Oecologia (2001) 129:1–20
DOI 10.1007/s004420100736

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The growth response of plants to elevated CO_2 under non-optimal environmental conditions

Received: 10 August 2000 / Accepted: 19 April 2001 / Published online: 25 July 2001

Abstract Under benign environmental conditions, plant growth is generally stimulated by elevated atmospheric CO_2 concentrations. When environmental conditions become sub- or supra-optimal for growth, changes in the biomass enhancement ratio (BER; total plant biomass at elevated CO_2 divided by plant biomass at the current CO_2 level) may occur. We analysed literature sources that studied CO_2×environment interactions on the growth of herbaceous species and tree seedlings during the vegetative phase. For each experiment we calculated the difference in BER for plants that were grown under 'optimal' and 'non-optimal' conditions. Assuming that interactions would be most apparent if the environmental stress strongly diminished growth, we scaled the difference in the BER values by the growth reduction due to the stress factor. In our compilation we found a large variability in CO_2×environment interactions between experiments. To test the impact of experimental design, we simulated a range of analyses with a plant-to-plant variation in size common in experimental plant populations, in combination with a number of replicates generally used in CO_2×environment studies. A similar variation in results was found as in the compilation of real experiments, showing the strong impact of stochasticity. We therefore caution against strong inferences derived from single experiments and suggest rather a reliance on average interactions across a range of experiments. Averaged over the literature data available, low soil nutrient supply or sub-optimal temperatures were found to reduce the proportional growth stimulation of elevated CO_2. In contrast, BER increased when plants were grown at low water supply, albeit relatively modestly. Reduced irradiance or high salinity caused BER to increase in some cases and decrease in others, resulting in an average interaction with elevated CO_2 that was not significant. Under high ozone concentrations, the relative growth enhancement by elevated CO_2 was strongly increased, to the extent that high CO_2 even compensated in an absolute way for the harmful effect of ozone on growth. No systematic difference in response was found between herbaceous and woody species for any of the environmental variables considered.

Keywords Nutrients · Water · Light · Temperature · Salt · Ozone

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The complex effect of elevated CO_2 on plant growth

The current increase in the atmospheric CO_2 concentration has triggered a wide variety of botanical investigations during the last two decades, at a range of integration levels. Notwithstanding this huge effort, we still have only a limited understanding about the effect of elevated CO_2 on plant growth. There is considerable variation in the direction and magnitude of growth responses to elevated CO_2, partly depending on the duration of the exposure, plant development, species (e.g. species that differ in inherent growth rate or type of photosynthetic pathway) and the availability of primary resources (Kimball 1986a; Idso and Idso 1994; Poorter et al. 1996; Curtis and Wang 1998; Saxe et al. 1998). However, there is still debate about when and where and to what extent these factors are important (Kimball 1986b; Idso and Idso 1994; Lloyd and Farquhar 1996, 2000; Poorter 1998; Stitt and Krapp 1999). The situation becomes even more complex if we take into account that concomitant with the increased level of CO_2, there are also increases in the level of air pollutants (ozone, nitrogen oxides, sulphur dioxide) and ultraviolet radiation. Enhanced deposition of air pollutants results in eutrophication and acidification of natural ecosystems. Increased emissions of CO_2, methane and chlorofluorocarbons might result in increased temperature and alterations in other climate

parameters, such as the distribution and intensity of clouds (light) and precipitation (water). We therefore need to analyse how these changing environmental factors may modify the impact of elevated CO_2 on plant growth.

A range of research papers and reviews has dealt with the interactions between elevated atmospheric CO_2 concentration and environmental factors (e.g. Kimball 1986b; Gifford 1992; Idso and Idso 1994; Curtis and Wang 1998; Poorter 1998; Luo and Mooney 1999). In most experiments, the CO_2 effect is analysed at two levels of another environmental factor, sometimes with quite contrasting results that hinder generalisations across experiments (Rawson 1992). Differences in response between species might be responsible for different results. Far less attention has been paid to the possibility that these differences are merely due to chance. In the first part of this paper, we analyse the degree of variability in the results of a CO_2×environment interaction when we repeatedly sample a limited number of plants from the same experimental population.

In the second part, we try to obtain an overall picture of the interaction between elevated CO_2 and environmental factors, such as primary resources, temperature and air pollutants. We will restrict our analysis to individually grown plants in the vegetative stage. Apart from the stochastic variation mentioned above, another factor may hinder generalisations across experiments, i.e. the range of environmental growth conditions applied in different experiments, which most likely stress plants to different degrees. Therefore, we follow a method that links the growth stimulation due to elevated CO_2 to the growth reduction at ambient levels of CO_2 due to the stress factor. That is, the severity of the applied environmental stress, as evident from the growth reduction in the control CO_2 plants, is used to scale the change in biomass response to elevated CO_2. This allows one to, at least partly, correct for differences between experiments. An additional advantage of this approach is that we can compare interactions between elevated CO_2 and a range of growth-limiting environmental factors at the same scale.

Methodology

SLB, a parameter to quantify CO_2×environment interactions

The minimal experimental design to analyse CO_2×environment interactions requires an orthogonal combination of two CO_2 concentrations (ambient and elevated) and two levels of the other environmental factor (optimal and non-optimal for growth). To quantitatively analyse those experiments, we used a method based on two main parameters. The first is an indicator of the stimulating effect of elevated CO_2 on total plant biomass (sum of above- and belowground biomass) and is calculated as the ratio of plant biomass at elevated and at ambient CO_2 levels. We call this the 'biomass enhancement ratio', using BER as an acronym. The second parameter is an indicator of the stress experienced by plants due to a non-optimal level of the environmental factor under study. For each experiment, we considered as the 'optimal' level, the treatment that resulted in the highest total biomass. The intensity of the stress was then calculated as the reduction in total biomass at ambient CO_2 of plants grown at the non-optimal level compared to the total biomass of plants grown at the optimal level. We call this the 'growth reduction due to stress' (GRS) and calculated it as:

$$\mathrm{GRS} = \frac{M_\mathrm{o} - M_\mathrm{s}}{M_\mathrm{o}} \quad (1)$$

with M_O and M_S being the total biomass of plants at the optimal level O and at a certain sub- or supra-optimal level S, respectively. We thereby assume that the higher the GRS, i.e. the larger the difference in biomass between the optimal and a non-optimal level, the stronger was the stress experienced by the plants. Because ratios are ln-normally distributed by nature, we first ln-transformed the BER values obtained under optimal and non-optimal conditions, and then scaled the difference between these two values by the growth reduction observed because of the interacting stress factor applied:

$$\mathrm{SLB} = \frac{\ln(\mathrm{BER_s}) - \ln(\mathrm{BER_o})}{\mathrm{GRS}} \quad (2)$$

where SLB is an acronym for 'slope of the line connecting the two BER values'. A graphical example of our method is given in Fig. 1. If plant biomass is as specified in the insert, then the ratio of plant biomass at elevated CO_2 relative to ambient CO_2 (BER) is 2 at the optimal level and 1.5 at the sub-optimal level. At ambient CO_2, we assume that the treatment with the highest biomass is optimal, with a GRS of 0 as the *x*-value at which we plot the BER of 2. The growth reduction due to the sub-optimal level is 0.6, the *x*-value at which we plot the BER of 1.5. These values result in an SLB of –0.48. A negative SLB indicates that at a given non-optimal level of the interacting factor, the relative growth response to elevated CO_2 is smaller than under optimal conditions. Note that in most of this paper we will focus on the relative growth response; the absolute growth response will almost always be lower under suboptimal conditions.

