

OPINION

Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO₂ concentrations: Has its importance been underestimated?

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Abstract. Climate change will include correlated increases in temperature and atmospheric CO₂ concentration (C_a). Rising temperatures will increase the ratio of photorespiratory loss of carbon to photosynthetic gain, whilst rising C_a will have an opposing effect. The mechanism of these effects at the level of carboxylation in C₃ photosynthesis are quantitatively well understood and provide a basis for models of the response of leaf and canopy carbon exchange to climate change. The principles of such a model are referred to here and used to quantitatively examine the implications of concurrent increase in temperature and C_a. Simulations of leaf photosynthesis show the increase, with elevation of C_a from 350 to 650 μmol mol⁻¹, in light saturated rates of CO₂ uptake (A_{sat}) and maximum quantum yields (ϕ) to rise with temperature. An increase in C_a from 350 to 650 μmol mol⁻¹ can increase A_{sat} by 20% at 10°C and by 105% at 35°C, and can raise the temperature optimum of A_{sat} by 5°C. This pattern of change agrees closely with experimental data. At the canopy level, simulations also suggest a strong interaction of increased temperature and CO₂ concentration. Predictions are compared with the findings of long-term field studies. The principles used here suggest that elevated C_a will alter both the magnitude of the response of leaf and canopy carbon gain to rising temperature, and sometimes, the direction of response. Findings question the value of models for predicting plant production in response to climate change which ignore the direct effects of rising C_a and the modifications that rising C_a imposes on the temperature response of net CO₂ exchange.

Key-words: climate change; greenhouse effect; C₃ photosynthesis; mathematical models; ecosystem processes; global warming; rising atmospheric CO₂ concentrations; quantum yield; plant canopies; primary production; Rubisco.

Introduction

Ability to predict the responses of the net carbon exchange and production of vegetation in response to climate change is critical to assessing potential of global warming on crop production, the dynamics of natural vegetation, and the potential feedbacks of the carbon balance of ecosystems on atmospheric CO₂ concentrations. Predicted global warming is driven by rising

concentrations of infra-red absorbing or 'greenhouse' gases in the atmosphere, predominantly CO₂. Any increase in temperature will be linked to a significant increase in atmospheric CO₂ concentration (C_a). Given current trends in, and projections of, future emissions of 'greenhouse gases', the UN-IPCC 'business-as-usual scenario' predicted that C_a will rise from 354 μmol mol⁻¹ in 1990 to 530 μmol mol⁻¹ in 2050, and could exceed 700 μmol mol⁻¹ by 2100 (Watson *et al.*, 1990). This increase in C_a, with parallel increases in other 'greenhouse gases', is predicted to produce an increase in mean global temperatures of ca. 3°C by 2050 and ca. 4°C by 2100 (Watson *et al.*, 1990).

In C₃ plants, both rising temperature and C_a are expected to influence the photosynthetic rate of CO₂ uptake (A) through their direct effects at the level of primary carboxylation. CO₂ and O₂ compete for the primary acceptor molecule of C₃ photosynthesis, ribulose bisphosphate (rubP). The enzyme rubP carboxylase/oxygenase (Rubisco) catalyses both rubP carboxylation and oxygenation. Carboxylation leads to photosynthesis via the photosynthetic carbon reduction cycle and oxygenation leads to photorespiration via the photosynthetic carbon oxidation or C₂ pathway, with the evolution of CO₂. Increased temperature favours oxygenation by decreasing, relative to O₂, both the solubility of CO₂ and the specificity of Rubisco for CO₂ (Jordan & Ogren, 1984; Fig. 1). For any given C_a, increase in temperature will increase the rate of oxygenation relative to carboxylation, so that the proportion of potential photosynthesis (i.e. rate in the absence of photoinhibition) lost to photorespiration will increase with temperature. Thus, inhibition of oxygenation by rising C_a and hence increase in net photosynthesis will have its greatest effect at higher temperatures.

There is then a fundamental basis for expecting an interactive effect of rising temperature and C_a at the very point of entry of carbon in photosynthesis and into ecosystems. Among the wide range of C₃ crops and wild species now examined, all show significant increases in photosynthesis and dry matter production in response to increase in C_a to between 500 and 1000 μmol mol⁻¹, with the larger increases apparently occurring at higher temperatures (reviewed: Cure, 1985; Idso, 1989; Patterson & Flint, 1990; Drake & Long, 1991; Lawlor & Mitchell, 1991, this issue, pp. 807–818).

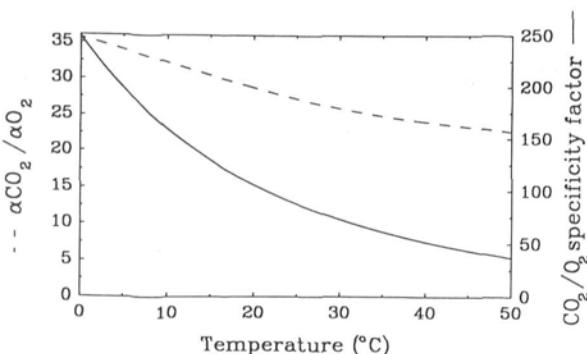


Figure 1. The specificity of Rubisco for CO_2 relative to O_2 ($V_c \cdot K_o$)/($V_o \cdot K_o$) and the ratio of solubilities (α) of CO_2 and of O_2 in water (pH 7) as functions of temperature. The relationships of K_c , K_o , V_c and V_o with temperature were determined from the data of Jordan & Ogren (1984). Solubilities are fitted to the data of Linke (1964) and Kaye & Laby (1973).

Despite this apparent wealth of experimental data, some of the key models designed purportedly to provide information for policy makers, nationally and internationally, have either ignored the direct effects of increased C_a or have considered these as an independent effect. The models of Parry & Carter (1988, 1990), used to predict regional patterns of change in crop production for the 'UNEP — World Climate Impact Studies Programme (WCIP)' make no allowance for any direct effect of rising C_a . The model of Esser (1987) and the approach proposed by Esser (1991), which underlies the 'Osnabrück Biosphere Model' and its progenitors (Esser, 1991), for assessing future changes in global primary productivity and spatial patterns of change, similarly ignore the direct implications of rising C_a and interaction with temperature to primary production. The '1990 — Greenpeace Assessment' (Schimmel, 1990) used the CENTURY model to predict the likelihood of ecosystem feedbacks on rising atmospheric CO_2 , yet this model only considers the indirect effect of rising C_a on the water use efficiency of vegetation and not its direct effects on photosynthesis (W.J. Parton, personal communication; Ågren *et al.*, 1991).

Given both the theoretical expectation of a strong interaction between rising C_a and temperature, and the quantity of experimental evidence for a potent direct effect of rising C_a on photosynthetic productivity, what justification is there for models which ignore these effects?

