

BOTANICAL BRIEFING

Modelling Plant Responses to Elevated CO₂: How Important is Leaf Area Index?

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• **Background and Aims** The problem of increasing CO₂ concentration [CO₂] and associated climate change has generated much interest in modelling effects of [CO₂] on plants. While variation in growth and productivity is closely related to the amount of intercepted radiation, largely determined by leaf area index (LAI), effects of elevated [CO₂] on growth are primarily via stimulation of leaf photosynthesis. Variability in LAI depends on climatic and growing conditions including [CO₂] concentration and can be high, as is known for agricultural crops which are specifically emphasized in this report. However, modelling photosynthesis has received much attention and photosynthesis is often represented inadequately detailed in plant productivity models. Less emphasis has been placed on the modelling of leaf area dynamics, and relationships between plant growth, elevated [CO₂] and LAI are not well understood. This Botanical Briefing aims at clarifying the relative importance of LAI for canopy assimilation and growth in biomass under conditions of rising [CO₂] and discusses related implications for process-based modelling.

• **Model** A simulation exercise performed for a wheat crop demonstrates recent experimental findings about canopy assimilation as affected by LAI and elevation of [CO₂]. While canopy assimilation largely increases with LAI below canopy light saturation, effects on canopy assimilation of [CO₂] elevation are less pronounced and tend to decline as LAI increases. Results from selected model-testing studies indicate that simulation of LAI is often critical and forms an important source of uncertainty in plant productivity models, particularly under conditions of limited resource supply.

• **Conclusions** Progress in estimating plant growth and productivity under rising [CO₂] is unlikely to be achieved without improving the modelling of LAI. This will depend on better understanding of the processes of substrate allocation, leaf area development and senescence, and the role of LAI in controlling plant adaptation to environmental changes.

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Key words: Elevated CO₂, leaf area index, modelling, photosynthesis, plant growth, scaling.

INTRODUCTION

It has been estimated that atmospheric CO₂ concentration [CO₂] will increase to between 540 and 970 µmol mol⁻¹ [CO₂] by 2100 (IPCC, 2001), which will affect plant and vegetation growth as demonstrated by numerous experiments and simulation studies. However, plant responses to rising [CO₂] vary (e.g. Kimball *et al.*, 2002) as a result of relationships that are not well understood and that involve complex responses of underlying growth and development to changes in [CO₂] and other environmental conditions.

Photosynthesis is without doubt the process that has been studied and modelled the most, not least because of the direct effect of [CO₂] on photosynthetic rate. However, at the more integrated plant and ecosystem level there is little evidence for a predictive relationship between leaf photosynthesis and growth. Instead, biomass production is closely related to light interception, which is mainly determined by leaf area index (LAI), as has been demonstrated for agricultural crops (e.g. Monteith, 1977) and other vegetation types (e.g. Hirose *et al.*, 1997). LAI varies depending on a number of factors including seasonal climate, water and nitrogen availability, and to some extent [CO₂] elevation (e.g. Drake *et al.*, 1997; Ewert and Pleijel, 1999; Hartz-

Rubin and DeLucia, 2001; Kimball *et al.*, 2002; Cowling and Field, 2003). Recent investigations suggest that canopy photosynthesis increases with LAI (Rochette *et al.*, 1995, 1996; Campbell *et al.*, 2001; Rodriguez *et al.*, 2001) and that effects of elevated [CO₂] on canopy photosynthesis decrease as LAI increases (Brooks *et al.*, 2000). Understanding of the relative importance of such relationships for vegetation growth and productivity is limited but essential for modelling systems responses to [CO₂].

Process-based models are increasingly used to predict effects of [CO₂] on crop and vegetation productivity (Amthor and Loomis, 1996; Tubiello and Ewert, 2002). These models integrate responses at the process level to the higher system level (van Oijen, 2002) and usually have some form of representation of LAI and photosynthesis depending on the underlying conceptual framework of the specific model. Results from comparison of models suggest that while model performance is often satisfactory at the system level, model behaviour at the process level is more critical (Ewert *et al.*, 2002). It is unclear to what extent uncertainties in estimating productivity changes due to rising [CO₂] are associated with inaccurate model assumptions about LAI.

