Tansley review

Plant growth and competition at elevated CO_2: on winners, losers and functional groups

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Contents

Key words: elevated CO_2, meta-analysis, seed mass, RGR, photosynthesis, growth, functional groups, competition.

Summary

The effects of increased atmospheric CO_2 concentrations on vegetative growth and competitive performance were evaluated, using five meta-analyses. Paying special attention to functional groups, we analysed responses at three integration levels: carbon economy parameters, vegetative biomass of isolated plants, and growth in competition. CO_2 effects on seed biomass and plant-to-plant variability were also studied. Underlying the growth stimulation is an increased unit leaf rate (ULR), especially for herbaceous dicots. This is mainly caused by an increase in the whole-plant rate of photosynthesis. The increased ULR is accompanied by a decrease in specific leaf area. The net result of these and other changes is that relative growth rate is only marginally stimulated. The biomass enhancement ratio (BER) of individually grown plants varies substantially across experiments/species, and size variability in the experimental populations is a vital factor in this. Fast-growing herbaceous C3 species respond more strongly than slow-growing C3 herbs or C4 plants. CAM species and woody plants show intermediate responses. When grown in competition, C4 species show lowest responses to elevated CO_2 at high nutrient conditions, whereas at low nutrient levels N_2-fixing dicots respond relatively strongly. No systematic differences were found between slow- and fast-growing species. BER values obtained for isolated plants cannot be used to estimate BER of the same species grown in interspecific competition – the CO_2 response of monocultures may be a better predictor.

Abbreviations

BER, Biomass enhancement ratio; FCI, Fraction of daily fixed C that is invested in growth; LAR, leaf area ratio; LMF, Leaf mass fraction; PS_A, daily rate of whole plant photosynthesis per unit leaf area; SLA, specific leaf area; RCI, relative competition intensity; RGR, relative growth rate; ULR, unit leaf rate.

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I. Introduction

The prospect of global changes in climate has triggered a wide variety of research in the past 25 years. One of the aspects that has received ample attention is the sharp rise in the atmospheric CO_2 concentration and the effects thereof on plant growth and functioning (Ward & Strain, 1999; Körner, 2001; Bazzaz & Catovsky, 2002). The primary and instantaneous responses of an increase in the CO_2 atmosphere around the plant are an increased rate of photosynthesis and a decreased rate of transpiration at the leaf level. The increase in C-fixation is due to repression of photorespiration and because of an increased substrate supply. The decreased water loss is due to a partial closure of the stomata (Lambers *et al.*, 1998). The effects on physiology and growth of the plant at the longer term are less clear. For example, the stimulation of photosynthesis may partially or totally disappear, due to negative feed-back effects that occur frequently, though not invariably (Woodward, 2002). The increased growth at elevated CO_2 may result in plants with a larger leaf area, which will diminish or nullify the reduction in water use shown at the leaf level (Field *et al.*, 1995; Samarakoon & Gifford, 1996). Secondary changes in morphology, allocation and chemical composition may also affect growth (Poorter *et al.*, 1997). Consequently, the picture emerging from experiments at the whole plant level is rather diffuse, and this holds even more if we try to scale up CO_2-induced growth responses from the individual to the stand level (Mooney *et al.*, 1999).

Given the wide range of experiments on the growth of plants at elevated CO_2 published so far there is a need for a more formal analysis of the accumulated data. Such a meta-analysis has been carried out for the growth response of agricultural species (Cure & Acock, 1986; Kimball, 1986), wild grasses (Wand *et al.*, 1999), CAM species (Drennan & Nobel, 2000) and woody species (Curtis & Wang, 1998; Kerstiens, 2001). However, we think that it is even more fruitful to bring together information of all the higher plant groups investigated so far, in a structured way that enables systematic comparison across widely different groups of species (Poorter, 1993).

Having said so, two problems arise. On the one hand, there is a huge amount of information available on a large number of species (±350) that all seem to respond more or less to CO_2. How can this information be structured? On the other hand, with 350 species investigated, we still have no clue about the response of far more than 99% of the total higher plant species on earth. It is evidently impossible to test all of them. How then could any systematic insight be obtained in the response of plants or vegetations in general? A possible solution to both these problems is the concept of 'functional groups', an approach pioneered by Raunkiaer (1934). The idea behind this concept is that a number of species that have 'functional' traits in common possibly show a relatively similar response in behaviour to a change in an environmental factor (Smith *et al.*, 1997; Lavorel, 2002). In the case of plants, this could imply that species that have a similar life history (e.g. annual as compared to perennial), life form (e.g. woody as compared to herbaceous), the same physiological characteristics (such as type of photosynthesis or phloem loading) or the possibility to form symbiotic relationships (with N_2-fixing organism, or with mycorrhizal fungi) would be more similar in their response to CO_2 than species belonging to different categories. If indeed several functional groups could be discerned, we would have a handle to design key experiments and to generalise across species, even those that have not been investigated yet.

The number of experiments that have described the growth response of isolated plants to elevated CO_2 is substantial (Körner, 2001). Unfortunately, given the comparative approach we want to take, most of the information is fragmentary. Hardly ever does the number of species tested in one experiment reach five or more, and even in those cases where a relatively high number of species was tested (10 or more: Carlson & Bazzaz, 1980; Morison & Gifford, 1984; Campbell *et al.*, 1991; Hunt *et al.*, 1991, 1993; Poorter, 1993; Mortensen, 1994; Körner *et al.*, 1995; Roumet *et al.*, 1996; Bunce, 1997; Ziska & Bunce, 1997; Atkin *et al.*, 1999; Bazzaz & Catovsky, 2002), species were generally taken from one or two functional groups. As long as this type of comparative data is not available from a number of screening programs that comprise a variety of functional groups – and this is apparently not easily achieved – the only way to test for functional groups is a retrospective quantitative analysis of the literature. Such a meta-analysis forms the subject of this paper.

Conceptually speaking, plant mass at a given time after the onset of germination is determined by three factors. The first is the mass of the seed, where both the size of the embryo and the reserves will determine the starting capital. The second

factor is the time required for such a seed to complete germination and to be transformed into a viable autotrophic seedling: the faster the germination rate, the quicker a seedling can start to fix carbon and gain biomass. The third is the growth rate achieved by the vegetative plant over the subsequent growth period. Each of these factors may contribute to the growth stimulation by elevated CO_2. Our first objective was therefore to analyse how the growth response to CO_2 is brought about at the level of the whole plant. We do so by studying CO_2 effects on seed mass as well as relative growth rate. By breaking down the growth rate of a plant into a number of underlying components, we can test in a top-down approach to what extent the various components of a plant's carbon budget are affected by elevated CO_2. The second aim is to analyze to what extent variation in the biomass response exists between and within species, for plants grown without mutual interference. Third, we wanted to know how much of the variation in response could be explained by categorising species into a limited number of functional groups.

One of the reasons for studying the growth and performance of isolated plants is that it is a relatively simple system by which we can characterise the response of a given species to elevated CO_2. The tacit assumption behind is that an inherent attribute of a plant, for example having a C4 type of photosynthesis or not, will determine its response not only in a glasshouse or growth room, but also in competition with other species in the field. However, such extrapolations towards a higher integration level do not always hold (Körner, 2001). Our fourth objective was to formally test how useful the observed functional types, derived from data of isolated plants, are in predicting the CO_2 response of species in a competitive environment.

II. Materials and methods

We reviewed the literature, concentrating on the effect of elevated CO_2 on seed mass, growth rate and its underlying parameters, and vegetative plant biomass. For the analysis of seed mass (section III) we set up a database with 150 observations in 80 experiments. For the growth parameters we build on Poorter & Nagel (2000), arriving at 180 observations in 40 experiments. As both seed mass data and growth analyses are relatively scarce, we were not very restrictive in the selection of the data and included experiments that studied plant responses at control levels between 280 and 410 μl l^{-1} (350 on average) and elevated levels between 500 and 1000 μl l^{-1} (670 on average). In case of multiple CO_2 levels, we selected those closest to 350 and 700 μl l^{-1} and in multifactorial experiments studying $CO_2 \times$ environment interactions we used that treatment where biomass production was highest at the control CO_2 level. Growth parameters were derived from isolated plants, but seed mass data were used from experiments on individuals, monostands as well as mixed stands.

For the analysis of the growth response to elevated CO_2 (sections IV to V), we build on a database from previous reviews (Poorter, 1993, 250 observations; Poorter *et al.*, 1996, 230 more observations) and added to that the literature of the last 6 years (340 observations). In this case we were more restrictive and only included those experiments where plants had been grown individually, at control CO_2 concentrations between 300 and 400 μl l^{-1} (350 on average) and at elevated CO_2 levels that were roughly twice higher (between 600 and 800 μl l^{-1}; 690 on average). We focused on plants that were in the vegetative stage. For a review on the effect of CO_2 on reproductive characteristics, the reader is referred to Ackerly & Bazzaz (1995) and Jablonski *et al.* (2002). In those experiments where plants were grown under different environmental conditions, we again selected data from that treatment where control plants were growing fastest. In this way we applied a filter, trying to ensure that plants were grown under relatively favourable conditions. However, in this type of analysis it is unavoidable that there will still be a considerable range in experimental conditions and duration of treatments. For an analysis of interactions with other environmental factors we refer to Idso & Idso (1994) or Poorter & Pérez-Soba (2001).

For the analysis of the response of plants grown in intra or interspecific competition (section VI), we build on the database from Navas (1998), arriving at 260 observations in 40 experiments. Again we based the analysis on dry mass data, in this case from above-ground material only, as below-ground biomass is often not measured at the species level because of technical difficulties. Control CO_2 concentrations were between 280 and 400 μl l^{-1} (350 on average) and elevated concentrations between 600 and 800 μl l^{-1} (660 on average). Plants were sometimes in the vegetative, but more often in the generative stage. Experiments were carried out mostly in artificial assemblages, but sometimes in the field. They were included only if the total above-ground biomass as well as the biomass of each of the composing species was known. If experiments were made at a range of nutrient levels, we only selected the two extreme cases. Apart from these studies along a nutrient gradient, some experiments were carried out with crop or weed species under fertile conditions, whereas others were with wild species under a strongly limiting nutrient supply. To differentiate between the two, we categorised for each experiment whether plants were grown at a relatively high or low nutrient level and analysed the responses separately.

For biomass the most simple and biologically meaningful way is to quantify the CO_2 response as the ratio between total plant mass of high-CO_2 grown plants and that of plants grown at control levels. We will call this the Biomass Enhancement Ratio, and use BER as an acronym. For other parameters we will use ratios as well. As ratios do have a $\log_e$-normal distribution by nature (Sokal & Rohlf, 1995), a $\log_e$-transformation was carried out before any statistical analyses. Mean values presented are based on back-transformed $\log_e$-based averages.

III. Factors underlying the growth response

1. Seed mass and germination

What will be the effect of elevated CO_2 on the size of the seeds produced? With an improved carbohydrate availability of the mother plant at elevated CO_2, one may expect that one of the constraints on seed mass would be lifted and that seed size would increase. On the other hand, seed mass *per se* is generally far less variable than the total number of seeds produced (Harper, 1977). The effects reported in the literature are variable, even within a species. Most of the studies have focused on the crop species *Triticum aestivum* and *Glycine max*. For both species decreases as well as increases in seed mass have been observed (Fig. 1a), the variation most likely depending on cultivar and/or environmental conditions. On average, both *Triticum* and *Glycine* seeds increase significantly in mass with CO_2 concentration, with a larger stimulation for the latter (2% vs 9%, $P < 0.05$).

Will all species be stimulated in seed mass? Not to give excessive weight to a frequently measured species we averaged all observations per species before the analysis, under the assumption that environmental effects are leveled out across groups of species. The results for a total of 50 species are shown in Fig. 1(b). In a number of cases, seeds of high CO_2 plants were found to be smaller, with differences ranging from almost nil to 25% (e.g. *Bromus rubens*, Huxman *et al.*, 1998). Others have reported increases in seed mass, up to 45% (e.g. *Cassia fasciculata*, Farnsworth & Bazzaz, 1995). Averaged over all herbaceous species, the effect of maternal CO_2 on seed mass was nil, and there were no significant differences ($P > 0.5$) between monocots, herbaceous legumes and other herbaceous dicots. Thus, we conclude that across these functional groups, seed mass will not contribute to a significant extent to the observed biomass stimulation. In a number of species, the difference may affect plant size of the next generation, though. A spectacular example is the seed mass of the only woody species investigated so far, *Pinus taeda* (Hussain *et al.*, 2001). High CO_2 plants produced 90% heavier seeds, with a much higher lipid concentration. Lipids do have a high C-concentration and it requires relatively large amounts of glucose to be synthesised (Penning de Vries *et al.*, 1974). If plants are C-limited, one could expect that species with a high lipid concentration in their seeds would show the largest increase in seed mass when mother plants were grown at high CO_2. The fact that a species like *Glycine max*, which also has a high lipid concentration, shows a strong response as well (Fig. 1a), does fit in with this idea. However, a third species with a high oil concentration in the seeds, *Brassica juncea*, is among the ones with the most negative response (–20%; Tousignant & Potvin, 1996). Clearly, more systematic experiments in this field are required before a proper answer can be provided.

Germination *per se* is generally not affected directly by a higher CO_2 concentration (Morse & Bazzaz, 1994; Andalo *et al.*, 1996; Huxman *et al.*, 1998). Given the overall high CO_2 concentration in the soil, it is questionable whether a doubling in the atmospheric CO_2 concentration would have any direct effect (Ward & Strain, 1999). However, maternal effects have been reported, with a much lower germination rate for seeds from high CO_2 parents of two *Ipomoea* species (Farnsworth & Bazzaz, 1995) up to an increased germination rate in *Pinus taeda* (Hussain *et al.*, 2001). The consequence of such maternal effects are as yet only scarcely studied (Tousignant & Potvin, 1996; Bezemer *et al.*, 1998), although they may have a profound impact on the growth and population dynamics of different species through changes in size hierarchy (Morse

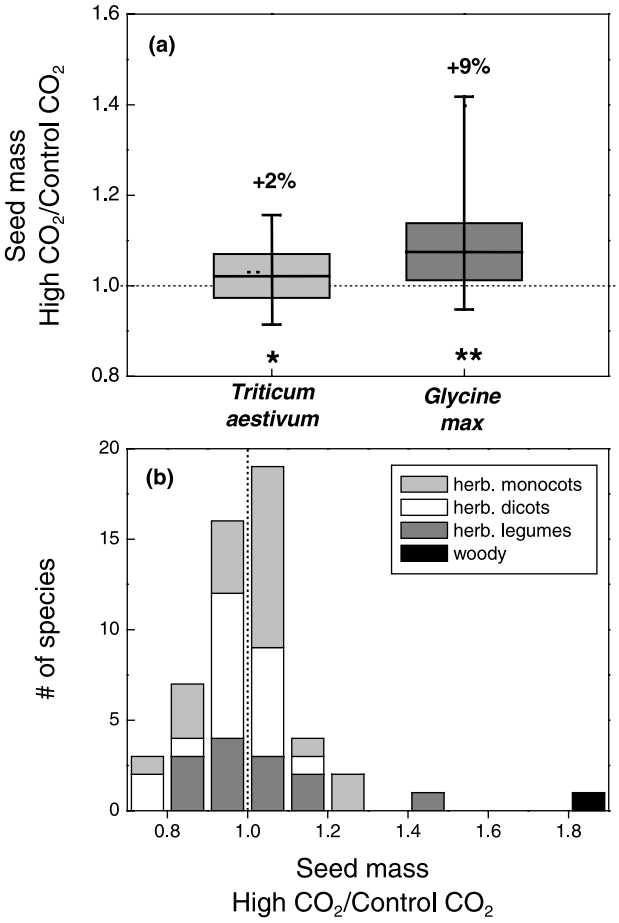

Fig. 1 (a) Box plots, characterizing the distribution of observed effects of elevated CO_2 on seed mass of *Triticum aestivum* ($n = 43$) and *Glycine max* ($n = 20$). Plotted is the ratio between individual seed mass produced by plants grown at high CO_2 and those grown at control CO_2 levels. Numbers above the boxplots indicate the average increase in seed mass. Asterixes below the boxplots show whether the response deviates significantly from zero (ratio = 1): *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. The boxplots indicate the 5th, 25th, 50th, 75th and 95th percentile of the distribution. (b) Distribution graph of the effect of CO_2 concentration on seed mass. Observations are averaged per species. Number of species per category: monocots 21, herbaceous legumes 13, other herbaceous species 18, woody species 1. Literature used for the analysis are listed in Appendix 1.

& Bazzaz, 1994) or reproductive behaviour (Bazzaz *et al.*, 1992). In most growth experiments discussed in this paper, however, seeds from the same batch were used for both control and high-CO_2 grown plants. Thus, in the analysis of biomass responses (section V), differences in seed mass or germination effects will not play a role.

