may fluctuate considerably during a 24 hour period as the balance between carbohydrate production and consumption alters.

The concept of feedback is central in temporal integration. As mentioned before, we need a method to ensure an upper limit to reserve levels, especially in periods of high radiation and low temperature. For such a stabilisation, one or more negative feedbacks are required. Such stabilisation can occur by an increase in the rate of conversion of assimilates into structural material with increasing reserve level or by a decrease in assimilation rate. We have used an instantaneous response of the carboxylation resistance to fluctuating reserve levels but a better description is badly needed. In the early spring period of growth we often simulate a high assimilation rate in the morning, consequently the reserve level builds up and severely reduces photosynthesis for the rest of the day. These unlikely results suggest the existence of a more subtle feedback with a much longer time-constant. Experimentally these effects may be confounded with a simultaneous afternoon depression due to water stress. Both water stress and high reserve levels are induced by high radiation levels. Manipulation of air humidity may be the key to distinguishing these two possible causes of an afternoon depression in photosynthesis.

ACTIVE AND PASSIVE GROWTH RESPONSE

When assimilation is stimulated by a higher level of CO_2, the reserve level is increased and, as a consequence, so is the growth rate of the plant. Therefore, increased CO_2 will always be beneficial for plant production until the upper level of reserves has been reached. However, its impact on future growth depends on whether the additional carbon gained is stored as passive material such as starch, or is used productively to increase leaf area. In the passive response mode, the leaf area growth is independent of the CO_2 concentration, even though the weight of the plant and of its organs may have increased. In the opposite type of response, which can be called the active response mode, the additional assimilates are not distinguished from the "reference assimilates" and are converted into active plant material as well. In that situation the time course of leaf area/plant weight ratio is not affected and is identical to the control. In this way the positive feedback loop from assimilation to leaf area to assimilation causes a steeper response to increased CO_2 than in the passive response mode.

In the real world, these response modes are often mixed. The active response mode can be expressed by increased tillering (wheat: Lemon, 1983), branching (faba bean) or increased individual leaf size (poplar: Goudriaan and de Ruiter, 1983). In the vegetative growth phase, plants have more opportunities to respond actively than after initiation of the storage organs. We have investigated both types of response by simulation and have used either a fixed time course of leaf area index, LAI, to represent the passive response mode, or a fixed time course of leaf area ratio, LAR, to represent the active response mode.

We started with a simulation of a field experiment on a C_3 species (faba bean) grown at Wageningen in 1979, to verify that the model behaved realistically under normal conditions. With the measured time course of LAI as input, we obtained reasonable results (Fig. 3). In the field, the maximum crop growth rate was about 140 kg ha^{-1} d^{-1}. We did not change the value of any parameter to improve the fit, because we felt that these results could serve as a point of reference for further investigation of the effect of CO_2 concentration. Preferably, the response curves for the active and the passive modes should intersect at normal ambient CO_2. This can only be achieved by using the same time course of LAR as simulated in the passive mode, and not the measured one.

The effect of CO_2 is now easily investigated by a sensitivity analysis. We changed the CO_2 level in the model and plotted the simulated above-ground dry matter and total transpiration at the end of the season as a function of CO_2 level (Fig. 4). Not surprisingly, the results show a diminishing response of dry matter