The aim of this Botanical Briefing is to provide some clarification about the relative importance of LAI for plant

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responses under rising [CO₂] and to discuss related implications for process-based modelling. Relationships are analysed between canopy assimilation, elevated [CO₂] and LAI for an example wheat crop with reference to experimental data from Rodriguez *et al.* (2001) and Manderscheid *et al.* (2003). For the simulations performed here, the WIMOVAC modelling system was used (Humphries and Long, 1995). This has been applied in earlier studies to assess responses of photosynthesis and its characteristics at leaf and canopy level in relation to environmental conditions such as temperature, radiation or tropospheric ozone and [CO₂] (e.g. Burkart *et al.*, 2000; Rogers and Humphries, 2000; Martin *et al.*, 2001; Sage, 2002). Results from selected simulation studies are also reviewed (Ewert *et al.*, 1999, 2002; van Oijen and Ewert, 1999; Jamieson *et al.*, 2000) in order to discuss model uncertainties related to simulations of LAI.

APPROACHES OF PROCESS-BASED MODELLING

Processes affected by [CO₂]

Process-based models calculate biomass production from underlying growth and development processes (van Oijen, 2002) that are affected directly or indirectly by elevated [CO₂] (Fig. 1). An enormous number of these models have been developed over the last few decades (see reviews by Reynolds *et al.*, 1996; Tubiello and Ewert, 2002) with substantial differences between models in their structure and mechanistic detail. As estimating the effects of rising [CO₂] was not an original modelling aim, most models were adapted for this application at a later stage with more or less extensive modifications of the original model version (Tubiello and Ewert, 2002). The emerging diversity of [CO₂] modelling approaches has been reviewed elsewhere (Amthor and Loomis, 1996; Reynolds *et al.*, 1996; Boote *et al.*, 1997; Tubiello and Ewert, 2002) and needs no repetition here. Instead, a brief overview is given of approaches that are most commonly used in productivity models to simulate growth, light interception (including LAI) and photosynthesis.

Growth

Growth in biomass is either calculated as proposed by Monteith (1977) for agricultural crops from intercepted radiation and the efficiency with which energy is converted into dry matter (Table 1, eqn 1), or from net assimilation, which is computed as the result of canopy gross assimilation and respiration, often distinguished into growth and maintenance respiration (Table 1, eqn 2). However, the approximate constancy of energy conversion (e.g. Monteith 1977; Sinclair and Muchow, 1999), henceforth 'radiation use efficiency' (RUE), has made the RUE approach rather attractive for modelling growth, avoiding more complicated calculation and parameterization of carbon accumulation from leaf photosynthesis and respiration. Increase in RUE with [CO₂] (e.g. Mulholland *et al.*, 1998, Ewert *et al.*, 1999) has been modelled empirically using linear (e.g. Jamieson

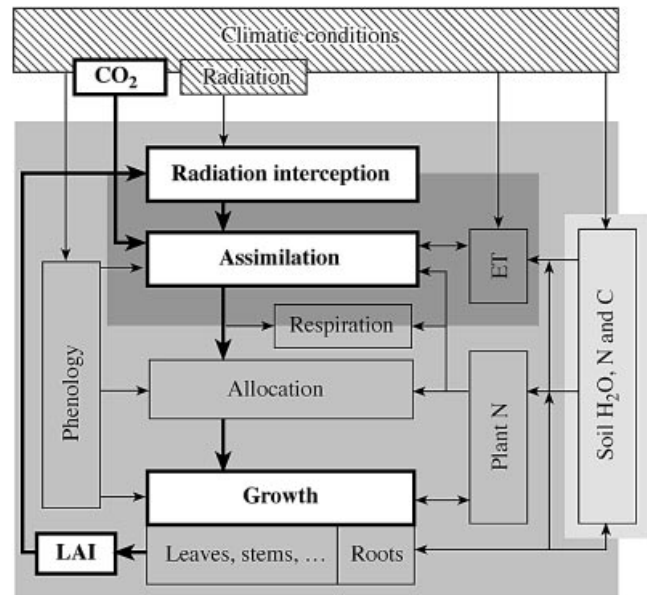


FIG. 1. Growth and developmental processes that are affected by elevated [CO₂] and are commonly used in process-based productivity models. Processes and relationships that are shown in white boxes and bold arrows are the ones primarily emphasized in the text. Grey areas indicate the temporal resolution of different processes ranging from seconds-to-hours (dark grey), to days (grey) and to decades-to-months (light grey).

et al., 2000) or curvilinear (e.g. Stockle *et al.*, 1992) multipliers (Table 1, eqn 1a). Recent studies report considerable variation in RUE depending on species, developmental stage and environmental conditions (e.g. Ruimy *et al.*, 1994; Sinclair and Muchow, 1999). Some attempts have been made to explore further such variations in RUE (Haxeltine and Prentice, 1996; Dewar, 1996; Ewert and Porter, 2000; Choudhury, 2001) and improve the modelling of RUE (Wolf *et al.*, 2002; Green *et al.*, 2003; Sitch *et al.*, 2003).