2. RGR, ULR and LAR

To analyse the growth response of plants to a given environmental factor, the concept of growth analysis can be used, a top-down approach tightly connected to the carbon budget of the plant. Growth then is analysed in terms of 'Relative Growth Rate' (RGR, the increase in biomass per unit time and per unit biomass present). This parameter can be factorised into the 'Unit Leaf Rate' (ULR, the increase in biomass per unit leaf area and per unit time), a factor closely related to the carbon gain and losses of the plant per unit leaf area, and the 'Leaf Area Ratio' (LAR), which indicates the amount of leaf area per unit plant mass (Evans, 1972). A problem is that the effect of CO_2 on RGR is relatively small and often time-dependent, occurring only at the early stage of plant growth (references in Poorter, 1993; Centritto *et al.*, 1999). In those experiments where seedlings were pregrown at control levels of CO_2 and then transferred to high CO_2, a transient stimulation of RGR is apparent (Fonseca *et al.*, 1996; Gibeaut *et al.*, 2001). In experiments where the seeds are germinated at different CO_2 levels, the CO_2-induced RGR stimulation is already partly over by the time of the first harvest (Wong, 1993; Roumet *et al.*, 1996; Bunce, 1997). This has to be kept in mind when the distribution of RGR data is considered. Averaged over a wide range of experiments with C3 species, RGR increases by 8% (Fig. 2a; 130 observations in 50 experiments), but the stimulation does not statistically differ from zero, due to quite a number of cases where RGR is not affected at all.

Although changes in RGR are small and only transient in time, the growth components underlying RGR do shift more substantially and over a longer time. The largest change is in ULR, with an average increase of 24% (Fig. 2a; $P < 0.001$). The increase in ULR is balanced by a decrease in LAR of on average 13% ($P < 0.001$). There are some differences between groups of species in this respect, but they are generally small and only marginally significant. The exception is formed by the herbaceous monocots and dicots: although there is no difference in RGR stimulation between the two groups, the dicots were showing a stronger increase in ULR at elevated CO_2 (28% vs 11%, $P < 0.001$) and a stronger decease in LAR (−17% vs −7%, $P < 0.001$).

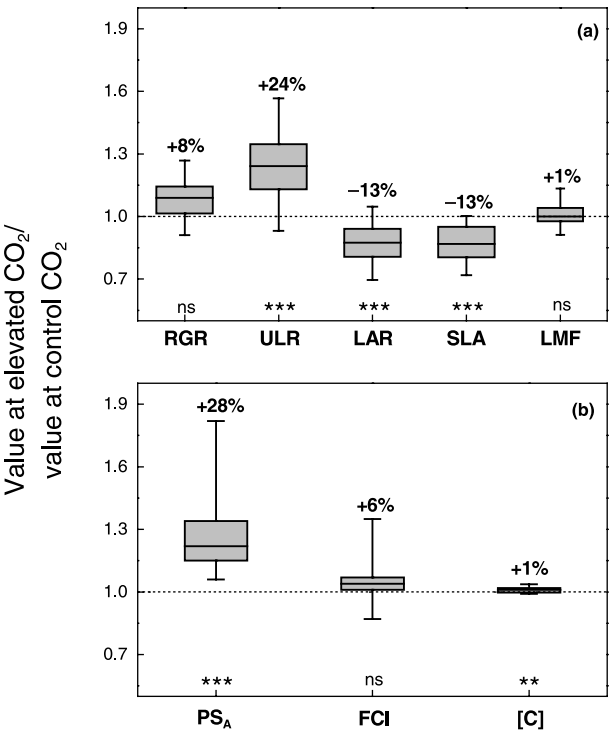

Fig. 2 Box plots of ratios of (a) the growth parameters relative growth rate (RGR; $n = 130$), unit leaf rate (ULR; $n = 130$), leaf area ratio (LAR; $n = 130$), specific leaf area (SLA; $n = 70$) and leaf mass fraction (LMF; $n = 70$), for plants grown at elevated and ambient CO_2 concentration. (b) Ratios of the rate of whole-plant photosynthesis per unit leaf area (PS_A; $n = 35$), the fraction of daily fixed C that is incorporated in the plant (FCI; $n = 29$) and the whole-plant carbon concentration ([c]; $n = 25$). Literature used for the analyses of RGR and growth components are listed in Appendix 2, for the analyses of C budgets in Appendix 3. For more information on boxplots see the legend of Fig. 1.

3. Components of ULR

A simple way to break down ULR is to consider it as composed of three parameters (Poorter, 2002). The first is the leaf-area based carbon gain in photosynthesis, not determined as a momentary rate at light saturation as in many physiological analyses, but under growth conditions and integrated over the day (PS_A). In this way, diurnal variation in light intensity and light distribution are taken into account. Moreover, different leaves on a plant may be in a different physiological stage, which necessitates measurements on whole plants rather than on one specific leaf. The second parameter is the fraction of the daily fixed C that is not spent in respiration, exuded or 'lost' in another way, such as volitalization, but retained in the plant to form part of its 'structural' biomass (FCI, fraction of fixed C incorporated). The third parameter is the carbon concentration of the plant material ([C]), which indicates how much C has to be invested in C-skeletons to build a given unit of biomass. In formula

$$\mathrm{ULR} = \frac{\mathrm{PS_A} \cdot \mathrm{FCI}}{[\mathrm{C}]} \qquad \text{eqn 1}$$

Although there is a wide range of information available at the level of the whole plant in terms of changes in growth, and even more at the individual leaf level in terms of C-fixation, we know very little about the whole-plant carbon fluxes and concentrations that basically link the two. In general, we may expect the daily rate of photosynthesis to increase with elevated CO_2, simply because it happens in most or all individual leaves. This indeed is confirmed by measurements in which the C-gain of whole plants is analyzed (Fig. 2b; $P < 0.001$), although the stimulation can be transient when measurements are made over longer time (Mousseau, 1993; Roumet *et al.*, 2000). Interestingly, although the dataset is small ($n = 35$) and does not adequately cover the various functional groups, herbaceous dicots showed a stronger increase in photosynthesis than the monocots (31% vs 12%, $P < 0.05$), which is in line with the stronger increase in ULR observed above.

Information on the fraction of daily fixed C that is incorporated into the plant's biomass is very scarce. With the rate of photosynthesis increased and the rate of respiration hardly affected by CO_2 (Bruhn *et al.*, 2002), one would expect the C-losses relative to the C-gain to decrease and – assuming exudation and volatilization to be constant – FCI would go up. This does indeed occur, although the average increase (6%; Fig. 2b) does not significantly differ from zero and is small compared to the average change in whole-plant photosynthesis (28%).

Carbon concentrations of whole plants are seldomly reported. The C-concentration of leaves generally decreases somewhat for plants that have a high C-concentration by nature, such as woody species, and increases somewhat for plants that inherently have a low C-concentration, such as fast-growing herbs, but the changes are mostly small and do not exceed the 3% (Poorter *et al.*, 1992; Poorter *et al.*, 1997). As changes in the C-concentration of stems and roots are generally less pronounced (Den Hertog *et al.*, 1993), and shifts in allocation between leaves, stems and roots are minimal (Poorter & Nagel, 2000), we expect changes in the C-concentration of the whole plant to be marginal. This is confirmed by the few data in the literature, showing an average increase of 1% only (Fig. 2b; $P < 0.05$). Thus, as far as information is present, it seems that the observed increase in ULR is mainly due to an increased rate of whole plant photosynthesis per unit leaf area, whereas changes in FCI or whole plant C concentration are minor factors (Fig. 2a,b). Similar conclusions were drawn by Wong (1990) and Evans *et al.* (2000) in comparisons of ULRs with photosynthetic rates measured on individual leaves.

4. Components of LAR

LAR is the product of the Leaf Mass Fraction (LMF, the fraction of total plant biomass that is allocated to leaves) and the Specific Leaf Area (SLA, amount of leaf area per unit biomass). The change in LMF at elevated CO_2 is generally small (Stulen & Den Hertog, 1993; Poorter & Nagel, 2000; Fig. 2a), although a CO_2-induced shift in allocation towards the roots may occur occasionally (Stulen & Den Hertog, 1993; Sigurdsson *et al.*, 2001), though not invariably (Maroco *et al.*, 2002) when plants are grown at a low nutrient availability. There was no difference in LMF change when various functional groups were compared.

The change in SLA is much stronger (Fig. 2a) and a decrease occurs in almost all C3 plants under a wide range of environmental conditions. SLA depends on differences in leaf anatomy, and should be reflected in the chemical composition on a leaf area basis. Although a meta-analysis is lacking, accumulation of nonstructural carbohydrates is likely to be the main factor for the decrease in SLA (Wong, 1990; Roumet *et al.*, 1996) resulting in an increase in leaf density (Roumet *et al.*, 1999). However, additional effects have been reported, such as an increase in the leaf thickness due to more cell layers or a larger cell size (Thomas & Harvey, 1983; Mousseau & Enoch, 1989; Sims *et al.*, 1998; Lin *et al.*, 2001). There is a substantial difference between the herbaceous monocots and dicots, with dicots decreasing 19% in SLA at elevated CO_2, and monocots decreasing only 7% ($P < 0.001$). We have no idea to what extent this can be a consequence of the observed larger stimulation of photosynthesis in dicots. Monocots more often accumulate soluble carbohydrates such as fructans, whereas most dicots accumulate more starch (Lambers *et al.*, 1998). If starch accumulation would have less of a feedback on photosynthesis than the accumulation of soluble sugars, this could perhaps form an explanation for the differential decrease in SLA. However, this is at the moment merely a speculative hypothesis.

5. Growth response along a CO_2 gradient

This paper focuses mainly on the effect of a twofold increase in the atmospheric CO_2 concentration, from *c.* 350 µl l^{-1}–700 µl l^{-1}. However, CO_2 concentrations have covered a much wider range throughout geological time scales, with values estimated as high as 6000 µl l^{-1} during the Paleozoïcum (500 million years ago) and as low 200 µl l^{-1} during the late Pleistocene (15 thousand years ago; Berner, 1997). How do growth parameters respond to a wider range of CO_2 levels? One of the most extended growth experiments is that of Neales & Nicholls (1978) on wheat. As can be seen in Fig. 3, strongest changes in parameters like ULR and SLA are in the low concentration range (200–400 µl l^{-1}). Similar to what happens with whole-plant photosynthesis, a clear saturation is shown for these growth parameters at higher CO_2 levels. Another point that should be stressed is that growth analyses generally deal with plants in the vegetative phase. Responses of plants in the generative phase are not necessarily similar to those of vegetative plants (Thomas *et al.*, 1999), a conclusion that probably holds strongest for annual plant species.

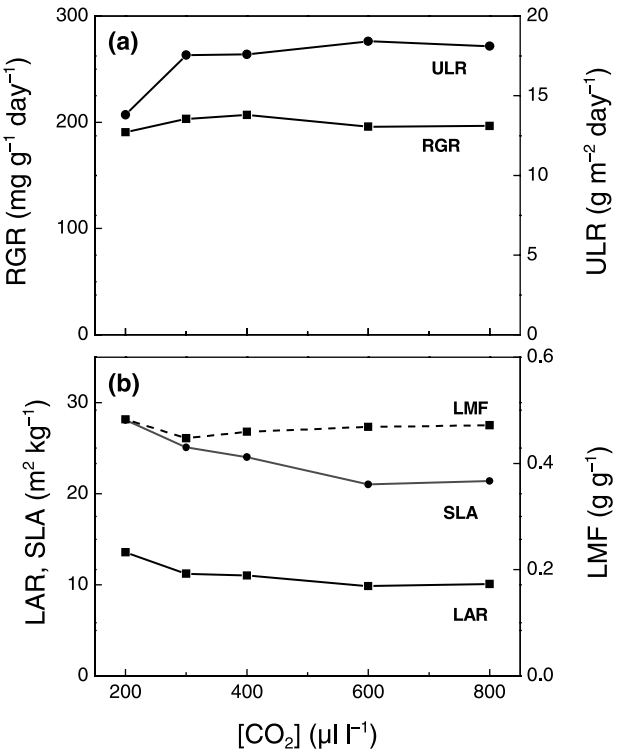

Fig. 3 Effect of a range of CO_2 concentrations on growth parameters of *Triticum aestivum*. Data from Neales & Nicholls (1978).

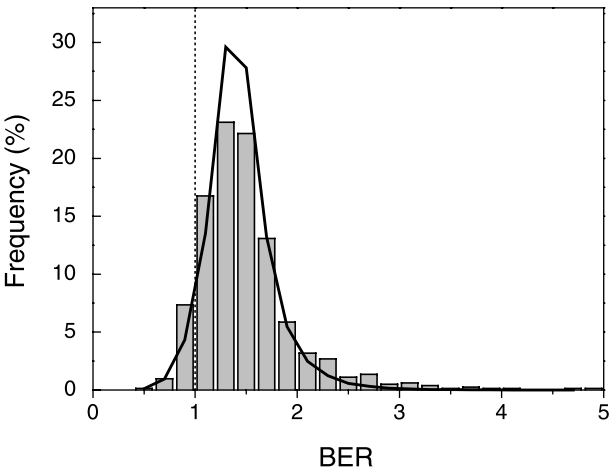

Fig. 4 The bars show the distribution graph of the observed biomass enhancement ratio (BER) data from 350 literature sources (±800 data points for 350 species). The bold line is the simulated distribution over artificial populations with a mean difference equal to the median of the observed data (41%). The artificial populations are of a low, intermediate or high variability in combination with a low (n = 5), intermediate (n = 8) or high (n = 12) number of plants harvested. For more information on the simulation see section IV. The dotted line is for BER = 1.0. BER values of the various sources are available as supplementary material (Table S1).

IV. Variation in biomass enhancement ratio

1. BER distribution

Our literature compilation on the growth response of plants to elevated CO_2 comprised approx. 350 experiments. Some of these were on one species, others on more, and in a number of cases the same species was studied in different experiments, yielding a total of 800 BER observations for approx. 350 species. The overall distribution of the observed BER values is shown in Fig. 4. Clearly, there is wide variation between observations, with some results showing a BER higher than four, implying an over 300% increase in plant mass due to elevated CO_2, and others a BER lower than 0.7, implying a more than 30% decrease in mass for high-CO_2 plants. The most simple and straightforward explanation would be that these differences are due to variation in response between species, with some species showing consistently high BER values across experiments and others showing low values. We tested this hypothesis by selecting only those data in the compilation for which at least three independent observations per species in different experiments had been made. We arrived at a total of 495 observations for 70 species, which were subjected to an analysis of variance with $\log_e$-transformed BER values as the dependent and species as the independent variable. The factor species explained 31% of the total sum of squares. If we would consider species as a random factor, assuming that these 65 were just a sample out of the total range of species that could be considered, then only 18% of the total variance is due to species. This leaves an uncomfortable 82% as 'unexplained'.

What may be the reason for such a high variability independent of species? A first possibility is that the biomass stimulation depends on developmental stage. Thus, starting with equally sized plants at the beginning of the CO_2 enrichment, one would expect BER to increase from one to a certain higher value, with possibly only small changes (mostly decreases) thereafter. That may apply to herbs that enter the generative phase (Thomas *et al.*, 1999) and has also been observed for tree seedlings (Norby *et al.*, 1995; Hättenschwiler *et al.*, 1997; Idso, 1999). However, there is as yet insufficient insight into the nature and reasons for these ontogenetic trends, especially in perennial plants. In most herbaceous species it seems that the main part of the growth stimulation occurs within a relatively short period of 2 wk after the start of the CO_2 treatment. Availability of extra sinks to which a high-CO_2 plant can allocate their extra fixed C may play an important role (Reekie *et al.*, 1998). We tried to filter out part of the effect of developmental stage by focusing on vegetative plants. However, even then BER may change nonpredictably during the growth period.

A second possibility for the high intraspecific variability in BER is that the CO_2-induced growth stimulation is strongly dependent on the environmental differences under which experiments are conducted. We expect controlled experiments,

which form the main topic of this review, to differ most in the integrated daily quantum flux and possibly in water supply (cf. Garnier & Freijsen, 1994). These two factors have, on average, only moderate effects on BER (see section VI), which are by far too small to explain the range in BER values of Fig. 4. Stronger effects are to be expected if nutrients become limited, in which case we expect BER to be 'underestimated', or in laboratories in high-ozone areas, where BER may be 'overestimated' due to a strong positive $CO_2 \times$ ozone interaction. Especially water and nutrient availability are strongly dependent on the relative size of plant and pot, whereas an environmental factor such as O_3 concentration is hardly ever determined. Therefore, there is not an easy way to statistically control for these environmental differences. Lloyd & Farquhar (2000) suggested an iterative restricted maximum likelihood approach to analyse the effect of species and experiment concurrently. Although less sensitive to unbalanced designs than most statistical tests, such an analysis is only fruitful when larger scale experiments are compared that have a range of species in common. This severely restricts the amount of information that can be used. The approach we will follow is to minimise the between-experiment effects by encompassing information from as many experiments as possible. However, we fully agree with Lloyd & Farquhar (2000) and Gurevitch *et al.* (2001) that factorial experiments with a range of species as well as environmental conditions are needed to further test our insights at this point.

