

## Interspecific variation in the growth response of plants to an elevated ambient CO<sub>2</sub> concentration

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### Abstract

The effect of a doubling in the atmospheric CO<sub>2</sub> concentration on the growth of vegetative whole plants was investigated. In a compilation of literature sources, the growth stimulation of 156 plant species was found to be on average 37%. This enhancement is small compared to what could be expected on the basis of CO<sub>2</sub>-response curves of photosynthesis. The causes for this stimulation being so modest were investigated, partly on the basis of an experiment with 10 wild plant species. Both the source-sink relationship and size constraints on growth can cause the growth-stimulating effect to be transient.

Data on the 156 plant species were used to explore interspecific variation in the response of plants to high CO<sub>2</sub>. The growth stimulation was larger for C<sub>3</sub> species than for C<sub>4</sub> plants. However the difference in growth stimulation is not as large as expected as C<sub>4</sub> plants also significantly increased in weight (41% for C<sub>3</sub> vs. 22% for C<sub>4</sub>). The few investigated CAM species were stimulated less in growth (15%) than the average C<sub>4</sub> species. Within the group of C<sub>3</sub> species, herbaceous crop plants responded more strongly than herbaceous wild species (58% vs. 35%) and potentially fast-growing wild species increased more in weight than slow-growing species (54% vs. 23%). C<sub>3</sub> species capable of symbiosis with N<sub>2</sub>-fixing organisms had higher growth stimulations compared to other C<sub>3</sub> species. A common denominator in these 3 groups of more responsive C<sub>3</sub> plants might be their large sink strength. Finally, there was some tendency for herbaceous dicots to show a larger response than monocots. Thus, on the basis of this literature compilation, it is concluded that also within the group of C<sub>3</sub> species differences exist in the growth response to high CO<sub>2</sub>.

*Abbreviations:* LAR, leaf area ratio; LWR, leaf weight ratio; NAR, net assimilation rate; PS<sub>a</sub>, rate of photosynthesis per unit leaf area; RGR, relative growth rate; RWR, root weight ratio; SLA, specific leaf area.

### Introduction

Plants grown at various ambient concentrations of CO<sub>2</sub> show numerous differences, including variation in photosynthesis, respiration, alloca-

tion, biochemical composition, morphology, flowering and fruit set (Gates *et al.* 1983; Percy & Björkman 1983; Cure & Acock 1986; Amthor 1991). Although the physiological background behind most of these alterations is not fully un-

derstood, it is clear that - at least for  $C_3$  species - two physiological processes are directly affected: photosynthesis and transpiration (Pearcy & Björkman 1983). Net photosynthesis per unit leaf area is raised at an increased  $CO_2$  concentration partly due to a decrease in photorespiration, partly due to an increased substrate supply. Transpiration is reduced due to a lower stomatal conductance.

As a result of the increase in photosynthesis and possibly also due to a decreased water loss, an increase in growth is expected. In almost all cases, high  $CO_2$  concentrations do indeed stimulate plant growth. To estimate the  $CO_2$ -induced increase in plant productivity, Kimball (1983) compiled a number of literature sources. Based mainly on data about flower-, fruit and grain crops and taking into account a wide range of elevated  $CO_2$  concentrations, he found an average stimulation of 33% in marketable yield. From an agricultural point of view marketable yield is an important parameter. However, it is not necessarily a proper indicator of plant growth (*cf.* Poorter *et al.* 1990). To understand how high  $CO_2$  levels stimulate plant growth it is preferable to concentrate on a less complicated system: the vegetative whole plant. The growth response of whole plants to a high  $CO_2$  concentration will be the main subject of this paper. Firstly, an estimation is made to what extent a doubling in the atmospheric  $CO_2$  concentration affects vegetative plant growth. Secondly, the mechanisms behind this growth stimulation will be assessed for 10 wild species. Finally, variation in the growth response amongst species is considered, both between  $C_3$ ,  $C_4$  and CAM species, and within the group of  $C_3$  plants.

### A literature review

To what extent does a high  $CO_2$  concentration stimulate the growth of plants? To answer this question literature data were compiled, using the same approach as Kimball's (1983), in which the weight ratio, the ratio of biomass produced at the end of the experiment at a high and at a control

$CO_2$  level, was calculated for various species. However, some extra constraints have been added. Firstly, I restricted the use of data to those cases where the dry weight of vegetative whole plants was reported. For the plants that had entered the reproductive phase before the end of the experiment, the dry weight prior to flowering was taken. Secondly, only experiments were considered in which the control  $CO_2$  concentration was between 300 and 360  $\mu\text{mol mol}^{-1}$  and the enriched  $CO_2$  level between 600 and 720  $\mu\text{mol mol}^{-1}$ . Thirdly, plants grown in competition were not included. Lastly, in those cases where plants were grown over a range of environmental conditions, I selected that condition where control plants were growing fastest.

The results of the compilation of 89 reports on 156 species are given in Table 1. A large variation in response is observed, even within a species. A striking result is that plants, which were described as unaffected in one report, are found to be highly responsive in others (*cf.* data on *e.g.* *Chenopodium album*, *Pinus taeda* or *Plantago lanceolata*). This may be caused by intraspecific variation (Potvin & Strain 1985) or by a  $CO_2 \times$  Environment interaction in growth (Tolley & Strain 1984; Potvin & Strain 1985; Wong 1992). An alternative and simpler explanation is that variation in plant weight within the experimental population may have affected the weight ratio, especially in experiments based on a limited number of plants. Most likely, all three factors played a role in causing variation in the weight ratio within a species. As it is impossible to discriminate between these alternatives and as the main interest of this paper is variation in response between species, I averaged all reported weight ratios for each species. The distribution of these weight ratios is shown in Figure 1.

Averaged over all the species, a doubling of the ambient  $CO_2$  concentration results in a stimulation of plant growth of 37%. This value is slightly higher than the one found by Kimball (1983). Taking into account the much wider range of  $CO_2$  concentrations in his compilation (up to 1200  $\mu\text{mol mol}^{-1}$ ) and the generally larger response of plants at higher  $CO_2$  levels, there is some suggest-

Table 1. Ratio of total weight of plants grown at a high (600-720  $\mu\text{mol mol}^{-1}$ ) and at a control concentration (300-360  $\mu\text{mol mol}^{-1}$ ) of  $\text{CO}_2$ . Final yield was taken when plants remained vegetative. In other cases plant weight before flowering or fruiting was used. In those cases where mean relative growth rates were given, these values were used for the calculation of the weight ratio, as they summarize data of more than one harvest. For each species and reference, the number (n) of days that the experiment lasted, and the total number of harvested plants on which the ratio is based, are given. Mean values per species and per category are backtransformed values of averaged log-transformed ratios, to correct for the intrinsically skewed nature of ratios. For the  $\text{C}_3$  wild species it is indicated whether they are potentially slow-growing ( $^{\circ}$ ), intermediate ( $^{\text{i}}$ ) or fast-growing ( $^{\text{f}}$ ). Unpublished data are from M.R. Badger & O. Björkman; M.C. Ball, M. Cochrane & H. Rawson; P.J. Mathias, J.E. Conroy & S.E.W.R. Barlow; M.E. Nicolas, R. Munns, A. Samarkoon & R.M. Gifford; C. Roumet, M.-P. Bel & J. Roy; S.C. Wong, P.E. Kriedemann & G.D. Farquhar.

Species	Weight ratio	n days	n plants	Reference	Averaged weight ratio
<b><math>\text{C}_3</math> CROP SPECIES:</b>					
<i>Abelmoschus esculentus</i>	1.08	34	10	Overdieck <i>et al.</i> 1988	1.08
<i>Beta vulgaris</i>	1.56	50	20	Sionit <i>et al.</i> 1982	1.56
<i>Brassica napus</i>	1.83	25	8	Morison & Gifford 1984	1.83
<i>Daucus carota</i>	2.10	28	?	Idso & Kimball 1989	2.10
<i>Glycine max</i>	1.23	45	16	Patterson & Flint 1980	1.71
	1.42	49	40	Rogers <i>et al.</i> 1984	
	1.49	16	256	Cure <i>et al.</i> 1989	
	1.50	35	24	Patterson & Flint 1982	
	1.51	24	24	Patterson <i>et al.</i> 1984	
	1.58	44	8	Cure <i>et al.</i> 1988	
	1.58	35	?	Carlson & Bazzaz 1980	
	1.63	57	20	Sionit <i>et al.</i> 1982	
	1.68	22	12	Bunce 1990	
	1.69	22	16	Cure <i>et al.</i> 1987	
	1.77	40	16	Sionit <i>et al.</i> 1987	
	1.83	38	24	Sionit 1983	
	4.95	20	36	Mauney <i>et al.</i> 1978	
<i>Gossypium hirsutum</i>	1.07	25	8	Morison & Gifford 1984	1.78
	1.46	28	12	Thomas & Strain 1991	
	1.61	35	16	Patterson <i>et al.</i> 1988	
	1.66	28	30	DeLucia <i>et al.</i> 1985	
	1.73	39	10	Wong 1992	
	2.72	20	36	Mauney <i>et al.</i> 1978	
<i>Helianthus annuus</i>	2.94	21	40	Wong 1990	1.64
	1.20	28	6	Carlson & Bazzaz 1980	
	1.51	25	8	Morison & Gifford 1984	
	1.58	25	24	Morison & Gifford 1984	
	1.62	24	?	Gifford <i>et al.</i> 1985	
	1.82	20	36	Mauney <i>et al.</i> 1978	
	1.91	25	8	Morison & Gifford 1984	
<i>Hordeum vulgare</i>	1.97	24	16	Hunt <i>et al.</i> 1991	2.07
	2.07	25	8	Morison & Gifford 1984	
<i>Lolium perenne</i>	1.23	70	30	Marks & Clay 1990	1.71
	1.34	49	16	Hunt <i>et al.</i> 1991	
	1.52	17	72	Poorter, this study	
	1.59	37	16	Roumet <i>et al.</i> unpubl.	
	2.32	25	8	Morison & Gifford 1984	
	2.72	36	16	Roumet <i>et al.</i> unpubl.	
<i>Lycopersicon esculentum</i>	1.14	18	?	Paez <i>et al.</i> 1984	1.30
	1.23	18	?	Paez <i>et al.</i> 1984	

Table 1. Continued.

