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Biomass Accumulation and Photosynthesis of Ornamentals in Elevated CO_2 Conditions

Steigerung von Biomasse und Photosynthese bei Zierpflanzen unter erhöhtem CO_2-Angebot

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Summary

Three species of ornamentals – *Dendranthema grandiflorum* hybrids (Ramat) 'Coral Charm', *Hibiscus rosasinensis* L. and *Schefflera arboricola* Hayatt. – were grown in open-top chambers in greenhouses at three different CO_2 concentrations: 350, 700, and 1050 ppm. The development of the above-ground biomass showed distinctive differences, indicating a growth-enhancing effect of CO_2. The response differed not only among the examined species but also between seasons.

All the species examined showed increased biomass accumulation due to elevated CO_2 (expressed by leaf number and overall dry and fresh weight), but the allocation of biomass to plant parts differed between species.

Light response curves indicated differences in maximum rate of photosynthesis, while no changes were found in quantum yield. The increases in gas exchange by triple ambient CO_2 were almost identical to the effect of double CO_2 concentration. There were no evident differences in gas exchange between plants of different ages. This suggests that CO_2 fumigation in greenhouses may need to be adjusted according to species and especially light conditions to reach the most efficient utilization.

Zusammenfassung

Drei Arten von Zierpflanzen – *Dendranthema grandiflorum*-Hybride (Ramat) 'Coral Charm', *Hibiscus rosasinensis* L. und *Schefflera arboricola* Hayatt – wurden in oben offenen Kammern im Gewächshaus mit drei verschiedenen CO_2-Konzentrationen: 350, 700 und 1050 ppm kultiviert. Die Entwicklung der oberirdischen Biomasse zeigte deutliche Unterschiede, die auf den wachstumsfördernden Effekt von CO_2 hinweist. Die Reaktion unterschied sich nicht nur unter den geprüften Arten, sondern auch zwischen den Jahreszeiten.

Alle geprüften Arten zeigten zunehmende biomasse-Akkumulation bei erhötem CO_2 Angebot (ausgedrückt durch Blattanzahl und Gesamttrocken- und -frischgewicht), aber die Verteilung der Biomasse auf die Pflanzenteile unterschied sich zwischen den Arten.

Lichtreaktionskurven zeigten Unterschiede in der maximalen Photosyntheserate, während keine Änderungen im Mengenertrag gefunden wurden. Die Steigerungen im Gasaustausch bei der dreifachen Menge an CO_2 waren ähnlich den Effekten der doppelten CO_2-Konzentration. Es gab keine gravierenden Unterschiede im Gasaustausch zwischen Pflanzen verschiedenen Alters. Dies bedeutet, daß CO_2-Begasung im Gewächshaus nützlich sein kann, wenn sie an die Arten und speziellen Lichtbedingungen angepaßt ist.

Introduction

Initially when selecting fast-growing clones of ornamental species traditional techniques based on the measurement of growth parameters such as plant height and number of lateral shoots were used (CHRISTENSEN and OTTOSEN 1992). In attempts to find an even more effective method for evaluating growth rates, measurements of the gas exchange of whole plants was compared to growth performance of clones of *Ficus benjamina* (OTTOSEN et al. 1989). The latter were not successful, as the clones appeared to respond differently to temperature and irradiance and to adapt differently to changes in environment, thus environmental effects can obscure any genetic effects (AUSTIN 1989). Furthermore, large differences in responsiveness have been observed (HUNT et al. 1991) .

Much research has focused on the effects of elevated CO_2 on plant growth and most reviewers have agreed on an average increase in biomass accumulation of approximately 30% (MORTENSEN 1983, MORISON and GIFFORD 1984, MORTENSEN and MOE 1992, MORTENSEN 1995). Reports of a downward regulation of photosynthesis under extended elevated CO_2 have indicated that responsiveness decreases with time (MORTENSEN 1992). However, reduced photorespiration and respiration due to elevated CO_2 have been observed (LONG et al. 1996); thus, efficiency of the photosynthesis may decrease with increasing CO_2 level.