Light interception and leaf area index

Computation of light interception usually follows Lambert–Beer's function (Monsi and Saeki, 1953; Table 1, eqn 3). Interception of photosynthetically active radiation is usually calculated separately for direct and diffuse light (e.g. Spitters, 1986; Goudriaan and van Laar, 1994; Choudhury, 2001). Recent analysis of multi-species and/or multi-site data-sets report substantial variation in LAI with ranges between 1–10 and more (Ewert and Pleijel, 1999; Choudhury, 2001; Cowling and Field, 2003). LAI depends on a number of environmental factors and modelling LAI remains difficult due to the complexity of relationships determining substrate allocation and growth and development of leaf area. Methodological differences and associated difficulties in measuring LAI cause additional errors (see Levy and Jarvis, 1999; Bréda, 2003), which are not further addressed in this report. Most productivity models simulate dry matter partitioning using descriptive allometry models based on empirically derived ratios between growth

TABLE 1. Summary of approaches with explanation of parameters for modelling responses to [CO₂] of growth, radiation interception and photosynthesis commonly used in crop and vegetation productivity models (see text for further explanation and references)

Approach	Equation no.	Parameters*
Growth rate		
I $dC/dt = S_i \varepsilon$	1	C , growth; t , time; S_i , intercepted solar radiation; ε , radiation use efficiency
$\varepsilon = \varepsilon f(c_a) f(n_c) f(F_{l,diff})$	1a	c_a , atmospheric CO ₂ concentration; n_c , canopy nitrogen content; $F_{l,diff}$, fraction of diffuse radiation
II $dC/dt = A_g - (R_g + R_m)$	2	A_g , gross photosynthesis; R_g , growth respiration; R_m , maintenance respiration
Radiation interception and LAI		
I $S_i/S_0 = e^{-kL}$	3	S_0 , solar radiation above canopy; k , light extinction coefficient; L , leaf area index
$L = C_l L_{sa}$	3a	C_l , leaf growth; L_{sa} , specific leaf area
Leaf photosynthesis		
I $\theta A_1^2 - A_1(\alpha I_1 + A_{sat})A_1 + \alpha I_1 A_{sat} = 0$	4	A_1 , leaf gross assimilation rate; A_{sat} , leaf maximum assimilation rate; I_1 , intercepted PAR at leaf; α , quantum efficiency; θ , curvator
$A_{sat} = A_{sat} f(c_a) f(T) f(n_1)$	4a	T , temperature; n_1 , leaf nitrogen content
$\alpha = \alpha f(c_a) f(T)$	4b	
II $A = \min\{A_q, A_r\} - R_d$	5	A , leaf net assimilation rate; A_q , light limited assimilation; A_r , Rubisco limited assimilation; R_d , day respiration
$A_q = V_m \frac{c_i - \Gamma^*}{c_i + K_c}$, $A_r = J \frac{c_i - \Gamma^*}{4.5c_i + 10.5\Gamma^*}$	5a, 5b	V_m , maximum carboxylation velocity; c_i , intercellular CO ₂ concentration; Γ^* , CO ₂ compensation point in the absence of respiration; K_c , function of enzyme; J , electron transport rate
$c_i = c_a - A/g_{sc}$	5c	g_{sc} , stomatal conductance
$g_{sc} = g_0 + a_1 f(D) A / (c_a - \Gamma)$	5d	$f(D)$, function of humidity deficit; Γ , CO ₂ compensation point; g_0 , residual conductance; a_1 , empirical parameter
Canopy photosynthesis		
I $A_g = \int_0^{LAI} A_1(L_z) dL_z$	6	LAI , leaf area index; L_z , LAI at level z of the canopy
II $A_n = A F_i / k$	7	A_n , canopy net photosynthesis; f_i , fraction of incident PAR absorbed by the canopy

* Explanation of each parameter is given at its first use in an equation

rates or relative growth rates (see review by Marcelis *et al.*, 1998; Table 1, eqn 3a). Such ratios are usually assumed to change with phenological development, but effects of environmental conditions have only recently been incorporated using more mechanistic modelling approaches (e.g. Dewar *et al.*, 1998; Marcelis *et al.*, 1998; Thornley, 1998).

