

Short note

## Effects of elevated carbon dioxide on leaf gas exchange and growth of cork-oak (*Quercus suber* L) seedlings

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**Summary** — Leaf gas exchange and growth were determined on cork-oak (*Quercus suber* L) seedlings which were grown from acorns for periods of up to 4 months in greenhouses at ambient ( $350 \mu\text{mol mol}^{-1}$ ) and at elevated ( $700 \mu\text{mol mol}^{-1}$ ) concentrations of carbon dioxide. In well-watered conditions, daily maximum photosynthesis ( $15 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) and stomatal conductance ( $440 \text{mmol m}^{-2} \text{s}^{-1}$ ) of plants grown and measured at  $700 \mu\text{mol mol}^{-1} \text{CO}_2$  did not differ from those of plants grown and measured at  $350 \mu\text{mol mol}^{-1}$ . In conditions of moderate drought, net  $\text{CO}_2$  assimilation was at least twice as great in elevated  $\text{CO}_2$ , but stomatal conductance was unchanged. Elevated  $\text{CO}_2$  affected total biomass production, the average increase being 76 and 97% at 3 and 4 months, respectively. Shoot biomass, root biomass, stem height and total leaf area were increased by elevated  $\text{CO}_2$ . Root and stem ramification were also enhanced by elevated  $\text{CO}_2$ , but no change in root/shoot ratio was observed.

***Quercus suber* / carbon dioxide / photosynthesis / stomatal conductance / growth**

**Résumé** — Effets d'une augmentation du  $\text{CO}_2$  atmosphérique sur les échanges gazeux et la croissance de plantules de chêne-liège (*Quercus suber* L). Des mesures de croissance et d'échanges gazeux ont été menées sur des plantules de chêne-liège (*Quercus suber* L) de 3 et 4 mois qui ont grandi avec une concentration en dioxyde de carbone de  $350 \mu\text{mol mol}^{-1}$  ou de  $700 \mu\text{mol mol}^{-1}$ . Dans des conditions non limitantes en eau, la photosynthèse ( $15 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) et la conductance stomatique ( $440 \text{mmol m}^{-2} \text{s}^{-1}$ ) maximales journalières, mesurées avec la concentration de  $\text{CO}_2$  de croissance, n'étaient pas différentes entre les deux traitements. En conditions de stress hydrique modéré, la photosynthèse nette était deux fois plus élevée en  $\text{CO}_2$  double, alors que les conductances stomatiques sont restées égales entre les deux traitements. La biomasse des jeunes chênes-lièges était plus élevée quand ils ont poussé à  $700 \mu\text{mol mol}^{-1}$ , le gain étant de 76 et 97 % à trois et quatre mois respectivement. La biomasse des tiges, des racines, la longueur de la tige principale et la surface foliaire totale ont été augmentées en  $\text{CO}_2$  double. Les ramifications des tiges et racines étaient plus nombreuses en  $\text{CO}_2$  élevé mais aucune variation du rapport racine/tige n'a été observée.

***Quercus suber* / dioxyde de carbone / photosynthèse / conductance stomatique / croissance**

## INTRODUCTION

To understand and predict the impact of increasing CO<sub>2</sub> upon natural vegetation, it is necessary to determine the nature and the direction of the responses in a range of plant species. In this paper, we investigate the effects of elevated CO<sub>2</sub> on *Quercus suber* L seedlings, a Mediterranean evergreen oak. Because the behaviour of a tree may significantly differ between its juvenile and its reproductive age, one cannot use the results concerning competitiveness of seedlings to predict mature tree behaviour. However, any change in environmental conditions during the first stages of a plant can have important consequences on the spatial and temporal vegetation patterns (Olsvig-Whittaker et al, 1992). Indeed, growth characteristics of seedlings will determine the success of a species and lead to a process of recruitment or extinction (Bazzaz, 1979).