The 'UN-IPCC Scientific Assessment of Climate Change' recognized that direct stimulation of production could result from rising C_a , but suggested that prolonged growth in elevated CO_2 will lessen this stimulation 'as other factors such as low nutrient availability eventually limit CO_2 uptake' (Melillo *et al.*, 1990). The implication being that, when limited by other environmental factors, plants are unable to respond to increased C_a . Schimmel (1990) in the '1990 Greenpeace Report' considers stimulation of carbon uptake by rising

C_a to be transient and attenuated by 'other limiting factors'; water, nutrients and light are mentioned. Indeed many controlled environment studies have shown that the stimulation of photosynthesis and relative growth rate, observed on transfer to elevated C_a environments declines with time; nevertheless, the end result is almost invariably more plant biomass and litter (Idso, 1989). Additionally, Arp (1991, this issue, pp. 869–875), suggests that much of the evidence for a decrease in photosynthetic capacity and growth rate with prolonged growth in elevated C_a could be an artifact of the growth conditions used in the experiments. Rather than other environmental limitations lessening the relative responses of production to increased C_a , experimental evidence suggests the opposite. Relative increases in photosynthesis and production have been shown to be larger rather than smaller in response to elevation of C_a in combination with nitrogen deficiency, water stress, low light and salinity stress (reviewed by Idso, 1989).

Only two field studies have so far examined the long-term (>2 years) effects of continual elevation of C_a on natural vegetation. In a tundra environment, a doubling of C_a produced only a transient initial stimulation of community CO_2 uptake in a 3-year study (Oechel & Strain, 1985; Oechel & Reichers, 1987). In a warm, temperate wetland, a doubling of C_a has produced an approximate doubling of canopy photosynthesis and biomass (Curtis *et al.*, 1989; Drake, 1989; Drake *et al.*, 1991). These conflicting findings may in fact be compatible with the interactive effects of temperature and C_a .

The objective of this article is to use the basic understanding of the interaction of temperature and CO_2 concentration at the biochemical level to assess, from a theoretical viewpoint, its significance for net carbon gain both at the leaf and canopy level, and to assess the errors that may be introduced by ignoring this interaction.

Theory and model

Leaf photosynthesis

Farquhar *et al.* (1980) and Farquhar & von Caemmerer (1982) provide a biochemically based mechanistic model of leaf photosynthesis, which has been widely tested and validated (e.g. von Caemmerer & Farquhar, 1981; Farquhar & von Caemmerer, 1982; Long, 1985). It encapsulates the primary mechanisms of response of Rubisco and photosynthesis to both CO_2 and O_2 concentration. Equations (see 'Appendix 1') from the models of Farquhar *et al.* (1980) and Farquhar & von Caemmerer (1982) were used here to predict leaf photosynthetic rates of CO_2 uptake and the significance of changes in temperature and C_a via their effects at the level of carboxylation and oxygenation of rubP (eqns 1–5). Parameters (see 'Appendix 2'), except where stated otherwise, were as given by Farquhar *et al.* (1980). The parameters of Farquhar *et al.* (1980) were

for a leaf temperature of 25°C. To examine the effects of variation in temperature, rate constants and solubilities were recalculated here relative to their values at 25°C (eqns 6–8). Although a gradient of CO₂ across the stomata is assumed in these equations, O₂ is to be constant, i.e. O_i = O_a. This is likely to slightly underestimate O_i, but with a background atmospheric concentration of 210 mmol mol⁻¹, the error was considered small. Neither O₂ nor CO₂ is a perfect gas, and because of their differing properties in aqueous solution, the ratio of their respective solubilities varies with temperature. In these simulations equivalent concentrations in solution, relative to 25°C, were calculated from polynomial relationships fitted to tabulated values of solubility at different temperatures (Linke, 1965; Kaye & Laby, 1973; eqns 7 & 8). Jordan & Ogren (1984) provide results on the response of the kinetic constants of Rubisco (K_c, K_o, V_{cmax}) to temperature. Activation energies have been determined here from these plots and were used (see 'Appendix 2') in preference to those of Farquhar *et al.* (1980). Possible decreases in Rubisco activity due to acclimatisation to elevated CO₂ were simulated by decreasing V_{cmax} and V_{omax}, each by either 20 or 40%. The quantum yield of CO₂ uptake (ϕ) was estimated as the predicted initial slope of A versus I_{abs}, and as it might be practically measured (eqn 9; Long & Drake, 1991). The light compensation point (LCP) was derived from this slope (eqn 10).

Canopy photosynthesis

To evaluate the significance of changes inferred at the leaf level to changes at the canopy level, a simplified model of canopy photosynthesis has been used. Norman (1980) compared different approaches to predicting light distribution in canopies for the calculation of canopy photosynthetic rates from relationships of A to I determined at the leaf level. This comparison showed that by treating the canopy as two populations of leaves, sunlit and shaded, and by calculating the mean I and in turn mean A for each category, estimated canopy photosynthesis differed little from estimates made with more complex models, which treated the canopy as several component leaf populations. However, this division into sunlit and shaded leaves did provide a substantial improvement in prediction over models which simply assumed the exponential decline in I through homogeneously lit canopy layers. This approach of dividing the canopy into dynamically variable sunlit and shaded populations of leaves was employed here to extrapolate from the leaf photosynthesis model to a whole canopy.

The photon flux of the shaded (I_{shade}) and sunlit (I_{sun}) leaves, and the leaf area index in direct sunlight (F_{sun}) were calculated throughout the day. These are functions of leaf area index (F), the ratio of the horizontally and vertically projected areas of the canopy (x), the quantities of direct (I_{dir}) and diffuse (I_{diff}), and the angular distribution of the light entering the canopy (eqns 13–15); after Campbell (1986) and Forseth & Norman

(1991). I_{dir} and I_{diff} were assumed to be a function of solar angle (θ), latitude (Ω), time of year (D_j) and atmospheric transmittance (α) (eqns 16–22); after Campbell (1977), Norman (1980) and Forseth & Norman (1991). Temperature was assumed to follow a sinusoidal pattern with a midnight minimum and noon maximum (eqn 11). For the simulations shown here, the 190th Julian day (July in the northern hemisphere) was used to derive diurnal variation in photon flux (I_{dir} and I_{diff}) and the angular distribution of light above the canopy (eqns 16–19). For these simulations, F was set to 3 and x to 1. In all cases, clear sky conditions were assumed ($\alpha = 0.75$). Maximum and minimum temperatures over 24 h were assumed to be +5°C and -5°C of the mean, respectively. Mean photosynthetic rates of CO₂ uptake by the shaded and by the sunlit leaf areas were then calculated (eqns 1–9) and canopy photosynthetic rate calculated (eqn 12). The daily sum of net CO₂ uptake (A_{c,tot}) was then obtained by integrating over the day (eqn 23) using the Euler method of numerical integration, with 5-min time steps.