A third reason for large variability within species may be that different researchers used different accessions or genotypes, which vary in their response to elevated CO_2. Such variation has been ascribed for a number of species (Wulff & Alexander, 1985; Curtis *et al.*, 1996; Schmid *et al.*, 1996; Klus *et al.*, 2001). In most cases, however, there are no independent experiments confirming that a specific genotype that responds strongly in experiment A is also the one with the strongest response in experiment B. As long as such information is not present, it may be questionable to what extent these genotypic differences really play a quantitative role. The reason for this will be discussed in the next paragraphs.

2. Plant-to-plant variability

The three causes given above are biological as well as deterministic by nature, and have been discussed on various occasions. A fourth reason for variation in BER, which has hardly received attention, is that individual plants within an experimental population vary in biomass (within group variation), sometimes to a large extent. Although all experiments in the literature are based on a number of replicates to avoid biased conclusions, plant-to-plant variability *per se* has hardly ever been the focus of attention of biologists, with the notable exception of size inequality in dense, highly competitive stands (Weiner *et al.*, 1990; Wyszomirski *et al.*, 1999). In the next three paragraphs we assess the importance of plant-to-plant variability. To this end we investigated the variation present in experimental plant populations, the effect of elevated CO_2 thereupon, and the consequences for the reliability of the BER estimate.

One way to characterise plant-to-plant variability is to calculate the standard deviation of the $\log_e$-transformed biomass data (S_{lnM}). In order to obtain an impression about the size of S_{lnM} in experimental populations used for growth analysis, Poorter & Garnier (1996) compiled such values for a variety of published experiments. We extended this compilation with data from a range of other studies, separating experiments with herbaceous species from those with tree seedlings. The distribution graphs of this compilation are shown in Fig. 5(a) and (b), respectively. In some cases investigators have selected for homogeneity of their plants before the onset of the experiment, others have taken a random sample from all seedlings available. The data on S_{lnM} therefore will underestimate the biological variability of the species, but gives a good indication about the homogeneity of the plants used in growth experiments. Taken over all species, the median value of S_{lnM} is 0.31, with 20% of the values below 0.21, and 20% above 0.51. Variability in populations of herbaceous species (Fig. 5a) is generally lower than that in populations of tree seedlings (Fig. 5b; $P < 0.001$). Possible reasons could be that a number of experiments on herbaceous species were carried out with genetically homogeneous crop plants and that in a number of tree species seeds are difficult to germinate, causing considerable variation in germination times and therefore large differences in plant size.

Having obtained an impression of plant variability in growth experiments, we turn to the next question to be answered: does the elevated CO_2 treatment affect plant-to-plant variability? This is a relevant question, not only because it could alter the population dynamics of various species, but also because it may affect the strength of the conclusions based on a given sampling scheme. Increases in population variability have been reported, for example, for plants fumigated with SO_2 (Coleman *et al.*, 1990). To test whether this is also the case for plants grown at elevated CO_2, we calculated the S_{lnM} observed per harvest in a range of CO_2-enrichment studies, with data kindly provided by a number of authors. Thereafter we calculated the ratio of the standard deviations in $\log_e$-transformed dry mass of the elevated-CO_2 and the control plants. The distribution of this ratio for 150 harvests on 60 species in 14 experiments is given in Fig. 5(c). The range is wide, most likely because a proper estimate of population variance is difficult to achieve with just 5 or 10 plants harvested. The average ratio, however, is 1.01 and does not deviate significantly from unity. Therefore, we conclude that plant populations do not become more variable at elevated CO_2. There is no indication of any difference between herbaceous and woody species in this respect ($P > 0.8$).

To what extent can plant-to-plant variability affect the outcome of CO_2 experiments? Let us assume an extreme case, i.e.

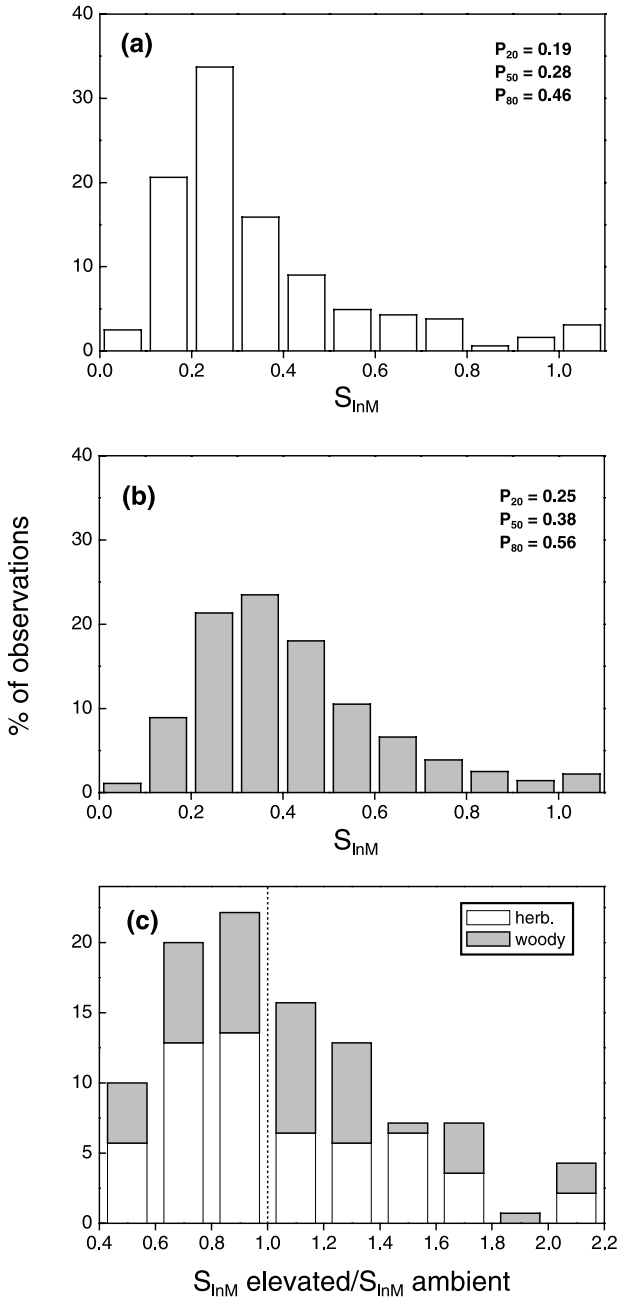

Fig. 5 Distribution graphs of variability in total plant dry mass in experimental populations used for the analysis of plant growth, for (a) herbs (n = 700) and (b) woody species (n = 350). (c) Distribution graph of the ratio in variability of plants grown at elevated CO_2 and ambient concentrations (n = 80). Variability is expressed as the standard deviation of the $\log_e$-transformed total dry mass for plants at a given harvest. The dotted line indicates where the variabilities are equal. Data for (C) are from Poorter *et al*. (1988), Poorter (1993), Roumet *et al*. (1996), Volin & Reich (1996), Reekie *et al*. (1998), Volin *et al*. (1998), Atkin *et al*. (1999), Cornelissen *et al*. (1999), Navas *et al*. (1999), Schortemeyer *et al*. (1999), Greer *et al*. (2000), Hoffmann *et al*. (2000), E. Garnier (unpublished) and M. Schortemeyer (unpublished). Data for (a) and (b) are from Poorter & Garnier (1996), supplemented by those listed above and by Cornelissen *et al*. (1998), Pattison *et al*. (1998), Poorter (1999), Wright & Westoby (1999), Van Rijn (2001) and R. Villar (unpublished).

the true BER for all 800 observations compiled in Fig. 4 was actually the same, with a value equal to the median of all observations (1.41). For most experiments we do not know the population variability, but we can arrive at an educated guess. Let us assume that the experimental populations can be categorised into three groups, with either a low, an intermediate or a high S_{lnM}, as derived from the 20th, 50th and 80th percentile of the distribution given in Fig. 5(a) and (b). The third part of information that has to be known is the number of plants harvested per treatment. For the 350 experiments compiled here, a low value is 5 (P20), the median is 8 and a high value is 12 (P80). Using all this information, we postulated a species with a high CO_2 and a control population that differed in mass by 41%, and with equal variability in plant mass. We then simulated experiments with three different population variabilities in plant mass (σ_{lnM} = 0.21, 0.31 and 0.51) and, for each variability, three different sample sizes (n = 5, 8 and 12). For each of the nine combinations we computer-generated 10 000 experiments, and for every experiment we calculated an average BER. The resulting distribution of 90 000 BER values, which we consider to be representative of what could be expected from a compilation of all of the actually observed BER results, is shown as the continuous line in Fig. 4. Compared to the actually observed distribution, the simulated distribution is surprisingly similar and no significant difference between the two could be found with a χ^2 test (df = 17, $P > 0.15$). Therefore, we have to conclude that variability in the plant population plays an unfortunate, but large role in determining the outcome of experiments. Clearly, the number of plants harvested is often insufficient given the range in plant mass within an experimental group of plants. This is especially problematic as variability in BER is the sum of the variability in both the numerator and denominator of the BER calculation (cf. Jasienski & Bazzaz, 1999).

3. Consequences for data interpretation

What are the take-home-messages of this analysis? The first conclusion is that in these type of experiments attention should be given to a sufficiently homogeneous experimental population. Clearly, the outcome of single experiments may vary to a large extent if highly variable populations are investigated. This is the more critical as the growth stimulating effect of CO_2 is relatively small compared to the effect of other environmental variables such as nutrient availability or light intensity, where plant masses may vary fivefold or more across treatments. Consequently, it requires more precision to separate the CO_2 effects from error variation than in the case of light or nutrient effects. Second, credibility for one or another hypothesis explaining interspecific variation in growth responses of plants cannot come from results of one or two specific experiments, because repeatability is not very high. Rather, we think that a wider range of experiments should be performed before we can conclude

that a (group of) species behaves differently with respect to CO_2 than another (group of) species. Such an approach bears the risk that experiments with different experimental conditions are compared. As discussed above, it is impossible to quantify these effects for each of the experiments described in the literature. This may imply that differences between species are confounded to a certain extent with growth conditions. However, given the large number of species and experiments, the chances that this may drastically affect the outcome of the analysis seem small. The other side of the coin is that the wide variety of experimental conditions allows for more general statements (Poorter, 1993). Thirdly, no matter what groups of species are compared, or how similar experimental conditions were, there will always be a lot of scatter, so the amount of variation explained by any contrast between groups of species will at best be modest. For the analysis of BER in the next section of this paper, we choose to consider variation at the level of species. Therefore, we averaged all data per species, assuming that most of the variation at the within-species level was random.

There is one other aspect that deserves attention. The timescale for the compiled experiments varies from 10 d to 50 months, with a median value of 4, 7 and 16 wk for crop, wild herbaceous and woody species, respectively. As discussed in section III, most of the CO_2-induced growth stimulation is generally found at the beginning of the treatment. However, for most species time-dependent changes have not been investigated and the phenomenon is in general ill-understood. It can be shown that it is the *absolute* difference in RGR that translates into a *relative* biomass stimulation after a given period of time. From the BER at the end of the experiment and the duration of the CO_2 fumigation we can back-calculate the average absolute stimulation in RGR over the whole experimental period, assuming equal seed or seedling size at the onset of CO_2 enrichment (for a mathematical derivation see Poorter *et al.*, 1996). In the analyses in section V, we decided to consider only those differences between groups relevant where both the average BER change and the RGR stimulation show similar direction and statistical significance.

V. Functional groups of species

1. C3, C4 and CAM

In this section we analyze to what extent functional groups of species differ in their growth response to elevated CO_2. The most obvious categorization that could be envisaged is based on the type of photosynthesis (Bazzaz & Catovsky, 2002). The commonest group of species, the C3 species, has a limiting CO_2 concentration at the level of the chloroplast and therefore can be expected to respond with an increased C-gain upon a rise in the CO_2 concentration around the leaves. Plants with a C4 type of photosynthesis posses a CO_2 concentrating mechanism that increases the CO_2 concentration at the site of

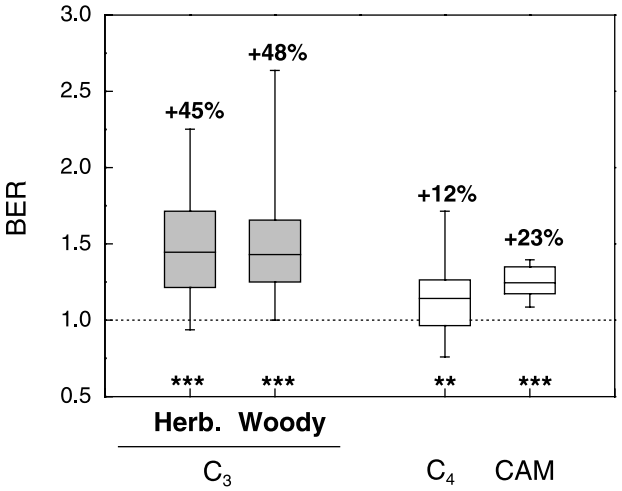

Fig. 6 Distribution of biomass enhancement ratio (BER) values for different categories of species (C3 herbs: $n = 144$, woody C3 species: $n = 160$, C4 species: $n = 41$; CAM species: $n = 9$). Graphs show boxplots. For more information on boxplots see the legend of Fig. 1.

Rubisco to *c.* 2000 µl l^{-1} (Sage, 2001). At this concentration the oxygenating function of Rubisco is repressed, and the carboxylating function is almost saturated. Purely on that basis, C4 plants are expected to respond not or at best marginally to a rise in atmospheric CO_2.

Analysis of the BER values complies with these notions. C3 plants show, on average, the strongest response (+45%; 300 species) and C4 plants the smallest (+12%; 40 species; Fig. 6). Both groups have BER values significantly higher than one, implying that at least a number of C4 species are stimulated in their growth as well. Several explanations are possible for this intriguing response (Ghannoum *et al.*, 2000). First, photosynthesis may not be completely saturated at current CO_2 concentrations in some or all C4 species. Second, CO_2-induced decreases in stomatal conductance may reduce transpiration, thereby conserving soil water that can be deployed for extra photosynthesis later in time. Thirdly, the decrease in transpiration could increase leaf temperature. As C4 photosynthesis is strongly dependent on temperature, this could be a likely explanation as well. A fourth alternative that has been mentioned is that cotyledons of C4 species may be C3 like, or that young developing leaves of C4 species are leaky and therefore may increase photosynthesis at elevated CO_2 (Dai *et al.*, 1995). However, this last option is not considered likely (Ghannoum *et al.*, 2000). The increase in daily photosynthesis required to explain the improved growth is in the range of 2% only (Poorter, 1993), a value that may easily be reached via any of these alternatives.

CAM species are also stimulated, with an average response in between that of C3 and C4 species (23%; $P < 0.001$). One of the physiological reasons for the positive growth response is that a number of these species are CAM-facultative, they can switch to a C3 type of photosynthesis when water is available. Others show direct CO_2 fixation by Rubisco early in

the morning or late in the afternoon. Under these circumstances an increased C-fixation is to be expected. However, CO_2 fixation by PEP-carboxylase during the night is also stimulated by elevated CO_2 (Li *et al.*, 2002). This is an ill-understood phenomenon, as it is generally thought that this enzyme is saturated at current CO_2 levels (Drennan & Nobel, 2000). Unfortunately the total number of CAM species measured is very low (nine), so any generalization for this group of species is premature. One interesting test would be to compare the response of species that are CAM facultative and those that are obligatory CAM in their CO_2 fixation. A point of attention is that in quite some cases CO_2 treatment did not start with seeds or recently germinated seedlings, but with larger plants or cuttings. Calculating a BER value on the basis of total biomass may then underestimate the real growth response. It would require a time-course of the growth stimulation to analyse whether the time-dependency of the stimulation, as observed for C3 species, also occurs in this group of plants.

Testing with a one-way ANOVA we found the differences between plants of the photosynthetic groups highly significant ($P < 0.001$). However, again the proportion of the sum of squares explained by the model is low, being 10% only. Notwithstanding this variation, the absolute differences between the functional groups of species are quite consistent and do hardly differ from earlier analyses, based on 1/3 or 2/3 of the now available data (Poorter, 1993; Poorter *et al.*, 1996). We checked the effect of data base size by randomly dividing the 800 observations into three groups, recalculating mean responses of C3, C4 and CAM species for each of the groups. Although small differences between the three data sets were present, they did not affect the main conclusion to any extent. Therefore, we conclude that the sample size of this database is sufficient for robust conclusions with regard to the investigated C3 and C4 species.