CO_2 feeding is commonly used in commercial greenhouses, although irradiance is the main limiting factor during most of the winter period, when CO_2 feeding is at its most intense. In previous experiments (OTTOSEN et al. 1989), *Ficus benjamina* has been shown to respond to a limited degree to increased CO_2 at low irradiance, that is, when CO_2 feeding is usually used in commercial greenhouses. Increasing levels of irradiance increased the CO_2 response (MORTENSEN and MOE 1992). Furthermore, in *Schefflera arboricola* clonal differences in CO_2 response were found (OTTOSEN 1994). The aim

Table 1. Growth and development of Schefflera arboricola at different CO_2 levels day 84 (the last harvest day). N=6.
Wachstum und Entwicklung von Schefflera arboricola bei verschiedenen CO_2-Konzentrationen in 84 Tagen (der letzte Erntetermin), N=6

	Summer grown (high PPFD)		Winter grown (decreasing PPFD)	
CO_2 level	750	1050	750	1050
Total leaf number	108 a	113 a	102 a	116 b
Total fresh weight of stem	182 b	171 b	182 b	213 c
Total dry weight of stem	182 b	185 b	219 b	286 c
Total dry weight of leaves	139 b	144 b	140 b	162 c
Dry matter content	102 a	105 a	118 b	135 c
Total dry weight	101 a	102 a	117 b	135 c
Avg. single leaf area	120 b	112 b	112 b	95 a

of this study was to examine the CO_2 uptake of three species assumed to differ in their growth rate under different irradiance conditions in order to evaluate whether elevated CO_2 has different growth-promoting effects during the season.

Materials and Methods

Cuttings from *Dendranthema grandiflorum* hybrid (Ramat.) 'Coral Charm', *Hibiscus rosa-sinensis* L. and *Schefflera arboricola* Hayatt. were rooted under polyethylene in fertilized peat. The rooting period lasted between three and nine weeks, depending on the species. Fully rooted uniform growing plants were pinched, if needed to ensure uniformity and transferred to nine Open-Top Chambers (OTC) located in two greenhouse compartments. Each OTC is a glass container of 1.1 × 1.1 m and a height of 1.8 m and contains one m² bench. The top lid is perforated to allow air to escape, while the front side is removable to give free access to plants. Fresh air at ambient CO_2, double and triple ambient CO_2 concentration was blown into the chamber at rate of 35 l m^{-1} from five outlets in the bottom of the OTC's. In combination with a horizontal fan, this ensured a uniform air distribution within the OTC.

The plants were exposed to continuous CO_2 fumigation during the entire experiment in OTCs. Concentrations at 350 ppm, 750 ppm and 1050 ppm of CO_2 were obtained by mixing pure CO_2 from a tank and compressed air using either electronic flow meters (Sierra Top-Track 822-1, Sierra, Amsterdam, The Netherlands) or ball flow meters (Brooks 5B4, Brooks, Amsterdam, The Netherlands). The concentration of CO_2, was monitored at intervals during the experiment, but no adjustments were needed. The plants were grown under natural irradiance, however, a movable screen was activated when PPFD (Photosynthetic Photon Flux Density) exceeded 600 μmol m^{-2} s^{-1} to avoid high irradiance. The temperature set points in the greenhouse were 25 °C day and 18 °C night.

At the beginning of the experiments, six plants were harvested and the leaf number, leaf area, and fresh and dry weight of above-ground plant parts were measured. Six plants per species and treatment were randomly collected from the OTC's and harvested as above at intervals of 14 days (*Dendranthema* and *Hibiscus*) and 21 days (*Schefflera*), respectively. Production time was therefore 56 or 84 days depending on species.

Oxygen evolution was measured on leaf discs of 10 cm^2 each freshly cut fully exposed leaves at 25 °C with an O_2 electrode disc mounted in a cooling jacket (LD-2, Hansatech, Hoddesdon, UK) at PPFD levels ranging from 0 to 1300 μmol m^{-2} s^{-1}. The PPFD level was obtained by a red LED light source (LS-36, Hansatech, Hoddesdon, UK). Leaf temperature was controlled using an external water bath.