Species	Weight ratio	n days	n plants	Reference	Averaged weight ratio
<i>Medicago sativa</i>	1.58	24	12	Bunce 1990	1.35
	0.79	28	20	MacDowall 1982	
	2.30	25	8	Morison & Gifford 1984	
<i>Oryza sativa</i>	1.42	58	18	Baker <i>et al.</i> 1991	1.47
	1.51	25	8	Morison & Gifford 1984	
<i>Pisum sativum</i>	1.05	14	42	Musgrave <i>et al.</i> 1986	1.36
	1.28	30	16	Paez <i>et al.</i> 1983	
	1.57	25	8	Morison & Gifford 1984	
	1.62	14	8	Musgrave <i>et al.</i> 1986	
<i>Raphanus sativus</i>	1.48	28	?	Idso & Kimball 1989	1.64
	1.51	32	10	Overdieck <i>et al.</i> 1988	
	1.57	27	20	Sionit <i>et al.</i> 1982	
	1.70	39	10	Wong 1992	
	1.99	25	8	Morison & Gifford 1984	
<i>Triticum aestivum</i>	1.07	24	20	Neales & Nicholls 1978	1.49
	1.25	14	?	Gifford <i>et al.</i> 1985	
	1.41	40	12	Nicolas <i>et al.</i> unpubl.	
	1.61	37	20	Sionit <i>et al.</i> 1981	
	1.83	29	24	Gifford <i>et al.</i> 1985	
	1.97	25	8	Morison & Gifford 1984	
<i>Triticum durum</i>	1.46	40	12	Nicolas <i>et al.</i> unpubl.	1.46
<i>Vicia faba</i>	1.44	25	8	Morison & Gifford 1984	1.44
<i>Vigna radicata</i>	1.45	27	?	Gifford <i>et al.</i> 1985	1.45
<i>Vigna unguiculata</i>	1.51	25	24	Morison & Gifford 1984	1.80
	1.64	33	10	Overdieck <i>et al.</i> 1988	
	1.99	25	8	Morison & Gifford 1984	
	2.12	43	16	Bhattacharya <i>et al.</i> 1985	
Mean Value:		30			1.58
<b>C<sub>3</sub> WILD SPECIES:</b>					
<i>Abutilon theophrasti</i> <sup>f</sup>	1.30	35	16	Patterson <i>et al.</i> 1988	1.41
	1.36	45	16	Patterson & Flint 1980	
	1.44	28	6	Carlson & Bazzaz 1980	
	1.56	20	12	Bazzaz <i>et al.</i> 1989	
<i>Agoseris heterophylla</i> <sup>s</sup>	1.71	64	40	Williams <i>et al.</i> 1988	1.71
<i>Agropyron smithii</i> <sup>i</sup>	1.57	70	20	Smith <i>et al.</i> 1987	1.57
<i>Agrostis capillaris</i> <sup>i</sup>	1.56	49	16	Hunt <i>et al.</i> 1991	1.56
<i>Ambrosia artemisiifolia</i> <sup>f</sup>	1.10	28	6	Carlson & Bazzaz 1980	1.10
<i>Anoda cristata</i> <sup>f</sup>	1.40	35	16	Patterson <i>et al.</i> 1988	1.40
<i>Arrhenatherum elatius</i> <sup>i</sup>	1.18	49	16	Hunt <i>et al.</i> 1991	1.18
<i>Artemisia tridentata</i> <sup>i</sup>	1.10	63	41	Johnson & Lincoln 1990	1.10
<i>Aster pilosus</i> <sup>i</sup>	1.13	56	20	Wray & Strain 1986	1.13
<i>Brachypodium pinnatum</i> <sup>s</sup>	1.00	49	16	Hunt <i>et al.</i> 1991	1.00
<i>Bromus erectus</i> <sup>s</sup>	1.51	49	16	Hunt <i>et al.</i> 1991	1.68
	1.88	42	16	Roumet <i>et al.</i> unpubl.	
<i>Bromus hordaceus</i> <sup>f</sup>	3.60	38	16	Roumet <i>et al.</i> unpubl.	3.60
<i>Bromus madritensis</i> <sup>i</sup>	2.50	38	16	Roumet <i>et al.</i> unpubl.	2.50
<i>Bromus mollis</i> <sup>i</sup>	1.16	49	16	Larigauderie <i>et al.</i> 1988	1.16
<i>Bromus riparius</i> <sup>s</sup>	2.92	43	16	Roumet <i>et al.</i> unpubl.	2.92

Table 1. Continued.

Species	Weight ratio	n days	n plants	Reference	Averaged weight ratio
<i>Bromus squarrosus</i> <sup>f</sup>	2.57	32	16	Roumet <i>et al.</i> unpubl.	2.57
<i>Bromus sterilis</i> <sup>f</sup>	1.04	49	16	Hunt <i>et al.</i> 1991	1.04
<i>Bromus tectorum</i> <sup>s</sup>	1.26	70	20	Smith <i>et al.</i> 1987	1.72
	2.33	40	16	Roumet <i>et al.</i> unpubl.	
<i>Bromus tomentellus</i> <sup>s</sup>	1.41	36	16	Roumet <i>et al.</i> unpubl.	1.41
<i>Bromus willdenowii</i> <sup>i</sup>	1.59	27	16	Roumet <i>et al.</i> unpubl.	1.59
<i>Callistephus chinensis</i> <sup>i</sup>	1.30	37	60	Hughes & Cockshull 1969	1.30
<i>Carex bigelowii</i> <sup>s</sup>	1.13	90	12	Oberbauer <i>et al.</i> 1986	1.13
<i>Carex diandra</i> <sup>s</sup>	1.10	17	72	Poorter, this study	1.10
<i>Cassia obtusifolia</i> <sup>f</sup>	1.60	35	24	Patterson & Flint 1982	1.60
<i>Cerastium fontanum</i> <sup>i</sup>	1.59	49	16	Hunt <i>et al.</i> 1991	1.59
<i>Chamerion angustifolium</i> <sup>f</sup>	3.66	49	16	Hunt <i>et al.</i> 1991	3.66
<i>Chenopodium album</i> <sup>f</sup>	1.00	49	16	Hunt <i>et al.</i> 1991	1.26
	1.60	28	?	Carlson & Bazzaz 1982	
<i>Crotolaria spectabilis</i> <sup>f</sup>	1.67	35	24	Patterson & Flint 1982	1.67
<i>Dactylis glomerata</i> <sup>i</sup>	1.24	49	16	Hunt <i>et al.</i> 1991	1.24
<i>Datura stramonium</i> <sup>f</sup>	1.70	28	?	Carlson & Bazzaz 1982	1.72
	1.74	28	6	Carlson & Bazzaz 1980	
<i>Deschampsia flexuosa</i> <sup>s</sup>	1.22	49	16	Hunt <i>et al.</i> 1991	1.28
	1.35	17	72	Poorter, this study	
<i>Desmazeria rigida</i> <sup>s</sup>	1.30	49	16	Hunt <i>et al.</i> 1991	1.30
<i>Digitalis purpurea</i> <sup>i</sup>	1.16	49	16	Hunt <i>et al.</i> 1991	1.16
<i>Eichornia crassipes</i> <sup>f</sup>	1.32	28	16	Spencer & Bowes 1986	1.33
	1.34	16	10	Drelon & Roy 1992	
<i>Epilobium hirsutum</i> <sup>f</sup>	1.11	49	16	Hunt <i>et al.</i> 1991	1.11
<i>Eriophorum vaginatum</i> <sup>s</sup>	1.19	49	16	Hunt <i>et al.</i> 1991	1.19
<i>Festuca ovina</i> <sup>s</sup>	1.23	49	16	Hunt <i>et al.</i> 1991	1.44
	1.69	17	72	Poorter, this study	
<i>Festuca rubra</i> <sup>s</sup>	1.00	49	16	Hunt <i>et al.</i> 1991	1.00
<i>Helianthemum</i>	1.00	49	16	Hunt <i>et al.</i> 1991	1.00
<i>Holcus lanatus</i> <sup>f</sup>	1.60	49	16	Hunt <i>et al.</i> 1991	1.60
<i>Koeleria macrantha</i> <sup>s</sup>	1.02	49	16	Hunt <i>et al.</i> 1991	1.02
<i>Lasthenia glabrata</i> <sup>s</sup>	0.78	64	40	Williams <i>et al.</i> 1988	0.78
<i>Layia platyglossa</i> <sup>s</sup>	1.46	64	40	Williams <i>et al.</i> 1988	1.46
<i>Lolium rigidum</i> <sup>f</sup>	1.61	30	16	Roumet <i>et al.</i> unpubl.	1.61
<i>Macropitilium purpureum</i> <sup>i</sup>	1.57	25	8	Morison & Gifford 1984	1.57
<i>Micropus californicus</i> <sup>s</sup>	1.17	64	40	Williams <i>et al.</i> 1988	1.17
<i>Microseris spec.</i> <sup>s</sup>	0.92	64	40	Williams <i>et al.</i> 1988	0.92
<i>Mimulus cardinalis</i> <sup>i</sup>	1.30	20	56	Badger & Björkman unpubl.	1.36
	1.43	20	56	Badger & Björkman unpubl.	
<i>Oryzopsis hymenoides</i> <sup>s</sup>	1.32	120	20	Smith <i>et al.</i> 1987	1.32
<i>Phalaris aquatica</i> <sup>f</sup>	1.43	25	8	Morison & Gifford 1984	1.43
<i>Pharus latifolius</i> <sup>f</sup>	2.72	95	8	Ziska <i>et al.</i> 1991	2.72
<i>Plantago erecta</i> <sup>s</sup>	1.02	64	40	Williams <i>et al.</i> 1988	1.02
<i>Plantago lanceolata</i> <sup>i</sup>	1.00	49	16	Hunt <i>et al.</i> 1991	1.23
	1.51	91	39	Fajer <i>et al.</i> 1991	
<i>Plantago major</i> <sup>i</sup>	1.32	17	72	Poorter, this study	1.48
	1.51	17	32	Den Hertog <i>et al.</i> 1992	
	1.63	49	192	Poorter <i>et al.</i> 1988	
<i>Poa annua</i> <sup>s</sup>	1.00	49	16	Hunt <i>et al.</i> 1991	1.00