2. Within C4 species

There are indications that not all C4 species respond to the same extent. Ziska & Bunce (1997), for example, found *Amaranthus retroflexus* and five other C4 weed species to respond more strongly than *Zea mays* and some other C4 crop species. Differences in BER between *Amaranthus retroflexus* and *Zea mays* have been quite systematic, indicating a species–specific response (Poorter *et al.*, 1996). These species belong to different C4-subtypes, which vary in leaf morphology as well as in the enzymes used for decarboxylation of the C4 product formed. The NAD-ME type is considered to have vascular bundle sheath cells that are the most leaky for CO_2, and therefore may respond more to an increase in CO_2. LeCain & Morgan (1998), however, found NAD-ME species to have lower BER values than NADP-ME species and a similar trend was observed by Wand *et al.* (2001). Ziska & Bunce (1997) could not relate differences in BER to the subtype. Averaged over all observations available, there was no difference between species of the two groups (Table 1). There are only few data for C4 species of the PCK subtype, so we did not include them in the tests, but contrary to the other subtypes the species investigated so far showed a negative growth response. A firm conclusion awaits more evidence.

Alternatively, a difference between *Amaranthus* and *Zea* might be caused by the very different genetic background, with one species belonging to the dicots, the other to the monocots. The number of dicots investigated is small and although they seem to respond more than monocots, the difference is not significant. Simply analyzing C4-subtype and lineage (monocots vs dicots) separately may ignore the fact that these factors could be confounded to a certain extent. This would be especially true if, by chance, the investigated monocots were almost all from the NADP-ME subtype and

Table 1 Average values for the biomass enhancement ratio (BER) and the relative growth rate (RGR) stimulation to CO_2 of C4 plants, as dependent on lineage (monocots/dicots) and C4 subtype (NAD-ME, NADP-ME and PCK)

	Simple contrast			*P*					
				BER			ΔRGR		
Class	BER	ΔRGR (mg g^{-1} day^{-1})	*n*	sc	mr	ba	sc	mr	ba
Monocot	1.11	3.0	37	ns	ns	ns	ns	ns	ns
Dicot	1.23	5.9	4						
NAD-ME	1.10	2.6	10	ns	ns	ns	ns	ns	ns
NADP-ME	1.18	4.8	23						
PCK	0.90	–2.6	4						

Also given are the number of species for each category. Significance levels are given for three types of analyses. The column 'sc' indicates the result of a two-sample *t*-test for each simple contrast. The column 'mr' gives the significance when all attributes are simultaneously analysed in a multiple regression, using dummy variables (0 and 1) for the various groups. The last column ('ba') gives the results if the simple contrasts were carried out on the data before all observations for a species were aggregated (cf. section IV). In the latter case n is much higher. Average values were rather similar for the 3 analyses. Significance levels are: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; +, $0.05 < P < 0.10$; ns, nonsignificant, $P > 0.10$.

the dicots from the NAD-ME subtype, or vice versa. Therefore we analysed the BER and RGR response of all NAD-ME and NADP-ME species with a multiple regression, in which we entered C4-subtype and lineage as dummy variables. As long as two traits are not completely correlated, such a regression can separate the effect of both factors. Finally, we also tested the significance of the difference between the groups without aggregating data per species. Table 1 shows the result of these analyses: there is no systematic effect of subtype or lineage in the compiled data set, independently of the way we tested the data and whether the growth stimulation was expressed as BER value or as increase in RGR. For the time being, with so few data on PCK species, we conclude that any systematic difference between C4 species has to be explained by other factors than subtype or lineage. Wand *et al.* (2001) suggested that C4 species with a large growth potential responded more than slower-growing species. This is a factor worth investigating, although it seems at variance with the meta-analysis of Wand *et al.* (1999). They found wild C4 species to respond more than what is generally found for weedy or crop C4 species, where we would presume these last two groups to be faster-growing.

3. Within C3 herbs

Plants within the group of C3 species share the same type of photosynthesis, but will that imply that they all behave the same in response to elevated CO_2? We considered three different contrasts: the one between monocots with dicots, the possibility to fix atmospheric nitrogen in one symbiotic relationship or another, and the effect of inherent differences in growth rate. Again we carried out a multiple regression with these factors as dummy variables to exclude to some extent the fact that these factors are not distributed randomly over our database. Table 2 shows that there was a significant increase in the RGR stimulation of those plants that are capable of symbiotic N_2 fixation. However, as the actual N_2-fixation strongly depends on nitrate availability in the root environment (Lambers *et al.*, 1998), it is not known to what extent these species really were relying on atmospherically fixed N. Moreover, there was no significant difference in BER. There was a tendency for monocots to respond more strongly than dicots, but again the statistical significance strongly depended on the way the data were treated, and whether the stimulation was expressed as BER difference or RGR increase. Therefore, we conclude for the moment that monocots and dicots show similar growth responses to elevated CO_2.

The largest and most consistent difference was the one between inherently fast- and slow-growing species. No matter how the data were analysed, fast-growing species showed a much greater response than slow-growing species, the difference being of the same magnitude as that for C3 and C4 plants in general. A simple explanation is that fast-growing species operate with a higher LAR than slow-growing species (Poorter & Van der Werf, 1998). If elevated CO_2 stimulates photosynthesis and also ULR to the same extent in slow- and fast-growing plants, then the proportional increase in RGR is the same for species of both groups, but the absolute increase in RGR is larger for the fast-growing species. And as it is the absolute increase in RGR that determines the relative response after a given period of time, this could explain the results. However, other differences between the species could play a role as well. Source–sink interaction is an important factor in determining the growth response, with the highest BER values observed for species with large sinks (Reekie *et al.*, 1998). We categorised all crop species as being fast-growing. They generally have growth rates that come close to those of the inherently fast-growing wild species. It may well be that such species are better able to lay down new meristems and invest the extra-fixed C in structural biomass than slow-growing species.

There have been other efforts in the literature to classify groups of species with contrasting characteristics. Indeterminate as opposed to determinate growth has been mentioned as a factor that may increase the growth response to CO_2 (Oechel & Strain, 1985; Ziska & Bunce, 2000), again because it will be easier to deploy extra-accumulated sugars. Mycorrhizal species may easily metabolise sugars in the fungal network, with possible beneficial effects (Díaz *et al.*, 1993), but in another experiment a nonmycorrhizal species like *Carex flacca* was responding better than all other species (Leadley & Körner, 1996). Another contrast that has been studied is

	Simple contrast			*P*					
				BER			ΔRGR		
Class	BER	ΔRGR (mg g^{-1} day^{-1})	*n*	sc	mr	ba	sc	mr	ba
Monocot	1.49	11.4	56	ns	**	ns	ns	*	*
Dicot	1.42	11.2	87						
N_2-fixing	1.50	14.5	23	ns	ns	*	+	*	***
others	1.44	10.6	120						
Slow-growing	1.25	5.8	41	***	***	***	***	***	***
Fast-growing	1.59	15.1	63						

Table 2 Average values for the biomass enhancement ratio (BER) and the relative growth rate (RGR) stimulation to CO_2 of herbaceous C3 species as dependent on lineage (monocots/dicots), the potential to fix N_2 symbiontically and the potential growth rate of the species. In the specific case of slow-, intermediate and fast-growing species we used 0, 0.5 and 1 as dummy variables. Only the estimated values for slow- and fast-growing species are given. For more information see the legend of Table 1

between plants that load their sugars differently into the phloem. These differences between symplastic and apoplastic phloem loaders are correlated with life form and ecological niche (Van Bel, 1999). Körner *et al.* (1995) investigated possible differences in starch accumulation between the groups, but were unable to find any. Differences in growth response have not been studied.

4. Within woody C3 species

In terms of number of species investigated, more work has been done on woody species than on herbaceous ones. With regard to the BER, no difference at all could be found between these two groups of species (Fig. 6). However, most experiments with woody species last longer than those for herbaceous species, implying that the RGR stimulation is much smaller in the case of woody species. It is obvious that most of the work on woody species is focused on young tree seedlings, with a median duration of CO_2 enrichment of 16 wk only. Therefore, it is difficult to forecast longer-term responses of larger trees on this basis. Longer-term enrichment studies on a few species indicate that an average stimulation of 30–50% is achieved in the field as well as in open-top chambers (Curtis & Wang, 1998; Idso, 1999). This is not different from the average stimulation for younger trees (Fig. 6).

In this analysis we considered possible functional groups on the basis of three contrasts: evergreen vs deciduous species, N_2-fixing plants compared to those without the possibility of N_2-fixation, and Gymnosperms vs Angiosperms. Only the last group showed a significant difference, with Angiosperm seedlings showing a somewhat stronger response than Gymnosperms (Table 3). This is in agreement with what was found by Ceulemans & Mousseau (1994), but Curtis & Wang (1998) did not find significant differences, and Saxe *et al.* (1998) even claimed the opposite. Another point of uncertainty is that evergreen species are generally slower-growing than deciduous species. Therefore, we had expected to see similar differences as for fast- and slow-growing herbaceous species.

Another attempt for classification has been made by Kerstiens (2001). In a meta-analysis of a more specific data set of woody species, he found BER to be higher for shade-tolerant species than for intolerant ones, especially at high light. This was partially confirmed in an experiment included in Bazzaz & Catovsky (2002) where coniferous seedlings complied with these expectations, but not the deciduous species. On the contrary, Winter & Lovelock (1999) found the shade-intolerant pioneer species to show larger responses than the shade-tolerant climax species. Combined with the fact that most experiments cover such a limited part of the life cycle of these plants, we have to conclude that classification of woody species into functional groups is still complicated.

5. Fast-growing versus slow-growing

In the above analysis of the woody species, we did not classify these species with respect to their growth rate, as we felt that we did not have a good overview over this parameter. For herbaceous C3 plants we were able to categorise species as slow-, intermediate and fast-growing. These categories are to some extent arbitrary, and attention has been drawn to the fact that these differences between fast- and slow-growing species may not show up in each experiment (Lloyd & Farquhar, 2000). Apart from the variability discussed in section IV, such 'inconsistencies' may also be due to misclassification of the species, or to specific conditions used in a particular experiment. We therefore extended the analysis, by selecting those experiments for which RGR of these species was specifically measured. Different experiments have different time-frames, and RGR is not always measured from the start of the CO_2 enrichment. Therefore, we derived the increase in RGR due to elevated CO_2 from the difference in the BER values and the duration of the CO_2 enrichment, as discussed in section IV. If the absolute increase in RGR is plotted against the measured growth rate of control plants, a strongly positive correlation is found: the higher the RGR at 350 µl l^{-1} CO_2, the stronger is the absolute RGR response (Fig. 7; $r^2 = 0.52$; $P < 0.001$).

The relationship shown in Fig. 7 comprises both herbaceous and woody species. The good fit may partly be fortuitous: by considering the absolute increase in RGR we

Table 3 Average values for the biomass enhancement ratio (BER) and the relative growth rate (RGR) stimulation to CO_2 of woody C3 species as dependent on lineage (Gymnosperms/Angiosperms), the potential to fix N_2 symbiontically and leaf phenology (evergreen/deciduous). For more information see the legend of Table 1

	Simple contrast			P					
				BER			ΔRGR		
Class	BER	ΔRGR (mg g^{-1} day^{-1})	*n*	sc	mr	ba	sc	mr	ba
Evergreen	1.51	4.5	83	ns	+	ns	ns	ns	ns
Deciduous	1.44	5.1	75						
N_2-fixing	1.49	5.3	26	ns	ns	ns	ns	ns	**
others	1.49	4.7	133						
Gymnosperms	1.36	2.6	30	+	*	*	***	*	***
Angiopserms	1.51	5.3	129						

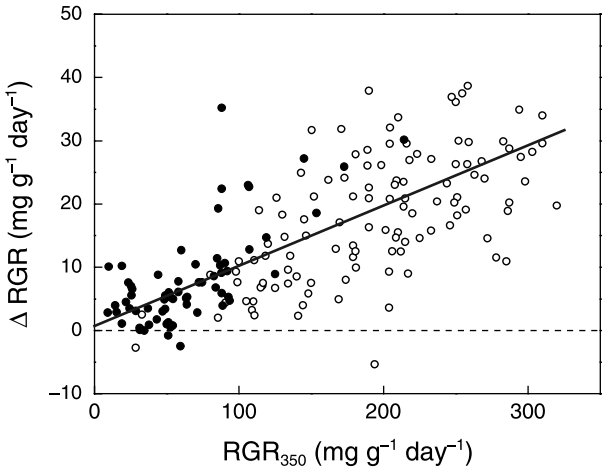

Fig. 7 The absolute increase in relative growth rate (RGR) due to an elevated CO_2 concentration plotted against the RGR at control conditions (n = 179, r^2 = 0.52). Open circles pertain to herbaceous plants, closed circles to woody species. In situations where RGR was not calculated over the exact period that CO_2 was applied, the increase in RGR was calculated from the different BER values, following the formula given in Poorter *et al*. (1996). Literature used for the analyses are listed in Appendix 4.

standardise time in the sense that the average growth stimulation per day over the whole experimental period is calculated. As most of the response is in the beginning of the growth period, and as experiments with tree seedlings are generally lasting for a longer time than those with herbaceous plants, the correlation may in part be due to the fact that tree seedlings grow more slowly than herbaceous plants, and are measured over a much longer time span. The positive relationship, however, also holds when herbaceous and woody species are considered separately, with some indication that woody species respond a bit stronger at a given RGR than herbaceous species ($P < 0.05$). An alternative test is to analyse the relationship within experiments, thereby minimizing the possibility that slow-growing species were experiencing less favourable conditions than the fast-growing species in the compilation. In almost all experiments where a range of species with different growth rates is compared (either tree seedlings or herbaceous plants), the faster-growing species respond more strongly than slow-growing species. In a number of cases the response is positive, but statistically above the 0.05 level (Campbell *et al*., 1991; Roumet *et al*., 1996; Cornelissen *et al*., 1999), whereas in others the response is significant (Poorter, 1993; Bunce, 1997; Atkin *et al*., 1999; Winter & Lovelock, 1999). For 20 out of the 24 experiments that included species comparisons and determined RGR values, slopes of the regression lines were positive, and the average slope (0.088, very similar to the overall slope of 0.095) was significantly higher than zero ($P < 0.001$). Therefore, we consider the broad picture emerging from the literature confirmed by most individual papers, and we conclude that under favourable conditions high-RGR species will respond more strongly to elevated CO_2 than low-RGR species. The mean difference in BER is of similar magnitude as the one observed between C3 and C4 species. The fact that fast-growing species respond more strongly to elevated CO_2 has a clear parallel in the growth responses observed at different light or nutrient availabilities. Also in those cases the inherently fast-growing species will respond strongest.

VI. The response in a more natural environment

1. Limiting conditions

One of the goals of the quantitative analysis presented in section V is to find a classification that might be helpful as a basis for prediction of changes in natural vegetations. Will C3 species expand relative to C4 species, and will fast-growing species thrive at the cost of slow-growing ones? There are a number of complications to which we briefly would like to draw the attention. First, the analysis in section V is carried out with species that were grown under more or less 'optimal' conditions. This will allow most plants to show their maximal response to CO_2, without environmental constraints or stresses. In a natural environment conditions will generally be less favourable. Poorter & Pérez-Soba (2001) reviewed the CO_2 response of isolated plants when grown under a variety of stresses. Table 4 gives the average BER of C3 species in the close-to-optimal situation as well as in the case that a given environmental factor causes biomass to be reduced by 50% at control levels of CO_2. For most of these factors (irradiance, water, salinity, UV-B) changes in BER are small. Interactions are more substantial in ozone-stressed plants, for which BER is strongly promoted, and for cold- or nutrient stressed plants, where the BER is clearly lower than for plants grown at close-to-optimal conditions. In most natural environments nutrient availability will be low, so purely on that basis we expect the response under those conditions to be small.

Table 4 Average biomass enhancement ratio (BER) of environmentally stressed C3 plants as compared to those of relatively unstressed plants. For each environmental factor it was calculated how the BER would be if the stress factor reduced growth of the 350 µl l^{-1} plants by 50% when compared with the 'optimal' conditions. After Fig. 6 of Poorter & Pérez-Soba (2001).

Environmental stress factor	BER
None	1.47
Low Nutrients	1.25
Low Temperature	1.27
High UV-B	1.32
High Salinity	1.47
Low Water availability	1.51
Low Irradiance	1.52
High Ozone	2.30

2. Competition versus isolated plants

The second factor that makes a difference between most laboratory experiments and the field is that plants in the lab often grow without any mutual interference at the leaf or root level. This implies that an extra investment in leaves or roots can immediately pay off in the form of extra carbon and nutrient capture, which will, in the absence of sink limitation, result in an extra stimulation in growth. The situation is different when plants are grown together. At low density, total biomass of a monoculture will increase linearly with density, but as crowding becomes stronger the biomass of the stand saturates to a maximum level, with only very limited space for each individual. Under crowded conditions, extra leaf area will not necessarily lead to extra carbon gain. Since both the threshold density and the slope vary among species, the simplest comparison is the biomass of isolated plants with those in crowded monocultures. Under those conditions, woody and herbaceous species are generally responding less to elevated CO_2 than individually grown plants (Du Cloux *et al.*, 1987; Wayne & Bazzaz, 1995; Retuerto *et al.*, 1996; Navas *et al.*, 1999). Taken over a range of experiments, no correlation was found between the response of a species grown in isolation and in monoculture (Fig. 8a, $r^2 = 0.06$).