Statistical analysis was carried out by comparing means by t-test for least significant difference after an analysis of variance. Growth data given as means with a common letter in the same line are not significantly different ($P>0.05$).

Results

Growth data

CO_2 fumigation increased the growth rate of all plant species, irrespective of season. The values in Tables 1–3 are indexed with ambient level (of 350 ppm CO_2) as 100 based on data from the last day of harvest.

The increase in above-ground biomass of *Schefflera* (Table 1) was mainly due to an increase in stem biomass, this being most pronounced under low irradiance. However, the increase was largely caused by the increase from ambient to double CO_2; a tripling of CO_2 concentration had a relative small additional effect on biomass accumulation. The number of leaves increased to a lesser degree than the total leaf area, indicating increased individual leaf size. Only during low light increases in dry matter content was observed. The height of the plants was not significantly affected. The differences between CO_2 treatments were evident after 40 days of treatment, but there was no significant difference between the two CO_2 treatments calculated on a leaf area basis (Fig. 1A) or on dry weight of stem and leaves (Fig. 1B).

The growth-promoting effects of *Dendranthema* were pronounced during winter and spring (Table 2). In

Table 2. Growth of Dendranthema grandiflorum at different CO_2 levels day 56 (the last harvest day). N=6.
Wachstum von Dendranthema grandiflorum bei verschiedenen CO_2-Konzentrationen in 56 Tagen (letzter Erntetag), N=6.

	Summer grown (high PPFD)		Winter grown (decreasing PPFD)		Winter grown (low PPFD)		Spring grown (increasing PPFD)	
CO_2-level	750	1050	750	1050	750	1050	750	1050
Total leaf number	113 b	123 b	110 a	110 a	111 b	134 b	116 b	139 c
Number of laterals	89 b	100 a	110 a	100 a	90 a	124 b	104 a	108 a
Total leaf area	109 b	119 c	121 b	125 b	122 b	140 c	111 b	129 c
Total plant fresh weight	113 b	125 c	123 b	130 b	128 b	152 c	116 b	136 c
Total dry weight	119 b	139 c	122 b	129 b	133 b	163 c	129 b	150 c

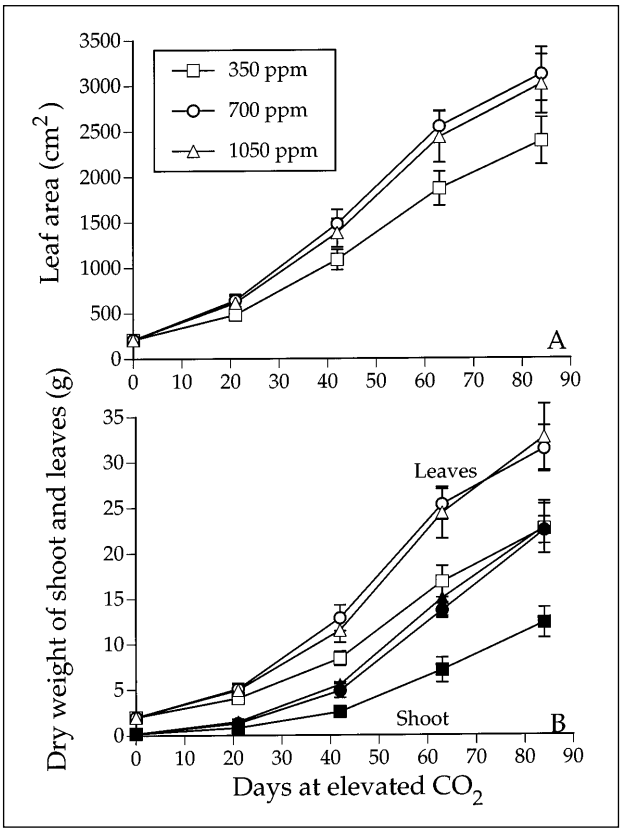


Fig. 1. Leaf area (A) and dry weights of leaves and stem (B) day 0 to 84 of Schefflera arboricola at three different CO_2 concentrations (350, 700 and 1050 ppm) during a summer experiment. Bars indicate standard error if larger than symbols.
Blattfläche (A) und Trockengewichte von Blättern und Stengeln (B) an 84 Tagen bei Schefflera arboricola bei drei verschiedenen CO_2-Konzentrationen (350, 700 und 1050 ppm) während eines Sommerversuches. Striche zeigen die Standardfehler, wenn sie größer als die Symbole sind.