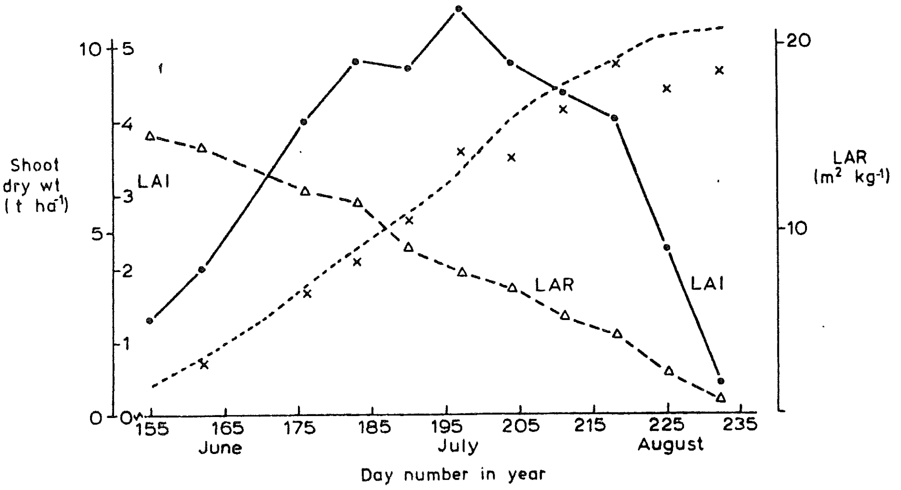

Fig. 3. Measured time courses of leaf area index (LAI, ●——●), leaf area ratio (LAR, △- -△), and of shoot dry weight (X) of faba bean. Shoot dry weight was also simulated (-----), using the measured LAI as an input.

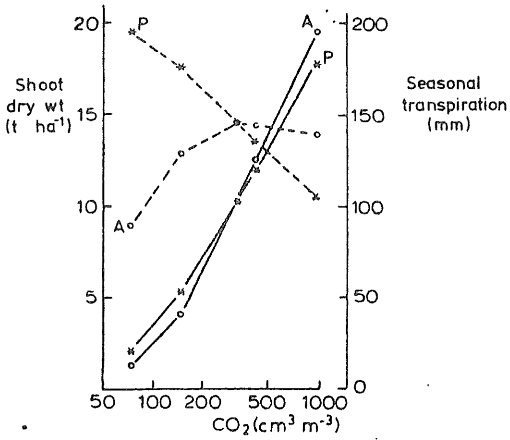

Fig. 4. Simulated shoot dry weight (———) and total transpiration (-----) at the end of the season as a function of ambient CO_2 level. In the passive response mode (P) LAI is a fixed function of time, in the active response mode (A) LAR is a fixed function of time.

with increasing CO_2. Plotting log (dry matter) against CO_2 concentration gives a remarkable linearity in response for both types of behaviour over the range from 200 to 1000 ppmv. Hence, the model results can be well represented by the equation:

$$Y = Y_o \; (1 + \beta \ln (\frac{C}{C_o})), \qquad (8)$$

where Y_o is the total dry matter at ambient CO_2 concentration, C_o.

This equation not only shows diminishing returns, but also allows for a non-zero CO_2 compensation point (Gifford, 1980). Graphically, the value of the CO_2 compensation point can be read from Fig. 4 by extrapolation to a zero yield. It is clear that the intercept is higher than the single leaf value of 50 ppmv, presumably because of respiration in other plant parts. However, there is also some upward curvature at the lower end of the graph, and the logarithmic relation does not seem valid in this region.

It is, of course, possible to find an alternative equation for the description of the CO_2 response of the model crop. The Michaelis-Menten equation (hyperbola) is attractive, because it allows for a saturation level. Within the range of 200 to 1000 ppmv, however, its behaviour is almost identical to that of the logarithmic equation. Because the logarithmic relation requires one parameter less, it is preferable for descriptive purposes. Moreover, the meaning of β is straightforward and can be interpreted as the relative sensitivity to CO_2 around the ambient concentration.

The concept of a logarithmic response is widely used in models for the global carbon cycle, more by virtue of its simplicity than because of its physiological meaning. In these studies the parameter β is termed "biotic growth factor", but the more neutral "relative sensitivity to CO_2" seems more appropriate. Our study gives a theoretical basis for the validity of the logarithmic equation. This relation was not introduced *a priori*, but was established *a posteriori* as a result of complex model relationships. It is valid, both in the active and in the passive response modes, although the values of β differ.

In the range of 200 to 1000 ppmv, β has a value of about 0.65 in the passive response mode and about 0.77 in the active one. With these relative sensitivities, a doubling of atmospheric CO_2 level will result in an increase of dry matter yields by a factor of 1.45 and 1.53 respectively. Such increases are not unrealistic and have been found under experimental conditions (Goudriaan and de Ruiter, 1983; Gifford and Evans, 1981; Lemon, 1983; Combe, 1981).