The next level of complexity comes in when mixed stands are analysed. The response to elevated CO_2 of a particular species will then not only depend on its own physiological and morphological characteristics, but is also determined by the secondary interactions that arise with the other species that are competing for the same resources (Firbank & Watkinson, 1990). Therefore, the correlation between the BER of a given species grown in isolation and in competition with other species can be expected to be even lower as the one between isolated plants and monocultures, and this happens to be the case (Fig. 8b, $r^2 = 0.00$). The most unpredictable step appears to be the transition from isolated plants to monocultures. The second step, from monostands to mixed stands, shows a much better correlation (Fig. 8c, $r^2 = 0.33$), confirming a previous study by Navas *et al.* (1999) on artificial herbaceous communities. Therefore, we conclude that any prediction of species responses in a vegetation would be better off with growth analyses at the stand level than at the level of the individual.

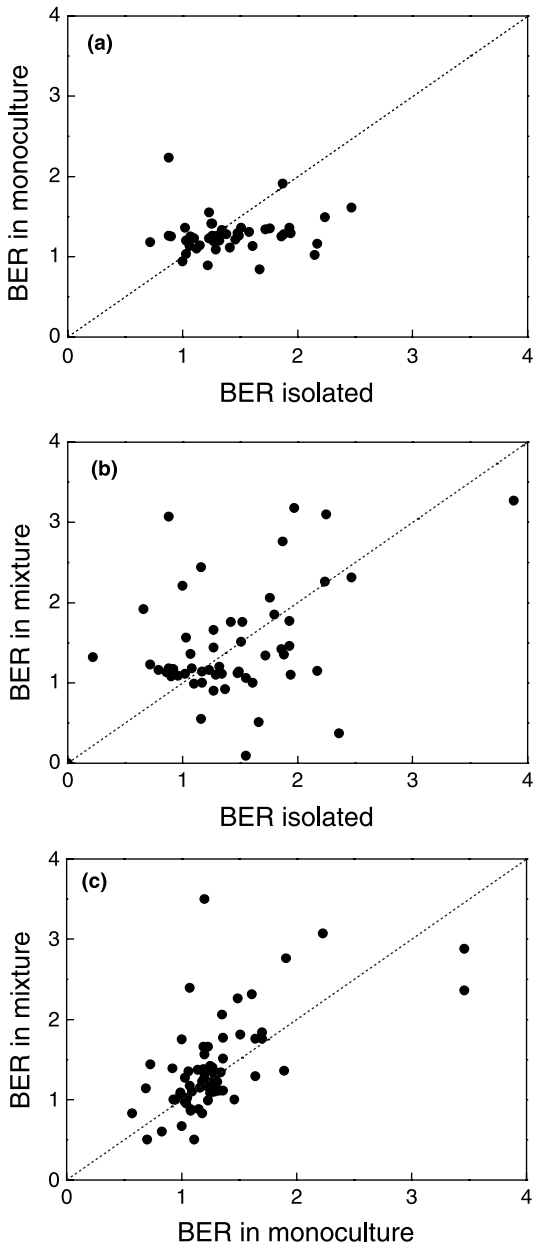

Fig. 8 (a) Biomass enhancement ratio (BER) of plants grown in a monoculture plotted against the BER of isolated plants ($r = -0.25$, $n = 27$, $P > 0.2$). (b) BER of plants grown in a mixed culture of plants plotted against the BER of isolated plants ($r = 0.04$, $n = 33$, $P > 0.8$). (c) BER of plants grown in a mixture of plants plotted against the BER of plants in monoculture ($r = 0.58$, $n = 50$, $P < 0.001$). The dotted line indicates a 1:1 relationship. Literature used for the analyses are listed in Appendix 5. Three species that represented less than 5% of the total biomass of the mixture at control levels of CO_2 were excluded from the analysis. Their effect on the analysis was negligible.

3. Functional groups

Alternatively, we could use published competition experiments, to test whether specific groups of plants profit more than others. A good example is shown in Fig. 9, where results of Winter & Lovelock (1999) and Lovelock *et al.* (1998) are combined. They grew isolated seedlings of nine tropical tree species in open top chambers at ambient and elevated CO_2, and found a stronger response for the fast-growing pioneer species as compared to the slow-growing climax species. This is in agreement with the conclusions of section V. However, when almost the same set of plant species was grown in competition, BER values for all species ranged around 1, with no difference between species that responded strongly or weakly in isolation. Another example of a very poor correlation between the prediction for isolated plants and those

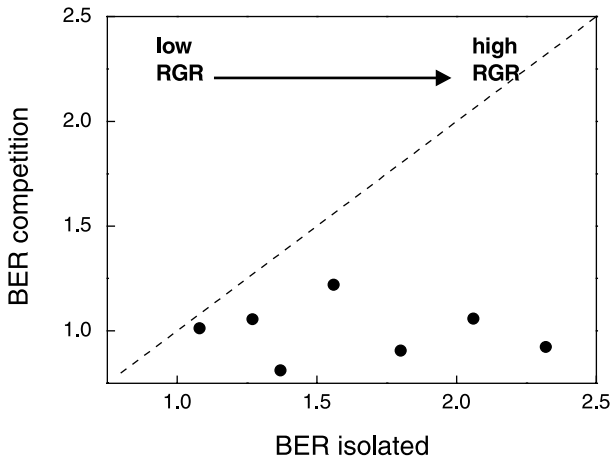

Fig. 9 Biomass enhancement ratio (BER) values of seven tropical plant species grown in isolation (Winter & Lovelock, 1999) and in a mixed community (Lovelock *et al*., 1998). The dotted line indicates a 1:1 relationship.

in competition are experiments in a calcareous grassland vegetation. The species that showed the strongest growth response, both in the field as in the lab was *Carex flacca* (Leadley & Körner, 1996; Stöcklin & Körner, 1999), a species with a very low potential growth rate (Van der Werf *et al*., 1993).

Is it possible to discriminate between groups of species that form 'winners' and 'losers' in competitive situations? An extended review is given by Reynolds (1996). Similarly as for isolated plants we analysed a number of competition experiments retrospectively for differences in response between functional groups of species. To this end, we used the BER of the whole artificial or natural vegetation as a calibration point. For each species of the mixture we calculated the BER of that species, and divided it by the BER value of the whole vegetation. If this ratio is higher than 1.0 the species is profiting disproportionately and is designated as a 'winner'. If the ratio is lower than 1.0 the plant would lose out compared to the whole vegetation. On the one hand, it may be naive to test for such a general response for a given group of species, as competition will strongly depend on the competing species that are present, as well as the specific environmental conditions. On the other hand, small differences between species that are hardly of relevance for plants grown in isolation can be of crucial importance in a competitive situation and may magnify differences in response between species. We felt it appropriate to formally test for these winners and losers anyway. We restricted our analysis to competition experiments carried out with herbs, as most of the work in this field has concentrated on this group, but excluded a-*priori* those species from the analysis that represented less than 2% of the total biomass of the vegetation, as the behaviour of these plants may be erratic if only a few individuals are present. Finally, given the strong difference in response of nutrient-rich and nutrient-stressed plants (Table 4), we classified experiments as carried out under either high or low nutrient conditions. A classical problem in this case is that the observations on different species within a competition experiment are definitely not independent of each other. A very conservative solution is to use only one species per experiment. This would have resulted in a serious loss of information, an aspect we considered more problematic than statistical independence (Gurevitch *et al*., 2001).

The results are shown in Table 5. As in section V, we analysed the differences both as simple contrasts and in a multiple regression. For experiments with high nutrient levels, the only significant difference found was between C3 and C4 species, with C4 species being the losers at elevated CO_2. However, the number of observations for C4 species is rather low (< 15). The difference remains significant in the multiple regression analysis and is in line with the difference we have seen between C3 and C4 species at the individual plant level (Fig. 6). By contrast with the observations at the individual plant level, fast- and slow-growing species respond exactly similar to elevated CO_2 under competition. Again, the number of species in one of the categories is low, but as it is in accordance with the idea that there is little scope for fast-growing plants in a vegetation to profit from the extra investments they made, we have as yet no reason to doubt these conclusions. No differences were found between N_2-fixing species and other dicots, or between monocots and dicots in general.

	High nutrients				Low nutrients			
			P				*P*	
Class	WinRatio	*n*	sc	mr	WinRatio	*n*	sc	mr
C3	1.04	74	**	***	0.94	72	ns	ns
C4	0.78	13			1.05	4		
Fast-growing	1.00	71	ns	ns	0.93	29	ns	ns
Slow-growing	0.97	16			0.96	44		
Monocots	0.95	41	ns	ns	0.86	29	+	ns
Dicots	1.04	46			1.00	47		
N_2-fixing species	0.96	12	ns	ns	1.19	16	**	**
others	1.00	75			0.88	60		

Table 5 Average values for the biomass enhancement ratio (BER) value of herbaceous plants grown in a mixed stand divided by the BER of the vegetation as a whole. Data are from a range of experiments, listed in Appendix 5. The averages and the number of species on which the average are based, are for simple contrasts of plants of different categories. For more information see the legend of Table 1

For competition at low nutrient levels, the situation is different. Here no differences between C3 and C4 species are observed, although we stress again that the number of C4 species investigated is low. The fact that C4 species are not negatively affected under these circumstances might well be due to the fact that at a low nutrient level a large CO_2 response of C3 species is precluded (Table 4). The exception to this rule is the group of species capable of symbiotic N_2 fixation, they are clearly the winners under these conditions. There is some indication of a difference between dicots and monocots, but closer analysis showed that the response only came from the nitrogen-fixing dicots. Decreases in grasses and increases in dicots, mostly due to an enhanced biomass of legumes, were found in most field studies (Schäppi, 1996; Clark *et al.*, 1997, Navas *et al.* 1997; Lüscher *et al.*, 1998; Warwick *et al.*, 1998; Reich *et al.*, 2001). The increase in leguminous species is particularly evident under conditions of low N and high P availability (Stöcklin & Körner, 1999; Körner, 2001).

Competition *per se* can be thought of as consisting of two components: the competitive effect, which is the ability of a plant to suppress neighbours, and the competitive response, the ability of a plant to tolerate its neighbours (Goldberg, 1990). An estimate of the first component is the dominance of a species in a community. In some field studies, not so much the dominant but some subordinate species were found to be highly responsive to CO_2 (Leadley & Körner, 1996; Clark *et al.*, 1997, Navas *et al.* 1997; Berntson *et al.*, 1998; Stöcklin & Körner, 1999). It has therefore been suggested that elevated CO_2 may reduce the overall size difference between dominant and subordinate plants (Catovsky & Bazzaz, 2002). Does that imply that we can consider subordinate species as a special 'response group', whose inherently low competitive effect is compensated for by a high responsiveness to CO_2? As mentioned above, just by the nature of the fact that a species forms a minority in a vegetation, it may show larger proportional fluctuations than dominant species. It could well be that large proportional increases in a species strongly draw the attention of the researchers. Considered over all competition experiments compiled, we tested whether subordinate species are more often winners than dominant species, calculating the percentage of the total stand biomass taken up by a given species as an estimate for dominance. Using this parameter as the independent variable and the winner scale as the dependent variable, we did not find any indication of a difference between subordinate and dominant species (Fig. 10a; $r^2 = 0.00$, $P > 0.4$), although the former show larger variability in their response to CO_2 than the latter.

The second factor that may play a role in the response to CO_2 is the reaction of a species to competition from neighbouring vegetation. It can be estimated by the Relative Competition Intensity (RCI; Wilson & Keddy, 1986; Keddy *et al.*, 1998), which is defined as the absolute decrease in the biomass of species because of competition, normalised against the biomass of isolated individuals. An RCI value of zero means that competition has no effect on plant performance, whereas an RCI value of one corresponds to complete competitive exclusion. Catovsky & Bazzaz (2002) suggested that tree species with a high response to elevated CO_2 were those that suffered less from neighbouring plants when grown in competition. However, tested for herbaceous plants, we were not able to find a correlation between our winner scale and RCI (Fig. 10b; $r^2 = 0.07$, $P > 0.1$).

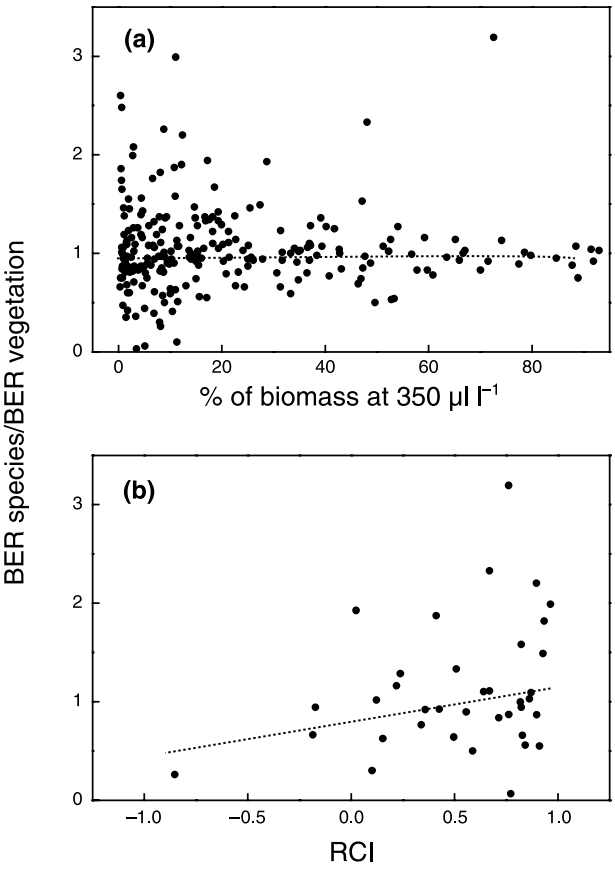

Fig. 10 Winning and loosing species in the response of mixed communities to elevated CO_2. The dependent variable is the ratio of the biomass enhancement ratio (BER) value of a species, growing in a mixed community, and the BER of the whole community. Independent variables are (a) the percentage of the biomass of a given species at control CO_2 levels, indicating the dominance of a species ($n = 204$, $r = 0.05$, $P > 0.4$) and (b) the Relative Competition Intensity (RCI), indicating to what extent the biomass of a species is suppressed by the growth of the neighbouring species ($n = 37$, $r = 0.26$, $P > 0.1$). Dotted lines indicate the nonsignificant linear regressions.

In conclusion, there is no scope for using the response of isolated plants as a predictor of changes in the vegetation. Furthermore, there is no relationship between the competitive ability of a species and its responsiveness to CO_2. As far as differences can be generalised over a larger group of experiments, C3 species may win from C4 species in vegetations with a high nutrient availability, and nitrogen-fixing dicots may profit at low nutrient availability.

VII. An outlook

In this paper we have covered only part of the data that deal with the effect of elevated CO_2 levels. There has been a strong research effort at both the physiological level (photosynthesis, respiration, chemical composition) as well as at the community level (Open Top Chambers or Free Air CO_2 Enrichment in various natural communities and agricultural settings), which has led to an impressive accumulation of publications. Playing the devil's advocate, what do we know more now than, say, 15–20 years ago? At that time it was clear that C3 species responded to elevated CO_2, whereas C4 species did not (Patterson & Flint, 1980). It had been found that the CO_2 response of growth parameters was quickly saturating beyond 450 μl l^{-1} (Neales & Nicholls, 1978) and that the growth stimulation was time-dependent (Wulff & Strain, 1982). Moreover, it was known that starch could accumulate to high levels (Cave *et al.*, 1981), that the N-concentration in the leaves would go down (Wong, 1979), and that photosynthetic acclimation could occur (Clough *et al.*, 1981). It was also known that leguminous species would increase nitrogen fixation, not so much per nodule mass, but because plants were larger, and that elevated CO_2 increased the amount of biomass produced per unit water transpired (Carlson & Bazzaz, 1980). Even the first experiment with an intact, natural vegetation was carried out during that time, showing that tundra vegetation did not respond to elevated CO_2 (Billings *et al.*, 1984).