Apart from seed size, physiological performances and allocation patterns play a major role in seedlings' adaptation to the environment. Most research on the effects of enhanced CO<sub>2</sub> emphasized photosynthesis because of its direct relationship to plant survival and growth through the carbon balance. However, the arrangement of foliage, branching patterns and root/shoot ratio are also important because they determine the access to environmental resources. CO<sub>2</sub> has been reported to be able to change both plant physiology and growth (Field et al, 1992; Mousseau and Saugier, 1992). Generally, total growth of a plant is increased by elevated CO<sub>2</sub> (Eamus and Jarvis, 1989), but leaf gas exchange appear more unpredictable. During long-term experiments (weeks or months), a down regulation of photosynthetic activity is often observed (Ceulemans and Mousseau, 1994). Moreover, interactive effects of CO<sub>2</sub> concentration and other environmental variables such as water availability may affect the response

of plants to CO<sub>2</sub> (Bowes, 1993; Guehl et al, 1994; Idso and Idso, 1994).

The objective of this study was to determine the effects of an increase in CO<sub>2</sub> concentration on the carbon gain of *Quercus suber* seedlings. We examined the effects of CO<sub>2</sub> enhancement i) on leaf gas exchange under well-watered conditions and moderate drought and ii) on biomass production and partitioning.

## MATERIALS AND METHODS

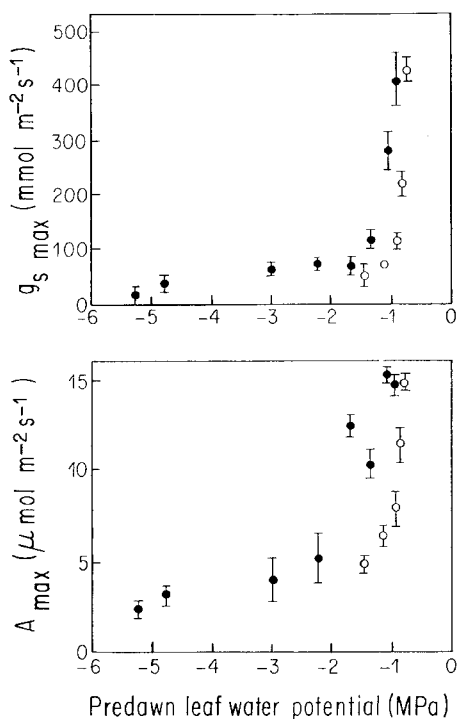
### *Growth conditons*

*Quercus suber* L acorns were potted in 5 L pots filled with a substrate made of 85% loamy soil and 15% compost. Each pot contained three acorns. Seedlings germinated in late April. Slow release fertilization (24 g per pot of Nutricote 100, N/P/K: 13/13/13) complemented with a mixture of oligoelements was added in order to avoid nutrient limitations. Seedlings were grown under ambient (350 µmol mol<sup>-1</sup>) or elevated (700 µmol mol<sup>-1</sup>) concentrations of atmospheric CO<sub>2</sub>. During growth, relative air humidity in the greenhouses was kept at outside values and plants received natural light with little effect of greenhouse structure. Minimum temperatures for May, June, July and August were 15.8, 19.1, 20.9 and 21.6 °C, respectively. For the same period, maximum temperatures were 25.5, 30.7, 31.3 and 33.6 °C. During the days with physiological measurements, relative air humidity was maintained at 60%. Maximum temperature and photosynthetically active radiation were 35 °C and 1 900 µmol m<sup>-2</sup> s<sup>-1</sup>, respectively.

### *Gas exchange and water potential measurements*

Seedlings were watered daily. Irrigation was discontinued for six pots per greenhouse from 15 July (d196) to 27 July 1993 (d208). Measurements were taken during 8 and 5 sunny days, respectively, in ambient and elevated CO<sub>2</sub>. Plant water status was characterized by predawn leaf

water potential measured with a pressure chamber (PMS Instrument Company, Corvallis, OR, USA). In each greenhouse, two seedlings with the same potential were chosen for leaf gas exchange. Measurements were made in the greenhouse where plants were grown, on three leaves per seedling, every 2 h from dawn to dusk. Stomatal conductance was measured with a LI:1600 steady-state porometer (LI-Cor, Inc, NE, USA) and net photosynthesis with an infrared CO<sub>2</sub> gas analyser model CI-301PS (CID, Inc, Vancouver, Canada), using a 2.5 cm<sup>2</sup> leaf chamber. Daily maximum photosynthesis and stomatal conductance were chosen to characterize leaf gas exchange. They occurred between 0900 and 1000 hours local solar time when air temperature was  $28 \pm 2$  °C and photosynthetically active radiation above  $1\ 600\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ .



**Fig 1.** Diurnal maximal stomatal conductance ( $g_{s\ max}$ ) and photosynthesis ( $A_{max}$ ) versus predawn leaf water potential for 3-month-old *Quercus suber* seedlings in 350 (open circles) and 700 (closed circles)  $\mu\text{mol mol}^{-1}$  CO<sub>2</sub>. Vertical bars indicate standard error of the mean of six replicates obtained with two seedlings.

## Growth measurements and nitrogen concentration

Twelve 3-month-old, and 15 4-month-old seedlings, maintained in well-watered conditions, were used for morphological analyses. Each seedling was harvested and divided into roots, stems and leaves. Expanding leaves, secondary roots and stems were segmented. Biomass of each part, length of the main root and stem, and total leaf area were recorded on an individual basis. Areas of the fresh leaves were determined with a video leaf-area meter (Delta-T Image Analysis System, Delta-T Devices, Ltd, UK). All the parts were dried at 60 °C for 2 days and then weighed.

Chemical analyses were done on the 4-month-old plants ( $n = 15$  for each CO<sub>2</sub> treatment). For each seedling, all its dried mature leaves were mixed and ground. The mass-based nitrogen concentration was measured by near-infrared spectroscopy following a procedure described by Joffre et al (1992). For each sampling date, growth data and nitrogen concentration between the two treatments were compared with Student's *t*-test. Differences were considered significant if probabilities were less than 0.05.

## RESULTS

### Leaf gas exchange

Figure 1 shows changes of maximal photosynthesis and stomatal conductance versus predawn leaf water potential. Under well-watered conditions, whatever the CO<sub>2</sub> partial pressure, maximal net photosynthesis and stomatal conductance measured during daytime were, respectively, about  $15\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$  and  $440\ \text{mmol m}^{-2}\ \text{s}^{-1}$ . In response to water stress, photosynthesis and stomatal conductance decreased at both 350 and 700  $\mu\text{mol mol}^{-1}$ . The relationships between predawn water potential and the stomatal conductance were similar for both CO<sub>2</sub> treatments. The decrease of net assimilation rates with predawn potential was slower under elevated CO<sub>2</sub> than under

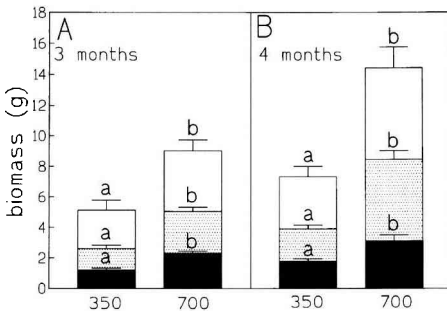
ambient CO<sub>2</sub>. At -1.2 MPa, maximal photosynthesis was around 5 and 10  $\mu\text{mol m}^{-2} \text{s}^{-1}$  at 350 and 700  $\mu\text{mol mol}^{-1}$ , respectively. Under elevated CO<sub>2</sub>, some substantial photosynthesis values (2.5  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) were observed at very low potentials (-5 MPa).

### Growth measurements and nitrogen concentration

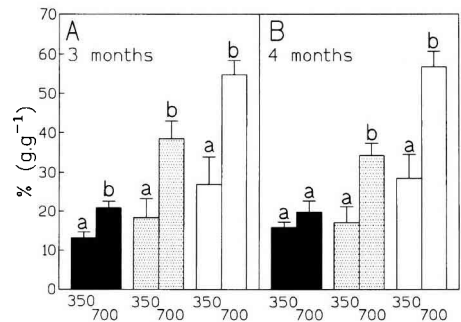
Exposure to elevated CO<sub>2</sub> resulted in a significant increase of total biomass in *Quercus suber* seedlings ( $t = -3.97$ ,  $P < 0.001$  at 3 months;  $t = -4.77$ ,  $P < 0.001$  at 4 months; fig 2). Increases were 76 and 97% at 3 and 4 months, respectively. On both dates, each biomass compartment was significantly larger at 700 than at 350  $\mu\text{mol mol}^{-1}$  (fig 2). At 3 months, leaf, root and stem dry mass increased respectively by 58, 92 and 95% in plants grown under elevated relative to ambient CO<sub>2</sub>. At 4 months, leaf and especially stem biomass increases were greater (72 and 148%, respectively) than at 3 months. On the contrary, the root biomass increase was less (76%). The ranking of

each plant compartment in terms of relative biomass was kept constant at both treatments (leaves > stems > roots).