Table 1. Continued.

Species	Weight ratio	n days	n plants	Reference	Averaged weight ratio
<i>Poa trivialis</i> <sup>i</sup>	1.03	49	16	Hunt <i>et al.</i> 1991	1.03
<i>Polygonum pensylvanicum</i> <sup>f</sup>	1.48	28	?	Carlson & Bazzaz 1982	1.48
<i>Rumex acetosella</i> <sup>s</sup>	1.31	49	16	Hunt <i>et al.</i> 1991	1.31
<i>Silene dioica</i> <sup>i</sup>	1.46	17	72	Poorter, this study	1.46
<i>Taraxacum officinale</i> <sup>f</sup>	1.70	17	72	Poorter, this study	1.70
<i>Trifolium repens</i> <sup>i</sup>	1.52	17	72	Poorter, this study	1.53
	1.55	25	8	Morison & Gifford 1984	
<i>Urtica dioica</i> <sup>f</sup>	1.29	21	64	Jansen <i>et al.</i> 1986	1.53
	1.30	49	16	Hunt <i>et al.</i> 1991	
	1.63	17	72	Poorter, this study	
	1.99	22	32	Den Hertog & Stulen 1990	
Mean value:		43			1.35
<b>C<sub>3</sub> WOODY SPECIES:</b>					
<i>Acacia mangium</i>	1.40	95	8	Ziska <i>et al.</i> 1991	1.40
<i>Acacia melanoxylon</i>	1.21	133	10	Mathias <i>et al.</i> unpubl.	1.21
<i>Acer saccharinum</i>	1.61	28	6	Carlson & Bazzaz 1980	1.61
<i>Alnus glutinosa</i>	1.39	17	72	Poorter, this study	1.44
	1.49	98	13	Norby 1987	
<i>Alnus rubra</i>	1.73	47	8	Arnone & Gordon 1990	1.73
<i>Banksia serrata</i>	4.13	100	10	Wong <i>et al.</i> unpubl.	4.13
<i>Betula nana</i>	0.90	90	12	Oberbauer <i>et al.</i> 1986	0.90
<i>Castanea saliva</i>	1.43	210	16	Mousseau & Enoch 1989	1.43
<i>Cecropia obtusifolia</i>	1.14	111	8	Reekie & Bazzaz 1989	1.14
<i>Elaeagnus angustifolia</i>	1.61	84	10	Norby 1987	1.61
<i>Eucalyptus camaldulensis</i>	2.11	84	80	Wong <i>et al.</i> unpubl.	2.11
<i>Eucalyptus cypelocarpa</i>	3.44	84	80	Wong <i>et al.</i> unpubl.	3.44
<i>Eucalyptus globulus</i>	1.57	133	10	Mathias <i>et al.</i> unpubl.	1.57
<i>Eucalyptus grandis</i>	1.05	133	10	Mathias <i>et al.</i> unpubl.	1.05
<i>Eucalyptus marginata</i>	1.45	133	10	Mathias <i>et al.</i> unpubl.	1.45
<i>Eucalyptus microcorys</i>	1.32	133	10	Mathias <i>et al.</i> unpubl.	1.32
<i>Eucalyptus pauciflora</i>	2.56	100	80	Wong <i>et al.</i> unpubl.	2.56
<i>Eucalyptus pttularis</i>	1.19	133	10	Mathias <i>et al.</i> unpubl.	1.19
<i>Eucalyptus pulverulenta</i>	2.74	98	80	Wong <i>et al.</i> unpubl.	2.74
<i>Ficus obtusifolia</i>	1.10	95	8	Ziska <i>et al.</i> 1991	1.10
<i>Gliricidia septum</i>	1.26	71	32	Thomas <i>et al.</i> 1991	1.26
<i>Ledum palustre</i>	0.90	90	12	Oberbauer <i>et al.</i> 1986	0.90
<i>Liquidambar styraciflua</i>	1.32	112	100	Tolley & Strain 1984	1.38
	1.44	224	30	Sionit <i>et al.</i> 1985	
<i>Liriodendron tulipifera</i>	1.73	168	12	O'Neill <i>et al.</i> 1987a	1.73
<i>Lonicera japonica</i>	2.35	54	24	Sasek & Strain 1991	2.35
<i>Lonicera sempervirens</i>	1.32	54	24	Sasek & Strain 1991	1.32
<i>Myriocarpa longipes</i>	0.92	111	8	Reekie & Bazzaz 1989	0.92
<i>Nerium oleander</i>	1.61	90	7	Downton <i>et al.</i> 1980	1.61
<i>Nothofagus fusca</i>	1.17	120	16	Hollinger 1987	1.17
<i>Ochroma lagopus</i>	1.79	60	10	Oberbauer <i>et al.</i> 1985	1.79
<i>Pentaclethra macroloba</i>	1.30	123	16	Oberbauer <i>et al.</i> 1985	1.30
<i>Pinus echinata</i>	1.15	263	20	Norby <i>et al.</i> 1987	1.38

Table 1. Continued.