A weak point in this approach is that we assume that BER changes linearly from optimal to non-optimal levels and that the environmental condition at which plants show the largest growth

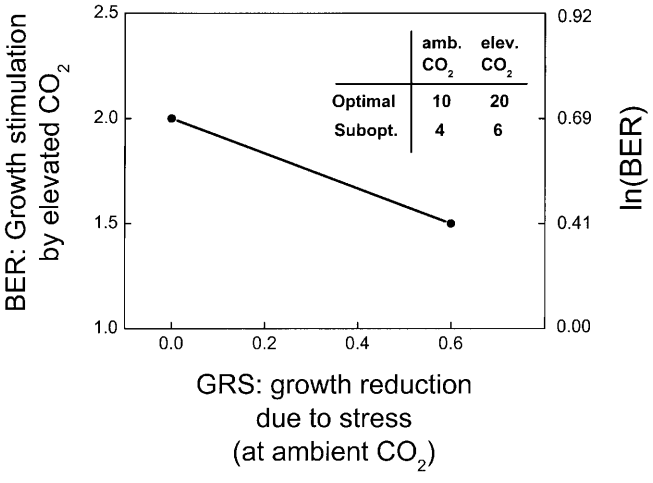

Fig. 1 Example to show the method used to calculate the effect of limiting factors on the biomass enhancement ratio (BER). The *x*-axis represents the reduction in total biomass at ambient CO_2 of plants grown at the sub- or supra-optimal level when compared to the total biomass of plants grown at the optimal level (growth reduction due to stress, GRS). The *y*-axis represents the ratio of plant biomass at elevated and ambient CO_2 levels. The positive, zero or negative sign of the slope of the line connecting the two BER values indicates the type of interaction (see text). For the calculations, all BER values have to be ln-transformed prior to any statistical analysis, as ratios are ln-normally distributed by nature. The slope in this case is –0.48

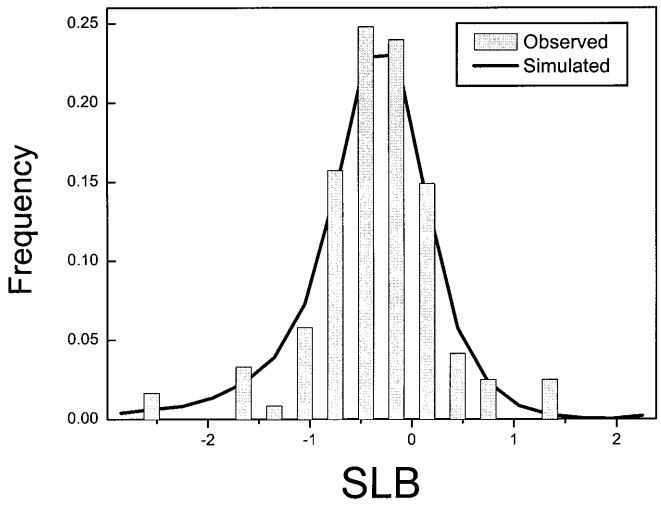

Fig. 2 Frequency distribution of CO_2×nutrient interactions. *Bars* indicate SLB values derived from 123 published observations. The *bold line* indicates the distribution of SLBs after simulating a range of experiments with a low (n=4), an intermediate (n=5) and a high (n=10) number of replicates per treatment, harvesting plant populations with either a low (σ_{lnM}=0.21), an intermediate (σ_{lnM}=0.31) or high (σ_{lnM}=0.51) variability in dry mass. The average mass for the four different treatments was chosen so that both GRS and SLB were exactly the same as the average values in the compiled data set. More information is given in the text

response is truly optimal; this may not necessarily be the case. An advantage is that the same method can be applied to different environmental variables, since the interactive effect with elevated CO_2 is related to the growth reduction caused by the non-optimal level and not to the environmental level itself. This enables a comparison of different treatments, using the growth reduction due to the stress factor as a biological yardstick.

Biomass responses were analysed based on a compilation of published and unpublished experiments on individually grown herbaceous and woody C_3 species (see Appendix 1 and 2). C_4 species were excluded, because the low number of CO_2×environment studies conducted with these plants hardly allows any generalisation. In addition, we did not consider those studies in which the non-optimal treatment caused a growth reduction of less than 10%, both because we felt that such a treatment was not stressful for the plants and because the GRS would become too small to accurately determine the slope of the line in Eq. 2. Following the above method, we calculated the SLBs for a range of factorial experiments, restricting the analysis to plants in the vegetative phase. The ambient CO_2 concentration ranged between 300 and 400 µl l^{-1}, and the elevated CO_2 concentration between 550 and 1,100 µl l^{-1}, except for one experiment with high salinity.

How precisely can an interaction be determined?

The SLB values may differ substantially between experiments. An example is given in Fig. 2, where we plotted the distribution of SLB values for 123 observations of plant species grown in a factorial combination of elevated CO_2 and nutrient supply (grey bars). In some cases, strong positive interactions were reported (e.g. Whitehead et al. 1997: SLB>1); in other cases, strong negative SLBs were found (e.g. Heath and Kerstiens 1997: SLB<–2). Most discussions almost automatically assume that such contrasting responses are due to the fact that different experiments use different species, another level of the stress factor, or simply a different combination of growth conditions (e.g. Lloyd and Farquhar 2000). A factor that has received less attention is plant variability within treatments. The slope calculated to determine a CO_2×environment interaction is based on the biomass of at least four differently treated groups of plants, each with its own variability in total biomass. Consequently, the estimate of the slope is affected by the added variability in all four experimental groups (cf. Poorter et al. 1996; Hedges et al. 1999; Jasienski and Bazzaz 1999). The precision of the slope is co-determined by the number of plants harvested per treatment. Because of constraints on space and labour, the number of replicates harvested per treatment in experiments that study CO_2 effects in combination with other factors will generally be low. This is unfortunate, because it decreases precision whereas, in fact, due to the added variability in *four* plant groups, a higher number of replicates would have been required than in a single-factor experiment with two groups of plants.