Photosynthesis

Physiology-based models that calculate growth in biomass from leaf photosynthesis (see Table 1, eqn 2) have some formulation to account for the non-linear relationship between assimilation rate and intercepted radiation. Simple empirical approaches employ exponential (Goudriaan and van Laar, 1994) or hyperbolic functions (Boote and Loomis, 1991; Table 1, eqn 4). Empirical relationships have been used to model [CO₂] effects on quantum efficiency and light-saturated photosynthesis rate (Table 1, eqn 4a, b). Despite its simplicity, this approach has been demonstrated satisfactorily to reproduce observed photosynthetic responses for a range of environmental conditions including elevated [CO₂] (Cannell and Thornley, 1998; Thornley, 1998; Rodriguez *et al.*, 2001). However, the most common approach to modelling photosynthesis is the one described first by Farquhar *et al.* (1980) (Table 1, eqn 5) where

photosynthesis rate, limited by either light or Rubisco, is modelled in more detail from underlying biochemical relationships (Table 1, eqn 5a, b). This approach and its improved versions (e.g. Collatz, 1990), and parameter responses to temperature and nitrogen (e.g. Long 1991; Harley *et al.*, 1992; Sage, 1994, 2002; Drake *et al.*, 1997; Medlyn *et al.*, 2002), have been described in detail many times and will not be repeated here. Effects of elevated [CO₂] on leaf photosynthesis are calculated from intercellular [CO₂] (Table 1, eqn 5a), which is often computed iteratively through coupling of a photosynthesis model with equations for stomatal conductance and intercellular [CO₂] (e.g. Leuning, 1995; Table 1, eqn 5c, d).

Scaling photosynthesis from leaf to canopy and acclimation to [CO₂]

Vegetation models that are based on photosynthesis need some approach to integrate responses from the leaf to the canopy level. The most conventional approach is the multi-layer model where leaf photosynthesis is integrated down the canopy, following radiation interception (e.g. Thornley, 1998; Table 1, eqn 6). Much emphasis has been on the development of simpler models such as the 'big-leaf approach' (e.g. Sellers *et al.*, 1992; Kull and Jarvis, 1995;

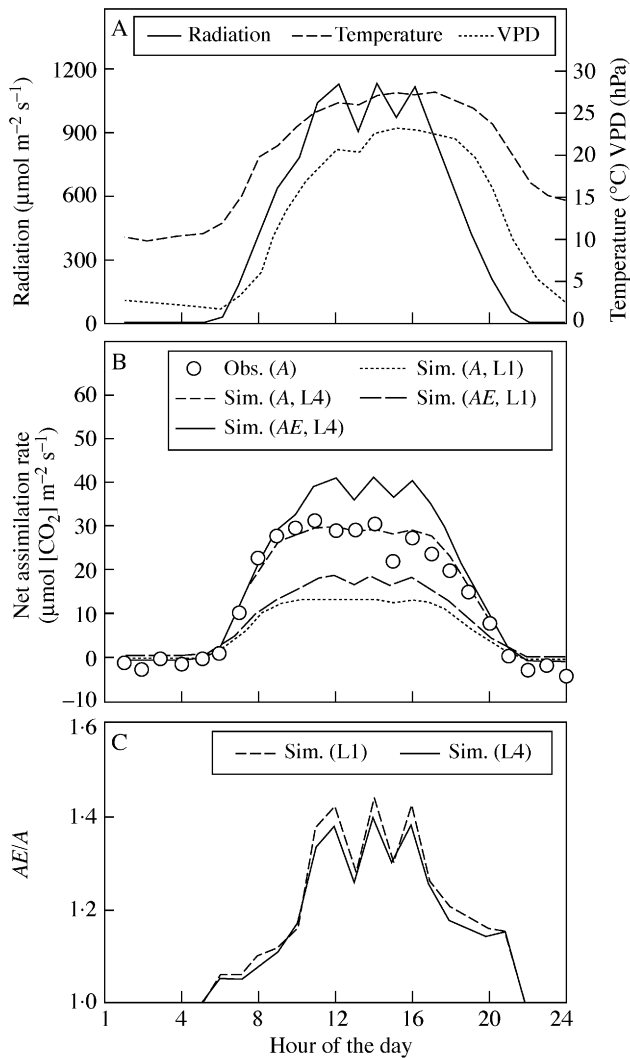


FIG. 2. Diurnal course of (A) measured air temperature, incident radiation and vapour pressure deficit (VPD) used as model input; (B) observed and simulated (WIMOVAC) instantaneous net assimilation rate of two wheat canopies with LAI = 1 (L1) and LAI = 4 (L4) at $360 \mu\text{mol mol}^{-1}$ [CO₂] (A) and $720 \mu\text{mol mol}^{-1}$ [CO₂] (AE); and (C) the simulated relative effects of [CO₂] elevation on canopy assimilation (AE/A) for L1 and L4. Measured assimilation rates are shown in (B) for A and LAI = 4.2. Information about experimental conditions and measurements are available in Rodriguez *et al.* (2001) and Manderscheid *et al.* (2003).