Results and discussion

Leaf photosynthesis

The effects of temperature on the solubility of CO₂ and Rubisco specificity for CO₂, relative to O₂, are illustrated in Fig. 1. Between 0 and 50°C, the solubility of CO₂ relative to O₂ decreases by 36%. By reference to eqns 2–23, it can be shown that this would decrease the rubP-saturated (W_c) and the rubP-limited (W_j) rates of carboxylation by 30 and 12%, respectively. This effect of decrease in the relative solubility of CO₂ with temperature is small by comparison to the independent decrease in the specificity of Rubisco for CO₂. Extrapolating from the data of Jordan & Ogren (1984), relative specificity would decrease by 86% between 0 and 50°C. The major cause of this change is a marked decrease in the affinity of the enzyme for CO₂ as indicated by a strong increase in the Michaelis constant for CO₂ (K_c) with temperature, whilst K_o shows no significant increase over the temperature range examined. The activation energies calculated here from this data were 65 800 J mol⁻¹ (K_c) and just 1400 J mol⁻¹ (K_o). Between 7 and 35°C, decrease in specificity accounts consistently for 68% of the decrease in the velocity of carboxylation relative to oxygenation (V_c/V_o), the remaining 32% being attributable to solubility changes (Jordan & Ogren, 1984). Both of these changes with increasing temperature will strongly depress V_c/V_o, leading to decreased efficiency of photosynthesis. However, this assumes that there is no compensatory increase in C_i with temperature and that C_i is directly proportional to the dissolved concentration of CO₂ within the chloroplast. The close agreement between the relationship of the CO₂ compensation point of photosynthesis with temperature and the relationship predicted from solubility and specificity changes (Jordan & Ogren, 1984), suggests that the second assumption holds. This is also

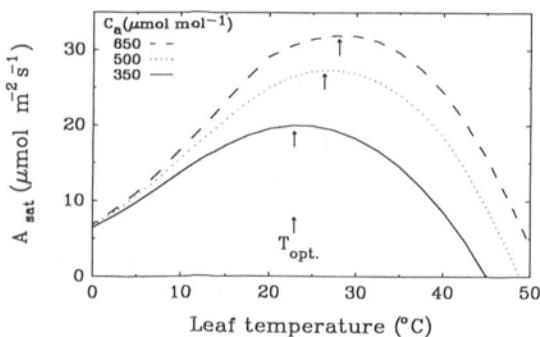


Figure 2. Predicted light-saturated rates of leaf CO_2 uptake (A_{sat}) with leaf temperature for three atmospheric CO_2 concentrations (C_a ; $\mu\text{mol mol}^{-1}$ of CO_2 in air). Arrows indicate T_{opt} , i.e. the temperature at which A_{sat} is maximal for each value of C_a .

suggested by the agreement between extractable activities of Rubisco and carboxylation efficiencies determined *in vivo* (reviewed: Long, 1985). A compensatory increase in C_i would need to be substantial to offset increased oxygenation with temperature, indeed by reference to eqns 2–4, it may be shown that even an increase in C_i to C_a , i.e. an infinite stomatal conductance, would be insufficient to counter the increase in oxygenation.

The implication of this strong dependence of the ratio of carboxylation rates to oxygenation rates (V_c/V_o) on temperature, is that as temperature increases, the proportion of potential carbon uptake, lost to photorespiration increases. This may be practically demonstrated by comparing photosynthetic CO_2 uptake in an atmosphere of $10 \text{ mmol mol}^{-1} \text{O}_2$, when $V_o \approx 0$, and in a normal atmosphere of $210 \text{ mmol mol}^{-1}$ (e.g. Berry & Björkman, 1980). Thus, the increase in photosynthesis that will be achieved by inhibiting oxygenation of rubP, and photorespiration, will increase with increase in temperature. Since the key effect of elevated CO_2 concentration (C_a) is increased competitive inhibition of oxygenation and hence photorespiration, it follows that the proportionate increase in photosynthesis resulting from elevated C_a will rise with temperature. This has been frequently demonstrated in leaf gas exchange studies (e.g. Sage & Sharkey, 1987) and is illustrated here for the predicted responses of light saturated CO_2 uptake (A_{sat}) to temperature (Fig. 2). Increase in C_a produces a progressive increase in A_{sat} with temperature. On elevation of C_a from 350 to $650 \mu\text{mol mol}^{-1}$, A_{sat} is predicted to increase by 14, 54 and 73% at leaf temperatures of 10, 20 and 30°C, respectively (Fig. 2). This increase is very similar to that observed with elevation of C_a and temperature, in a study of three C_3 species (Sage & Sharkey, 1987). It also follows from this interaction of C_a and temperature, that the temperature optimum (T_{opt}) of A_{sat} will increase. T_{opt} increases by 3°C at $C_a = 500 \mu\text{mol mol}^{-1}$ and 5°C at $C_a = 650 \mu\text{mol mol}^{-1}$ (Fig. 2). The predicted upper temperature at which positive A_{sat} may be maintained is also increased

by 4 and 7°C, respectively. The change in these characteristic temperatures underlies the importance of considering rise in C_a , not simply as a factor which increases photosynthetic rate, but also as a variable that modifies the response to temperature. In Fig. 3, two approaches to examining the stimulatory effect of C_a on photosynthesis are compared. In one case, A_{sat} predicted for $C_a = 350 \mu\text{mol mol}^{-1}$ is multiplied by 1.25, the average increase observed across the temperature range on increase in C_a to $500 \mu\text{mol mol}^{-1}$. Therefore, this simulates an increase in photosynthesis which is independent of temperature. The second approach takes account of the interaction of C_a and temperature. If the effect of increase in C_a to $500 \mu\text{mol mol}^{-1}$ is considered to be independent of temperature, then increase in A_{sat} is overestimated at low temperatures and underestimated at higher temperatures. Further, the use of a constant multiplier to simulate the effect of elevated C_a predicts that increase in leaf temperature from 25 to 30°C would decrease A_{sat} . When the interactive effects of increased C_a and temperature are taken into account, a small increase in A_{sat} is indicated on increasing leaf temperature from 25 to 30°C (Fig. 3). Thus, failure to take account of the interaction might not only fail to predict the magnitude of change in photosynthesis with temperature, but also the direction of change.