Species	Weight ratio	n days	n plants	Reference	Averaged weight ratio
<i>Pinus radiata</i>	1.65	144	30	O'Neill <i>et al.</i> 1987b	1.37
	1.24	798	40	Conroy <i>et al.</i> 1990	
	1.31	798	40	Conroy <i>et al.</i> 1990	
	1.34	154	30	Conroy <i>et al.</i> 1988	
	1.43	154	10	Conroy <i>et al.</i> 1986	
<i>Pinus taeda</i>	1.55	154	10	Conroy <i>et al.</i> 1986	1.03
	0.67	84	100	Tolley & Strain 1984	
	1.56	224	30	Sionit <i>et al.</i> 1985	
<i>Piper auritum</i>	1.15	111	8	Reekie & Bazzaz 1989	1.15
<i>Platanus occidentalis</i>	1.13	28	6	Carlson & Bazzaz 1980	1.13
<i>Poncirus spec.</i>	2.11	154	140	Koch <i>et al.</i> 1986	2.13
	2.15	154	140	Koch <i>et al.</i> 1986	
<i>Populus deltoides</i>	1.65	28	6	Carlson & Bazzaz 1980	1.65
<i>Populus euramericana</i>	1.73	129	?	Goudriaan & De Ruiter 1983	1.73
<i>Populus spec.</i>	1.14	92	6	Radoglou & Jarvis 1990	1.30
	1.15	92	6	Radoglou & Jarvis 1990	
	1.33	92	6	Radoglou & Jarvis 1990	
	1.66	92	6	Radoglou & Jarvis 1990	
<i>Pseudotsuga menziesii</i>	1.03	120	16	Hollinger 1987	1.03
<i>Psychotria limonensis</i>	1.43	95	8	Ziska <i>et al.</i> 1991	1.43
<i>Pueraria lobata</i>	1.20	60	20	Sasek & Strain 1988	1.20
<i>Quercus alba</i>	1.71	210	12	O'Neill <i>et al.</i> 1987b	1.78
	1.85	280	12	Norby <i>et al.</i> 1986	
<i>Rhizophora apiculata</i>	1.17	105	10	Ball <i>et al.</i> unpubl.	1.17
<i>Rhizophora stylosa</i>	1.07	105	10	Ball <i>et al.</i> unpubl.	1.07
	1.32	105	20	Norby 1987	
<i>Senna multijuga</i>	1.19	111	8	Reekie & Bazzaz 1989	1.19
<i>Tabebuia rosea</i>	2.64	95	8	Ziska <i>et al.</i> 1991	2.64
<i>Trichospermum mexicanum</i>	1.21	111	8	Reekie & Bazzaz 1989	1.21
Mean value:		136			1.41
C <sub>4</sub> SPECIES					
<i>Amaranthus edulis</i>	1.26	25	8	Morison & Gifford 1984	1.26
<i>Amaranthus hypochondria</i>	1.02	20	12	Bunce 1990	1.02
<i>Amaranthus retroflexus</i>	1.27	28	?	Carlson & Bazzaz 1982	1.41
	1.56	20	12	Bazzaz <i>et al.</i> 1989	
<i>Andropogon glomeratus</i>	0.63	56	14	Bowman & Strain 1987	0.63
<i>Andropogon virginicus</i>	1.14	56	20	Wray & Strain 1986	1.14
<i>Bouteloua gracillis</i>	1.23	21	20	Riechers & Strain 1988	1.23
<i>Digitaria ciliaris</i>	1.06	30	16	Patterson 1986	1.06
<i>Digitaria sanguinalis</i>	1.61	21	16	Sionit & Patterson 1984	1.61
<i>Echinochloa crus-galli</i>	0.95	30	16	Patterson 1986	1.37
	1.35	48	18	Potvin & Strain 1985	
	1.53	48	18	Potvin & Strain 1985	
	1.55	48	18	Potvin & Strain 1985	
	1.59	21	16	Sionit & Patterson 1984	
<i>Eleusine indica</i>	1.02	30	16	Patterson 1986	1.11
	1.11	48	18	Potvin & Strain 1985	
	1.21	21	16	Sionit & Patterson 1984	

Table 1. Continued.

Species	Weight ratio	n days	n plants	Reference	Averaged weight ratio
<i>Eragrostis orcuttiana</i>	1.45	70	20	Smith 1987	1.45
<i>Paspalum conjugatum</i>	1.22	95	8	Ziska <i>et al.</i> 1991	1.22
<i>Rottboetia exaltata</i>	1.21	45	16	Patterson & Flint 1980	1.21
<i>Setaria faberii</i>	0.92	28	?	Carlson & Bazzaz 1982	1.11
	1.34	21	16	Sionit & Patterson 1984	
<i>Setaria lutescens</i>	1.73	28	?	Carlson & Bazzaz 1982	1.73
<i>Sorghum bicolor</i>	1.26	25	8	Morison & Gifford 1984	1.52
	1.82	20	36	Mauney <i>et al.</i> 1978	
<i>Sorghum halepense</i>	1.10	24	24	Patterson <i>et al.</i> 1984	1.10
<i>Tridens flavus</i>	0.94	70	24	Marks & Clay 1990	0.94
<i>Zea mays</i>	0.98	45	16	Patterson & Flint 1980	1.09
	1.00	49	16	Hunt <i>et al.</i> 1991	
	1.04	25	8	Morison & Gifford 1984	
	1.06	55	4	King & Greer 1986	
	1.24	40	20	Sionit <i>et al.</i> 1982	
	1.24	28	6	Carlson & Bazzaz 1980	
Mean value:		38			1.22
CAM SPECIES:					
<i>Aechmea magdalene</i>	1.36	95	8	Ziska <i>et al.</i> 1991	1.36
<i>Agave deserti</i>	1.22	365	12	Nobel & Hartsock 1986	1.22
<i>Agave vilmoriniana</i>	1.08	183	26	Idso <i>et al.</i> 1986	1.08
<i>Anana comosus</i>	0.90	95	8	Ziska <i>et al.</i> 1991	0.90
<i>Ferocactus acanthodes</i>	1.14	365	12	Nobel & Hartsock 1986	1.14
<i>Opuntia ficus-indica</i>	1.15	183	12	Nobel & Garcia de Cortazar 1991	1.15
Mean value		214			1.15
All species:		66			1.37

ion that the response of whole plants may be somewhat larger than that for marketable yield. However, a stimulation of 37% is still rather modest. Using eq. 1, which will be introduced in the next paragraph, the effect of a change in the rate of photosynthesis on growth can be calculated. Given the median duration of the experiments listed in Table 1 (45 days) and assuming that the rate of photosynthesis was the only parameter responsible for the growth stimulation, the increase in photosynthesis due to an increased CO<sub>2</sub> level would only need to be 2-5 % to explain the growth difference. In CO<sub>2</sub> response curves a much higher stimulation (20-50%) of the rate of

photosynthesis is found. Why then is the growth stimulation so small?

### The mechanisms behind the growth stimulation

To find out why the growth stimulation is relatively small, more insight into the mechanisms behind this growth stimulation is required. Weight ratios are then inadequate as a starting point, with a major shortcoming of not correcting for the duration of the experiment. If a high CO<sub>2</sub> concentration stimulates growth each day, then long-term experiments will show a larger stimulation



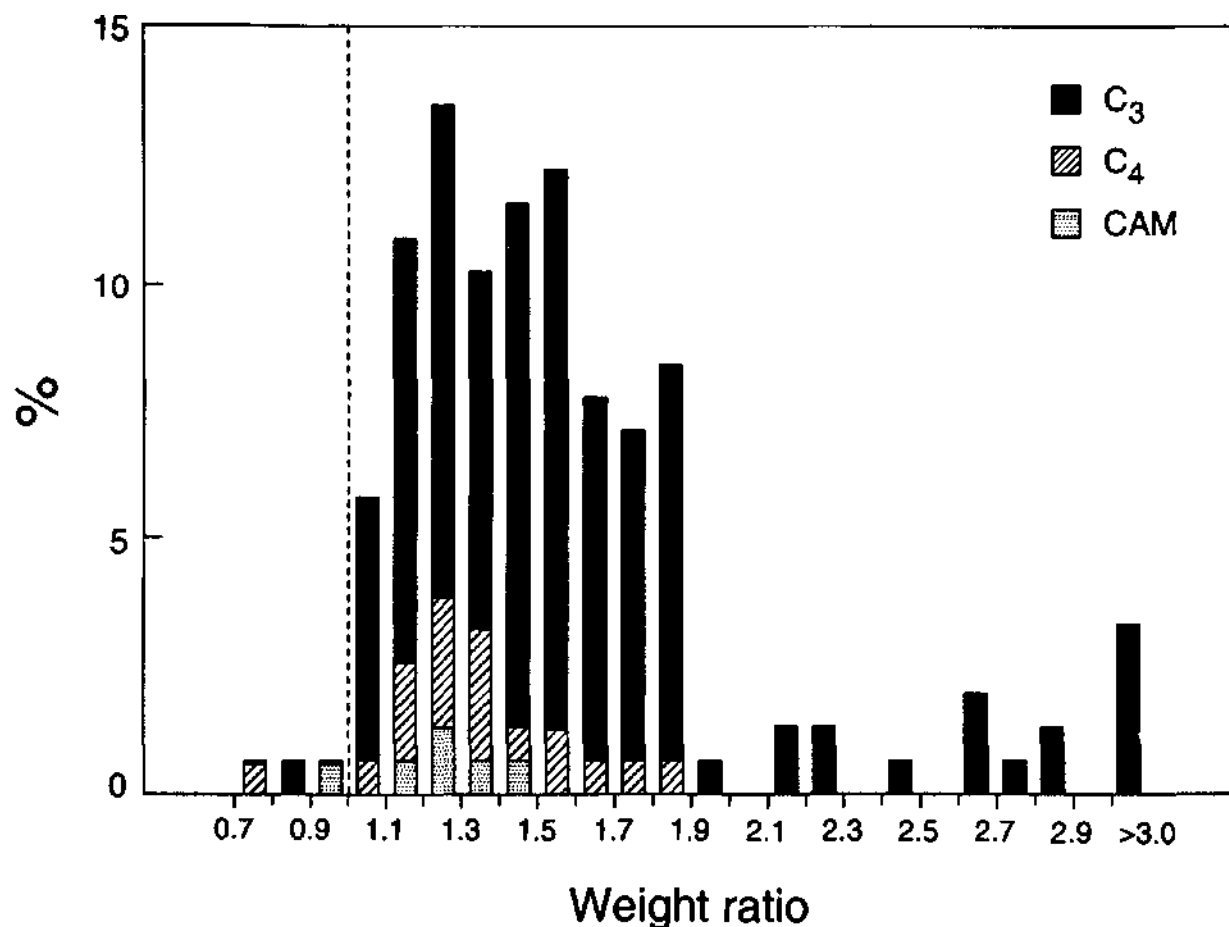


Fig. 1. Distribution of the weight ratios of CO<sub>2</sub> enriched (600-720  $\mu\text{mol mol}^{-1}$ ) and control plants (300-360  $\mu\text{mol mol}^{-1}$ ). Data are compiled from the literature. Each datum is the average of all the weight ratios reported for a species. Total number of species is 156.