After 3 months of exposure to elevated CO<sub>2</sub>, main root, main stem length and leaf mass per area were increased respectively by 72, 25 and 28% (table I). These increases were significant at both dates. Total leaf area was higher at 700  $\mu\text{mol mol}^{-1}$ , but this difference was only significant at 4 months. High CO<sub>2</sub> did not lead to a significant effect on the root/shoot ratio. At 3 months, the ratio of secondary root mass to total root mass was significantly different between the two CO<sub>2</sub> treatments (fig 3). This difference disappeared at 4 months. The ratio of secondary stem mass to total stem mass and the ratio of non-fully expanded leaves to total leaf biomass were significantly higher at 700 than for 350  $\mu\text{mol mol}^{-1}$  at both dates. Growth under elevated CO<sub>2</sub> resulted in a significant decrease of leaf nitrogen concentration (table I).



**Fig 2.** Biomass allocation to roots (black section), stems (dotted section), leaves (white section) ( $\pm$  SE) in *Quercus suber* seedlings at 3 (A) and 4 (B) months in 350 and 700  $\mu\text{mol mol}^{-1}$  CO<sub>2</sub>. For each age, means with different letters are significantly different ( $P < 0.05$ , Student's  $t$ -test).



**Fig 3.** Proportion of secondary roots to total root biomass (black bars), secondary branches to total stem biomass (dotted bars) and non-fully expanded leaves to total leaf biomass (white bars) of *Quercus suber* seedlings at 3 months (A) and 4 months (B) in 350 (left bars) and 700 (right bar)  $\mu\text{mol mol}^{-1}$  CO<sub>2</sub>. Error bars indicate  $\pm 1$  standard error. For each age, means with different letters are significantly different ( $P < 0.05$ , Student's  $t$ -test).

**Table I.** The effects of two levels of atmospheric CO<sub>2</sub> on stem and root length, total fully-expanded leaf area, leaf mass per area, root/shoot ratio and nitrogen concentration (mean ± SE) in *Quercus suber* seedlings.

	3 months		4 months	
	350	700	350	700
Mean stem length (cm)	39.8 (2.79) <sup>a</sup>	49.9 (2.38) <sup>b</sup>	51.9 (3.09) <sup>a</sup>	66.7 (2.61) <sup>b</sup>
Mean root length (cm)	40.7 (3.78) <sup>a</sup>	69.9 (5.49) <sup>b</sup>	51.0 (5.49) <sup>a</sup>	70.4 (4.81) <sup>b</sup>
Total leaf area (cm <sup>2</sup> )	198.6 (27.40) <sup>a</sup>	257.0 (28.04) <sup>a</sup>	270.1 (30.15) <sup>a</sup>	383.3 (37.32) <sup>b</sup>
Leaf mass area (g m <sup>-2</sup> )	105.3 (2.04) <sup>a</sup>	134.9 (2.42) <sup>b</sup>	112.9 (2.71) <sup>a</sup>	134.5 (2.73) <sup>b</sup>
Root/shoot ratio (g g <sup>-1</sup> )	0.36 (0.05) <sup>a</sup>	0.37 (0.04) <sup>a</sup>	0.35 (0.03) <sup>a</sup>	0.29 (0.04) <sup>a</sup>
Nitrogen (% dry weight)	—	—	2.2 (0.05) <sup>a</sup>	1.8 (0.05) <sup>b</sup>

Means with a different letter are significantly different ( $P < 0.05$ , Student's *t*-test,  $n = 12$ ,  $n = 15$  for 350 and 700  $\mu\text{mol mol}^{-1}$  CO<sub>2</sub>, respectively). Comparisons apply within one date only

## DISCUSSION

After 3 months, and under well-watered conditions, daily maximum photosynthesis and stomatal conductance of *Quercus suber* seedlings at ambient and elevated CO<sub>2</sub> were similar. Bunce (1992) measured similar values of leaf conductance on seedlings of two deciduous oaks (*Quercus prinus* and *Q. robur*) under 700 and 300  $\mu\text{mol mol}^{-1}$  CO<sub>2</sub>. Between 350 and 700  $\mu\text{mol mol}^{-1}$ , one could have expected an enhancement of net photosynthesis. However, contradictory results are reported in the literature. Even within the same genus, responses to CO<sub>2</sub> enhancement differ among species. For example, Idso et al (1991) reported an increase of carbon exchange rate at elevated CO<sub>2</sub> on a deciduous oak, *Q. alba*, but, as with *Q. suber* in this study, they found similar photosynthetic rates between CO<sub>2</sub> treatments for *Q. robur*. We observed a decrease of leaf nitrogen concentration of *Q. suber* seedlings in elevated CO<sub>2</sub>. As photosynthesis is often strongly positively related with nitrogen in leaves (Evans, 1989), this decrease could lead to a limitation of photosynthesis capacity under ele-