Increase in the temperature optimum of photosynthesis with rising C_a is of particular significance to putative climate change. The 'IPCC business-as-usual scenario' suggests an increase in mean temperatures of 3°C by about 2050 (Watson *et al.*, 1991). In temperate climates, this would increase the frequency of temperatures which are supra-optimal for A_{sat} . However, the results here suggest that this inhibitory effect can be negated if C_a increases to $500 \mu\text{mol mol}^{-1}$, as has been projected, since this increase in C_a would apparently increase T_{opt} by 3°C (Figs 2 & 3). However, predicted temporal patterns of temperature increase

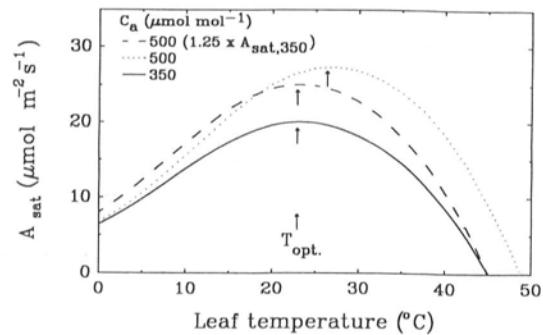


Figure 3. Predicted light-saturated rates of leaf CO_2 uptake (A_{sat}) at the current atmospheric CO_2 concentration (C_a) of $350 \mu\text{mol mol}^{-1}$ and in an elevated C_a of $650 \mu\text{mol mol}^{-1}$. The model predicted increase which takes account of the interactive effect of temperature and C_a (broken line) is compared to the effect of a simple multiplication of A at all temperatures by 1.25 (dotted line); where 1.25 is the mean increase predicted across the temperature range. Arrows indicate T_{opt} , i.e. the temperature at which A_{sat} is maximal.

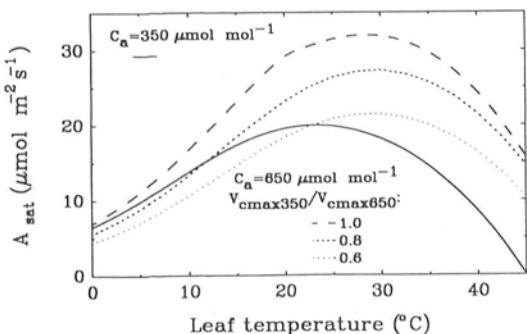


Figure 4. Predicted light-saturated rates of leaf CO₂ uptake (A_{sat}) at the current atmospheric CO₂ concentration (C_a) of 350 $\mu\text{mol mol}^{-1}$ and with an elevated C_a of 650 $\mu\text{mol mol}^{-1}$. The effects of decreased Rubisco activity with acclimation to the elevated C_a are simulated by decreasing the maximum rubP saturated velocities of carboxylation and oxygenation to 0.8 (a 20% decrease) and 0.6 (a 40% decrease) of the values assumed for plants grown at a C_a of 350 $\mu\text{mol mol}^{-1}$ ($V_{\text{cmax},650}/V_{\text{cmax},350}$).

with global warming suggest that in cool temperate climates, temperature increase will be greatest in the winter (Bretherton *et al.*, 1990; Mitchell *et al.*, 1990), when T is commonly sub-optimal for A_{sat} . However, should rising CO₂ concentrations fail to produce any increase in mean summer temperatures, in temperate zones, leaf temperatures might still increase. Several studies suggest that C₃ leaves, in the absence of water stress, maintain a constant ratio of C_i to C_a (reviewed by Long, 1985). This will require a decrease in stomatal conductances and, given a constant VPD, a decrease in the latent heat losses. To maintain a constant (C_i/C_a) with the same rate of CO₂ uptake at $C_a = 350$ and 500 $\mu\text{mol mol}^{-1}$ could require a 30% decrease in g_s. In full sunlight ($I = 1800 \mu\text{mol mol}^{-1} \text{ s}^{-1}$) at 25°C and a VPD of 0.5 kPa, this would increase leaf temperature by ca. 1°C, assuming an average boundary layer conductance (calculated from the equations of Forseth & Norman, 1991). Thus, even without any change in air temperatures, the stimulatory effect of elevated CO₂ on A_{sat} may be further increased by an indirect elevation of leaf temperature.

A frequent, but variable, response of species to long-term growth in elevated CO₂ are decreases in the *in vivo* carboxylation efficiency, correlated with decreases in the extractable activity of Rubisco (e.g. Sage *et al.*, 1989). Decreases in Rubisco activity range from 0 to 60% and result from either a decrease in the amount of Rubisco protein or/and a decrease in the activation state of the enzyme, depending apparently on the species (Campbell *et al.*, 1988; Sage *et al.*, 1989; Rowland-Bamford *et al.*, 1991). The significance of these decreases to light saturated photosynthesis may be simply simulated by decreasing V_{cmax} and V_{oxygen} accordingly in the model. Figures 4 and 5 show that even with a decrease in total activity, by 40% of the controls ($V_{\text{cmax},650}/V_{\text{cmax},350} = 0.6$), A_{sat} will still be greater in leaves in a C_a of 650 $\mu\text{mol mol}^{-1}$ than in leaves in a C_a of 350 $\mu\text{mol mol}^{-1}$, when leaf

temperatures exceed 22.5°C. At 40°C, A_{sat} will be 75% greater, despite the 40% loss in activity. However, below 22.5°C, depression of V_c due to decreased Rubisco activity exceeds the increase attributable to inhibition of oxygenation by elevated CO₂ (Figs 4 & 5). Thus, if acclimatization to elevated CO₂ does result in a decrease in the activity of Rubisco, then at low temperatures, this could be one instance where rising CO₂ results in decreased photosynthesis. Since photorespiration must also be decreased by such a loss of Rubisco activity, photochemical dissipation of intercepted light energy will also be depressed; these are conditions which may be expected to increase susceptibility to photoinhibition at low temperatures (Powles, 1984). The studies which have shown a decrease in Rubisco activity or carboxylation efficiency in leaves grown in elevated CO₂ have used relatively high temperatures (>20°C) (e.g. Campbell *et al.*, 1988; Sage *et al.*, 1989). The significance of the low temperature decrease in photosynthesis suggested here (Figs 4 & 5) will depend on a similar decrease in Rubisco activity developing in plants grown at high C_a , but low temperatures.

The interactive effects of temperature and elevated C_a suggested by this analysis assume that when rubP limits V_c , its regeneration is limited by the rate of electron transport. As noted by Farquhar & von Caemmerer (1982), regeneration could also be limited by the rate of exchange of triose phosphates and inorganic phosphate between chloroplasts and the cytoplasm. If phosphate recycling became an increasing restraint with increasing C_a , then the increases in A_{sat} indicated might not be realized. However, increase in temperature makes this less likely Farrar & Williams (1991, this issue, pp. 819–830), note that increased temperature will be expected to increase the rate of sucrose synthesis, increasing the degree of phosphate recycling and permitting higher rates of CO₂ synthesis. They also suggest

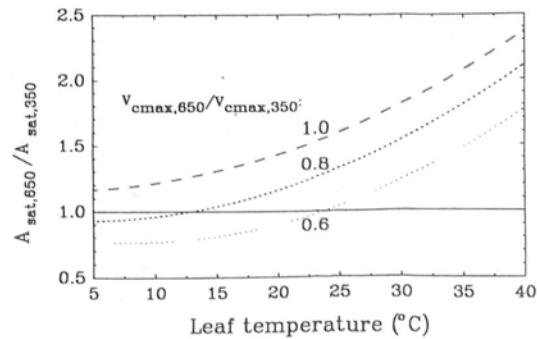


Figure 5. The predicted change in the ratio of light-saturated rates of leaf CO₂ uptake (A_{sat}) in an elevated CO₂ atmosphere of 650 $\mu\text{mol mol}^{-1}$ relative to that predicted for a C_a of 350 $\mu\text{mol mol}^{-1}$ ($A_{\text{sat},650}/A_{\text{sat},350}$), and the potential effects of a decrease in Rubisco activity produced by putative acclimatization to elevated C_a . The three lines assume: (1) no change in Rubisco activity; (2) a decrease to 0.8; and (3) a decrease to 0.6 of the Rubisco activity of leaves grown in a C_a of 350 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ($V_{\text{cmax},650}/V_{\text{cmax},350}$).