than short-term ones. Another flaw is that the weight ratio does not correct for the plant weight at the beginning of the experiment. Moreover, in calculating weight ratios no correction is normally made for the log-normal distribution in plant weight, and it is difficult to relate time-dependent changes in the weight ratio to the physiological functioning of the plant. Better insight into the mechanisms behind the growth stimulation can be obtained by using the techniques of growth analysis (*cf.* Lambers *et al.* 1989). In this approach growth is calculated as the increase in biomass per unit plant weight already present and per unit of time: the 'Relative Growth Rate' (RGR). A first clue to the basis of growth differences can be provided by factorizing RGR into

the 'Net Assimilation Rate' (NAR), the increase in plant weight per unit leaf area and per unit of time on one hand and the 'Leaf Area Ratio' (LAR), the amount of leaf area per unit total plant weight, on the other hand (*cf.* Hurd 1968). However, to arrive at a good insight into the causes of the - relatively small - growth stimulation, it is preferable to directly analyze growth in terms of the underlying carbon economy (Lambers & Poorter 1992):

$$\text{RGR} = \frac{\text{PS}_a \cdot \text{SLA} \cdot \text{LWR} - \text{S}_h \text{R} \cdot \text{S}_h \text{WR} - \text{RR} \cdot \text{RWR}}{[\text{C}]} \quad (1)$$

where PS<sub>a</sub> is the rate of photosynthesis per unit leaf area ( $\text{mol C m}^{-2} \text{ day}^{-1}$ ), SLA the specific leaf area (leaf area:leaf weight), LWR the leaf weight

ratio (leaf weight: total plant weight), ShR the rate of shoot respiration per unit shoot weight ( $\text{mol C g}^{-1} \text{ day}^{-1}$ ), ShWR the shoot weight ratio (leaf + stem weight: total plant weight), RR the rate of root respiration per unit root weight ( $\text{mol C g}^{-1} \text{ day}^{-1}$ ), RWR the root weight ratio (root weight: total plant weight) and where [C] is the carbon concentration of the plant biomass ( $\text{mol g}^{-1}$ ).

The techniques of growth analysis were followed in an experiment set up to analyze the effect of an elevated  $\text{CO}_2$  concentration on the growth and physiology of 10 wild species. These species differ in the RGR they can attain under optimum conditions (*cf.* Poorter 1989). For each of the species, seeds were germinated at  $350 \pm 20 \mu\text{mol mol}^{-1} \text{ CO}_2$  and transferred to a nutrient solution as soon as the roots reached a length of 3–4 cm. Photosynthetic photon flux density was  $270 \mu\text{mol m}^{-2} \text{ s}^{-1}$  and the daylength 14 hours. After acclimation (3–5 days) half of the plants were transferred to a growth chamber with a  $\text{CO}_2$  concentration of  $700 \pm 20 \mu\text{mol mol}^{-1}$  (day 0). At day 0, 3, 8, 9, 13 and 17, six plants of each  $\text{CO}_2$  concentration were harvested and leaf area and dry weight of leaves, stem and roots were determined. At day 8 and 9,  $\text{CO}_2$ -fixation was measured on whole shoots of four plants under conditions similar as in the growth rooms. Further details on growth conditions and photosynthesis determinations are given in Poorter *et al.* (1988). The overall response of the 10 species was tested in a t-test with the  $H_0$ -hypothesis that the average change in a parameter due to the high  $\text{CO}_2$  treatment was 0%.

Averaged over the 10 species, the growth parameter NAR was increased due to the elevated  $\text{CO}_2$  concentration by 19% (Fig. 2A,  $P < 0.001$ ). LAR was affected in the opposite direction, being on average 6.5% lower for the  $\text{CO}_2$ -enriched plants (Fig. 2B,  $P < 0.01$ ). The rate of photosynthesis expressed per unit leaf area was 20% higher (Fig. 3A,  $P < 0.001$ ), but expressed on a leaf weight basis only 6.5% ( $0.05 < P < 0.10$ ). SLA decreased by an average value of 8% (Fig. 3B,  $P < 0.001$ ). In general, allocation was hardly affected by the  $\text{CO}_2$  treatment. LWR increased slightly (on average 1.5%, Fig. 4A,  $P < 0.05$ ),

whereas RWR decreased slightly (on average 2.5%, Fig. 4B,  $P < 0.05$ ).

Respiration and carbon content of the plant biomass were not measured in this experiment and seem to be neglected by almost all authors. However, the growth-stimulating effect of a high  $\text{CO}_2$  concentration can only be fully understood if these parameters are taken into account (*cf.* eq. 1). Both increases and decreases in the rate of respiration have been reported (Gifford *et al.* 1985; Poorter *et al.* 1988, Bunce & Caulfield 1991). In general, respiration rates expressed on a dry weight basis may decrease somewhat (Amthor 1991). This is at least partly due to accumulation of starch in the plant, which does not require a high amount of metabolic energy, but increases total biomass. Few data exist on the effect of  $\text{CO}_2$  enrichment on the carbon content of the plant. Johnson & Lincoln (1990) found the C-content of leaves of enriched plants to be  $35 \text{ mmol g}^{-1}$  as compared to  $36.5 \text{ mmol g}^{-1}$  in control plants. If a similar change occurred in stem and roots, this alone could increase RGR by 4%. Thus, changes in both respiration and C-content may contribute to the stimulated growth.

As far as the other parameters are concerned, they seem to fit in with the majority of earlier data, where the increase in  $\text{PS}_a$  is partly offset by a decrease in SLA (*e.g.* Hicklenton & Jolliffe 1980, Wulff & Strain 1982; Spencer & Bowes 1986; Poorter *et al.* 1988). This decrease in SLA is at least partly due to accumulation of starch (*cf.* Sasek *et al.* 1985; Wong 1990). Thus, one of the causes of the relatively minor stimulation of high  $\text{CO}_2$  concentrations is that the increased photosynthetic supply is not used for investment in new actively growing material (*e.g.* leaf area) but rather is accumulated as starch in the chloroplasts.

### Time dependence of the growth stimulation

In the above-given analysis of the 10 species, average values of the growth parameters over a 17 day period were presented, together with values of photosynthesis in the middle of this period. However, the effect of elevated  $\text{CO}_2$  concentra-