Friend *et al.*, 1997; Woodward and Lomas, 2001; Table 1, eqn 7) where the whole canopy is treated as one big leaf, often separated into a sunlit and sun-shaded part. Despite its wide acceptance, the physiological basis of the assumptions behind the big-leaf approach have recently been questioned (Kull and Kruijt, 1998; Friend, 2001). Since leaf assimilation rate is closely related to leaf incident radiation and nitrogen content, a number of studies have aimed at improving the understanding and modelling of radiation and nitrogen distribution within the canopy (see Dewar, 1996; Medlyn, 1998; Choudhury, 2001; Kull 2002) including relationships to [CO₂] elevation (Long and Drake, 1991; Hirose *et al.*, 1997; Hartz-Rubin and DeLucia, 2001). Optimization of nitrogen distribution within the canopy

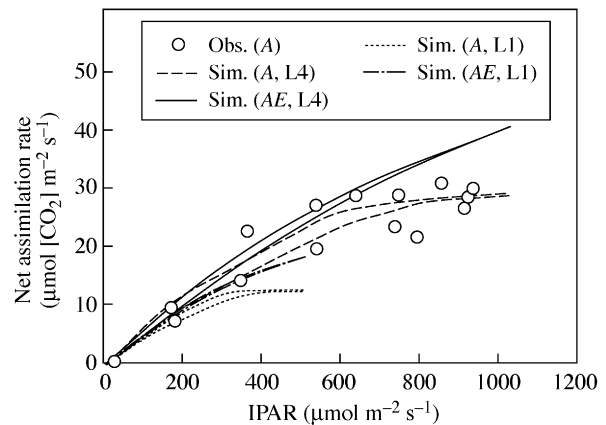


FIG. 3. Relationships between simulated (WIMOVAC) and observed (only for A and LAI = 4.2) instantaneous canopy net assimilation rate and intercepted photosynthetically active radiation (IPAR) for LAI = 1 (L1) and LAI = 4 (L4) at ambient (A) and elevated (AE) [CO₂]. Data refer to simulations and observations presented in FIG. 2.

(Field 1983; Hirose and Weger, 1987; Badeck, 1995) is commonly used to explain photosynthetic acclimation to low radiation.

Acclimation to [CO₂], i.e. the failure of plants to sustain the initial, maximal stimulation of photosynthesis (e.g. Gunderson and Wullschlegel, 1994; Drake *et al.*, 1997), can occur after long-term exposure to elevated [CO₂] and reduced N supply (Sage, 1994; Drake *et al.*, 1997). A related decrease in maximum carboxylation velocity of Rubisco (Rogers and Humphries, 2000) is caused by limitation of sink development (Rogers *et al.*, 1998) and a temporal shift of leaf ontogeny (Ludewig and Sonnewald, 2000). Mechanisms that explain acclimation and adaptation to [CO₂] at the whole-plant level are more complex and are not well understood (Wolfe *et al.*, 1998), and modelling remains difficult.

EFFECTS ON CANOPY ASSIMILATION

A well-validated multi-layer model of canopy photosynthesis was used to demonstrate characteristic responses of instantaneous and daily canopy net assimilation to LAI reported for annual, single-species vegetation stands (Figs 2–4). Briefly, canopy photosynthesis increases with LAI (Baldocchi, 1994; Rochette *et al.*, 1995, 1996; Campbell *et al.*, 2001; Rodriguez *et al.*, 2001; Sakai *et al.*, 2001) but the effect of LAI depends on radiation level and is particularly high at noon when incident radiation is high (Fig. 2). LAI largely affects the canopy radiation saturation point (Fig. 3; see also Baldocchi, 1994; Rochette *et al.*, 1995, 1996; Campbell *et al.*, 2001), so that in dense canopies assimilation further increases with incident radiations above the radiation saturation point of individual leaves. The effect of LAI on the initial slope of the regression between canopy assimilation and intercepted radiation is comparably small (Fig. 3). This suggests that for canopy sub-saturated radiation conditions effects on instantaneous RUE of LAI are small (Fig. 3; see also Medlyn,