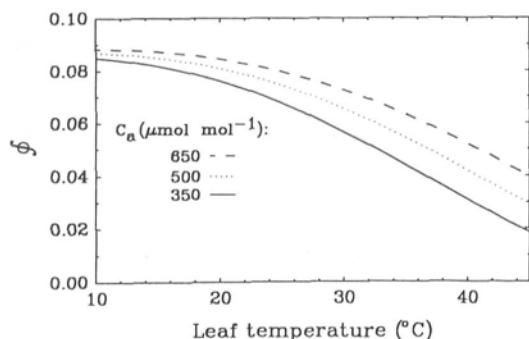


Figure 6. The predicted response of the maximum quantum yield of CO_2 uptake (ϕ) to leaf temperature at three atmospheric CO_2 concentrations (C_a).

that increased temperature is likely to increase utilization of carbohydrate leading to a positive rather than negative feedback effect. Further, under conditions of high CO_2 and temperatures, photosynthesis is more likely to be limited by the capacity of Rubisco for carboxylation than the rate of phosphate recycling (Sage, Sharkey & Pearcy 1990; Labate, Adcock & Leegood, 1990).

Because increased temperature decreases V_c/V_o , net rates of CO_2 uptake will also be depressed under light-limiting conditions, since an increasing proportion of the NADPH and ATP produced by electron transport must be diverted into photorespiration. Thus, the maximum quantum yield of CO_2 uptake (ϕ) in C_3 species decreases with increase in temperature (Fig. 6; Ehleringer & Björkman, 1977). As increase in C_a will decrease photorespiration, the decline in ϕ with increase in leaf temperature will be less when C_a is elevated. Figure 6 shows that whilst increase in C_a from 350 to $650 \mu\text{mol mol}^{-1}$ would increase ϕ by just 4% at 10°C , it would increase ϕ by 64% at 40°C (Fig. 6). At 28°C , ϕ is predicted to be 0.062 at $C_a = 350 \mu\text{mol mol}^{-1}$ and 0.078 at $C_a = 650 \mu\text{mol mol}^{-1}$. These values are close to the measured values of 0.064 and 0.078 for shoots of the C_3 sedge *Scirpus olneyi* at 28°C growing in atmospheres of $C_a = 350$ and $680 \mu\text{mol mol}^{-1}$, respectively (Long & Drake, 1991). Maximum quantum yield (ϕ) represents the initial and maximal slope of the response of A to I_{abs} . Under these light limiting conditions, A will be rubP limited (i.e. $V_c = W_j$). Therefore, decreases in Rubisco activity resulting from putative acclimatization to elevated CO_2 should not decrease ϕ . Although decrease in active Rubisco will decrease V_{cmax} , $V_{\text{o max}}$ is assumed to decrease in direct proportion (see 'Appendix 2'), and so Γ^* and W_j will be unchanged (eqns 2 and 4). Acclimation in Rubisco could only affect ϕ , if loss of activity was accompanied by a change in the kinetic properties of the enzyme, leading to a change in its specificity for CO_2 , but as noted earlier, this enzyme is remarkable for the constancy of this value (Jordan & Ogren, 1984; Woodrow & Berry, 1988). Despite three years of growth in a C_a of $680 \mu\text{mol mol}^{-1}$, shoots of *S. olneyi* showed a ϕ , measured at $C_a = 350 \mu\text{mol mol}^{-1}$,

that was identical to the ϕ of plants grown at $C_a = 350 \mu\text{mol mol}^{-1}$ (Long & Drake, 1991).

In the absence of change in the rate of dark respiration with increase in C_a , it follows that the light compensation point of photosynthesis (LCP) must decrease if ϕ rises (Fig. 7). At all temperatures, LCP is depressed by increase in C_a , again the effect being greatest at high temperatures. For example, at 35°C the predicted LCP decreases from $67 \mu\text{mol m}^{-2}\text{s}^{-1}$ at $C_a = 350 \mu\text{mol mol}^{-1}$ to $43 \mu\text{mol m}^{-2}\text{s}^{-1}$ at $C_a = 650 \mu\text{mol mol}^{-1}$. Such decreases could be of considerable significance in warm-shade environments. Such a large decrease in LCP would significantly alter the number of leaf layers that a canopy could maintain above the light compensation point for net carbon gain, and the productivity of forest ground-flora and under-story plants, which exist at photon fluxes little above the LCP. Decreases in LCP in accordance with these predictions were observed in *S. olneyi* growing in an elevated CO_2 atmosphere (Long & Drake, 1991).

Canopy photosynthesis

Figure 8 uses predictions of A at the leaf level to calculate net canopy CO_2 uptake over 24 h ($A_{\text{c,tot}}$), where the quantity and angular distribution of light is continually varying with change in sun angle. For a canopy of leaf area index (F) 3, a substantial portion of the leaf area will be shaded even during the course of a summer day with clear skies at latitude 52°N , and thus, the canopy response to temperature will not be solely determined by the response of A_{sat} to temperature. Nevertheless, the pattern of response of $A_{\text{c,tot}}$ to temperature with increase in C_a is similar to that described for A_{sat} (Fig. 8). $A_{\text{c,tot}}$ at 35°C is predicted to double with increase in C_a from 350 to $650 \mu\text{mol mol}^{-1}$. Temperature optima of $A_{\text{c,tot}}$ are also shifted upwards by 3 and 5°C with increase in C_a to 500 and $650 \mu\text{mol mol}^{-1}$, respectively (Fig. 8). However, the larger part (58%) of the increase in $A_{\text{c,tot}}$ is attributable to increase in the contribution of the shaded rather than sunlit leaves, emphasizing the significance of increase in both ϕ and LCP.

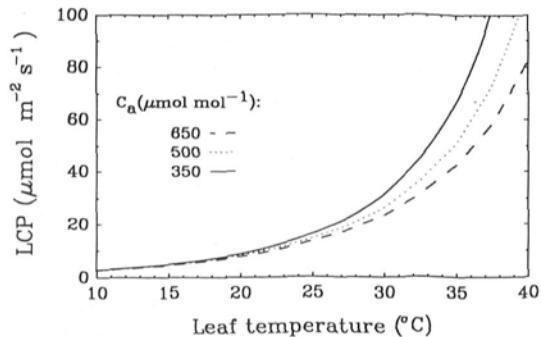


Figure 7. The predicted response of the light compensation point of photosynthesis, in terms of photon flux (LCP), to leaf temperature, at three atmospheric CO_2 concentrations (C_a).