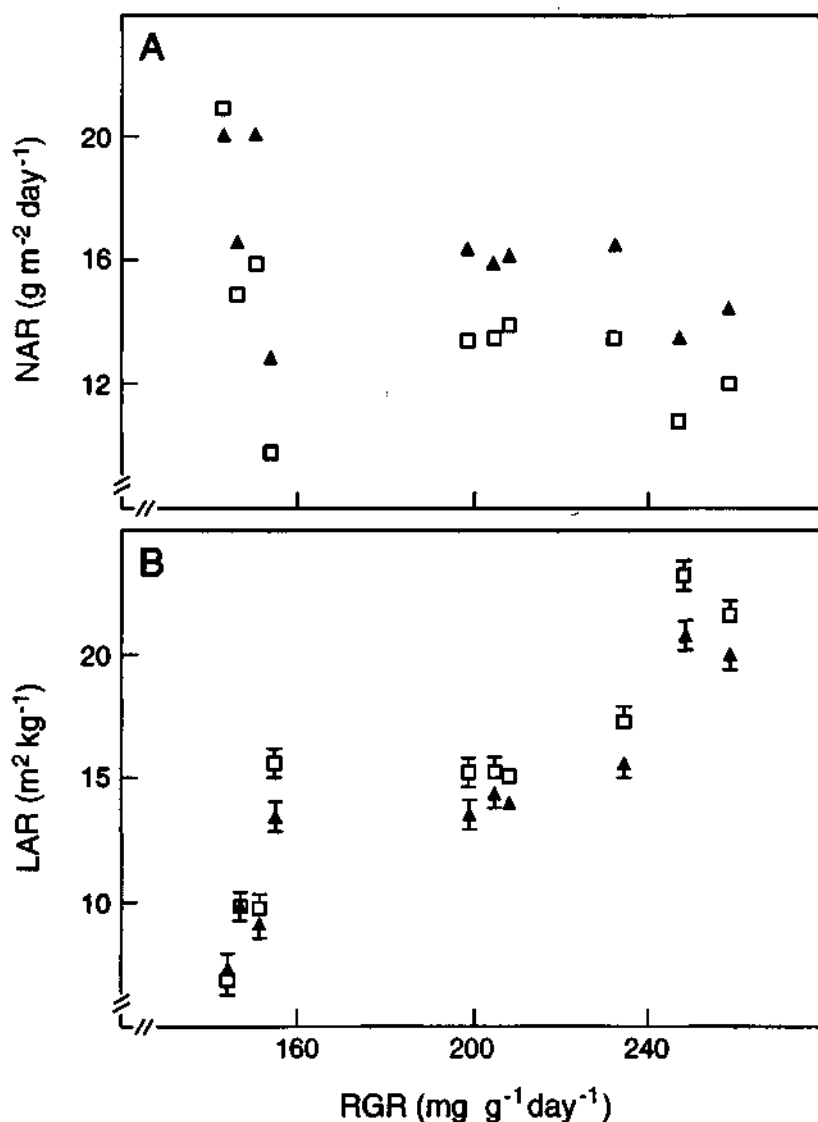


Fig. 2. A, Mean Net Assimilation Rate (NAR); and B, mean Leaf Area Ratio (LAR) of 10 species grown for a 17-day period at 700  $\mu\text{mol mol}^{-1}$  CO<sub>2</sub> (filled triangles) or 350  $\mu\text{mol mol}^{-1}$  CO<sub>2</sub> (open squares). All values are plotted against the mean RGR of each species at 350  $\mu\text{mol mol}^{-1}$  CO<sub>2</sub>. The 10 species are (from low to high RGR) *Carex diandra*, *Deschampsia flexuosa*, *Festuca ovina*, *Alnus glutinosa* (tree species), *Lolium perenne*, *Trifolium repens*, *Plantago major* ssp. *major*, *Silene dioica*, *Taraxacum officinale* and *Urtica dioica*. Error bars in B indicate 2 times the mean SE during the experiment.

tions on growth is often time-dependent. For *Triticum aestivum* a stimulation in RGR was found only during the first week of CO<sub>2</sub>-enrichment (Neales & Nicholls 1978). Thereafter, no stimulation was found, or even an inhibition of RGR. Similar results, amongst others, have been obtained for *Triticum aestivum* stands (Du Cloux *et al.* 1987), for *Abutilon theophrasti* (Garbutt *et al.*

1990), *Brassica pekinensis* (Kriedemann & Wong 1984), *Cucumis sativus* (Kriedemann & Wong 1984, Peet 1986), *Desmodium paniculatum* (Wulff & Strain 1982), *Gliricidia sepium* (Thomas *et al.* 1991), *Glycine max* (Rogers *et al.* 1984), *Gossypium hirsutum* (Wong 1990), *Lycopersicon esculentum* (Hurd 1968; Hicklenton & Jolliffe 1980), *Phaseolus vulgaris* (Jolliffe & Ehret 1985),

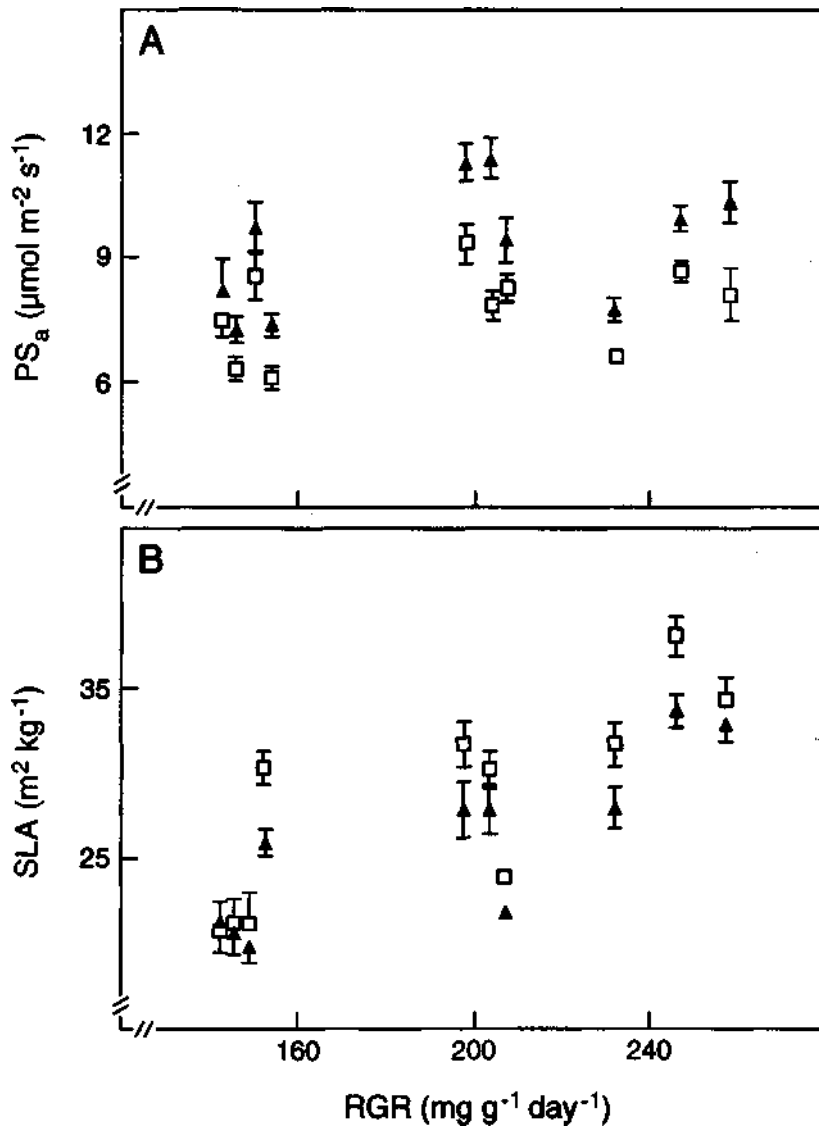


Fig. 3. A, Mean rate of photosynthesis per unit leaf area at day 8 and 9; and B, mean Specific Leaf Area (SLA) of 10 species grown for a 17-day period at 700  $\mu\text{mol mol}^{-1}$   $\text{CO}_2$  (filled triangles) or 350  $\mu\text{mol mol}^{-1}$   $\text{CO}_2$  (open squares). Error bars in A indicate  $\pm$  SE (n = 8). For further information see the legend of Fig. 2.

and for *Plantago major* (Poorter *et al.* 1988). Only in rare cases is the growth stimulation found to be continuous (Downton *et al.* 1980).

The diminished response with time can be explained in at least three ways. First, it may be a consequence of the experimental setup used. If plants are grown in small pots or close to each other, roots may get potbound, nutrient and water supply may fall short and/or mutual shading may

occur. As high  $\text{CO}_2$  plants are bigger, they will suffer at an earlier time from these growth restrictions than the control plants and their RGR will decline more rapidly (*cf.* Brown 1991). Second, acclimation in the rate of photosynthesis per unit leaf area of individual leaves is often observed (*e.g.* Hicklenton & Jolliffe 1980; Clough *et al.* 1981). As mentioned before, photosynthesis is stimulated to such an extent, that the extra sup-