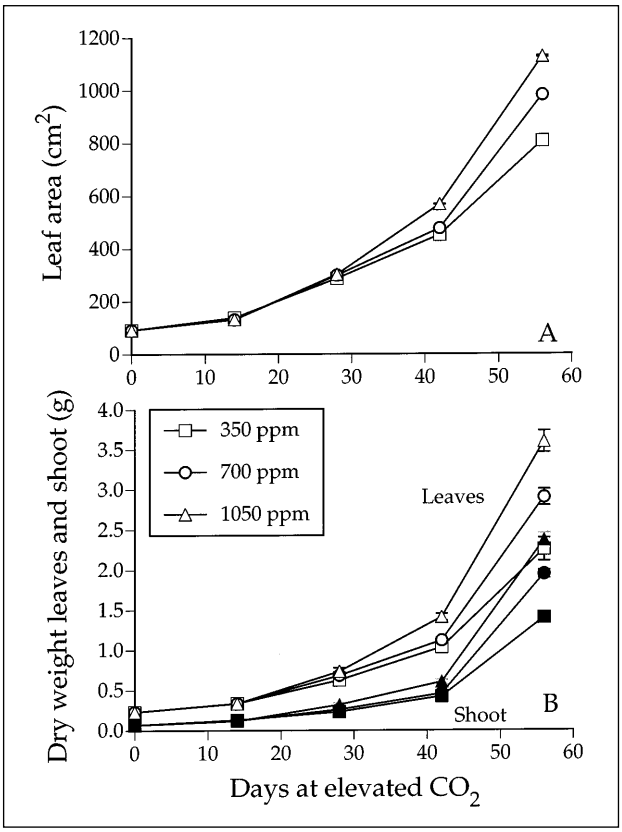


Fig. 2. Leaf area (A) and dry weights of leaves and stem (B) day 0 to 56 of Dendranthema grandiflorum hybrids (Ramat) 'Coral Charm' at three different CO_2 concentrations: 350, 700 and 1050 ppm during a spring experiment. Bars indicate standard error if larger than symbols.
Blattfläche (A) und Trockengewichte von Blättern und Stengeln (B) an 56 Tagen von Dendranthema grandiflorum-Hybriden (Ramat) 'Coral Charm' bei drei verschieenen CO_2-Konzentrationen: 350, 700 und 1050 ppm während eines Frühjahrsversuches. Striche zeigen Standardfehler an, wenn sie größer als die Symbole sind.

Table 3. Growth of Hibiscus rosa-sinensis at different CO_2 levels day 56 (the last harvest day). N=6.
Wachstum von Hibiscus rosa-sinensis bei verschiedenen CO_2-Konzentrationen in 56 Tagen (letzter Erntetag), N=6.

	Summer grown (high PPFD)		Winter grown (low PPFD)	
CO_2 level	**750**	**1050**	**750**	**1050**
Total leaf area	95 a	125 b	95 a	125 b
Bud number	117 b	161 c	117 b	127 b
Fresh weight of stem	100 a	161 b	116 b	139 c
Fresh weight of leaves	96 a	132 b	115 b	123 b
Dry weight of leaves	96 a	134 b	120 b	199 c
Area per leaf	110 a	98 a	116 b	120 b
Fresh weight per leaf	75 a	127 b	123 b	138 b

contrast to *Schefflera*, the leaf numbers increased, but not the size of the individual leaf. The total fresh and dry weight increased, but there was no effect on the dry matter content irrespective of season. It was possible to distinguish the effects of CO_2 treatments after 28 days, and the relative differences between treatments seemed to increase during the experimental period irrespective of whether the effect was examined on leaf area or dry weight basis (Fig. 2A and B).