Obviously, these early observations are now supported by a wealth of additional experiments, which have shown that the phenomena observed in those early days are more generally valid. Moreover, we now know that some C4 plants may also show a growth stimulation and the possible courses thereof (Poorter, 1993; Ghannoum *et al.*, 2000) and we are unraveling the molecular mechanisms that may control the amount of Rubisco (Paul & Foyer, 2001) and nitrate reductase (Fonseca *et al.*, 1997) when sugars accumulate. We have gained insight into the possibly strong effect at the ecosystem level that is exerted by the increased soil moisture level due to a decreased transpiration (Mooney *et al.*, 1999) including effects on the nitrogen cycle (Hungate *et al.*, 1999). With the application of the free-air carbon dioxide enrichment, we are now able to study intact crops and natural vegetations (Huxman & Smith, 2001), as well as young developing forests (Hamilton *et al.*, 2002). However, at the same time there is a range of issues that are not solved at all. What exactly is sink limitation and why has an increase in C-fixation due to an increased CO_2 concentration so little effect on the growth of a plant compared to a quantitatively similar increase in photosynthesis due to extra light? What hinders a plant to deploy the extra fixed C and why is it accumulated in the leaves? How exactly is maintenance and growth respiration affected by CO_2 and how can we quantitatively summarise the carbon budget of various plants? How do the chemical composition and the anatomy of stems and roots change with CO_2 enrichment, and what are actually the changes in the leaf except for the increase in starch and decrease in organic N? How valuable are experiments with plants in pots, and why may those experiments differ so much from those in hydroponics? Is the overwhelming variation in response to, for example, $CO_2 \times$ nutrient interactions just a matter of variability, or are there systematic differences between species? What exactly makes the growth responses of isolated plants so different from those in monocultures? What are the maternal effects on seed quality, size, germination and subsequent growth? Are there really systematic differences between genotypes and how will this affect plant populations? How will mature forests respond to elevated CO_2?

Undoubtedly, this list can be extended with many more relevant questions, where the research community still has not been able to come up with more or less clear answers, notwithstanding a huge investment in manpower and finances. In a time that molecular biologists make impressive advances in understanding gene regulation, we are still quarreling over very basic questions as whether plants at low nutrient availability respond more to CO_2 or less (Poorter, 1998; Lloyd & Farquhar, 2000). In a review by Bazzaz & Catovsky (2002) the overall message is that CO_2 effects on almost all levels investigated are highly variable and this is partly echoed in the current paper. How is it possible that our view is so diffuse? Is that only because plant responses are really so variable and so heavily dependent on external conditions? We wonder whether that is the only reason. It seems that we eco-(physio)logists are dividing our energy over too many species, grown under too many experimental conditions. Will we gain any extra insight if a new experiment is set up that will determine the rate of photosynthesis and biomass accumulation of yet another C3 species? Will we ever find out what the $CO_2 \times$ temperature interaction is if one experiment is carried out with small pots and infrequent watering, whereas another is using hydroponics at a much lower light level? It does not seem very likely. We are clearly lacking model organisms like *Drosophila* and *Arabidopsis*, which have facilitated major breakthroughs in population biology and plant molecular biology. In this field, one model species would not be enough, but what if we could focus on, for example, six herbaceous wild C3 species (grasses, leguminous dicots, other dicots, both an annual and a perennial from each group), six C3 crop species (grasses and dicots), six woody species (deciduous, evergreen, N_2 fixing) and two C4 species? We could also profit from systematic experiments, where the same protocols are used in different laboratories. Although not easy to agree on, such a concerted effort would provide a good opportunity to make substantial achievements and arrive at much stronger generalisations than we are able to make now. Moreover, such species could form a focus point to subsequently compare their response with other representatives from the functional group they belong to.

V. Conclusions

The growth response to elevated CO_2 of isolated plants is mainly determined by the increased rate of photosynthesis per unit leaf area and the decreased SLA. Variation in the Biomass Enhancement Ratio is large and a disturbing factor in comparisons across experiments. There were differences between groups of species, with C4 species responding less than average, and fast-growing C3 species responding above average. However, such functional groups based on data for isolated plants are only poor predictors for the response of species grown in competition. One avenue to arrive at a more accurate prediction of variation in response between species is to grow plants in dense monocultures rather than in isolation. Finally, it is our conviction that the research field would profit from a more structured approach with a set of preselected species.

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Supplementary material

The following material is available from http://www.blackwellpublishing.com/products/journals/suppmat/NPH/NPH680/NPH680sm.htm

Table S1 BER values

References

Ackerly DD, Bazzaz FA. 1995. Plant growth and reproduction along CO_2 gradients: non-linear responses and implications for community change. *Global Change Biology* **1**: 199–207.

Andalo C, Godelle B, Lefranc M, Mousseau M, Till-Bottraud I. 1996. Elevated CO_2 decreases seed germination in *Arabidopsis thaliana*. *Global Change Biology* **2**: 129–135.

Atkin OK, Schortemeyer M, McFarlane N, Evans JR. 1999. The response of fast- and slow-growing *Acacia* species to elevated atmospheric CO_2: an analysis of the underlying components of relative growth rate. *Oecologia* **120**: 544–554.

Bazzaz FA, Ackerly DD, Woodward FI, Rochefort L. 1992. CO_2 enrichment and dependence of reproduction on density in an annual plant and a simulation of its population dynamics. *Journal of Ecology* **80**: 643–651.

Bazzaz FA, Catovsky S. 2002. Impact of global environmental change on plants: From cells to ecosystems. In: Mooney HA, Canadell JG, eds. *Encyclopedia of global environmental change, Vol. 2*. Chichester, UK: Wiley, 94–111.

Berner RA. 1997. The rise of plants and their effect on weathering and atmospheric CO_2. *Science* **276**: 544–546.

Berntson GM, Rajakaruna N, Bazzaz FA. 1998. Growth and nitrogen uptake in an experimental community of annuals exposed to elevated atmospheric CO_2. *Global Change Biology* **4**: 607–626.

Bezemer TM, Thompson LJ, Jones TH. 1998. *Poa annua* shows inter-generational differences in response to elevated CO_2. *Global Change Biology* **4**: 687–691.

Billings WD, Peterson KM, Luken JO, Mortensen DA. 1984. Interaction of increasing atmospheric carbon dioxide and soil nitrogen on the carbon balance of tundra microcosms. *Oecologia* **65**: 26–29.

Bruhn D, Mikkelsen TN, Atkin OK. 2002. Does the direct effect of atmospheric CO_2 concentration on leaf respiration vary with temperature? Responses in two species of *Plantago* that differ in relative growth rate. *Physiologia Plantarum* **114**: 57–64.

Bunce JA. 1997. Variation on growth stimulation by elevated carbon dioxide in seedlings of some C3 crop and weed species. *Global Change Biology* **3**: 61–66.

Campbell BD, Laing WA, Newton PCD. 1991. Variation in the response of pasture plants to carbon dioxide. Proceedings of the XVII International Grassland Congress, 1125–1126.

Catovsky S, Bazzaz FA. 2002. Plant competition in an elevated CO_2 world. In: Mooney HA, Canadell JG, eds. *Encyclopedia of global environmental change, Vol. 2*. Chichester, UK: Wiley, 471–481.

Cave G, Tolley LC, Strain BR. 1981. Effect of carbon dioxide enrichment on chlorophyll content, starch content and starch grain structure in *Trifolium subterraneum* leaves. *Physiologia Plantarum* **51**: 171–174.

Centritto M, Lee HS, Jarvis PG. 1999. Increased growth in elevated [CO_2]: an early short-term response? *Global Change Biology* **5**: 623–633.

Ceulemans R, Mousseau M. 1994. Effects of elevated atmospheric CO_2 on woody plants. *New Phytologist* **127**: 425–446.

Clark H, Newton PCD, Bell CC, Glasgow EM. 1997. Dry matter yield, leaf growth and population dynamics in *Lolium perenne*/*Trifolium repens* dominated pasture turves exposed to two levels of elevated CO_2. *Journal of Applied Ecology* **34**: 304–316.

Clough JM, Peet MM, Kramer PJ. 1981. Effects of high atmospheric CO_2 and sink size on rates of photosynthesis of a soybean cultivar. *Plant Physiology* **67**: 1007–1010.

Coleman JS, Mooney HA, Winner WE. 1990. Anthropogenic stress and natural selection: variability in radish biomass accumulation increases with increasing SO_2 dose. *Canadian Journal of Botany* **68**: 102–106.

Cornelissen JHC, Carnell AL, Callaghan TV. 1999. Generalities in the growth, allocation and leaf quality responses to elevated CO_2 in eight woody species. *New Phytologist* **141**: 401–409.

Cornelissen JHC, Castro-Díez P, Carnelli AL. 1998. Variation in relative growth rate among woody species. In: Lambers H, Poorter H, Van Vuuren MMI, eds. *Inherent variation in plant growth physiological mechanisms and ecological consequences*. Leiden, The Netherlands: Backhuys Publishers, 363–392.

Cure JD, Acock B. 1986. Crop responses to carbon dioxide doubling: a literature survey. *Agricultural and Forest Meteorology* **38**: 127–145.

Curtis PS, Klus DJ, Kalisz S, Tonsor SJ. 1996. Intraspecific variation in CO_2 responses in *Raphanis raphanistrum* and *Plantago lanceolata*: assessing the potential for evolutionary change with rising atmospheric CO_2. In: Körner C, Bazzaz FA, eds. *Carbon dioxide, populations, communities*. San Diego, CA, USA: Academic Press, 13–22.

Curtis PS, Wang X. 1998. A meta-analysis of elevated CO_2 effects on woody plant mass, form, and physiology. *Oecologia* **113**: 299–313.

Dai Z, Ku MSB, Edwards GE. 1995. C4 photosynthesis. The effects of leaf development on the CO_2-concentrating mechanisms and photorespiration in maize. *Plant Physiology* **107**: 815–825.

Den Hertog J, Stulen I, Lambers H. 1993. Assimilation, respiration and allocation of carbon in *Plantago major* as affected by atmospheric CO_2 levels. *Vegetatio* **104/105**: 369–378.

Díaz S, Grime JP, Harris J, McPherson E. 1993. Evidence of a feedback mechanism limiting plant response to elevated carbon dioxide. **364**: 616–617.

Drennan PM, Nobel PS. 2000. Responses of CAM species to increasing atmospheric CO_2 concentrations. *Plant, Cell & Environment* **23**: 767–781.

Du Cloux HC, André M, Daguenet A, Massimino J. 1987. Wheat response to CO_2 enrichment: growth and CO_2 exchange at two plant densities. *Journal of Experimental Botany* **38**: 1421–1431.

Evans GC. 1972. *The quantitative analysis of plant growth*. Oxford, UK: Blackwell Scientific Publications.

Evans JR, Schortemeyer M, Mcfarlane N, Atkin OK. 2000. Photosynthetic characteristics of 10 *Acacia* species grown under ambient and elevated atmospheric CO_2. *Australian Journal of Plant Physiology* **27**: 13–25.

Farnsworth EJ, Bazzaz FA. 1995. Inter- and intra-generic differences in growth, reproduction, and fitness of nine herbaceous annual species grown in elevated CO_2 environments. *Oecologia* **104**: 454–466.

Field CB, Jackson RB, Mooney HA. 1995. Stomatal responses to increased CO_2: implications from the plant to the global scale. *Plant, Cell & Environment* **18**: 1214–1226.

Firbank LG, Watkinson AR. 1990. On the effects of competition: from monocultures to mixtures. In: Grace JB, Tilman D, eds. *Perspectives on plant competition*. London, UK: Academic Press, 165–192.

Fonseca F, Bowsher CG, Stulen I. 1997. Impact of elevated atmospheric CO_2 on nitrate reductase transcription and activity in leaves and roots of *Plantago major*. *Physiologia Plantarum* **100**: 940–948.

Fonseca F, Den Hertog J, Stulen I. 1996. The response of *Plantago major* ssp. *pleiosperma* to elevated CO_2 is modulated by the formation of secondary shoots. *New Phytologist* **133**: 627–635.

Garnier E, Freijsen AHJ. 1994. On ecological inference from laboratory experiments conducted under optimum conditions. In: Roy J, Garnier E, eds. *A whole plant perspective on carbon–nitrogen interactions*. The Hague, The Netherlands: SPB Academic Publishing, 267–292.

Ghannoum O, Von Caemmerer S, Ziska LH, Conroy JP. 2000. The growth response of C4 plants to rising atmospheric CO_2 partial pressure: a reassessment. *Plant, Cell & Environment* **23**: 931–942.

Gibeaut DM, Cramer GR, Seemann JR. 2001. Growth, cell walls, and UDP-Glc dehydrogenase activity of *Arabidopsis thaliana* grown in elevated carbon dioxide. *Journal of Plant Physiology* **158**: 569–576.

Goldberg DE. 1990. Components of resource competition in plant communities. In: Grace JB, Tilman D, eds. *Perspectives on plant competition*. London, UK: Academic Press, 27–49.

Greer DH, Laing WA, Campbell BD, Halligan EA. 2000. The effect of perturbations in temperature and photon flux density on the growth and photosynthetic response of five pasture species to elevated CO_2. *Australian Journal of Plant Physiology* **27**: 301–310.

Gurevitch J, Curtis PS, Jones MH. 2001. Meta-analysis in ecology. *Advances in Ecological Research* **32**: 199–247.

Hamilton JG, DeLucia EH, George K, Naidu SL, Finzi AC, Schlesinger WH. 2002. Forest carbon balance under elevated CO_2. *Oecologia* **131**: 250–260.

Harper JL. 1977. *Population biology of plants*. London, UK: Academic Press.

Hättenschwiler S, Miglietta F, Raschi A, Körner C. 1997. Thirty years of situ tree growth under elevated CO_2: a model for future forest response? *Global Change Biology* **3**: 463–471.

Hoffmann WA, Bazzaz FA, Chatterton NJ, Harrison PA, Jackson RB. 2000. Elevated CO_2 changes resprouting of a tropical savanna. *Oecologia* **123**: 312–317.

Hungate BA, Dijkstra P, Johnson DW, Hinkle CR, Drake BG. 1999. Elevated CO_2 increases nitrogen fixation and decreases soil nitrogen mineralization in Florida scrub oak. *Global Change Biology* **5**: 781–789.

Hunt R, Hand D, Hannah MA, Neal AM. 1991. Response to CO_2 enrichment in 27 herbaceous species. *Functional Ecology* **5**: 410–421.

Hunt R, Hand D, Hannah MA, Neal AM. 1993. Further responses to CO_2 enrichment in British herbaceous species. *Functional Ecology* **7**: 661–668.

Hussain M, Kubiske ME, Connor KF. 2001. Germination of CO_2-enriched *Pinus taeda* L. seeds and subsequent seedling growth responses to CO_2 enrichment. *Functional Ecology* **15**: 344–350.

Huxman TE, Hamerlynck EP, Jordan DN, Salsman KJ, Smith SD. 1998. The effects of parental CO_2 environment on seed quality and subsequent seedling performance in *Bromus rubens*. *Oecologia* **114**: 202–208.

Huxman TE, Smith SD. 2001. Photosynthesis in an invasive grass and native forb at elevated CO_2 during an El Nino year in the Mojave Desert. *Oecologia* **128**: 193–201.

Idso SB. 1999. The long-term response of trees to atmospheric CO_2 enrichment. *Global Change Biology* **5**: 493–495.

Idso KE, Idso SB. 1994. Plant responses to atmospheric CO_2 enrichment in the face of environmental constraints: a review of the past 10 years' research. *Agricultural and Forest Meteorology* **69**: 153–203.

Jablonski LM, Wang X, Curtis PS. 2002. Plant reproduction under elevated CO_2 conditions: a meta-analysis of reports on 79 crop and wild species. *New Phytologist* **156**: in press.

Jasienski M, Bazzaz FA. 1999. The fallacy of ratios and the testability of models in biology. *Oikos* **84**: 321–326.

Keddy P, Fraser LH, Wisheu IC. 1998. A comparative approach to examine competitive response of 48 wetland plant species. *Journal of Vegetation Science* **9**: 777–786.

Kerstiens G. 2001. Meta–analysis of the interaction between shade-tolerance, light environment and growth response of woody species to elevated CO_2. *Acta Oecologia* **22**: 61–69.

Kimball BA. 1986. Influence of Elevated CO_2 on Crop Yield. In: Enoch HZ, Kimball BA, eds. *Carbon dioxide enrichment of greenhouse crops*, *Vol. II.* Physiology, yield and economics. Boca Raton, FL, USA: CRC Press, 105–115.

Klus DJ, Kalisz S, Curtis PS, Teeri JA, Tonsor SJ. 2001. Variation in responses to atmospheric CO_2 concentration: gas exchange and the allocation of C, N, and biomass in *Plantago lanceolata* (Plantaginaceae). *American Journal of Botany* **88**: 1080–1087.

Körner C. 2001. Biosphere responses to CO_2 enrichment. *Ecological Applications* **10**: 1590–1619.

Körner C, Pelaez-Riedl S, Van Bel AJE. 1995. CO_2 responsiveness of plants: a possible link to phloem loading. *Plant, Cell & Environment* **18**: 595–600.