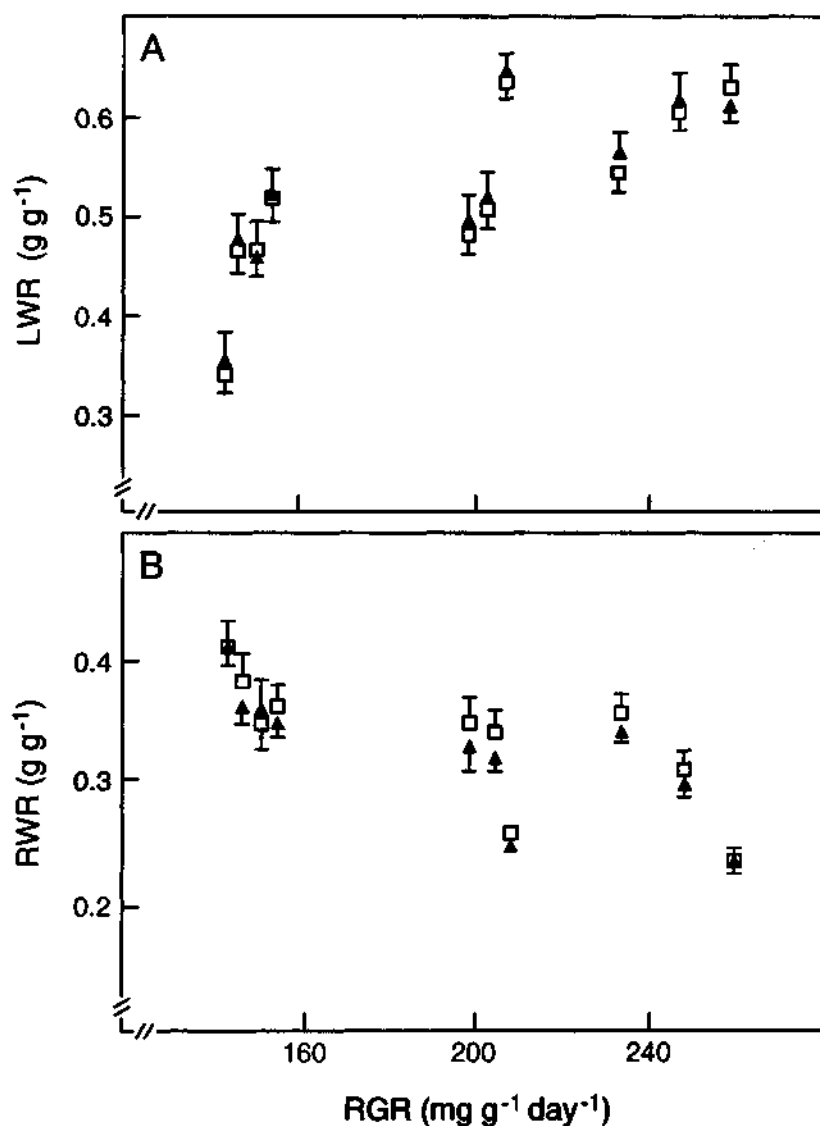


Fig. 4. A, Mean Leaf Weight Ratio (LWR); and B, mean Root Weight Ratio (RWR) of 10 species grown for a 17-day period at  $700 \mu\text{mol mol}^{-1} \text{CO}_2$  (filled triangles) or  $350 \mu\text{mol mol}^{-1} \text{CO}_2$  (open squares). For further information see the legend of Fig. 2.

ply of sugars cannot be used by the plant for growth. Due to a feed-back inhibition, accumulation of starch will occur in the chloroplasts and, finally, a decrease in the rate of photosynthesis (*cf.* Nafziger & Koller 1976; Clough *et al.* 1981). Sometimes, this negative feedback on the rate of photosynthesis may be even stronger in the case where starch accumulation causes disruption of the chloroplasts (Cave *et al.* 1981; Wulff & Strain 1982). The importance of this mechanism has

been shown frequently. However, there is also a third possibility that may explain the transient nature of the growth stimulation. Especially in fast-growing plants, RGR has been shown to decrease with time. This can be attributed to the change in plant size. As plants grow taller, they invest more biomass in support tissue (*cf.* Givnish 1986; Konings *et al.* 1989), and suffer more from self-shading. Thus, the stimulation in growth rate of the plant due to a high  $\text{CO}_2$  environment can

be totally offset after a certain period by the increased size of the high CO<sub>2</sub> plants and the concomitantly lower RGR (*cf.* Jolliffe & Ehret 1985; Du Cloux *et al.* 1987; Poorter *et al.* 1988). However, the absolute growth rate of these plants may still be higher than that of the - smaller - control plants. To support this explanation in specific situations, an extended analysis of growth and carbon economy is required. In most cases both acclimation and size constraints play a role in causing the growth-stimulating effect of a high CO<sub>2</sub> concentration to be transient.

In conclusion, several ways exist by which the growth stimulation at a high CO<sub>2</sub> level can vanish. The source-sink balance of the plant seems to play a crucial role in determining to what extent a growth stimulation can take place. However, the mechanisms behind this feedback are rather poorly understood, especially at the level of the sink. How can sink strength be defined exactly and in what way can the sink strength of a vegetative plant be increased? The main challenge at this moment in this field of research may be the question why exactly a high CO<sub>2</sub> concentration no longer stimulates growth after some time.

### Interspecific variation in the stimulation of growth

Up till now I did not consider variation between species in their growth response to an elevated CO<sub>2</sub> level. To what extent does interspecific variation in growth response exist and is it possible to relate this to functional groups of species? A full answer to this question would require a growth analysis for a wide range of species. To my knowledge, such an experiment has not been carried out yet and is probably beyond the opportunities for most research groups. Alternatively, a combination of published experiments may be used. Such an approach may have the drawback that different experiments are conducted under different, and sometimes fluctuating, environmental conditions. As there is no straightforward way to correct for these differences, it cannot be excluded that the main point of interest, *i.e.* the response of various groups of species on a high

CO<sub>2</sub> concentration, is confounded by a major difference in, *e.g.*, quantum flux density. Therefore, it should be borne in mind that such a literature analysis cannot yield results as conclusive as an experiment. On the other hand, if the effect of confounding variables is small, the wide variety of conditions used in the various experiments permits more general conclusions than results of one experiment, carried out under only one, specific combination of environmental conditions.

In this section the above compilation of literature data is used to detect possible growth differences between groups of species in response to CO<sub>2</sub> enrichment. A complicating factor is that the duration of the different experiments varied from two weeks to more than two years (Table 1). One can assume that most of the growth response will have occurred in the first two weeks of the experiment, and that differences more or less stabilized thereafter. In that case the weight ratios can be analyzed. Alternatively, if the growth stimulating effect extends over a longer period, it is more appropriate to correct for the duration of the experiment. Given the length of the experiment and the weight ratio, it can be calculated what the stimulation in RGR should have been, assuming equal weights at the beginning of the experiment and steady state RGRs. As time courses of the growth stimulation are often not investigated, it is difficult to choose between the two scenarios. Most probably, something in between these two alternatives happens, and therefore I analyzed both. If each of these tests resulted in the same answer, I considered the difference to be consistent. However, if both tests did not agree, the difference is apparently less straightforward. A second point of concern is that differences between groups possibly can be biased by a few outlying observations. Therefore, I analyzed the data after removing the 10% highest and 10% lowest observations from each of the categories of interest.

### *C*<sub>3</sub>, *C*<sub>4</sub> and CAM species

The most obvious difference in response can be expected when species with different types of

photosynthesis are compared. C<sub>4</sub> species possess a CO<sub>2</sub>-concentrating mechanism at the site of Rubisco and therefore often do not show a response in their rate of CO<sub>2</sub> fixation with a doubling of the ambient CO<sub>2</sub> concentration, in contrast to C<sub>3</sub> species, where such a response is almost invariably found (Percy & Björkman 1983). In the compilation of literature sources the growth-stimulating effect on C<sub>4</sub> species is indeed less than for C<sub>3</sub> species (Table 2), although it certainly exists (P < 0.001 in a t-test with the H<sub>0</sub>-hypothesis that the growth stimulation of C<sub>4</sub> plants is nil). In fact, the difference between C<sub>3</sub> and C<sub>4</sub> plants is relatively small (41% vs. 22%)

and not consistent. The difference in RGR stimulation becomes significant when the tree species are excluded from the analysis. Remarkably, the C<sub>4</sub> species that is kind of 'standard' for its group (*Zea mays*) showed a very small response.

What is the reason for the observed growth stimulation of C<sub>4</sub> species? Possibly, the decreased stomatal conductance at high CO<sub>2</sub>, also found for C<sub>4</sub> species, has relieved water stress in some of the reported experiments, thus increasing growth. However, this is unlikely to be so for all cases. An alternative explanation comes from the observation that CO<sub>2</sub>-response curves of photosynthesis of various C<sub>4</sub> species indicate that photosynthe-

Table 2. Average weight ratio and RGR stimulation (mg g<sup>-1</sup> day<sup>-1</sup>) of groups of species listed in Table 1 (x), the range into which 80% of the species fall (Range), total number of species on which the average is based (n) and significance of tests for differences between groups of species (P). Mean values of the weight ratios are backtransformed values of averaged log-transformed ratios, to correct for the intrinsically skewed nature of ratios. For the statistical tests the log-transformed ratios were used as well. The RGR stimulation gives the absolute increase due to the high CO<sub>2</sub> environment. Calculations and statistical tests were carried out after removing the 10% largest and the 10% smallest observations in each category. This may cause the number of species in a group to be different for the weight ratio and the RGR stimulation. P-values show the probability of differences between groups on adjacent lines. All tests were t-tests, except for the 3 groups within the C<sub>3</sub> wild species with a difference in potential growth rate, where a regression was carried out with the three groups as dummy variables, ns, non-significant; \*, P < 0.05; \*\*, P < 0.01; \*\*\*, P < 0.001.