To what extent might plant-to-plant variability explain the observed variation in SLBs as in Fig. 2? Because we do not know all the details of each experiment, we can only answer this question by a simulation of the most likely situation. From the specifications of the CO_2×nutrient experiments provided by the authors, we know that the median number of plants harvested per treatment was five. A low number is four, and a high number is ten, as judged from the 20th and 80th percentile, respectively, of the compiled number of plants harvested in these experiments. We do not know the variability in the plant populations under investigation. Poorter and Garnier (1996) used the standard deviation in ln-transformed dry mass (σ_{lnM}) as a way to characterise variability in experimental plant populations. From their compilation of a range of experiments, we derive an average σ_{lnM} of 0.31 (50th percentile), a low value of 0.21 (20th percentile) and a high value of 0.51 (80th percentile). Assuming now that the true GRS and SLB values were the average of the 123 experimental observations (0.55 and –0.41, respectively), and that plant-to-plant variability is not altered by elevated CO_2, we simulated experiments in which we randomly 'harvested' four, five or ten plants out of three artificial populations with a σ_{lnM} of 0.21, 0.31 or 0.51, respectively. In this way, we arrived at nine different scenarios, and for each of these combinations of n and σ_{lnM}, we simulated 5,000 experiments. We assume that the aggregated distribution of calculated slopes gives us a reasonable estimate of the extent to which slopes vary due to random variation in biomass alone. The simulated distribution of SLB values is shown as the continuous line in Fig. 2. Although the 'true' (average) SLB value was negative, positive interactions were observed in 22% of the simulations. Moreover, variation was largely similar to that observed in the literature. Based on this simulation, we conclude that the relatively low number of plants harvested from rather variable populations can explain most of the observed variability in CO_2×nutrient interactions. We do not doubt that variation in SLB is also partly due to differences between species or growth conditions. However, in our opinion, support for these alternative explanations has to be found in an a posteriori analysis of a range of experiments and not in the mere observation that species A in experiment 1 responded differently from species B in experiment 2 (see also General discussion below). In the analysis to follow, we will consider the average response across all observations, and only test for possible differences between herbaceous and woody species in general, unless otherwise stated.

Interaction of CO_2 with primary resources

Low nutrient supply

From the literature data listed in Appendix 1 and 2 and plotted in Fig. 2, we obtained the distribution of the slopes represented by the boxplots of Fig. 3. On average, the SLB for nutrients was negative (P<0.001), with no indication of a difference between herbaceous and woody species (P>0.5). This implies that a decrease in nutrient availability reduces the relative growth response

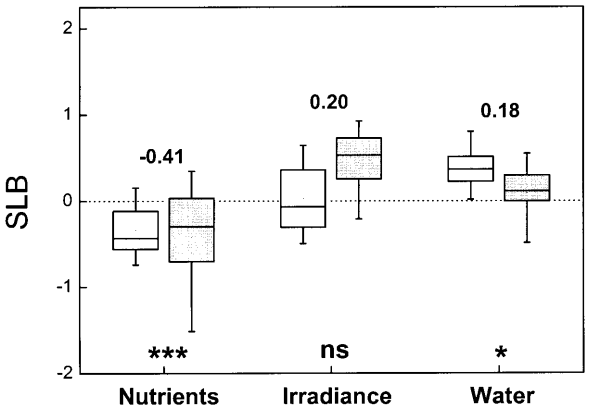

Fig. 3 Distribution of slopes (SLB), indicating the strength of the interaction between elevated CO_2 and the primary resources (nutrients, irradiance and water) on plant growth. For each of the environmental factors, data are separated for herbaceous species (*open boxplots*) and tree seedlings (*shaded boxplots*). Data are based on a literature review of factorial experiments with combinations of elevated CO_2 and nutrients (n=51 and n=72 for herbaceous and woody species, respectively, in 83 papers), irradiance (n=11 and n=8, respectively, in 8 papers) and water (n=12 and n=30, respectively, in 25 papers). An explanation of SLB values is given in Methodology and Fig. 1. *Numbers* in the graph are the 10%-trimmed means of SLB values for herbs and woody species together. *Boxplots* indicate the distribution of a range of observations. The lower part of the box shows the 25th percentile. The highest part of the box gives the 75th percentile, and the line in between, the median (50th percentile). The *whiskers* indicate the 10th (lower) and 90th (higher) percentile

of plants to elevated CO_2. Similar conclusions have been drawn for CO_2-enriched crops (Kimball 1986a) and vegetations (Stöcklin et al. 1998). Overall, the pattern of response was not affected by the type of nutrient in short supply, as judged from the similarity in interaction between experiments where nitrogen, phosphorus or all nutrients together were modified (Poorter 1998). Although the average SLB is negative, positive slopes are found in 20% of the experiments. As discussed below, more detailed research, including a range of nutrient levels, should show whether these positive slopes are merely caused by chance or are a systematic response of specific species.

At low nutrient levels, growth is apparently not restricted by carbon availability, since high concentrations of starch and other non-structural carbohydrates are usually found in nutrient-limited plants. Therefore, we do not expect an increase in carbon fixation to lead to a similar stimulation in growth, unless plants at elevated CO_2 would acquire more nutrients or use them more efficiently (BassiriRad et al. 2001). In the case of N, one of the ways to use the acquired nutrients more efficiently is to invest less of the available N into Rubisco, and more into other compounds that limit growth. Interestingly, this does not happen (Medlyn 1996; Makino et al. 2000). We are only beginning to understand the mechanism by which plants with a low nutrient status adjust their growth and how this limits the response to elevated CO_2 (Stitt and Krapp 1999).

Low light availability

Theoretically, the relative stimulation of photosynthesis by elevated CO_2 is strongest close to the light compensation point (Kimball 1986a), and this has indeed been observed (Idso and Idso 1994). At low light, plant growth is strongly carbon limited, and therefore one would expect this stimulation of photosynthesis by elevated CO_2 to be translated into increased growth. However, analysis of the limited information (Fig. 3; 19 observations) shows that this interaction is small: the average SLB does not deviate significantly from zero, although it comes close ($0.05<P<0.1$). Similar results have been found for crop yield (Kimball 1986a). Although not significant ($P>0.3$), there seems to be a tendency for tree seedlings to have positive SLB values, whereas the herbaceous plants in our compilation showed – on average – no response. One might expect tree seedlings to be generally more shade-tolerant than the five crop species that represent the herbaceous plants in this case. Such observations would be in line with the conclusion of Kerstiens (1998) that within the group of woody species, the shade-tolerant ones are the strongest in their growth response. He suggests that shade-tolerant species have a lower leaf area per unit leaf mass, which is less reduced than in other tree species at elevated CO_2. In addition, species-specific differences in response in tree seedlings may change with small increases in light availability (Hättenschwiler and Körner 2000). Clearly, the number of experiments with low light is far too limited to allow any firm conclusion. Moreover, other factors like the quality of light used in the experiments may play a role as well (Hodinott and Scott 1996).

Low water supply

Overall, the results obtained for a range of different herbaceous and woody species confirmed that a reduced water supply modestly enhances the relative growth response to elevated CO_2 (Fig. 3; 42 observations; $P<0.05$), with again a small but non-significant difference between herbs and trees ($0.05<P<0.1$). As in the case of nutrients, 20% of the observations show an interaction deviating from the general trend.

Elevated CO_2 decreases stomatal conductance by 30–60% on average (Morison 1993), which in turn reduces water loss in the plant. Consequently, CO_2 may alleviate plant water stress by reducing water use. However, plants that are stimulated in growth by high CO_2 will have an increased leaf area. This will result in increased transpiration at the whole-plant level, thereby moderating the interaction (Samarakoon and Gifford 1996). The effect of CO_2 on stomatal conductance is observed in both C_3 and C_4 species and is generally persistent throughout plant development, with little evidence for acclimation. There is growing experimental evidence suggesting that elevated CO_2 may have small or insignificant effects on stomatal conductance of many forest tree

species, especially conifers (Curtis 1996). Hence, the reduced use of water in coniferous forests growing under elevated CO_2 and the subsequent growth response may be smaller than predicted. In our compilation, however, we did not find a difference in the strength of the interaction between conifers and hardwoods (P>0.7).