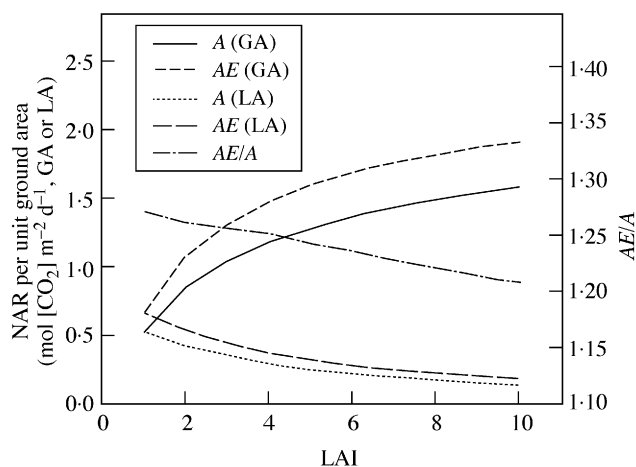


FIG. 4. Simulated (WIMOVAC) relationships between daily canopy net assimilation rate per unit ground area (GA) and per unit leaf area (LA) and LAI for ambient (A) and elevated (AE) [CO₂]. Relative [CO₂] effects are calculated from AE/A. Climate input data and [CO₂] concentrations were the same as in Figs 2 and 3.

1998) and are likely to be insignificant (Choudhury, 2001, Green *et al.*, 2003; but see Campbell *et al.*, 2001). The implication for daily integrated responses is shown in Fig. 4. Clearly, as LAI increases more radiation is intercepted per unit ground area resulting in higher assimilation rates, which tend to level out at high LAI. In contrast, intercepted radiation and assimilation rate decrease with increasing LAI on a per unit leaf area basis (Fig. 4).

The present simulations further demonstrate that elevated [CO₂] increases canopy assimilation, particularly at noon (Fig. 2; see also Brooks *et al.*, 2000; Rodriguez *et al.*, 2001) and in sparse canopies (Figs 3, 4; Brooks *et al.*, 2000). Thus, as LAI increases less radiation is intercepted per unit leaf area. This results in a smaller stimulation of photosynthetic assimilation at elevated [CO₂], a mechanism apparently sufficient to explain interactions between LAI and [CO₂] observed in the field (Brooks *et al.*, 2000).

It can be seen from the simulations (Fig. 4) that an additional increase in LAI by 10–30 % due to [CO₂] elevation (e.g. Ewert *et al.*, 1999; Rodriguez *et al.*, 2001; Kimball *et al.*, 2002) would have a relatively small effect on radiation interception (not shown) and canopy assimilation, particularly when LAI is high and close to radiation saturation (see also Drake *et al.*, 1997; Brooks *et al.*, 2000; Manderscheid *et al.*, 2003).

Acclimation and adaptation to [CO₂] were not considered in the present example since simulations were performed for unstressed conditions. However, modification in canopy architecture (Brooks *et al.*, 2000) may reduce the stimulatory effect of [CO₂] elevation (Figs 2–4). Leaves of C₃ plants tend to be more erectophile in ambient compared to elevated [CO₂], with the implication that solar radiation is distributed more uniformly (i.e. increase in *k*, eqn. 3), which results in increased canopy assimilation (Brooks *et al.*, 2000).

Importantly, for the range of conditions considered here, canopy assimilation was largely affected by LAI below

canopy radiation saturation and to a lesser extent by [CO₂] elevation. Interactive effects between [CO₂] elevation and LAI were relatively small.

EFFECTS ON BIOMASS: EVIDENCE FROM MODEL TESTING

There is a remarkable imbalance between the large number of models available and applied for estimating [CO₂] effects on field-grown plants and the limited number of studies that have actually tested models against the few available data sets (Tubiello and Ewert, 2002). Most model-testing exercises have demonstrated satisfactory model results even for conditions where resources such as H₂O or N were limiting (see Tubiello and Ewert, 2002). However, a few studies have reported unsatisfactory simulations and differences among models, particularly for experiments that represented a larger range in climatic and growing conditions (Ewert *et al.*, 1999, 2002; van Oijen and Ewert, 1999). Further analysis indicates that difficulties in estimating LAI form an important source of model uncertainty (Fig. 5; see also Wolf *et al.*, 2002). Accurate prediction of LAI can improve model behaviour at the systems level significantly, both under ambient and elevated [CO₂] (Fig. 5). This even applies to conditions of limited N or H₂O supply and seems independent of the model's approach for canopy assimilation (Jamieson *et al.*, 2000; Ewert *et al.*, 2002). However, there are large differences among models in simulating LAI, with important implications for simulations of biomass (e.g. Jamieson *et al.*, 1998), which has also been reported for elevated [CO₂] (Ewert *et al.*, 2002).