Group of species	Weight ratio		n	P	RGR stimulation		n	P
	X	Range			X	Range		
C <sub>3</sub> ALL	1.41	1.13-1.72	106	***	8.2	1.4-17.1	109	ns
C <sub>4</sub> ALL	1.22	1.09-1.37	15		6.4	2.0-11.6	17	
C <sub>3</sub> HERBS	1.41	1.11-1.70	67	**	10.9	2.1-19.3	68	*
C <sub>4</sub> HERBS	1.22	1.09-1.37	15		6.4	2.0-11.6	17	
C <sub>3</sub> N <sub>2</sub> -FIXING	1.50	1.40-1.61	15	*	12.3	3.5-18.0	14	*
C <sub>3</sub> OTHERS	1.41	1.10-1.73	93		8.1	1.3-17.0	100	
C <sub>3</sub> HERBS	1.41	1.11-1.70	67	ns	10.9	2.1-19.3	68	ns
C <sub>3</sub> WOODY	1.41	1.15-1.73	39		3.7	1.3-9.4	41	
C <sub>3</sub> HERB. CROP	1.58	1.44-1.83	17	**	16.7	11.2-24.2	17	***
C <sub>3</sub> HERB. WILD	1.35	1.10-1.61	50		9.0	1.5-17.1	51	
C <sub>3</sub> WILD slow-growing	1.23	1.00-1.46	20		4.5	0.0-10.9	20	
C <sub>3</sub> WILD intermediate	1.38	1.16-1.57	16	***	10.6	3.0-18.0	17	***
C <sub>3</sub> WILD fast-growing	1.54	1.11-1.72	18		14.4	3.4-26.5	19	
C <sub>3</sub> HERB. DICOTS	1.44	1.16-1.67	38	ns	13.1	4.5-21.1	37	*
C <sub>3</sub> HERB. MONOCOTS	1.42	1.13-1.68	27		9.7	3.0-15.9	27	
CAM ALL	1.15	1.08-1.22	4		0.5	0.4-0.8	4	
ALL SPECIES	1.37	1.10-1.70	125		7.7	1.2-17.1	130	

sis is not saturated at an ambient CO<sub>2</sub> concentration as high as 600 μmol mol<sup>-1</sup> (S. von Caemmerer and C. Potvin, pers. comm.). It seems that in some species the C<sub>4</sub> pathway is not as tightly controlled as usually suggested and therefore allows for some response to CO<sub>2</sub>. As stated above, a stimulation of 2 % in the rate of photosynthesis throughout the whole experiment may already explain the growth enhancement. Finally, changes in allocation, respiration and carbon content (*cf.* eq. 1) are poorly documented for the group of C<sub>4</sub> species, and may also explain part of their enhanced growth.

Physiological data on CAM plants under CO<sub>2</sub> enrichment are even more scarce. An increase in the growth of CAM plants might be expected if photosynthesis takes place during the day. Few experiments on the growth of CAM species at higher CO<sub>2</sub> concentrations are reported. For the six CAM-species included in this literature compilation, there was a smaller response than for C<sub>4</sub> plants (0.05 < P < 0.10; Table 2).

#### *Within C<sub>3</sub> species*

Less attention has been paid to interspecific variation in the growth stimulation within the group of C<sub>3</sub> species. Is it possible to discern groups of C<sub>3</sub> species which differ in their growth response to a high CO<sub>2</sub> concentration? With the source-sink ratio being so crucial in the response of plants, one could expect plant species with strong sinks, or with the ability to increase sink size, to be more responsive. Some observations fit with this idea. Mauney *et al.* (1978) ascribed the larger growth stimulation of *Gossypium hirsutum* and *Glycine max* as compared to the relatively small stimulation of *Helianthus annuus* to the indeterminate nature of the growth of the first two species. This can be caused by the larger number of meristems that indeterminate species can develop (Hofstra & Hesketh 1975). A second suggestion which has been made, is that N<sub>2</sub>-fixing species could profit more from CO<sub>2</sub> enrichment than others because their nodules represent a large sink (Arnone & Gordon 1990). A test of this hypo-

thesis can be carried out with the data of Table 1. Indeed, on average the response of C<sub>3</sub> species capable of symbiosis with N<sub>2</sub>-fixing organisms (both herbaceous and woody plants) is higher than that of other species (Table 2). However, a complication in this simple dichotomy is that plant species, capable of symbiotic N<sub>2</sub>-fixation, will not necessarily have symbionts under the often nutrient-rich conditions used in these experiments. Thus, this comparison might be somewhat misleading.

A group of plants where selection for vigorous growth and strong sinks can be expected are crop species. Assuming there was no major difference in the way wild species and crop plants were grown, the data in Table 1 were analyzed for a possible difference between these two groups. On average, C<sub>3</sub> crop plants show a significantly larger response to CO<sub>2</sub> enrichment than wild species (Table 2). The difference in yield ratio is comparable to the one between C<sub>3</sub> and C<sub>4</sub> species. The difference in RGR-stimulation is even more pronounced in this case.

A similar line of reasoning regarding growth and sink strength may hold within the group of wild C<sub>3</sub> species. Do species that grow relatively fast under optimum conditions respond more strongly than species with a low maximum relative growth rate? Partly on the basis of some large-scale growth experiments, partly on information about phenology (annual/perennial) and the soil fertility in their natural habitat, I divided the group of wild C<sub>3</sub> species into three categories: slow-growing, intermediate, and fast-growing. There was a significant positive correlation between the potential growth rate of a plant and its response to a high CO<sub>2</sub> concentration (Table 2). In fact, the difference between fast-growing and slow-growing species is the largest of all the contrasts investigated here. However, the relationship between growth response and potential growth rate is not very close ( $r^2 = 0.21$  for the weight ratio; 0.28 for the RGR stimulation). A weak point in this analysis is that no exact data on the growth rates of these species are available. Alternatively, the experiment with the 10 species may be used to test this hypothesis. There was a



significant positive correlation between RGR at control  $\text{CO}_2$  level and growth stimulation in this experiment as well (Fig. 5), although again the relationship is not very close. Given that the growth stimulation is small, and that variation in response between species always exists, the number of species in this experiment is apparently too limited to compensate for the normal uncertainty related to RGR determinations. Nevertheless, all tests point into the same direction and although it awaits stronger evidence, this hypothesis certainly cannot be dismissed.

In the previous paragraphs, growth responses have been discussed in terms of variation in sink strength and, consequently, variation in the feedback of sinks on the rate of photosynthesis. However, interspecific variation in the weight ratio is not necessarily caused by a difference in the proportional stimulation of photosynthesis. For example, fast-growing species are found to differ largely in LAR, but only marginally in NAR or the rate of photosynthesis per unit leaf area (Fig. 2 and 3; Poorter and Remkes 1990, Poorter *et al.* 1990). Suppose that the rate of photosynthesis and NAR are stimulated to the same proportional extent for a fast- and a slow-growing species then, as a consequence of the larger leaf area per unit

plant weight, the absolute carbon gain per unit plant weight will be higher. Indeed, in the experiment with the 10 species, no difference in the proportional stimulation of the rate of photosynthesis was found (Fig. 3A), although the weight ratios of the fast-growing species at the end of the experiment were significantly higher than that of the slow-growing ones.

The last contrast that will be presented here is between monocots and dicots. In a review on the effect of a high  $\text{CO}_2$  level on 10 crop species, Cure and Acock (1986) found the growth stimulation of the monocotyledons (*Triticum aestivum*, *Hordeum vulgare*, *Oryza sativa*) to be smaller than that of the dicotyledonous *Glycine max*. To test whether this is a more general phenomenon, all data on herbaceous  $\text{C}_3$  species were analyzed. When the dicots and monocots in this compilation are compared, there is a similar tendency as that observed by Cure and Acock. However, this difference is only present when the growth stimulations are corrected for the duration of the experiments (Table 2). Although a reason behind this possible difference is not immediately obvious, variation between monocots and dicots in physiology and growth parameters have been observed more often (*cf.* Poorter and Remkes 1990, Garnier 1991).

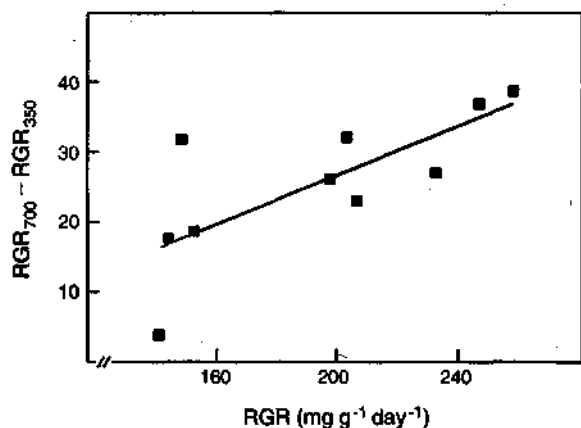


Fig. 5. Mean RGR stimulation ( $\text{RGR at } 700 \mu\text{mol mol}^{-1} - \text{RGR at } 350 \mu\text{mol mol}^{-1}$ ) plotted against the mean RGR at  $350 \mu\text{mol mol}^{-1}$  for 10 species grown for a 17-day period at  $700 \mu\text{mol mol}^{-1} \text{CO}_2$  and at  $350 \mu\text{mol mol}^{-1} \text{CO}_2$ . RGR values of the high  $\text{CO}_2$  plants were corrected for their larger size. For further information see the legend of Fig. 2.

## Conclusions

A doubling in the ambient  $\text{CO}_2$  concentration leads to only a small increase in growth, much smaller than could be expected on the basis of short-term measurements of photosynthesis. A negative feed-back on photosynthesis, as a consequence of a change in the source-sink ratio, and a size-constraint in growth cause the growth stimulation to be time-dependent. Compared to  $\text{C}_3$  species, the growth-stimulating effect is less in  $\text{C}_4$  plants, but certainly not nil. Within the group of  $\text{C}_3$  plants, crop species respond more strongly than wild plants. Potentially fast-growing wild species have a larger response than slow-growing ones.

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