Interaction with temperature and salinity

Temperature

Our analysis shows that the average SLB is negative for sub-optimal temperatures, which indicates that at close-to-optimal temperatures, the relative biomass increase by elevated CO_2 is higher than at low temperatures (Fig. 4; 59 observations, P<0.001). This result is in agreement with results from previous analyses, which also concluded that low temperature reduced the growth response to elevated CO_2 (Idso et al. 1987; Rawson 1992; Curtis and Wang 1998), although, again, 20% of the observations differ in direction from the other experiments, with a BER higher at low temperature. No statistical difference was detectable between herbs and woody species (P>0.15). In a few experiments, the highest temperature was supra-optimal for growth. In those cases, the largest growth response was at the highest temperature as well, although the difference was not statistically significant (Fig. 4; 9 observations, P>0.15).

There are at least two explanations for the CO_2×temperature interaction. In the short term, an increase in ambient CO_2 concentration results in increased photosynthesis in C_3 species, not only by increasing the concentration of substrate but also by suppressing oxygenation (Long 1994). An increase in temperature promotes oxygenation relative to carboxylation through decreases in the affinity of the enzyme Rubisco for CO_2. Moreover, the solubility of CO_2 decreases faster than that of O_2 at high temperature, diminishing the relative abundance of CO_2 in the chloroplasts (Jordan and Ogren 1984). Therefore, the stimulating effect of elevated CO_2 on photosynthesis is strongest under warmer conditions. An alternative explanation for the low response at low temperatures is that growth is more impaired by sub-optimal temperatures than photosynthesis (Körner 1991; Rawson 1992). As in the case of low nutrient supply, this will result in the accumulation of non-structural carbohydrates. With sink strength being so crucial for the growth response of plants (e.g. Reekie et al. 1998), plants at low temperature are probably not able to profit much from an increased sugar supply due to elevated CO_2 (Greer et al. 2000).

Salinity

Salinity has a negative effect on both the water status and the photosynthetic apparatus of plants (Ball and Munns 1992). As elevated CO_2 has exactly the opposite effects, one might expect elevated CO_2 to ameliorate the negative effects of a supra-optimal salt (NaCl) concentration on growth. This has indeed been found in a number of cases, but not all, and the mean SLB does not deviate significantly from zero (Fig. 4; 18 observations, P>0.4). Hardly any data have been published for woody species. Munns et al. (1999) suggested a positive CO_2×salt interaction at low salinity, but no CO_2 effect at high salinity. From the present compilation we conclude that most halophytes have a higher BER at supra-optimal salinity, whereas most glycophytes have a lower BER under these conditions (Appendix 1 and 2). However, the few observations available preclude any firm conclusion at this stage.

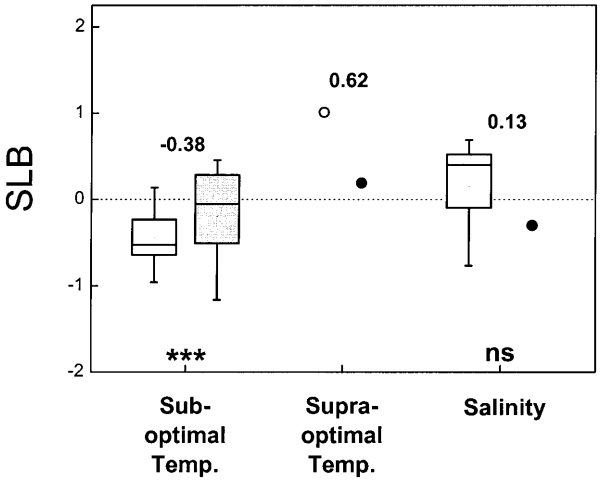

Fig. 4 Distribution of SLB values, indicating the strength of the interaction between elevated CO_2 and sub-optimal temperature, supra-optimal temperature and salinity. Data are based on a literature review (sub-optimal temperature: n=48 and n=11 for herbaceous and woody species, respectively, in 24 papers; supra-optimal: n=5 and n=4 in 6 papers; salinity: n=16 and n=2 in 12 papers). Because of the low number of observations for supra-optimal temperatures and for woody species at high salinity, we only calculated the average values (*open circles* herbaceous plants, *closed circles* woody plants). For more information see the legend to Fig. 3

Interaction with air pollutants

Ozone

Of all factors considered here, ozone shows the strongest interaction with CO_2. The slope is positive (Fig. 5; 29 observations, P<0.001), and this is true for 95% of the observations, with no indication of a difference between woody and herbaceous species (P>0.7). This implies that CO_2 strongly ameliorates the detrimental effect of ozone. There is good evidence that in plants in which stomatal conductance is reduced by CO_2 enrichment, O_3 flux into the leaf interior is reduced and this contributes to reducing the injurious impact of O_3 on plant growth and physiology (Turcsányi et al. 2000). Three major questions remain with regard to the protection against O_3 damage

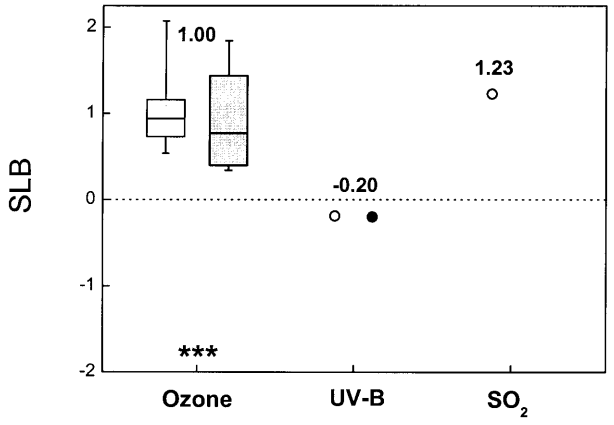

Fig. 5 Distribution of SLB values, indicating the intensity of the interaction between elevated CO_2 and air pollutants. Data are based on a literature review of interactions with O_3 (n=16 and n=13 for herbaceous and woody species, respectively, in 19 papers), UV-B (n=2 and n=6 in 8 papers) or SO_2 (n=3 and n=0 in 2 papers). Because of the low number of observations for UV-B and SO_2, we only calculated the average values (*open circles* herbaceous plants, *closed circles* woody plants). For more information see the legend to Fig. 3

provided by elevated CO_2. First, does elevated CO_2 induce other advantageous mechanisms in addition to stomatal closure, such as detoxification or repair processes (J. Cardoso-Vilhena, personal communication)? Second, what is the combined effect of elevated CO_2 and O_3 on the growth and productivity of species in which the stomata are less responsive to CO_2 enrichment, such as many conifers? Data indicate that for these species, there may be similar effects of O_3 at ambient and elevated CO_2, or at least much less amelioration of O_3 damage than observed in herbaceous species (Pérez-Soba et al. 1995). However, the data on conifers in the literature are at present too sparse to be conclusive at this stage. And third, what is the combined effect of elevated CO_2 and O_3 on photosynthesis? Long-term exposure to elevated CO_2 is accompanied by a decrease in Rubisco activity or amount of Rubisco protein in many species (Drake et al. 1997). Likewise, both short-term exposures to peak concentrations of O_3 and to high background concentrations of O_3 show a decline in Rubisco activity (Pell et al. 1994). If the effects of elevated CO_2 and elevated O_3 on Rubisco were additive, then the decrease in activity would result in a reduction of photosynthetic capacity.