Hibiscus (Table 3) showed a limited response to elevated CO_2, especially with respect to leaf number, where a tendency to decreasing leaf number was seen at elevated CO_2, but in this case the individual leaf size increased. However, the increases in biomass accumulation were most evident in the stem of the plants under summer conditions, but still significant under winter conditions. The number of buds increased strongly during high PPFD conditions. The effect of CO_2 treatments on plant biomass accumulation was evident after 42 days, and the relative differences did not change during the remaining period (Fig. 3).

Photosynthesis

CO_2 fumigation increased the net photosynthesis rate of all species; however, the increase in maximum rate of photosynthesis was the most evident, as figures 4 illustrate. The respiration level did not differ signifi-

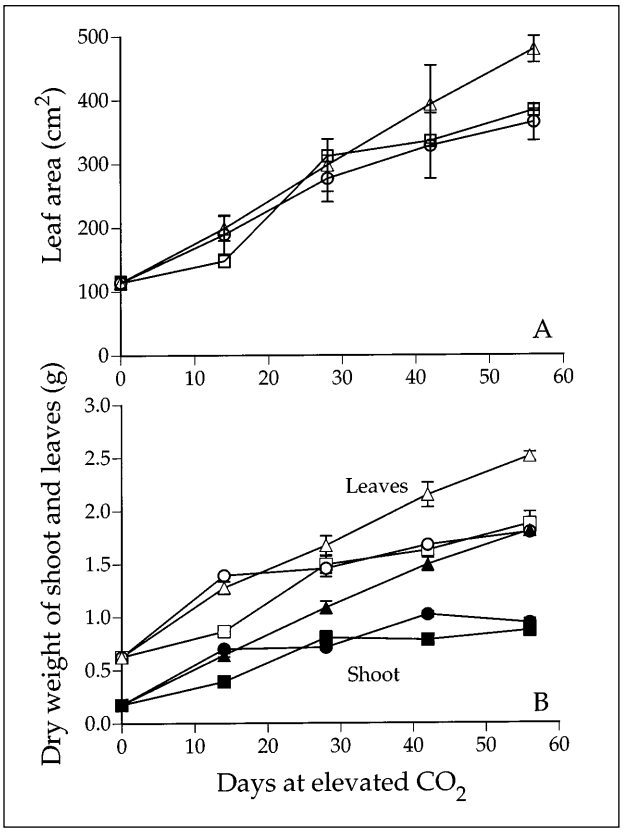


Fig. 3. Leaf area (A) and dry weights of leaves and stem (B) day 0 to 56 of Hibiscus rosa-sinensis L. at three different CO_2 concentrations: 350, 700 and 1050 ppm during a spring experiment. Bars indicate standard error if larger than symbols. (Symbols as in Fig. 1)
Blattfläche (A) und Trockengewichte von Blättern und Stengeln (B) an 56 Tagen von Hibiscus rosa-sinensis L. bei drei verschiedenen CO_2-Konzentrationen: 350, 700 und 1050 ppm während eines Frühjahrsversuches. Striche zeigen Standardfehler an, wenn sie größer als die Symbole sind. (Symbole wie in Abb. 1)

cantly between treatments and there were no significant differences between the light response curves for all species grown at 350 and 750 ppm, while plants of all species grown at 1050 ppm showed increased Pmax.

Discussion

In short-term CO_2 treatments, increases in gas exchange of up to 100% have been found; however, the long-term effects on biomass accumulation have not shown such increases. By comparison, small increases in the gas exchange rates were found (ranging from zero to 50%) when analyzing the effect on P_{max}. As a general rule, for all three species an increase in the above-ground biomass ranging from 0 to 100% was observed as a response to elevated CO_2. The differences appeared very early during the experiment, that is after 4-6 weeks of exposure. Furthermore, there are clear interspecific differences in the response to elevated CO_2 under different light regimes (equal to seasons). The woody species *Schefflera* and *Hibiscus* increased the stem biomass under low light conditions, perhaps reflecting a storage strategy under unfavorable growing conditions.