THE PROBLEM OF SCALING-UP

Numerous studies have aimed at scaling responses of leaf photosynthesis to changes in [CO₂] and other environmental conditions from the leaf to the canopy, plant, ecosystem and even global level. However, aggregation of fine (leaf-) scale photosynthetic variability to higher spatial and temporal scales remains difficult since systems' functions and responses to environmental conditions generally change with scale. Hierarchy theory (Allen and Star, 1982; O'Neill, 1986) suggests that it is seldom necessary to look more than one level down in search of a mechanistic explanation of a system's behaviour. Instead, representation of important processes and consistency in modelling detail within hierarchical layers are important criteria for process-based modelling (Leffelaar, 1999). Photosynthesis models such as the one by Farquhar *et al.* (1980) were originally developed to explain [CO₂] exchange by leaves to environmental conditions (Farquhar *et al.*, 1980, 2001). Such detail in process modelling with a time-step of seconds to hours is in contrast to other processes that are also important at the plant and ecosystem level with characteristic time-steps of days and larger (Fig. 1). It has recently been shown that the temporal resolution (hours, days, months or years) of input data has a significant impact on RUE (Ruimy *et al.*, 1994; Medlyn, 1998; van Wijk and Bouten, 2002). As the time scale increases, RUE becomes less variable (e.g. Medlyn,

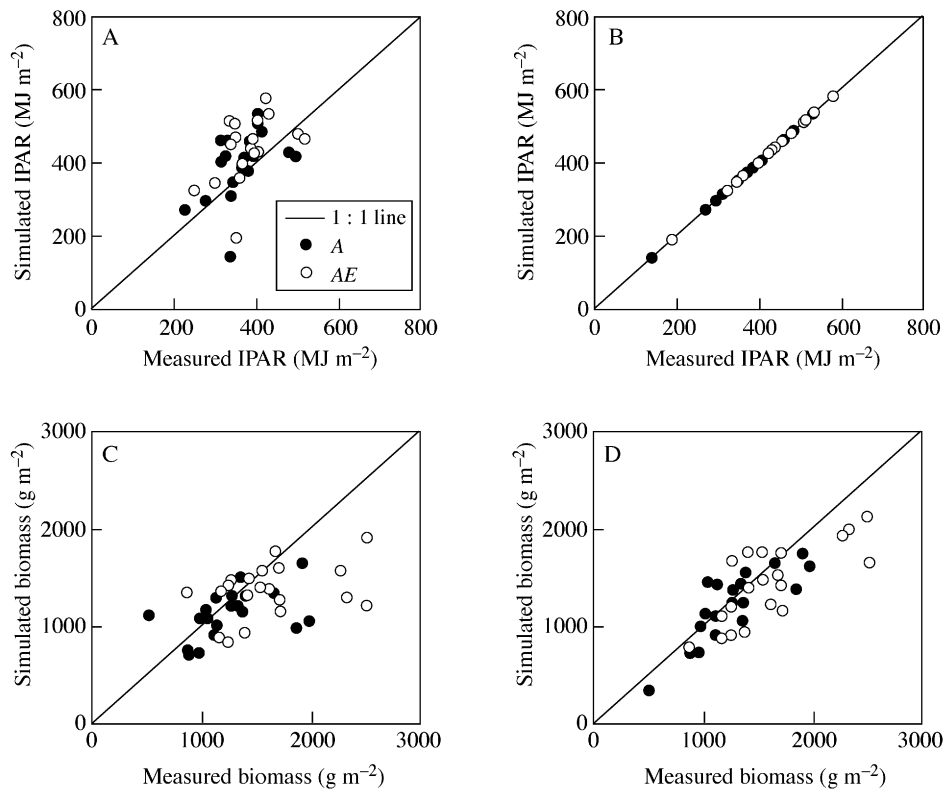


FIG. 5. Simulated (AFRCWHEAT2-O3) vs. measured IPAR (A, B) and biomass at harvest maturity (C, D) for spring wheat 'Minaret' grown at ambient (A) and elevated ($2 \times$ ambient, AE) [CO₂] at eight location across Europe between 1994–1996. Simulations were performed using simulated LAI (A, C) or observed LAI (B, D) as model input. Original simulations of biomass (C) that used model estimates of LAI were unsatisfactory (see also Ewert *et al.*, 1999) but improved substantially when observed LAI data were used as model input (D). The remaining unexplained variability was due to factors mainly associated to the use of open-top chambers that were not considered in the model (see Ewert and Porter, 2000; Ewert *et al.*, 2002).