UV-B radiation

Experiments with CO_2×UV-B interactions are scarce (8 observations). As with other interactions, data are variable, and the average SLB does not deviate significantly from 0 (Fig. 5; P>0.5). Thus, elevated CO_2 may not compensate for the harmful effect of UV-B. The reason for this could be that UV-B primarily affects photosystem II, whereas CO_2 influences carboxylation and stomatal conductance. On the other hand, elevated CO_2 generally increases the concentrations of soluble phenolic compounds (Poorter et al. 1997; Peñuelas and Estiarte 1998), some of which are known to decrease plant sensitivity to UV-B. Most results to date have been obtained under artificial-environment conditions, which could result in stronger damage than in the field situation. First, the UV-B levels used in the experiments are generally very high (Rozema 1993). Second, leaves developed under high light adapt morphologically and physiologically in a way that may also confer protection against UV-B (Teramura and Murali 1987). Consequently, plants in growth chambers, in which the daily irradiance is about two times lower than under field conditions (Garnier and Freijsen 1994), may be more sensitive to UV-B than plants in the field.

Sulphur dioxide

The very few data available on the combined effects of elevated CO_2 and supra-optimal SO_2 (3 observations) show a positive interaction, with high SLB values. This suggests that CO_2 enrichment reduces the adverse effects of SO_2 on plant growth. SO_2 is probably used as a source of sulphur and assimilated to proteins and other organic compounds. The presence of elevated CO_2 results in higher metabolic rates that may stimulate the sulphur assimilation and accelerate repair processes (Rao and De Kok 1994). In addition, high CO_2 decreases stomatal conductance, which in turn may reduce the SO_2 flux into the leaf. However, when SO_2 levels are very high, as in many East European countries, elevated CO_2 may not be able to counteract the detrimental effect of SO_2.

General discussion

How useful is a meta-analysis?

We would like to make a strong case for meta-analysis as a tool that allows generalisation across a wide range of experiments (Gurevitch and Hedges 1999). It provides a framework to judge whether a new result falls within the low, high or average range of previous observations. Moreover, it may allow the detection of contrasting responses between (groups of) species or environments, before such differences have been explicitly tested in a specifically designed experiment. Finally, because the strength of the interaction is prone to random variation (Fig. 2), average values across experiments may give a better estimate of the strength of the interaction under study. However, when interpreting the results of a meta-analysis, one should keep in mind that this approach has some limitations. First, unnoticed mistakes may have occurred in the experimental phase or during calculation of the data on which the compilation is based. Second, researchers may have chosen to refrain from publishing data that were found to be statistically non-significant, which may bias the overall picture (Gurevitch and Hedges

1999). Third, the available studies are not necessarily a weighted random sample of global vegetation, implying that estimates of the response of the 'average' C_3 plant or vegetation are extrapolations with unknown confidence margins. Fourth, we can never exclude that an observed class difference in SLB (e.g. woody plants versus herbs) is confounded with another difference across species (e.g. sun versus shade species), or a difference in experimental conditions (cf. Lloyd and Farquhar 2000). Such a risk is particularly evident when only a few studies have been carried out, as in the case of CO_2×light interactions. A last point to consider, especially in the context of the present review, is that we assumed that interactions would be similar for CO_2 concentrations ranging between 550 and 1100 µmol mol^{-1}, and that the BER values change linearly between the assumed optimal and non-optimal level.

Given these considerations we face a dilemma. Ideally, conclusions would be based on large-scale experiments that study CO_2×environment interactions for a wide range (say >15) of ecologically contrasting species. Even in this case, true generality is only achieved if researchers at different laboratories independently arrive at similar conclusions. As such large-scale screenings are rare, and the vast majority of experiments is restricted to one to four species, we have to accept that most of the generalisations will come from combining information from a variety of experiments. To minimise the chance effect alluded to in Fig. 2, we suggest using an experimental design with more than two levels of the interacting factor, giving more degrees of freedom to estimate the overall response. Moreover, if plant-to-plant variation is not of prime interest, all precautions possible should be taken to minimise and control plant-to-plant variability within the experimental population (Poorter and Garnier 1996), which will also improve the precision of the SLB estimation.

An overview of interactions

The effect of an interaction between CO_2 and any environmental factor will not only depend on the slopes of the lines (Figs. 3, 4 and 5), but also on the magnitude of the growth reduction due to the stress factor at ambient CO_2. This is taken into account in Fig. 6, where we plot the average BER values against the average GRS, as explained in Fig. 1. At optimal conditions (GRS=0), we assumed a BER value of 1.47 (average from the compilation by Poorter et al. 1996). The BER values at non-optimal conditions were then derived from the average SLB and GRS values in the present compilation. The dashed line in the figure indicates the extent to which the enhancement in plant biomass by elevated CO_2 should increase in order to compensate for growth losses at non-optimal conditions, not only in a proportional but also in an absolute way. Clearly, propositions that plants under stress will always respond relatively more strongly to CO_2 enrichment than those under optimal conditions

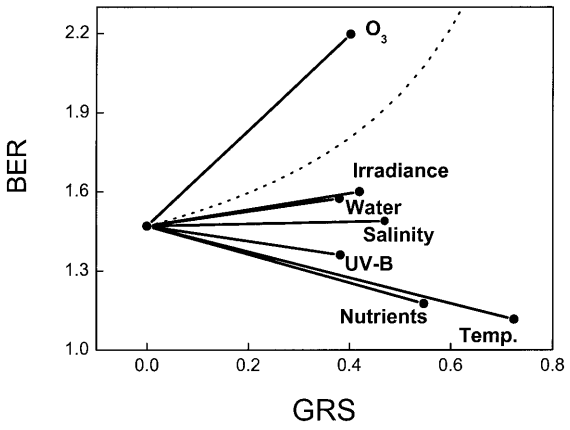

Fig. 6 Summary of the average growth response of plants for an interaction between elevated CO_2 and other environmental factors. Responses are calculated using a biomass enhancement ratio of 1.47 for plants grown under optimal conditions. The average slope was calculated from the data of Figs. 4, 5 and 6, and the average reduction in growth at 350 µl l^{-1} CO_2 as calculated in the compiled literature. The *dashed line* indicates the biomass enhancement by elevated CO_2 that would compensate for biomass reduction under stress conditions, not only in a proportional but also in an absolute way

(e.g. Idso and Idso 1994) do not hold. The growth enhancement by elevated CO_2 is severely reduced at low temperatures or poor nutrient supply. This is not only explained by the more negative SLB values, but also by the generally strong growth reduction in those experiments (GRS >0.5). The average growth enhancement by elevated CO_2 at optimal conditions is not significantly altered by high UV-B, high salinity or low irradiance, mainly because the average SLB values were only marginally different from zero. The interaction with water was significant, but the effect was small. The interaction between elevated CO_2 and O_3 was strong. This is the only type of stress where biomass is stimulated more than twofold under elevated CO_2 (BER values at high O_3 are often larger than 2). The average value is above the dotted line, indicating that the loss of biomass at elevated O_3 is more than compensated by the presence of elevated CO_2. However, the biomass of high-CO_2 plants at high O_3 concentrations is not as large as that of high-CO_2 plants grown at low O_3 levels.