The effects on gas exchange appeared to remain at a constant level during the entire experimental period. The use of a constant CO_2 level may have caused some adaptation of the gas exchange of the plants, as it has been shown that intermittent use of elevated CO_2 in tomato can result in more vegetative growth promotion than constant CO_2 (BEHBOUDIAN and LAI 1994). This fact has been confirmed in a number of potted plants (POORTER 1993). In some cases it has also been possible to ascribe some of the relatively low effects of

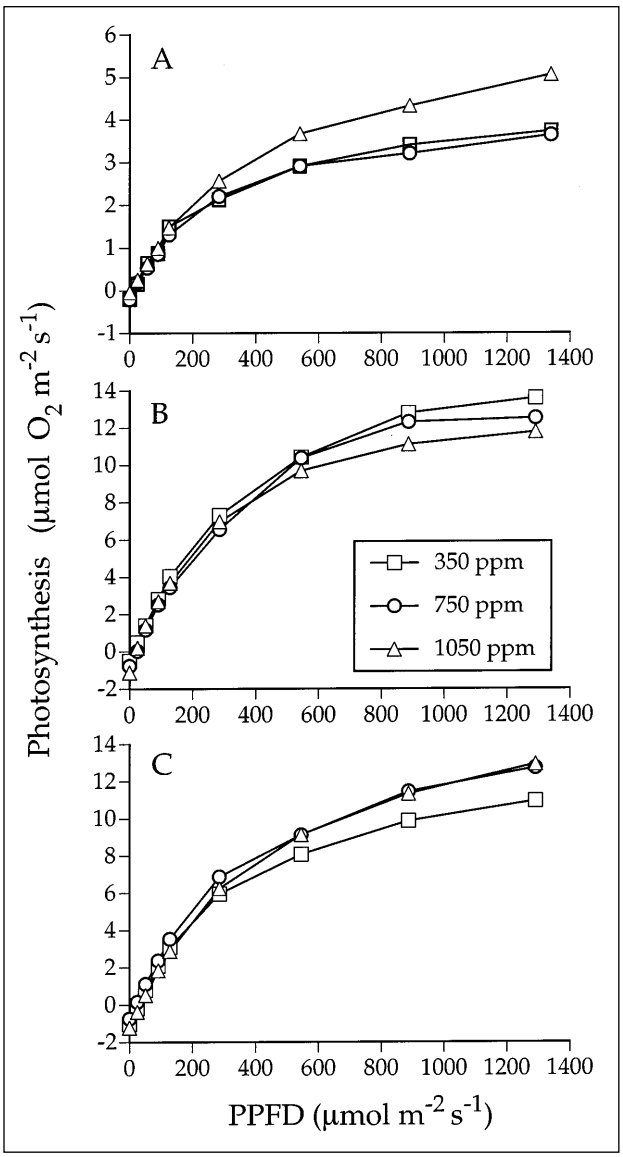


Fig. 4. Light response of single fully exposed leaves of Schefflera arboricola Hayatt. (A), Dendranthema grandiflorum hybrids (Ramat) 'Coral Charm' (B), Hibiscus rosa-sinensis L. (C) grown at three different CO_2 concentrations: 350, 700 and 1050 ppm during a winter experiment using full sized plants.
Lichtreaktionen von einzelnen voll beleuchteten Blättern von Schefflera arboricola Hayatt. (A), Dendranthema grandiflorum-Hybriden (Ramat) 'Coral Charm' (B), Hibiscus rosa-sinensis L. (C) bei drei verschiedenen CO_2-Konzentrationen: 350, 700 und 1050 ppm während eines Winterversuches mit ausgewachsenen Pflanzen.

CO_2 as due to nutrient dilution, since all plants irrespective of growth rate are supplied with the same nutrient concentration (BAXTER et al. 1997), but this cannot be the case in this experiment since an adequate nutrient supply was used.