Lambers H, Chapin FS, Pons TL. 1998. *Plant physiological ecology*. New York, USA: Springer.

Lavorel S. 2002. Plant Functional types. In: Mooney HA, Canadell JG, eds. *Encyclopedia of global environmental change*, *Vol. 2*. Chichester, UK: Wiley.

Leadley PW, Körner C. 1996. Effects of elevated CO_2 on plant species dominance in a highly diverse calcareous grassland. In: Körner C, Bazzaz FA, eds. *Carbon dioxide, populations, communities*. San Diego, CA, USA: Academic Press, 159–175.

LeCain DR, Morgan JA. 1998. Growth, gas exchange, leaf nitrogen and carbohydrate concentration in NAD-ME and NADP-ME C4 grasses grown in elevated CO_2. *Physiologia Plantarum* **102**: 297–306.

Li CR, Gan LJ, Xia K, Zhou X, Hew CS. 2002. Responses of carboxylating enzymes, sucrose metabolising enzymes and plant hormones in a tropical epiphytic CAM orchid to CO_2 enrichment. *Plant, Cell & Environment* **25**: 369–377.

Lin J, Jack ME, Ceulemans R. 2001. Stomatal density and needle anatomy of Scots pine (*Pinus sylvestris*) are affected by elevated CO_2. *New Phytologist* **150**: 665–674.

Lloyd J, Farquhar GD. 2000. Do slow-growing species and nutrient-stressed plants consistently respond less to elevated CO_2? A clarification of some issues raised by Poorter (1998). *Global Change Biology* **6**: 871–876.

Lovelock CE, Winter K, Mersits R, Popp M. 1998. Responses of communities of tropical tree species to elevated CO_2 in a forest clearing. *Oecologia* **116**: 207–218.

Lüscher A, Hendrey GR, Nössberger J. 1998. Long-term responsiveness to free air CO_2 enrichment of functional types, species and genotypes of plants from fertile permanent grassland. *Oecologia* **113**: 37–45.

Maroco JP, Breia E, Faria T, Pereira JS, Chaves MM. 2002. Effects of long-term exposure to elevated CO_2 and N fertilization on the development of photosynthetic capacity and biomass accumulation in *Quercus suber* L. *Plant, Cell & Environment* **25**: 105–113.

Mooney HA, Canadell J, Chapin FS, Ehleringer JR, Körner C, McMurtrie RE, Parton WJ, Pitelka LF, Schulze ED. 1999. *Ecosystem* physiology responses to global change. In: Walker BH, Steffen WL, Canadell J, Ingram JSI, eds. *The terrestrial biosphere and global change*. Cambridge, UK: Cambridge University Press, 141–189.

Morison JIL, Gifford RM. 1984. Plant growth and water use with limited water supply in high CO_2 concentrations. II. Plant dry weight, partitioning and water use efficiency. *Australian Journal of Plant Physiology* **11**: 361–374.

Morse SR, Bazzaz FA. 1994. Elevated CO_2 and temperature alter recruitment and size hierarchies in C3 and C4 annuals. *Ecology* **75**: 966–975.

Mortensen LM. 1994. The influence of carbon dioxide or ozone concentration on growth and assimilate partitioning in seedlings of nine conifers. *Acta Agriculturae Scandinavica Section B, Soil et Plant Sciencea* **44**: 157–163.

Mousseau M. 1993. Effects of elevated CO_2 on growth, photosynthesis and respiration of sweet chestnut (*Castanea sativa* Mill.). *Vegetatio* **104/105**: 413–419.

Mousseau M, Enoch HZ. 1989. Carbon dioxide enrichment reduces shoot growth in sweet chestnut seedlings (*Castanea sativa* Mill.). *Plant, Cell & Environment* **12**: 927–934.

Navas ML. 1998. Individual species performance and response of multi-specific comunities to elevated CO_2: a review. *Functional Ecology* **12**: 721–727.

Navas ML, Garnier E, Austin MP, Gifford RM. 1999. Effect of competition on the responses of grasses and legumes to elevated atmospheric CO_2 along a nitrogen gradient: differences between isolated plants and multi-species mixtures. *New Phytologist* **143**: 323–331.

Navas ML, Sonie L, Richarte J, Roy J. 1997. The influence of elevated CO_2 on species phenology, growth and reproduction in a Mediterranean old-field community. *Global Change Biology* **3**: 523–530.

Neales TF, Nicholls AO. 1978. Growth response of young wheat plants to a range of ambient CO_2 levels. *Australian Journal of Plant Physiology* **5**: 45–59.

Norby RJ, Wullschleger SD, Gunderson CA, Nietch CT. 1995. Increased growth efficiency of *Quercus alba* trees in a CO_2-enriched atmosphere. *New Phytologist* **131**: 91–97.

Oechel WC, Strain BR. 1985. Native responses to increased carbon dioxide concentration. In: Strain BR, Cure JD, eds. *Direct effects of carbon dioxide on vegetation*. Washington DC, USA: United States Department of Energy, 117–154.

Patterson DT, Flint EP. 1980. Potential effects of global atmospheric CO_2-enrichment on the growth and competitiveness of C3 and C4 weed and crop plants. *Weed Science* **28**: 71–75.

Pattison R, Goldstein G, Ares A. 1998. Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rainforest species. *Oecologia* **117**: 449–459.

Paul MJ, Foyer CH. 2001. Sink regulation of photosynthesis. *Journal of Experimental Botany* **52**: 1383–1400.

Penning de Vries FWT, Brunsting AHM, van Laar HH. 1974. Products, requirements and efficiency of biosynthetic processes: a quantitative approach. *Journal of Theoretical Biology* **45**: 339–377.

Poorter H. 1993. Interspecific variation in the growth response of plants to an elevated ambient CO_2 concentration. *Vegetatio* **104/105**: 77–97.

Poorter H. 1998. Do slow-growing species and nutrient-stressed plants respond relatively strongly to elevated CO_2? *Global Change Biology* **4**: 693–697.

Poorter H. 2002. Plant Growth and Carbon Economy. In: *Encyclopedia of Life Sciences*. [WWW document] URL http://www.els.net. London, UK: Nature Publishing Group.

Poorter H, Garnier E. 1996. Plant growth analysis: evaluation of experimental design and computational methods. *Journal of Experimental Botany* **47**: 1343–1351.

Poorter H, Gifford RM, Kriedemann PE, Wong SC. 1992. A quantitative analysis of dark respiration and carbon content as factors in the growth response of plants to elevated CO_2. *Australian Journal of Botany* **40**: 501–513.

Poorter H, Nagel O. 2000. The role of biomass allocation in the growth response of plants to different levels of light, CO_2, nutrients and water. *Australian Journal of Plant Physiology* **27**: 595–607.

Poorter H, Pérez-Soba M. 2001. The growth response of plants to elevated CO_2 under non-optimal environmental conditions. *Oecologia* **129**: 1–20.

Poorter H, Pot CS, Lambers H. 1988. The effect of an elevated atmospheric CO_2 concentration on growth, photosynthesis and respiration of *Plantago major*. *Physiologia Plantarum* **73**: 553–559.

Poorter H, Roumet C, Campbell BD. 1996. Interspecific variation in the growth response of plants to elevated CO_2: A search for functional types. In: Körner C, Bazzaz FA, eds. *Carbon dioxide, populations, communities*. San Diego, CA, USA: Academic Press, 375–412.

Poorter H, Van Berkel Y, Baxter B, Bel M, Den Hertog J, Dijkstra P, Gifford RM, Griffin KL, Roumet C, Wong SC. 1997. The effect of elevated CO_2 on the chemical composition and construction costs of leaves of 27 C_3 species. *Plant, Cell & Environment* **20**: 472–482.

Poorter H, Van der Werf A. 1998. Is inherent variation in RGR determined by LAR at low irradiance and by NAR at high irradiance? A review of herbaceous species. In: Lambers H, Poorter H, Van Vuuren MMI, eds. *Inherent variation in plant growth physiological mechanisms and ecological consequences*. Leiden, The Netherlands: Backhuys Publishers, 309–336.

Poorter L. 1999. Growth response of 15 rain-forest tree species to a light gradient: the relative importance of morphological and physiological traits. *Functional Ecology* **13**: 396–410.

Raunkiaer C. 1934. *The life forms of plants and statistical plant geography*. Oxford, UK: Clarendon Press.

Reekie EG, MacDougall G, Wong I, Hicklenton PR. 1998. Effect of sink size on the growth response to elevated atmospheric CO_2 within the genus *Brassica*. *Canadian Journal of Botany* **76**: 829–835.

Reich PB, Knops J, Tilman D, Craine J, Ellsworth D, Tjoelker M, Lee T, Wedin D, Naeem S, Bahauddin D, Hendrey G, Jose S, Wrage K, Goth J, Bengston W. 2001. Plant diversity enhances ecosystem responses to elevated CO_2 and nitrogen deposition. *Nature* **410**: 809–812.

Retuerto R, Rochefort L, Woodward FI. 1996. The influence of plant density on the responses of *Sinapis alba* to CO_2 and windspeed. *Oecologia* **108**: 241–251.

Reynolds HL. 1996. Effects of elevated CO_2 on plants grown in competition. In: Körner C, Bazzaz FA, eds. *Carbon dioxide, populations, communities*. San Diego, CA, USA: Academic Press, 273–286.

Roumet C, Bel MP, Sonie L, Jardon F, Roy J. 1996. Growth response of grasses to elevated CO_2: a physiological plurispecific analysis. *New Phytologist* **133**: 595–603.

Roumet C, Garnier E, Suzor H, Salager JL, Roy J. 2000. Short and long-term responses of whole-plant gas exchange to elevated CO_2 in four herbaceous species. *Environmental and Experimental Botany* **43**: 155–169.

Roumet C, Laurent G, Roy J. 1999. Leaf structure and chemical composition as reflected by elevated CO_2: genotypic responses of two perennial grasses. *New Phytologist* **143**: 73–81.

Sage RF. 2001. Environmental and evolutionary preconditions for the origin and diversification of the C4 photosynthetic syndrome. *Plant Biology* **3**: 202–213.

Samarakoon AB, Gifford RM. 1996. Water use and growth of cotton in response to elevated CO_2 in wet and drying soil. *Australian Journal of Plant Physiology* **23**: 63–74.

Saxe H, Ellsworth DS, Heath J. 1998. Tree and forest functioning in an enriched CO_2 atmosphere. *New Phytologist* **139**: 395–436.

Schäppi B. 1996. Growth dynamics and population development in an alpine grassland under elevated CO_2. *Oecologia* **106**: 93–99.
Schmid B, Birrer A, Lavigne C. 1996. Genetic variation in the response of plant populations to elevated CO_2 in a nutrient-poor, calcareous grassland. In: Körner C, Bazzaz FA, eds. *Carbon dioxide, populations and communities*. Physiological Ecology Series. San Diego, CA, USA: Academic Press, 31–50.
Schortemeyer M, Atkin OK, McFarlane N, Evans JR. 1999. The impact of elevated atmospheric CO_2 and nitrate supply on growth, biomass allocation, nitrogen partitioning and N_2 fixation of *Acacia melanoxylon*. *Australian Journal of Plant Physiology* **26**: 737–747.
Sigurdsson BD, Thorgeirsson H, Linder S. 2001. Growth and dry-matter partitioning of young *Populus trichocarpa* in response to carbon dioxide concentration and mineral nutrient availability. *Tree Physiology* **21**: 941–950.
Sims DA, Seemann JR, Luo Y. 1998. Elevated CO_2 concenttration has independent effects on expansion rates and thickness of soybean leaves across light and nitrogen gradients. *Journal of Experimental Botany* **49**: 583–591.
Smith TM, Shugart HH, Woodward FI. 1997. *Plant functional types*. Cambridge, UK: Cambridge University Press.
Sokal RR, Rohlf FJ. 1995. *Biometry*. New York, USA: Freeman.
Stöcklin J, Körner C. 1999. Interactive effects of elevated CO_2, P availability and legume presence on calcareous grassland: result of a glasshouse experiment. *Functional Ecology* **13**: 200–209.
Stulen I, Den Hertog J. 1993. Root growth and functioning under CO_2 enrichment. *Vegetatio* **104/105**: 99–115.
Thomas JF, Harvey CN. 1983. Leaf anatomy of four species grown under continuous CO_2 enrichment. *Botanical Gazette* **144**: 303–309.
Thomas SC, Jasienski M, Bazzaz FA. 1999. Early vs. asymptotic growth responses of herbaceous plants to elevated CO_2. *Ecology* **80**: 1552–1567.
Tousignant D, Potvin C. 1996. Selective responses to global change: Experimental results on *Brassica juncea* (L.) Czern. In: Körner C, Bazzaz FA, eds. *Carbon dioxide, populations and communities*. Physiological Ecology Series. San Diego, CA, USA: Academic Press, 23–30.
Van Bel AJE. 1999. Evolution, polymorphology and multifunctionality of the phloem system. *Perspectives in Plant Ecology, Evolution and Systematics* **2**: 163–184.
Van der Werf A, Van Nuenen M, Visser AJ, Lambers H. 1993. Contribution of physiological and morphological plant traits to a species' competitive ability at high and low nitrogen supply. A hypothesis for inherently fast- and slow-growing monocotyledonous species. *Oecologia* **94**: 434–440.
Van Rijn CPE. 2001. *A Physiological and Genetic Analysis of Growth Characteristics in* Hordeum spontaneum. PhD thesis, Utrecht University.
Volin JC, Reich PB. 1996. Interaction of elevated CO_2 and O_3 on growth, photosynthesis and respiration of three perennial species grown in low and high nitrogen. *Physiologia Plantarum* **97**: 674–684.
Volin JC, Reich PB, Givnish TJ. 1998. Elevated carbon dioxide ameliorates the effects of ozone on photosynthesis and growth: species respond similarly regardless of photosynthetic pathway or plant functional group. *New Phytologist* **138**: 315–325.
Wand SJE, Midgley GF, Jones MH, Curtis PS. 1999. Responses of wild C4 and C3 (Poaceae) species to elevated atmospheric CO_2 concentration: a meta-analytic test of current theories and perceptions. *Global Change Biology* **5**: 723–741.
Wand SJE, Midgley GF, Stock WD. 2001. Growth responses to elevated CO_2 in NADP-ME, NAD-ME and PCK C4 grasses and a C3 grass from South Africa. *Australian Journal of Plant Physiology* **28**: 13–25.
Ward JK, Strain BR. 1999. Elevated CO_2 studies: past, present and future. *Tree Physiology* **19**: 211–220.
Warwick KR, Taylor G, Blum H. 1998. Biomass and compositional changes occur in chalk grassland turves exposed to elevated CO_2 for two seasons in FACE. *Global Change Biology* **4**: 375–385.
Wayne PM, Bazzaz FA. 1995. Seedling density modifies the growth responses of yellow birch maternal families to elevated carbon dioxide. *Global Change Biology* **1**: 315–324.
Weiner J, Mallory EB, Kennedy C. 1990. Growth and variability in crowded and uncrowded populations of dwarf marigolds (*Tagetes patula*). *Annals of Botany* **65**: 513–524.
Wilson SD, Keddy PA. 1986. Measuring diffuse competition along an environmental gradient: results from a shoreline plant community. *American Naturalist* **127**: 862–869.
Winter K, Lovelock CE. 1999. Growth responses of seedlings of early and late succesional tropical forest trees to elevated atmospheric CO_2. *Flora* **194**: 221–227.
Wong SC. 1979. Elevated atmospheric partial pressure of CO_2 and plant growth. I. Interactions of nitrogen nutrition and photosynthetic capacity in C3 and C4 plants. *Oecologia* **44**: 68–74.
Wong SC. 1990. Elevated atmospheric partial pressure of CO_2 and plant growth. II. Non-structural carbohydrate content and its effect on growth parameters. *Photosynthesis Research* **23**: 171–180.
Wong SC. 1993. Interaction between elevated atmospheric CO_2 and humidity on plant growth: comparison between cotton and radish. *Vegetatio* **104/105**: 211–221.
Woodward FI. 2002. Potential impacts of global elevated CO_2 concentrations on plants. *Current Opinion in Plant Biology* **5**: 207–211.
Wright IJ, Westoby M. 1999. Differences in seedling growth behaviour among species: trait correlations across species, and trait shifts along nutrient compared to rainfall gradients. *Journal of Ecology* **87**: 85–97.
Wulff RD, Alexander HM. 1985. Intraspecific variation in the response to CO_2 enrichment in seeds and seedlings of *Plantago lanceolata* L. *Oecologia* **66**: 458–460.
Wulff RD, Strain BR. 1982. Effects of CO_2 enrichment on growth and photosynthesis in *Desmodium paniculatum*. *Canadian Journal of Botany* **60**: 1084–1091.
Wyszomirski T, Wyszomirska I, Jarzyna I. 1999. Simple mechanisms of size distribution dynamics in crowded and uncrowded virtual monocultures. *Ecological Modelling* **115**: 253–273.
Ziska LH, Bunce JA. 1997. Influence of increasing carbon dioxide concentration on the photosynthetic and growth stimulation of selected C4 crops and weeds. *Photosynthesis Research* **54**: 199–208.
Ziska LH, Bunce JA. 2000. Sensitivity of field-grown soybean to future atmospheric CO_2: selection for improved productivity in the 21st century. *Australian Journal of Plant Physiology* **27**: 979–984.