Differences between species

The responses in Fig. 6 are average values of literature data for both herbaceous and woody species. Some time ago, Curtis and Wang (1998) reviewed the growth response of woody plants to elevated CO_2. To the extent that they studied CO_2×environment interactions, their conclusions and ours are in agreement. This can be explained by the fact that we did not find systematic differences between woody seedlings and herbaceous species for any of the environmental factors, although some (irradiance, water) are on the verge of significance. Con-

clusions deviate strongly for the factor ozone, where we calculated much stronger responses both for herbaceous and woody species. The fact that Curtis and Wang (1998) had only two data points for this factor may explain the different results. We were not able to find systematic differences in the compiled literature between responses of gymnosperms and hardwood seedlings. This may imply that the differential response of stomatal conductance with respect to increased CO_2 does not necessarily lead to a strongly different CO_2×environment interaction.

We have not paid attention to C_4 and Crassulacean acid metabolism species, because far less information is available for the response of these species under sub- or supra-optimal conditions. However, as their response to elevated CO_2 is generally smaller than that of C_3 species (Poorter et al. 1996), we expect the CO_2×environment interactions to be smaller as well.

Conclusions

Plant-to-plant variability in biomass within treatments is one of the factors that explains contrasting CO_2×environment interactions published in the literature. On average, the growth stimulation by elevated CO_2 is smaller at low nutrient availability and low temperature, increases somewhat at low water supply, and is substantially higher at high ozone concentrations. There is a strong paucity of data on the interaction with light, salt, UV-B, nitrogenous air pollutants and SO_2, but, with the exception of SO_2, average responses are small. No systematic differences were found between woody and herbaceous species for any of the interactions.

Acknowledgements We thank Ep Heuvelink, Eric Garnier, Gina Adams and Manuela Chaves for trustfully providing us with (partially unpublished) data for incorporation in our analyses. Ineke Stulen, Jan Goudriaan, Marcel van Oijen and an anonymous reviewer thoughtfully commented on a previous version of the manuscript.

Appendix 1

SLB values for herbaceous species

SLB values used for the analysis of different types of CO_2×environment interaction. Data are for herbaceous species and listed in alphabetical order. References are given as first author and year of the publication[a]

Species	Nutrients	Light	Water	Temperature	Salinity	Ozone	UV-B	SO_2
Abutilon theophrasti	–0.65 Bernacci (2000) –0.57 McConnaughay (1993) –0.30 Coleman (1993)		0.83 Ward (1999)	–0.24 Coleman (1992) –0.02 Patterson (1988 0.12 Tremmel (1993				
Agropyron smithii	0.15 Volin (1996)					–0.18 Volin (1996) 2.02 Volin (1998)		
Agrostis capillaris	–0.80 Bowler (1996) –0.33 Newbery (1996) –0.00 Newbery (1996) 0.16 Bowler (1993)			–0.50 Campbell (1993)				
Anoda cristata				–0.28 Patterson (1988)				
Anthoxantum odoratum				–0.42 Campbell (1993)				
Arrennatherum elatius	–0.48 Arp (1998) –0.43 Arp (1998) –0.13 Hunt (1995)		0.41 Arp (1998)					
Aster tripolium					–2.03 Rozema (1990) 0.25 Lenssen (1990) 0.25 Lenssen (1993a 0.51 Lenssen (1993a)			
Atriplex glabriuscala					0.72 Adams (1996)			
Atriplex halimus					1.41 Schwarz (1984)			

Appendix 1 (continued)

Species	Nutrients	Light	Water	Temperature	Salinity	Ozone	UV-B	SO_2
Bellis perennis				1.53 Stirling (1998)				
Brassica oleracea	–0.54 Sritharan (1992)							
Bromus mollis	–0.52 Larigauderie (1988)							
Bromus sterilis				–0.90 Stirling (1998)				
Bromus willdenowii				–0.58 Campbell (1993)				
Carex bigellowi	–0.44 Oberbauer (1986)							
Cassia obtusifolia	–0.11 Patterson (1982)			–0.01 Tremmel (1993)				
Chenopodium album				0.71 Stirling (1998)				0.91 Carlson (1982)
Chrysanthemum morifolium		–0.80 Hughes (1971) –0.07 Hughes (1971)						
Cichorium intybus				–0.51 Campbell (1993)				
Crotolaria spectabilis	–1.05 Patterson (1982)							
Cynosurus cristatus				–0.67 Campbell (1993)				
Dactylis glomerata	0.10 Harmens (2000)			–0.53 Campbell (1993)				
Dantonia richardsonii	–0.11 Garnier (personal communication)							
Datura stramonium								0.80 Carlson (1982)

Species	Nutrients	Light	Water	Temperature	Salinity	Ozone	UV-B	SO_2
Elymus athericus					0.51 Lenssen (1993b)		–1.31 Van de Staaij (1993) 0.93 Rozema (1997)	
Elymus pycnanthes					–0.01 Lenssen (1990)			
Elytrigia repens				0.06 Tremmel (1993)				
Festuca arundinacea				–0.11 Campbell (1993)				
Festuca ovina	–0.29 Hunt (1995)							
Festuca rubra	–0.33 Hunt (1995)							
Fragaria vesca	–0.35 Chen (1997)							
Glycine max	–1.70 Sionit (1983) –1.49 Nakamura (1999) –1.00 Sa (1998) –0.54 Cure (1988) –0.46 Israel (1990) –0.29 Patterson (1982) –0.23 Yong (2000) –0.11 Williams (1981) –0.09 Israel (1990)	0.05 Sionit (1982)	0.33 Serraj (1999) 0.59 Serraj (1999)	–0.54 Imai (1979) –0.01 Sionit (1987) 0.19 Tremmel (1993) 0.44 Ziska (1997)		0.84 Miller (1998)		
Gossypium hirsutum	–0.44 Wong (1990) –0.22 Barett (1995)	–0.44 Rufty (1994) –0.18 Rufty (1994) 0.38 Rufty (1994)		–0.25 Patterson (1988) 0.48 Reddy (1998)		0.64 Heagle (1999)		
Helianthus annuus	–0.16 Zerihun (2000)							
Holcus lanataus				–0.44 Campbell (1993)				
Koeleria cristata						2.14 Volin (1998)		
Lolium multiflorum				–0.54 Campbell (1993) –0.20 Campbell (1993)				
Lolium perenne	–0.69 Goudriaan (1983)			–0.89 Campbell (1993)				

Appendix 1 (continued)

Species	Nutrients	Light	Water	Temperature	Salinity	Ozone	UV-B	SO_2
Lolium perenne	–0.22 Goudriaan (1983) 0.61 Marks (1990)			–0.77 Campbell (1993) –0.64 Campbell (1993)				
Lotus corniculatus				–0.53 Campbell (1993)				
Lotus pedunculatus				–0.54 Campbell (1993)				
Lycopersicon esculentum			0.00 Paez (1984) 0.84 Paez (1984)			1.15 Reinert (1997) 0.78 Olszyk (1997)		
Medicago sativa	–0.56 Goudriaan (1983)		–0.43 De Luis (1999)	–1.17 Campbell (1993) –0.99 Campbell (1993)		0.51 Johnson (1996)		
Molinia caerulea	–0.74 Arp (1998) –0.47 Arp (1998)		0.24 Arp (1998)					
Nardus stricta	–0.56 Bowler (1993) –0.67 Bowler (1996)							
Oryza sativa	–0.80 Imai (1978) –0.36 Aben (1999)	–0.14 Imai (1979)		–0.57 Imai (1979)		1.10 Olszyk (1997) 1.18 Olszyk (1997)		
Panicum laxum	–0.33 Ghanoum (1998)							
Phalaris aquatica	0.13 Garnier (personal communication)			–0.59 Campbell (1993)				
Phaseolus vulgaris	0.01 Radoglou (1992)				–0.58 Schwarz (1984)			
Phleum pratense				–0.42 Campbell (1993)				
Plantago lanceolata				–0.97 Campbell) (1993				
Poa annua	–0.54 Hunt (1995)			–1.17 Campbell (1993) –0.93 Stirling (1998)				
Polygonum pensylvanicum								1.98 Carlson (1982)