TRANSPIRATION AND ROOT/SHOOT RATIO

Both short- and long-term feedback mechanisms influence the relation between transpiration and root/shoot ratio. In the short term, water stress may limit transpiration. Then the root/shoot ratio constrains the transpiration rate. This effect only shows up during a part of the day, but its duration and intensity decreases with higher CO_2 levels. Water stress changes the partitioning of dry matter in favour of the root system, so that a long-term negative feedback mechanism accounts for some adaptation of the root/shoot ratio to the transpirational demand. In the simulated example, the root/shoot ratio dropped from 0.19 at 200 ppmv to 0.12 at 1000 ppmv in the active growth response. In reality increased CO_2 does not always lead to lower root/shoot ratio. Sometimes the opposite happens, possibly because of earlier saturation of shoot compared to root growth by the accumulation of reserves. Such a preferential demand of the shoot was not modelled because of lack of data. An interesting result of the simulation is the calculated maximum value of total transpiration at around 300 ppmv of CO_2, in the active response mode. Leaf transpiration per unit area decreases with increasing CO_2 level because of stomatal closure, but this effect is more than compensated for by an increase in leaf area index. Only above 300 ppmv does total crop transpiration decrease again. Of course, the ratio of transpiration to dry matter production declines sharply over the entire range of CO_2 levels.

INTERNAL AND EXTERNAL STIMULATION OF PHOTOSYNTHESIS

Stimulation of photosynthesis by external factors, such as radiation or CO_2, almost invariably results in increased plant production and dry matter accumulation. Although some problem areas remain, such as the effect of CO_2 on partitioning, the main features of model calculations and CO_2 experiments agree, showing that assimilate supply does limit growth. Once the assimilates are in the reserve pool, it does not seem to matter whether they have been brought there by improved external conditions or by an improved photosynthetic response. Therefore our model seems ideally suited to evaluate the growth response to genetic (internal) changes of the leaf photosynthetic properties. We have investigated the effect of changes in the potential light use efficiency, ε_o, and the carboxylation conductance, g_x. In the control situation the values of these parameters are 17×10^{-9} kg CO_2 J^{-1} and 4×10^{-3} m s^{-1} respectively. The results of the model computations are presented in Fig. 5. It is immediately clear that the relative effect of changes in light use efficiency is much larger than that of carboxylation conductance. The relative sensitivity to ε_o is about 0.7 and to g_x only about 0.25. These results suggest that a much larger potential exists in breeding for improved quantum use

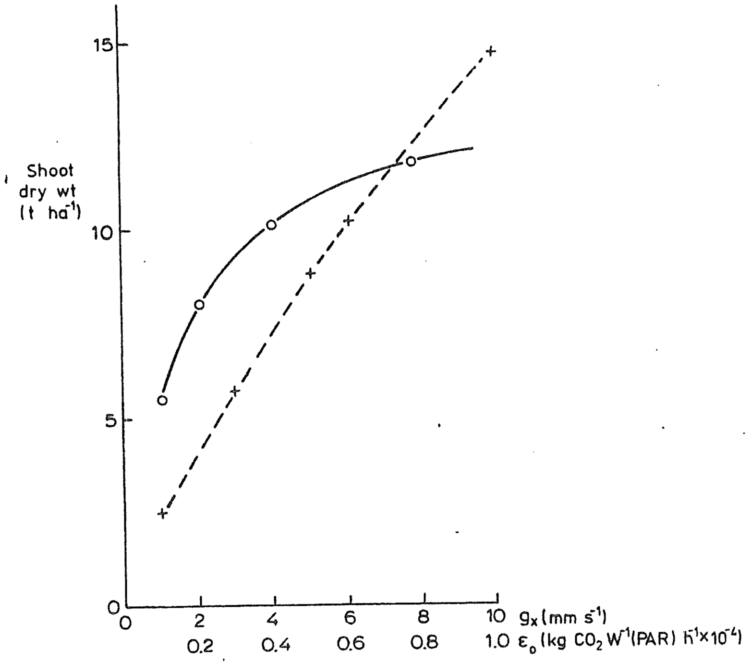

Fig. 5. Simulated shoot dry matter at the end of the season as a function of carboxylation conductance, g_x (———), and of light use efficiency, ε_o (-----).

efficiency rather than for improved carboxylation properties. Austin (1982) found a higher sensitivity to $F_{n,max}$ but this value includes the resistance of the stomata. The idea of improving photosynthetic properties has been evaluated by many plant breeders working with a large number of species. It is surprising and theoretically challenging that so far the practical results of such efforts have been disappointing. Gifford and Evans (1981) mentioned in a review on this subject that

a) The relationship between assimilation and yield is tenuous,

b) No indirect increase of maximum assimilation rate has occurred during domestication and improvement of wheat in the past (Khan and Tsunoda, 1970) nor in other species (maize, sorghum, millet, sugarcane, cotton, cowpea),

c) Breeding for lower photorespiration (CO_2 compensation point) has been unsuccessful.