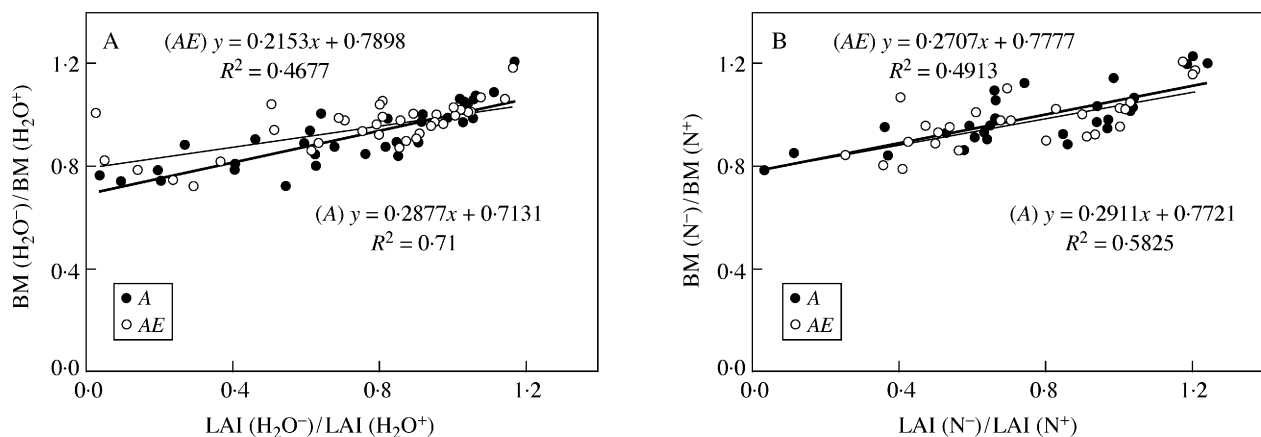


FIG. 6. Relationships between effects on biomass (BM) and effects on LAI of limited (A) water and (B) N supply for ambient (A) and elevated ($1.5 \times$ ambient, AE) [CO₂] of wheat 'Yecora Rojo' grown at Maricopa, Arizona in 1992–93 and 1993–94 (H₂O limitation) and 1995–96 and 1996–97 (N-limitation). Ratios were calculated from measurements of biomass and LAI at different occasions throughout each growing season in water-stressed (H₂O⁻) and well-watered (H₂O⁺) and N-limited (N⁻) and non-limited (N⁺) treatments, respectively. References about data sources with information about experimental performances can be obtained from Jamieson *et al.* (2000) and Ewert *et al.* (2002).

1998). Consequently, other processes become more important for explaining systems' behaviour.

In this brief report I have tried to demonstrate the importance of LAI for determining variation in plant productivity under ambient and elevated [CO₂]. The

examples considered here refer to unstressed conditions. However, recent evidence suggests that limited supply of H₂O (Jamieson *et al.*, 1998) and N (Jamieson *et al.*, 2000; Poorter and Nagel, 2000) also affect plant growth significantly via changes in LAI. Interactions between these

factors and [CO₂] elevation for growth and productivity at field and larger scales are not well understood but are likely to be small. There is recent evidence that elevated [CO₂] has little or no effect, respectively, on the role of LAI to control growth responses to H₂O and N limitation (Fig. 6).

Modelling LAI is still in its infancy, particularly for stressed conditions. Recent advances in modelling allocation (Dewar *et al.*, 1998), leaf area development and senescence (Jamieson and Semenov, 2000; Yin *et al.*, 2000; Franklin and Ågren, 2002) offer promising concepts but require further evaluation and, eventually, consideration in plant productivity models. Importantly, processes determining LAI should be viewed as properties of the canopy (Franklin and Ågren, 2002) or even of the ecosystem rather than of that of a single leaf. In this respect, investigations about the role of LAI in controlling plant adaptation to environmental changes (Hirose *et al.* 1997; Jamieson *et al.*, 1998; Jamieson and Semenov, 2000), including optimization of canopy photosynthesis (Anten *et al.*, 1995, Franklin and Ågren, 2002), are of particular interest.

SUMMARY

This brief report has demonstrated the relative importance of LAI for canopy assimilation and growth in biomass under conditions of rising [CO₂] and the need for satisfactory representation of LAI in plant productivity models. Interactions between LAI and [CO₂] effects on canopy assimilation are relatively small but require further investigation. Effects of LAI on RUE are also not well understood but are likely to be small. My conclusion is that progress in estimating future plant productivity under conditions of rising [CO₂] is unlikely to be achieved without improving the modelling of LAI, particularly for vegetation types with a large variability in LAI, such as agricultural crops. Improved modelling of LAI will depend on better understanding of the processes of substrate allocation, leaf area development and senescence, and the role of LAI in controlling plant adaptation to environmental changes.

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