Species	Nutrients	Light	Water	Temperature	Salinity	Ozone	UV-B	SO_2
Puccinellia maritima					0.66 Lenssen (1993a)			
Raphanus sativus	0.24 Jablonski (1997)	–0.49 Sionit (1982)				0.88 Barnes (1992)		
Rumex obtusifolius	–0.73 Arp (1998) –0.63 Arp (1998)		0.28 Arp (1998)					
Rytidosperma clavatum				–0.95 Campbell (1993)				
Sanguisorba minor			0.40 Ferris (1995)					
Senecio vulgaris				0.21 Stirling (1998)				
Solanum tuberosum		0.34 Wheeler (1991) 0.65 Wheeler (1991) 1.27 Wheeler (1991)						
Spergularia maritima					0.50 Rozema (1990)			
Stipa occidentalis	–3.17 Wilsey (1996)							
Trifolium dubium				–0.64 Campbell (1993)				
Trifolium fragiferum				–0.59 Campbell (1993)				
Trifolium hybridum				–0.59 Campbell (1993)				
Trifolium pratense				–0.29 Campbell (1993)				
Trifolium repens	–0.51 Almeida (1999)			–1.10 Greer (2000) –0.77 Campbell (1993) –0.64 Campbell (1993) –0.52 Campbell (1993) –0.37 Campbell (1993)		0.99 Heagle (1993)		
Trifolium subterraneum				–1.05 Campbell (1993)		0.76 Van der Eerden (1993)		

Appendix 1 (continued)

Species	Nutrients	Light	Water	Temperature	Salinity	Ozone	UV-B	SO_2
Triticum aestivum	0.57 Sionit (1981)		0.17 Samarakoon (1995) 0.49 Samarakoon (1995)		–0.95 Rozema (1993) 0.30 Nicolas (1993) 0.52 Nicolas (1993) 0.77 Heuvelink (personal communication)	0.56 Barnes (1995) 1.04 Dueck (personal communication)		
Urtica dioica					–0.38 Jansen (1986)			
Vulpia bromoides				–0.87 Campbell (1993)				
Xanthium occidentale	0.20 Hocking (1985)							
Xanthium strumarium					0.53 Schwarz (1984)			

[a] Aben (1999) Aust J Plant Physiol 26:759–766; Adams (1996) PhD thesis, University of Sheffield; Almeida (1999) Plant Soil 210:159–166; Arp (1998) Plant Cell Environ 21:1–11; Barett (1995) J Biogeogr 22:331–339; Barnes (1992) New Phytol 121:403–412; Barnes (1995) Global Change Biol 1:129–142; Bernacci (2000) Global Change Biol 6:855–863; Bowler (1993) New Phytol 144:515–522; Bowler (1996) New Phytol 132:391–401; Campbell (1993) Proc 17th Grassland Conf, Palmerston North, New Zealand, pp 1125–1126; Carlson (1982) Oecologia 54:50–54; Chen (1997) Gartenbauwissenschaft 62:30–37; Coleman (1992) Ecology 73:1244–1259; Coleman (1993) Oecologia 93:195–200; Cure (1988) Crop Sci 28:671–677; De Luis (1999) Physiol Plant 107:84–89; Ferris (1995) New Phytol 131:491–501; Ghanoum (1998) Aust J Plant Physiol 25:627–636; Goudriaan (1983) Neth J Agric Sci 31:157–169; Greer (2000) Aust J Plant Physiol 27:301–310; Harmens (2000) Ann Bot 86:833–839; Heagle (1993) New Phytol 123:751–762; Heagle (1999) Crop Sci 39:731–744; Hocking (1985) Ann Bot 55:835–844; Hughes (1971) Ann Bot 35:933–945; Hunt (1995) Ann Bot 75:207–216; Imai (1978) Jpn J Crop Sci 47:118–123; Imai (1979) Jpn J Crop Sci 48:409–417; Israel (1990) J Plant Nutr 13:1419–1433; Jablonski (1997) Can J Bot 75:533–545; Jansen (1986) Biological control of photosynthesis, Nijhoff, Dordrecht, pp 143–146; Johnson (1996) J Environ Qual 25:908–916; Larigauderie (1988) Oecologia 77:544–549; Lenssen (1990) In: Goudriaan et al (eds) The greenhouse effect and primary productivity in European agro-ecosystems, Pudoc, Wageningen, pp 64–67; Lenssen (1993a) PhD thesis, Free University, Amsterdam; Lenssen (1993b) Vegetatio 104/105:379–388; Marks (1990) Oecologia 84 207–214; McConnaughay (1993) Oecologia 94:550–557; Miller (1998) Crop Sci 38:122–128; Nakamura (1999) Photosynthetica 37:61–72; Newbery (1996) New Phytol 132:403–411; Nicolas (1993) Aust J Plant Physiol 20:349–360; Oberbauer (1986) Can J Bot 64:2993–2998; Olszyk (1997) Agric Ecosyst Environ 66:1–10; Paez (1984) J Agric Sci 102:687–693; Patterson (1982) Weed Sci 30:389–394; Patterson (1988) Weed Sci 36:751–757; Radoglou (1992) Ann Bot 70:245–256; Reddy (1998) Environ Exp Bot 39:117–129; Reinert (1997) New Phytol 137:411–420; Rozema (1990) In: Beukema et al (eds) Expected effects of climate change on marine coastal ecosystems, Kluwer, Dordrecht, pp 49–54; Rozema (1993) Vegetatio 104/105:173–192; Rozema (1997) Plant Ecol 128:182–191; Rufty (1994) Physiol Plant 91:503–509; Sa (1998) J. Plant Nutr 21:2207–2218; Samarakoon (1995) Aust J Plant Physiol 22:33–44; Schwarz (1984) J Exp Bot 35:193–196; Serraj (1999) Global Change Biol 5:283–291; Sionit (1981) Agron J 73:1023–1027; Sionit (1982) Agron J 74:721–725; Sionit (1983) Crop Sci 23:329–333; Sionit (1987) Can J Plant Sci 67:59–67; Sritharan (1992) Gartenbauwissenschaft 57:246–251; Stirling (1998) New Phytol 140:343–354; Tremmel (1993) Can J Plant Sci 73:1249–1260; Van de Staaij (1993) Vegetatio 104/105:433–439; Van der Eerden (1993) NATO ASI Ser 16:125–137; Volin (1996) Physiol Plant 97:674–684; Volin (1998) New Phytol 138:315–325; Ward (1999) Global Change Biol 5:857–867; Wheeler (1991) Crop Sci 31:1209–1213; Williams (1981) Plant Physiol 68:1406–1409; Wilsey (1996) Oecologia 108:321–327; Wong (1990) Photosyn Res 23:171–180; Yong (2000) Plant Physiol 124:767–779; Zerihun (2000) Ann Bot 86:723–730; Ziska (1997) Physiol Plant 100:126–132