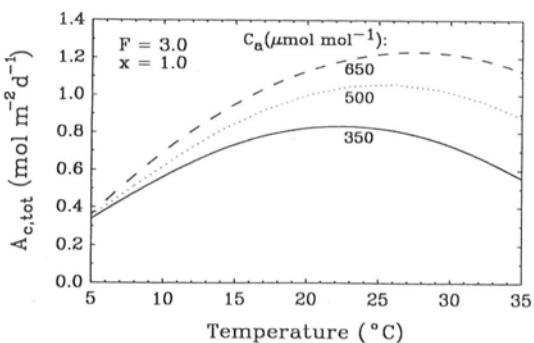


Figure 8. The predicted response of net canopy CO₂ uptake rate, integrated over 24 h ($A_{c,\text{tot}}$), to temperature at three atmospheric CO₂ concentrations (C_a). The simulation is for a canopy with a leaf area index (F) of 3 and a ratio of horizontally to vertically projected leaf area (x) of 1, on Julian date 190, latitude 52°N and assuming clear sky conditions (atmospheric transmittance, $\alpha = 0.75$). The total photon flux simulated over the course of the day was 36 mol m⁻².

Diurnal courses of canopy photosynthesis were simulated for July days at three latitudes, assuming the same canopy characteristics and sky conditions at each site. At the 'high latitude site', with a mean temperature of 5°C and a day-time maximum of 10°C, enhancement of A_c by increased CO₂ concentration, is small and amounts to less than 8% over the day (Fig. 9). At the 'mid-latitude site', with a mean temperature of 17.5°C and a maximum of 22.5°C, a 33% increase over the day is predicted for elevation of C_a from 350 to 650 μmol mol⁻¹ (Fig. 9). The equivalent increase for the lower latitude site, with a mean temperature of 30°C and maximum of 35°C is 110%. The much greater increase in net carbon gain at the 'low latitude site', results from the interaction between temperature and elevated CO₂. Whilst temperatures of 30°C and above may be common in warm temperate climates during the summer months, they can be supra-optimal for carbon gain by C₃ canopies. Thus, a greater net carbon gain is predicted for a canopy of the same structure and size at the cooler 'mid-latitude site', at the current atmospheric CO₂ concentration of 350 μmol mol⁻¹. When C_a is elevated to 650 μmol mol⁻¹, this pattern is reversed (Fig. 10), with the 'low-latitude site' showing a greater $A_{c,\text{tot}}$, which reflects the increase in T_{opt} produced by elevation of C_a (Figs 2–4). The contrast between the three sites, with respect to the predicted increases in $A_{c,\text{tot}}$ with elevation of C_a , is consistent with findings of the two long-term field CO₂ enrichment studies undertaken. Enrichment of tundra vegetation at a high latitude site, Alaska, produced no significant long-term increase in canopy carbon exchange (Oechel & Strain, 1985; Oechel & Reichers, 1987). Enrichment of warm temperate wetland vegetation on a low latitude site, Maryland, produced marked increases in $A_{c,\text{tot}}$, which during the warmest months of the year approach the 110% increase suggested here for a doubling of C_a (Drake *et al.*, 1991).

Conclusion

The simulations presented here are for a very limited subset of possible climatic conditions, leaf properties and canopy structures and sizes. Leaves within and between species vary markedly in their contents of active Rubisco (V_{cmax}) and maximum rates of electron transport (J_{max}). However, these variations will lead to variation primarily in the magnitude rather than patterns of the response. Critical to the predictions is the specificity constant of Rubisco for CO₂, fortunately this seems a remarkably constant value between taxonomically separate photosynthetic organisms and growth conditions, varying only with temperature (Jordan & Ogren, 1984; Woodrow & Berry, 1988). A constant

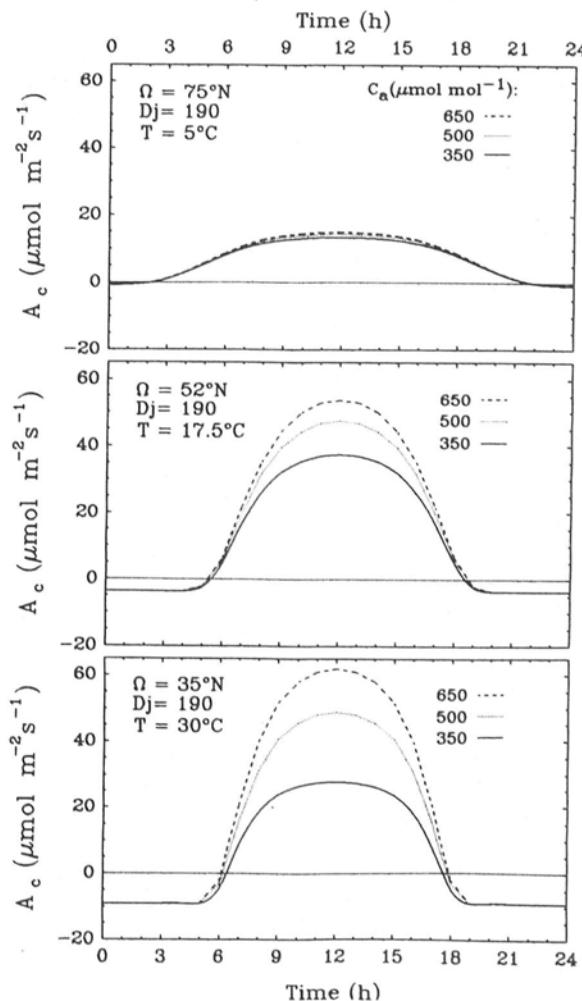


Figure 9. The predicted diurnal course of net canopy CO₂ uptake at three atmospheric CO₂ concentrations (C_a). The simulations are for canopies with a leaf area index (F) of 3 and a ratio of the horizontally to vertically projected leaf area (x) of 1, on Julian date 190, and assume clear sky conditions (atmospheric transmittance, $\alpha = 0.75$). Simulations are for three locations; latitude (Ω) 75°N, with a (T_{max}) and minimum (T_{min}) temperatures of 0 and 10°C, giving a total photon flux over the day (I_{tot}) of 28 mol m⁻² d⁻¹; $\Omega = 52^{\circ}\text{N}$, with $T_{\text{max}} = 22.5^{\circ}\text{C}$ and $T_{\text{min}} = 12.5^{\circ}\text{C}$, giving a I_{tot} of 36 mol m⁻² d⁻¹; and $\Omega = 35^{\circ}\text{N}$, with $T_{\text{max}} = 35^{\circ}\text{C}$ and $T_{\text{min}} = 25^{\circ}\text{C}$, giving a I_{tot} of 40 mol m⁻² d⁻¹.