Appendices

Appendix 1: literature used for the analysis of seed mass

Gifford (1979) Aust. J. Plant Physiol. 6: 367–378; Sionit *et al.* (1980) Crop Sci. 20: 687–690; Goudriaan and De Ruiter (1983) Neth. J. Agric. Sci. 31: 157–169; Garbutt and Bazzaz (1984) New Phytol. 98: 433–446; Bhattacharya *et al.* (1985) J. Agric. Sci. 105: 527–534; Wulff and Alexander (1985) Oecologia 66: 458–460; Khan and Madsen (1986) New Phytol. 104: 215–223; Sionit *et al.* (1987) Can. J. Plant Sci.

67: 629–636; Allen *et al.* (1998) Crop Sci. 28: 84–94; Cure *et al.* (1988) Agron J. 80: 897–902; Larigauderie *et al.* (1988) Oecologia 77: 544–549; Baker *et al.* (1989) Crop Sci. 29: 98–105; Baker *et al.* (1990) J. Agric. Sci. 115: 313–320; Chaudhuri *et al.* (1990) Agron. J. 82: 637–641; Garbutt *et al.* (1990) Ecology 71: 1185–1194; Allen *et al.* (1991) Agron. J. 83: 875–883; Fajer *et al.* (1991) Oecologia 87: 37–42; Baker *et al.* (1992) J. Exp. Bot. 43: 959–964; Bazzaz *et al.* (1992) J. Ecol. 80: 643–651; Miglietta *et al.* (1993) Plant Cell Environ. 16: 909–918; Mitchell *et al.* (1993) Plant Cell Environ.16: 521–529; Müller (1993) J. Agron. Crop Sci 171: 217–235; Pettersson *et al.* (1993) Vegetatio 104/105: 462–463; Chen *et al.* (1994) Physiol. Plant. 90: 79–85; Conroy *et al.* (1994) Aust. J. Plant Physiol. 21: 741–758; Jackson *et al.* (1994) Oecologia 98: 257–262; Morse and Bazzaz (1994) Ecology 75: 966–975; Seneweera *et al.* (1994) Aust. J. Plant Physiol. 21: 281–292; Thompson & Woodward (1994) J. Exp. Bot. 45: 937–942; Weigel *et al.* (1994) Agric. Ecosys. Environ. 48: 231–240; Farnsworth and Bazzaz (1995) Oecologia 104: 454–466; Mitchell *et al.* (1995) Plant Cell Environ. 18: 736–748; Rawson (1995) Aust. J. Plant Physiol. 22: 23–32; Fangmeier *et al.* (1996) Environ. Poll. 91: 381–390; Mitchell *et al.* (1996) Plant Cell Environ. 19: 615–621; Tousignant and Potvin, 1996) Oecologia 108: 683–693; Rudorff *et al.* (1996) Environ. Poll. 94: 53–60; Saebo & Mortensen (1996) Agric. Ecosys. Environ. 57: 9–15; Schäppi (1996) Oecologia 106: 93–99; Ziska *et al.* (1996) J. Exp. Bot. 47: 1353–1359; Baker *et al.* (1997) Glob. Change Biol. 3: 119–128; Fischer *et al.* (1997) J. Ecol. 85: 681–691; Lee *et al.* (1997) Env. Exp. Bot. 37 : 85–93; Manderscheid & Weigel (1997) Agric. Ecosys. Environ. 64: 65–73; McKee *et al.* (1997) Plant Cell Environ. 20: 77–84; Mulholland *et al.* (1997) J. Exp. Bot 48: 113–122; Prior *et al.* (1997) J. Env. Qual. 26: 244–252; Sharma-Natu *et al.* (1997) Photosynthetica 34: 537–543; Wheeler *et al.* (1996) J. Agric. Sci. 127: 37–48; Ziska and Bunce, 1997) Agron. J. 89: 45–53; Andalo *et al.* (1998) Ann. Bot. 81: 405–411; Batts *et al.* (1998) J. Agric. Sci. 130: 17–27; Hakala (1998) Eur. J. Agron. 9: 41–52; Heagle *et al.* (1998) Crop Sci. 38: 128–134; Huxman *et al.* (1998) Oecologia 114: 202–208; Mulholland *et al.* (1998) Glob. Change Biol. 4: 375–385; Rogers *et al.* (1998) Aust. J. Plant Physiol. 25: 387–393; Ziska *et al.* (1998) Aust. J. Plant Physiol. 25: 801–807; Dijkstra *et al.* (1999) Glob. Change Biol. 5: 563–576; Fangmeier *et al.* (1999) Eur. J. Agron. 10: 215–229; Ferris *et al.* (1999) Crop Sci. 39: 710–718; Heagle *et al.* (1999) J. Environ. Qual. 28: 666–675; Huxman *et al.*, 1998) Funct. Ecol. 13 : 769–777; Leishmann (1999) New Phytol. 144: 455–462; Rüegg *et al.* (1999) Agrarforschung 6: 141–144; Van Oijen *et al.* (1999) Glob. Change Biol. 5: 411–421; Körner, 2001) Glob. Change Biol. 6: 631–638; Steinger *et al.* (2000) Oecologia 123: 475–480; Ziska and Bunce (2000) Aust. J. Plant Physiol. 27: 979–984; Ziska and Bunce (2000) Glob. Change Biol. 6: 899–905; Edwards *et al.* (2001) New Phytol. 150: 359–369; Grünzweig and Körner (2001) Oikos 95: 112–124; Hussain *et al.* (2001) Funct. Ecol. 15: 344–350; Kim *et al.* (2001) New Phytol. 150: 223–229; Kimball *et al.* (2001) New Phytol. 150: 295–303; Mitchell *et al.* (2001) Glob. Change Biol. 7: 599–611; Steinger *et al.* (2001) Oecologia 123: 475–480; Wagner *et al.* (2001) Plant Cell Environ. 24: 957–965.

Appendix 2: literature used for the analysis of RGR and its components

Hurd & Thornley (1974) Ann. Bot. 38: 375–388; Collins (1976) HortSci. 11: 467–469; Mauney *et al.* (1978) Crop Sci. 18: 259–263; Neales and Nicholls (1978) Aust. J. Plant Physiol. 5: 45–59; Patterson and Flint (1980) Weed Sci. 28: 71–75; Wyse (1980) Crop Sci. 20: 456–458; Patterson & Flint (1982) Weed Sci. 30: 389–394; Sionit *et al.* (1982) Agron. J. 73: 1023–1027; Carter & Peterson (1983) Oecologia 58: 188–193; Sionit (1983) Crop Sci. 23: 329–333; Rogers *et al.* (1984) Crop Sci. 24: 361–366; Battacharya *et al.* (1985) J. Agric. Sci. 105: 527–534; Joliffe & Ehret (1985) Can. J. Bot. 63: 2021–25; Jansen *et al.* (1986) In: Biological Control of Photosynthesis, pp 143–146; Patterson (1986) Weed Sci. 34: 203–210; Peet (1986) Plant Physiol. 80: 59–62; Cure *et al.* (1988) Crop Sci. 28: 671–677; Musgrave and Strain (1988) Proc. Natl. Acad. Sci. USA 83: 8157–8161; Overdieck *et al.* (1988) Angew. Bot. 62: 119–134; Patterson *et al.* (1988) Weed Sci. 36: 751–757; Bazzaz *et al.* (1989) Oecologia 79: 223–235; Bunce (1990) Ann. Bot. 65: 637–642; Wong (1990) Photosynth. Res. 23: 171–180; Badger (1992) Aust. J. Bot. 40: 421–429; Chu *et al.* (1992) Oecologia 89: 580–587; Coleman & Bazzaz (1992) Ecology 73: 1244–1259; Pettersson & McDonald (1992) Plant Cell Env. 15: 911–919; Ryle *et al.* (1992) J. Exp. Bot. 43: 811–818; Wong *et al.* (1992) Aust. J. Bot. 40: 457–472; Bowler and Press (1993) New Phytol. 124: 515–522; Den Hertog *et al.* (1993) Vegetatio 104/105: 369–387; Poorter (1993) Vegetatio 104/105: 77–97; Rozema (1993) Vegetatio 104/105: 173–190; Van de Staaij *et al.* (1993) Vegetatio 104/105: 433–439; Wong (1993) Vegetatio 104/105: 211–221; Baxter *et al.* (1994) J. Exp. Bot. 45: 305–315; Lovelock *et al.* (1996) Funct. Ecol. 10: 662–667; Roden and Ball (1996) Glob. Change Biol. 2: 115–228; Roumet *et al.* (1996) New Phytol. 133 : 595–603; Bunce (1997) Glob. Change Biol. 3: 61–66; Makino *et al.* (1997) Plant Physiol. 115: 199–203; Tjoelker *et al.* (1998) New Phytol. 140 : 197–210; Volin *et al.* (1998) New Phytol. 138: 315–325; Atkin *et al.* (1999) Oecologia 120: 544–556; Cornelissen *et al.* (1999) New Phytol. 141: 401–409; De Luis *et al.* (1999) Physiol. Plant. 107: 84–89; Winter and Lovelock (1999) Flora 194: 221–227; Carswell *et al.* (2000) Tree Physiology 20: 977–986; Poorter & Wierda, unpubl.

Appendix 3: literature used for the analysis of whole plant photosynthesis, FCI and whole plant C concentration

Jansen *et al.* (1986) Biological Control of Photosynthesis, 143–146; Poorter *et al.* (1988) Physiol. Plant. 73 : 553–559; Bunce (1990) Ann. Bot. 65: 637–642; Vessey *et al.* (1990) Crop Sci. 30 : 287–294; Gifford (1991) Report no. 37 Energy Research and Development Corporation; Chu *et al.* (1992) Oecologia 89: 580–587; Den Hertog *et al.* (1993) Vegetatio 104/105; Mousseau (1993) Vegetatio 104/105: 413–419; Poorter (1993) Vegetatio 104/105; Read & Strain (1994) Oecologia 98: 31–39; Gifford (1995) Glob. Change Biol. 4: 879–893; Wullschleger *et al.* (1997) Ann. Bot. 80: 289–297; Ziska and Bunce (1997) Physiol. Plant. 100: 126–132; Ziska (1998) Ann. Bot. 81: 717–721; Dijkstra *et al.* (1999) Glob. Change Biol. 5: 563–576; Santruckova *et al.* (1999) Photosynthetica 36: 341–354; Tjoelker *et al.* (1999) Glob. Change Biol. 5: 679–692; Cheng *et al.* (2000) Glob. Change Biol. 6: 931–941; Roumet *et al.* (2000) Env. Exp. Botany 43: 155–169; Klus *et al.* (2001) Am. J. Bot. 88: 1080–1087; Sakai *et al.* (2001) New Phytol. 150: 241–249; Jifon *et al.* (2002) New Phytol. 153: 133–142; E. Heuvelink, unpubl.; M.L. Navas *et al.* unpubl.; H. Poorter & A. Wierda, unpubl.; S.C. Wong & P. Kriedeman, unpubl.

Appendix 4: literature used for the analysis of the RGR response for species varying in RGR

Neales and Nicholls (1978) Aust. J. Plant Physiol. 5: 45–59; Patterson and Flint (1980) Weed Sci. 28: 71–75; Patterson & Flint (1982) Weed Sci. 30: 389–394; Tolley & Strain (1984) Can. J. For. Res. 14: 343–350; Rogers *et al.* (1984) Crop Sci. 24: 361–366; Peet (1986) Plant Physiol. 80: 59–62; Cure *et al.* (1988) Crop Sci. 28: 671–677; Musgrave and Strain (1988) Plant Physiol. 87: 346–350; Overdieck *et al.* (1988) Angew. Bot. 62 : 119–134; Patterson *et al.* (1988) Weed Sci. 36: 751–757; Bunce (1990) Ann. Bot. 65: 637–642; Wong (1990) Photosynth. Res. 23: 171–180; Badger (1992) Aust. J. Bot. 40 : 421–429; Chu (1992) Oecologia 89: 580–587; Ryle *et al.* (1992) Ann. Bot. 70: 221–228; Wong *et al.* (1992) Aust. J. Bot. 40: 457–472; Bowler and Press (1993) New Phytol. 124: 515–522; Campbell *et al.* (1993) Proc. Int. Grasl. 1125–1126; Den Hertog *et al.* (1993) Vegetatio 104/105: 369–378; Lindroth (1993) Ecology 74 : 763–777; Poorter (1993) Vegetatio 104/105: 77–97; Tremmel and Patterson (1993) Can. J. Plant Sci. 73: 1249–1260; Van der Staaij *et al.* (1993) Vegetatio 104/105 : 433–439; Wong (1993) Vegetatio 104/105: 211–221; Baxter *et al.* (1994) J. Exp. Bot. 45: 305–315; Mortensen (1994) Acta Agric. Scan. 44 : 164–169; Mortensen (1994) Acta Agric. Scan. 44: 157–163; Hunt *et al.* (1995) Ann. Bot. 75: 207–216; Roden and Ball (1996) Glob. Change Biol. 2: 115–228; Roumet *et al.* (1996) New Phytol. 133 : 595–603; Bunce (1997) Glob. Change Biol. 3: 61–66; Fonseca *et al.* (1997) Physiol. Plant. 100: 940–948; Makino *et al.* (1997) Plant Physiol. 115: 199–203; Tjoelker *et al.* (1998) New Phytol. 140: 197; Atkin *et al.* (1999) Oecologia 120: 544–554; Cornelissen *et al.* (1999) New Phytol. 141: 401–409; Winter and Lovelock (1999) Flora 194: 221–227; Carswell *et al.* (2000) Tree Physiology 20: 977–986; Tischler *et al.* (2000) Int. J. Plant Sci. 161: 779–783; Wiggins, Ball, Gifford & Farquhar, unpubl.; Poorter & Wierda, unpubl.

Appendix 5: literature used for the analysis of competition in monostands and mixed cultures

Carter & Peterson (1983) Oecologia 58: 188–193; Bazzaz & Carlson (1984) Oecologia 62: 196–198; Patterson *et al.* (1984) Weed Sci. 32: 101–105; Zangerl & Bazzaz (1984) Oecologia 62: 412–417; Hardacre *et al.* (1986) New Zeal. J. Agric. Res. 29: 567–573; Williams *et al.* (1986) Oecologia 69: 454–459; Du Cloux *et al.* (1987) J. Exp. Bot. 38: 1421–1431; Wray & Strain (1987) Ecology 68: 1116–1120; Bazzaz & Garbutt (1988) Ecology 69: 937–946; Williams *et al.* (1988) Env. Exp. Bot. 28: 123–130; Reekie & Bazzaz (1989) Oecologia 79: 212–222; Wong *et al.* (1991) Austr. J. Plant Physiol. 18 : 137–152; Körner *et al.*, 1995) Oecologia 104: 61–71; Firbank *et al.* (1995) Funct. Ecol. 9: 432–441; Reining (1995) Photosynthetica 31: 501–508; Schenk *et al.* (1995) J. Exp. Bot. 46: 987–993; Teughels *et al.* (1995) J. Biogeogr. 22: 297–305; Wayne and Bazzaz (1995) Glob. Change Biol. 1: 315–324; Chiariello & Field (1996) in Körner & Bazzaz (eds), 'Carbon dioxide, Populations and Communities'; Leadley & Stöcklin (1996) Glob. Change Biol. 2: 389–397; Lüscher *et al.* (1996) in Körner & Bazzaz (eds), 'Carbon dioxide, Populations and Communities'; Retuerto *et al.* (1996) Oecologia 108: 241–251; Arnone & Kestenholz (1997) Funct. Ecol. 11: 209–214; Hebeisen *et al.* (1997) Glob. Change Biol. 3: 149–160; Schenk *et al.* (1997) New Phytol. 135: 67–80; Berntson *et al.* (1998) Glob. Change Biol. 4: 607–626; Bucher *et al.* (1998) Chemosphère 36: 777–782; Jongen & Jones (1998) Ann. Bot. 82: 111–123; Lovelock *et al.* (1998) Oecologia 116 : 207–218; Catovsky & Bazzaz (1999) Glob. Change Biol. 5: 507–518; Navas *et al.* (1999) New Phytol. 143: 323–331; Norton *et al.* (1999) Funct. Ecol. 13 (Suppl. 1) 38–44; Stöcklin and Körner (1999) Funct. Ecol. 13: 200–209.