Appendix 2

SLB values for woody species

SLB values used for the analysis of different types of CO_2×environment interaction. Data are for woody species listed in alphabetical order. References are given as first author and year of the publication[a]

Species	Nutrients	Light	Water	Temperature	Salinity	Ozone	UV-B
Acacia melanoxylon	–0.65 Schortemeyer (1999)						
Acer pensylvanicum	0.04 Bazzaz (1993) 0.22 Bassow (1994)	0.57 Bazzaz (1993)					
Acer rubrum	–0.36 Bazzaz (1993)	0.15 Bazzaz (1993)	–0.46 Miao (1992)				
Acer saccharum						–0.54 Gaucher (1998)	
Alnus rubra	–0.94 Arnone (1990)		0.29 Hibbs (1995)				
Beilschmiedia pendula	–0.25 Lovelock (1996)						
Betula alleghaniensis	0.21 Bazzaz (1993) –0.42 Bassow (1994)	0.74 Bazzaz (1993)	–0.04 Catovsky (1999)	1.07 Wayne (1998)			
Betula nana	–0.21 Oberbauer (1986)						
Betula papyrifera			0.78 Catovsky (1999)	–0.05 Tjoelker (1998)			
Betula pendula	0.27 Silvola (1995)						–0.22 Lavola (2000)
Betula platyphylla			0.65 Koike (1993)				
Betula populifolia	–0.35 Bassow (1994) –0.19 Bazzaz (1993)	0.50 Bazzaz (1993)	0.25 Miao (1992)				
Betula pubescens				–1.16 Mortensen (1995)		0.40 Mortensen (1995)	
Calluna vulgaris	–0.24 Arp (1998) –0.21 Arp (1998) 0.69 Whitehead (1997) 1.36 Whitehead (1997) 1.37 Whitehead (1997)		0.54 Arp (1998)				

Appendix 2 (continued)

Species	Nutrients		Light		Water		Temperature		Salinity	Ozone		UV-B
Castanea sativa	–0.11 –0.10	El-Kohen (1992) El-Kohen (1994)										
Citrus aurantum	1.31	Syvertsen (1999)										
Citrus sinensis	–2.49	Syvertsen (1999)										
Erica tetralix	–0.60	Arp (1998)			0.06	Arp (1998)						
Eucalyptus camaldulensis	–0.68	Wong (1992)										
Eucalyptus cladocalyx	0.70	Gleadow (1998)										
Eucalyptus cypellocarpa	–0.70	Wong (1992)										
Eucalyptus grandis	–0.98 –0.30	Conroy (1992) Conroy (1992)										
Eucalyptus pauciflora	0.35	Wong (1992)										
Eucalyptus pulverulenta	–0.32	Wong (1992)										
Fagus sylvatica	–4.80	Heath (1997)					–0.09	Bruhn (2000)				
Fraxinus americana	–0.81	Bazzaz (1993)	0.29	Bazzaz (1993)								
Fraxinus excelsior					0.47	Broadmeadow (2000)				1.88	Broadmeadow (2000)	
Kielmeyera coriacea	–1.72	Hoffmann (2000)										
Larix laricina							–0.11	Tjoelker (1998)				
Ledum palustre	–0.06	Oberbauer (1986)										
Leucadendron coniferum	0.35 0.39	Midgley (1995) Midgley (1995)										
Leucadendron xanthocorus	–0.63	Midgley (1995)										
Liquidambar styraciflua			–1.06	Tolley (1984a)	0.16 0.30	Tolley (1984b) Tschaplinski (1995)						
Liriodendron tulipifera	0.03	Norby (1991)										

Species	Nutrients	Light	Water	Temperature	Salinity	Ozone	UV-B
Picea glauca	–0.24 Brown (1986)						–0.12 Yakimchuk (1993)
Picea mariana	–0.21 Johnsen (1993)		0.17 Johnsen (1993)	0.03 Tjoelker (1998)			0.03 Yakimchuk (1993)
Picea sitchensis	–0.71 Townend (1995) –0.54 Murray (2000)		0.11 Townend (1993) 0.12 Townend (1995) 0.39 Townend (1993)				
Pinus banksiana				–0.91 Tjoelker (1998)			–0.07 Stewart (1993) –0.89 Yakimchuk (1993)
Pinus palustris	–0.97 Prior (1997)		0.67 Runion (1999)				
Pinus pinaster			–0.72 Guehl (1994)				
Pinus ponderosa	–0.65 Johnson (1995) 0.05 Johnson (1997)			0.46 DeLucia (1997)			
Pinus radiata	–0.91 Conroy (1986) –0.51 Conroy (1990) –0.17 Conroy (1988)		0.03 Conroy (1986) 0.05 Conroy (1990) 0.11 Conroy (1986) 0.20 Conroy (1988)				
Pinus sylvestris	–1.03 Griffin (1995)		–0.35 Broadmeadow (2000)			0.27 Broadmeadow (2000)	
Pinus taeda	–0.86 Griffin (1997) –0.57 Lewis (1996) –0.45 Griffin (1993) –0.18 Gebauer (1996)	0.72 Tolley (1984a)	0.03 Tschaplinski (1993)				0.04 Sullivan (1994)
Platanus occidentalis			0.35 Tschaplinski (1995)				
Populus	–0.27 Zak (2000)						
Populus deltoides× P. nigra						0.33 Dickson (1998) 0.68 Dickson (1998) 0.77 Dickson (1998) 1.44 Dickson (1998)	
Populus nigra× P. maximowiczii						0.52 Dickson (1998)	
Populus tremuloides	–0.35 Volin (1996) –0.23 Wang (2000) 0.23 Brown (1986)			0.41 Tjoelker (1998)		1.49 Volin (1996) 1.70 Volin (1998)	
Populus× euramericana	–1.61 Goudriaan (1983) –0.82 Curtis (1995) –0.74 Pregitzer (1995)						

Appendix 2 (continued)

Species	Nutrients	Light	Water	Temperature	Salinity	Ozone	UV-B
Prunus avium	–2.51 Wilkins (1994) 0.21 Kerstiens (1994)		0.09 Centritto (1999)				
Quercus petrea			–1.36 Guehl (1994) 0.29 Broadmeadow (2000)			1.22 Broadmeadow (2000)	
Quercus robur			–0.99 Picon (1996) –0.01 Vivin (1997)				
Quercus rubra	0.20 Bazzaz (1993)	1.35 Bazzaz (1993)				2.34 Utriainen (1998)	
Quercus suber	–0.66 Chaves (personal communication) –0.26 Chaves (personal communication)						
Robinia pseudoacacia	–0.30 Uselman (2000)			0.16 Uselman (2000)			
Rhizopora apiculata					–0.67 Ball (1997)		
Rhizopora stylosa					–0.41 Ball (1997)		
Salix phylicifolia	–1.57 Silvola (1993)						
Salix× dasyclados	–0.32 Silvola (1992)						
Schima superba				–1.46 Sheu (1999)			
Vaccinium myrtillus	–0.17 Arp (1998) –0.09 Arp (1998)		0.08 Arp (1998)				

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