They conclude that selection for photosynthetic properties may be failing because of counterproductive associations. If this statement is true then our next task is to find these associations and to devise ways to counter them.

DISCUSSION

Both internal and external stimulation of photosynthesis lead to the same end products, so that feedback mechanisms through end-product inhibition or through increased respiratory losses cannot explain the difference between the apparent lack of success in breeding for improved photosynthesis and the effect of CO_2 enrichment. Presumably the crucial difference is the high cost of building the photosynthetic structure itself.

The light-saturated rate of assimilation ($F_{n,c}$) is strongly related to leaf thickness (Louwerse and van der Zweerde, 1977), to leaf nitrogen content (van Keulen, 1984) and to RuBP carboxylase/oxygenase concentrations. RuBP carboxylase is known to account for up to half of the leaf protein, and therefore it is understandable that photosynthetic capacity is related to both nitrogen and RuBP concentrations. This brings us to the agriculturally trivial conclusion that nitrogen uptake must be improved, or that the efficiency of nitrogen use must be improved by a better distribution. But this latter conclusion poses difficulties because a relatively small increase in nitrogen involved in photosynthesis implies a relatively large decrease in other nitrogenous compounds. If there is little scope for changing the allocation of nitrogen from non-photosynthetic functions to photosynthetic ones, another possibility is a more efficient, but perhaps uneven, redistribution between the leaves in the canopy. The photosynthetic capacity of single leaves may then be quite variable, because a locally high rate of photosynthesis can only be achieved at the expense of a lower value somewhere else. Since leaf position is correlated with leaf age, this would also imply that high rates cannot be maintained for a long time in the same leaf. Measurement of single leaf photosynthesis then requires intensive sampling, and it is probably necessary to measure whole canopy photosynthesis as well.

The remarkable constancy of the quantum use efficiency also indicates physical and biochemical limits. Osborne and Garrett (1983) found no worthwhile variation with ploidy in the quantum use efficiency of absorbed radiation. Optical properties of the leaves did vary slightly, but because of counteracting effects of light loss to soil and sky, and of improved light distribution, the overall effect was small (Goudriaan, 1977). Even small improvements in this area are attractive, however, because of the high sensitivity of plant production to this factor. The steepness of the transition between the light-limited and the CO_2-limited part of the photosynthetic response curve can influence assimilation. With equal ε and $F_{n,c}$, crop photosynthesis can still be improved by a steeper transition. The extreme effect is obtained by replacing Equation (6) by a Blackman-type curve. The effect of such a change is a calculated increase of final dry matter of almost 10%. Experimentally, the detection of differences between leaves with respect to the shape of the photosynthesis curve requires measurements at a number of light levels and is therefore labour intensive. The scope for genetic improvement in this characteristic is only modest.

Finally, it is interesting to return to the response to changes in CO_2 concentration, because it partly consists of an effect through ε (Equation (5)) and partly through $F_{n,c}$ (Equation (2)). Using these equations, together with the chain rule for derivatives and the sensitivities just mentioned, we find that the CO_2 effect of 0.77 is composed of an ε effect of 0.28, a carboxylation effect of 0.3, and a remainder of 0.19. The latter may be attributed to improved water use efficiency, leading to more prolonged periods free of water stress, and to a shift in partitioning in favour of the shoot. Nutrient-imposed limitations reduce the CO_2 response of the crop but there is no reason to abandon the concept of a logarithmic response. The value of the relative sensitivity will fall, dependent on the degree and character of the nutrient shortages. An important prediction is that water shortage should not reduce the CO_2 response, because the water-use efficiency increases and there is some evidence that the efficiency of nitrogen use but not that of phosphorus slightly improves at higher CO_2 concentrations (Wong, 1979; Goudriaan and de Ruiter, 1983).

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