Furthermore, additional growth-promoting effects have been seen with elevated CO_2 in combination with increased temperatures (BAKER et al. 1992). The variations in photosynthesis may vary with species and in combination with the higher temperatures during the summer; therefore, an experiment performed under constant higher temperatures and low light conditions might have performed differently. *Dendranthema* subjected to triple ambient CO_2 has a marked higher temperature optimum for photosynthesis (ROSENQVIST pers. comm). Perhaps ornamental plants may be slower in their response to CO_2 as shown in general, or perhaps the species used for ornamentals are light-loving plants that have a lower ability to utilize CO_2 (KERSTIENS 1998).

The use of elevated CO_2 result in a direct growth-promoting effect during the whole year; however, it has to be considered in practical production whether the use of CO_2 can be extended into the high irradiance period, since the growth-promoting effects are more prominent than under low light. This could be done by a more efficient distribution of CO_2 between the plants, or under open benches as is done in tomato crops, where a mixture of air and CO_2 are blown into the crops.

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Literature

AUSTIN, R. B. 1989: Genetic variation in photosynthesis. Journal of Agricultural Science, Cambridge **112**, 287–294.

BAKER, J. T., L. H. ALLEN and K. J. BOOTE 1992: Temperature effects on rice at elevated CO_2 concentration. Journal of Experimental Botany **43**, 959–964.

BEHBOUDIAN, M. H. and R. LAI 1994: Carbon dioxide enrichment in "Virosa" tomato plant: responses to enrichment duration and to temperature. HortScience **29**: 1456–59.

CHRISTENSEN, O. V. and C.-O. OTTOSEN 1992: Selection of fast growing seed propagated clones of Schefflera arboricola Hayatt. Tidsskrift for Planteavl **96**, 37–43.

HUNT, R., D. W. HAND, M. A. HANNAH and A. M. NEAL 1991: Response to CO_2 enrichment in 27 herbaceous species. Functional Ecology **5**, 410–421.

KERSTIENS, G. 1998: Shade tolerance as a predictor of response to elevated CO_2 in trees. Physiologia Plantarum **102**, 472–480.

LONG, S. P., P. K. FARAGE and R. L. GARCIA 1996: Measurement of leaf and canopy photosynthetic CO_2 exchange in the field. Journal of Experimental Botany **73**, 1629–1642.

MORISON, J. I. L. and R. M. GIFFORD 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**, 375–384.

MORTENSEN, L. M. 1983: Growth responses of some greenhouse plants to environment: X: Long term effects of CO_2 enrichment on photosynthesis, photorespiration and carbohydrate content Chrysanthemum morifolium Ramat. Medelelser fra Norges Landbohøgskole **62**, 1–11.

MORTENSEN, L. M. 1995: Diurnal carbon dioxide exchange rates of greenhouse roses under artifical light as compared with daylight conditions in summer. Acta Agricultural Scandinavica Sect. B **45**, 148–152.

MORTENSEN, L. M. and R. MOE 1992: Effects of CO_2 enrichment and different day/night temperature combinations on growth and flowering of Rosa L. and Kalanchoe blossfeldiana. v. Poelln. Scientia Horticultura **51**, 145–153.

OTTOSEN, C.-O. 1990: Growth versus net photosynthesis in clones of Ficus benjamina. HortScience **25**, 956–57.

OTTOSEN, C.-O. 1994: Net photosynthesis of Schefflera arboricola Hayata clones at different CO_2 concentration and photosynthetic flux densities. Acta Agricultural Scandinavica Sect. B **44**, 248–250.

OTTOSEN, C.-O., Å. ANDERSEN and O. V. CHRISTENSEN 1989: Clonal variation of net photosynthetic rate of Ficus benjamina in relation to height growth. Gartenbauwissenschaft **54**, 208–211.

POORTER, H. 1993: Interspecific variation in the growth response of plants to an elevated ambient CO_2 concentration. Vegetatio **104/105**, 77–95.

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