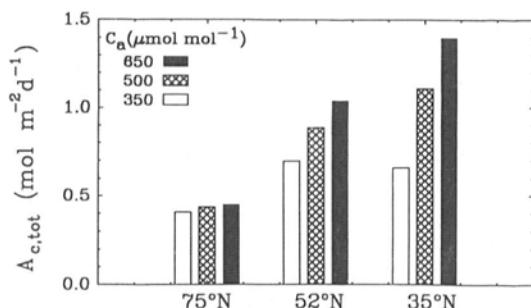


Figure 10. As for Fig. 9, but illustrating A_c integrated over the 24-h period (A_{c,tot}) for the three locations.

ratio of C_i/C_a is assumed in these simulations and no account is taken of the possibility that climate change (e.g. through increased VPDs) may force even lower stomatal conductances than would be necessary to simply maintain this ratio (see McMurtrie & Wong, 1991, for a mathematical treatment of this response). In the absence of concurrent elevation of C_a, a decrease in C_i/C_a would promote photorespiration; in an elevated CO₂ atmosphere, this effect would again be lessened.

Schimmel (1990) suggested that at the ecosystem level a longer-term effect of climate change will be decreased availability of nitrogen, negating the 'CO₂ fertilization effect'. Since Rubisco can account for a large proportion of plant protein and nitrogen, a likely result of any decreased availability of nitrogen would be decreased concentrations of Rubisco. However, it is demonstrated here that even if plants grown in elevated C_a show a 40% loss of their active Rubisco, net photosynthetic rates will still be enhanced by elevated CO₂ when temperatures exceed 22.5°C.

At the canopy level, different leaf areas, sky conditions and angular distributions of leaves would all lead to different spatial and temporal patterns of light within the canopy (see McMurtrie & Wong, 1991, for a more detailed treatment). However, since increased temperature increases the response of A to elevated C_a at all photon fluxes, it follows that a strong interaction of C_a and temperature will result in all canopies.

The simulations used here assume that respiration increases as a simple function of temperature, with a Q₁₀ of ca. 2.2. The use of more appropriate models of respiration which partition between 'maintenance' and 'growth' components (Charles-Edwards, 1982; Long & Hutchin, 1991) suggest that the 'growth' component might increase as a constant proportion of photosynthesis. In this case, the patterns of response reported here would be maintained, but their magnitude decreased. However, there is little evidence that large increases in respiration result from growth in elevated CO₂ concentration (Farrar & Williams, 1991, this issue, pp. 819–830) and some evidence that growth in elevated CO₂ may even depress respiration (Idso, 1989; Amthor, 1991). If growth in elevated CO₂ leads to increased C/N ratios, as suggested, then the 'maintenance' and 'growth' components of respiration might be expected to

decline, as proportions of total biomass in a given time (Charles-Edwards, 1982).

The results of these simulations, based on understanding of the interaction of temperature and CO₂ at the point of carbon uptake, predict that the interaction of these two variables of climate change will invalidate conclusions based on their individual effects on photosynthetic productivity. At the leaf and canopy level, under light-saturating and light-limiting conditions, it has been shown that elevated C_a may not only alter the scale of the response of canopy carbon gain to rising temperature, but can alter the direction of response. These points bring into serious question the value of any predictions of plant production which ignore not only the direct effect of CO₂ on carbon gain, but also the basic interaction of temperature and CO₂. Given the detailed information on the primary basis for this interaction at the biochemical level, and the apparently robust nature of the equations developed by Farquhar *et al.* (1980), it is surprising that more models of the response of vegetation to climate change have not made use of this information. Yet a survey of models being developed for assessments of crop and ecosystem production in relation to climate change (Ågren *et al.*, 1991), showed only two which attempted to utilize this information: BIOMASS (McMurtrie *et al.*, 1990; McMurtrie & Wang, 1991) and MAESTRO (Wang, 1988).

Although it may be argued that parametrizing such models at the biochemical level for different species and community types may be difficult and time-consuming, there is a wealth of data available for such a task. The approach has also been criticized for the increased computational power required by its incorporation (Ågren *et al.*, 1991). However, these implications for computer time and power seem small compared to those used in other areas of climate change research (e.g. Bretherton *et al.*, 1990; Mitchell *et al.*, 1990). At the least, the approach could be used to develop response surfaces of the interaction of temperature and C_a, perhaps averaged over a daily time-step, which would at least capture the broad pattern of interaction of temperature and C_a. Such simplifications could be tested against more detailed models run over shorter time-steps.

In the opinion of the author, ignoring both the direct effects of elevated CO₂ concentration and the modification of temperature responses produced by rising CO₂ concentration when modelling the responses of plant and ecosystem production to climate change is akin to trying to model change in lake levels without knowing how inputs will change.

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Appendix 1

Equations

Model of leaf photosynthesis:

$$A = [1 - \Gamma^*/C_i] \cdot \min[W_c, W_j] - R_d \quad (1)$$

$$\Gamma^* = \frac{0.5V_{omax} \cdot K_c \cdot O_i}{V_{cmax} \cdot K_o} \quad (2)$$

$$W_c = \frac{V_{cmax} \cdot C_i}{C_i + K_c[1 + O_i/K_o]} \quad (3)$$

$$W_j = \frac{J \cdot C_i}{4.5C_i + 10.5\Gamma^*} \quad (4)$$

$$J = \frac{J_{max} \cdot f \cdot I}{f \cdot I + 2.1J_{max}} \quad (5)$$

$$K_T = e^{[E(Tk-298)/(298Tk.R)]} \cdot [Tk/298]^{0.5} \quad (6)$$

$$C_i = 0.7C_a \cdot [(1.6740 - 6.1294 \cdot 10^{-2}T + 1.1688 \cdot 10^{-3}T^2 - 8.8741 \cdot 10^{-6}T^3)/0.73547] \quad (7)$$

At 25°C, C_i = 0.7C_a

$$O_i = 210[(4.7000 \cdot 10^{-2} - 1.3087 \cdot 10^{-3}T + 2.5603 \cdot 10^{-5}T^2 - 2.1441 \cdot 10^{-7}T^3)/2.6934 \cdot 10^{-2}] \quad (8)$$

At 25°C, O_i = O_a

$$\phi = \frac{A_{(I=50)} - A_{(I=25)}}{25f} \quad (9)$$

$$LCP = R_d/\phi \quad (10)$$

$$T_t = T_{min} + (T_{max} - T_{min})\cos(15[t - t_{sn}]) \quad (11)$$

$$A_c = f(I_{sun} \cdot T_t \cdot C_i \cdot O_i)F_{sun} + f[I_{shade} \cdot T_t \cdot C_i \cdot O_i]F_{shade} \quad (12)$$

Where *f* indicates a function as described in eqns 1–9.

$$F_{sun} = [1 - e^{(-kF/\cos\theta)}] \cos\theta/k \quad (13)$$

$$F_{shade} = F - F_{sun} \quad (14)$$

$$k = \frac{[x^2 + \tan^2\theta]^{0.5} \cos\theta}{x + 1.744 [x + 1.182]^{-0.733}} \quad (15)$$

$$\cos\theta = \sin(\Omega) \cdot \sin(\delta) + \cos(\Omega) \cdot \cos(\delta) \cdot \cos(15[t - t_{sn}]) \quad (16)$$

$$\delta = -23.5 \cdot \cos[360(D_j + 10)/365] \quad (17)$$

$$I_{dir} = I_s \cdot \alpha^{[(P/P_0)/\cos(\theta)]} \quad (18)$$

$$I_{diff} = 0.5I_s[1 - \alpha^{[P/P_0]/\cos(\theta)}] * \cos(\theta) \quad (19)$$

$$I_{shade} = I_{diff} \cdot e^{[-0.5F^{0.7}]} + I_{scat} \quad (20)$$

$$I_{scat} = 0.07 \cdot I_{dir} \cdot [1.1 - 0.1F]e^{[-\cos\theta]} \quad (21)$$

$$I_{sun} = I_{dir} \cdot [\cos\theta/\cos\theta] + I_{shade} \quad (22)$$

$$A_{c,tot} = \int_0^t A_c \cdot dt \quad (23)$$

Appendix 2

Definition of symbols

Values in parenthesis are those used in simulations, unless stated otherwise

| Term | Units | Definition |
|--------------------|--------------------------------------|--|
| A | $\mu\text{mol m}^{-2} \text{s}^{-1}$ | Net leaf rate of CO ₂ uptake per unit leaf area |
| A _c | $\mu\text{mol m}^{-2} \text{s}^{-1}$ | Net canopy rate of CO ₂ uptake per unit ground area |
| A _{c,tot} | $\text{mol m}^{-2} \text{d}^{-1}$ | A _c integrated over the course of 1 d |
| A _{sat} | $\mu\text{mol m}^{-2} \text{s}^{-1}$ | Light saturated value of A |
| C _a | $\mu\text{mol mol}^{-1}$ | Atmospheric CO ₂ concentration (350) |
| C _i | $\mu\text{mol mol}^{-1}$ | Intercellular concentration of CO ₂ in air, corrected for solubility relative to 25°C |
| D _j | d | Julian date (190) |
| f | (dimensionless) | Fraction of light not absorbed by functional photosynthetic pigments (0.23) |
| E | (J mol ⁻¹) | Activation energy; k _c (65 800), k _o (1400), R _d (66 405), V _{cmax} (68 000) |
| F | (m ² m ⁻²) | Leaf area index, i.e. the ratio of leaf area per unit ground area |
| F _{shade} | (m ² m ⁻²) | Shaded leaf area index |
| F _{sun} | (m ² m ⁻²) | Sunlit leaf area index |
| I | $\mu\text{mol m}^{-2} \text{s}^{-1}$ | Photon flux (2000) |
| I _{abs} | $\mu\text{mol m}^{-2} \text{s}^{-1}$ | Absorbed photon flux |
| I _{dir} | $\mu\text{mol m}^{-2} \text{s}^{-1}$ | Photon flux in direct beam solar radiation |
| I _{diff} | $\mu\text{mol m}^{-2} \text{s}^{-1}$ | Photon flux in diffuse radiation |
| I _s | $\mu\text{mol m}^{-2} \text{s}^{-1}$ | Solar constant, photon flux in a plane perpendicular to the solar beam above the atmosphere (2600) |
| I _{scat} | $\mu\text{mol m}^{-2} \text{s}^{-1}$ | Direct beam radiation scattered by surfaces within the canopy |
| I _{shade} | $\mu\text{mol m}^{-2} \text{s}^{-1}$ | Mean I for leaves shaded from direct sunlight within a canopy |
| I _{sun} | $\mu\text{mol m}^{-2} \text{s}^{-1}$ | Mean I for sun illuminated leaves within a canopy |
| I _{tot} | $\text{mol m}^{-2} \text{d}^{-1}$ | Total photon flux received in a horizontal plane above the canopy over the course of one day |
| J | $\mu\text{mol m}^{-2} \text{s}^{-1}$ | Potential rate of electron transport |
| J _{max} | $\mu\text{mol m}^{-2} \text{s}^{-1}$ | Light-saturated potential rate of electron transport (210) |
| k | dimensionless | Foliar absorption coefficient |
| K _c | $\mu\text{mol mol}^{-1}$ | Michaelis constant for CO ₂ (460) |
| K _o | mmol mol^{-1} | Michaelis constant for O ₂ (330) |
| O _a | mmol mol^{-1} | Atmospheric O ₂ concentration (210) |
| O _i | mmol mol^{-1} | Intercellular concentration of O ₂ in air, corrected for solubility relative to 25°C |
| P | kPa | Atmospheric pressure |
| P _o | kPa | Standard atmospheric pressure at sea level (101.324) |
| R | $\text{J K}^{-1} \text{mol}^{-1}$ | Gas constant (8.314) |
| R _d | $\mu\text{mol m}^{-2} \text{s}^{-1}$ | 'Dark respiration rate' (1.1) |
| t | h | Time of day |
| t _{sn} | h | Time of solar noon |
| T | °C | Leaf temperature |
| T _k | K | Absolute temperature |
| T _{opt} | °C | The optimum leaf temperature for net CO ₂ uptake |
| T _{max} | °C | The maximum daily temperature |
| T _{min} | °C | The minimum daily temperature |
| T _t | °C | Temperature at time t |
| V _c | $\mu\text{mol m}^{-2} \text{s}^{-1}$ | Carboxylation velocity |
| V _{cmax} | $\mu\text{mol m}^{-2} \text{s}^{-1}$ | Maximum rubP saturated rate of carboxylation (98) |
| V _o | $\mu\text{mol m}^{-2} \text{s}^{-1}$ | Oxygenation velocity |
| V _{omax} | $\mu\text{mol m}^{-2} \text{s}^{-1}$ | Maximum rubP saturated rate of oxygenation (0.21 V _{c,max}) |
| VPD | kPa | Leaf-air water vapour pressure deficit |
| W _c | $\mu\text{mol m}^{-2} \text{s}^{-1}$ | rubP saturated rate of carboxylation |
| W _j | $\mu\text{mol m}^{-2} \text{s}^{-1}$ | rubP limited rate of carboxylation |
| x | (dimensionless) | The ratio of horizontal:vertical projected area of a canopy (1) |
| Γ* | $\mu\text{mol mol}^{-1}$ | CO ₂ compensation point of photosynthesis in the absence of dark respiration |
| α | dimensionless | Atmospheric transmittance (0.75) |
| ϕ | mol mol^{-1} | The quantum yield of CO ₂ uptake determined from the initial slope of the response of A versus I _{abs} |
| δ | ° | Solar declination |
| Ω | ° | Latitude |
| θ | ° | Solar zenith angle |
| τ | ° | Angle between the leaf surface and the direct beam solar radiation |

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