vated CO<sub>2</sub>. Such a decrease has been observed in a range of tree species (Johnsen, 1993; Julkunen-Tiitto et al, 1993; Lindroth et al, 1993; Duff et al, 1994). By comparing oaks growing naturally in elevated CO<sub>2</sub> with those growing in ambient CO<sub>2</sub>, Körner and Miglietta (1994) found a decrease of the leaf nitrogen concentration for a deciduous oak, *Q. pubescens*, but an increase for an evergreen oak, *Q. ilex*.

When water stress takes place under 350  $\mu\text{mol mol}^{-1}$ , the decrease patterns of maximal net photosynthesis and stomatal conductance with respect to predawn leaf water potential were similar to those obtained for the same species by Acherar et al (1991) on 3-year-old seedlings under controlled conditions, and by Tenhunen et al (1987) on mature trees in the field. As water stress occurred, intrinsic water-use efficiency, defined as the ratio of maximal photosynthesis to maximal leaf conductance, increased under elevated CO<sub>2</sub>.

If we only consider the photosynthesis results related to leaf gas exchange, an elevation of CO<sub>2</sub> would not be of benefit for the water and carbon balances of well-watered seedlings. However, results regard-

ing the growth of seedlings indicate that enhanced CO<sub>2</sub> significantly increased carbon balance at the whole-plant level. These increments were closer to the average increment observed in deciduous (+63%) than in coniferous trees (+38%), as reported by Ceulemans and Mousseau (1994). They are comprised between the biomass increase over one growing season observed in *Q petraea* (+138%) and *Pinus pinaster* (+63%) (Guehl et al, 1994). In *Q suber*, root and shoot biomass, and total leaf area were increased, like in *Populus grandidentata* Michx (Curtis and Teeri, 1992). An increase of root/shoot ratio is frequently observed in elevated CO<sub>2</sub> (Ceulemans and Mousseau, 1994). Nevertheless, as Bunce (1992) observed for *Q robur*, we found no change in the investment of biomass to roots relative to shoots. The greater proportion of fully-expanded leaves at 700 μmol mol<sup>-1</sup> suggests that shoot growth was almost continuous.

Stem and root biomass as well as their degree of ramification were increased by an elevation of CO<sub>2</sub>. This different architecture could improve *Q suber* establishment in elevated CO<sub>2</sub> in the field where competition with grasses plays an important role in tree seedlings establishment (Griffin 1971; McPherson, 1993). The increase in twig growth in elevated CO<sub>2</sub> could lead to a rapid construction of sun leaves above the grass layer (McCarthy and Dawson, 1990). The increases of root growth, root length and the higher number of ramifications may allow the exploitation of a greater volume of soil and thus, water and nutrient extraction in soil layers not exploited by competitors (Gordon and Rice, 1993). Enhancement of root growth, root length and fine root mass have been already reported on tree species (Idso and Kimball, 1992; Norby et al, 1992; Pettersson et al, 1993). Experiments with competitors under elevated CO<sub>2</sub> are needed to determine ultimately the success of *Q suber* seedling

establishment in a future CO<sub>2</sub> environment. It is surprising to find an increase of total biomass when at the same time, leaf photosynthesis is not improved by elevated CO<sub>2</sub>. This may be due to an acclimation to elevated CO<sub>2</sub>, similar to the one described by El Kohen et al (1993) on *Castanea sativa*. The enhancement of net photosynthesis only in the first days after emergence leads to a greater initial growth rate and to a greater total leaf area (Gaudillère and Mousseau, 1989) which could promote a large difference of biomass production at the plant level.

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## REFERENCES

- Acherar M, Rambal S, Lepar J (1991) Évolution du potentiel hydrique foliaire et de la conductance stomatique de quatre chênes méditerranéens lors d'une période de dessèchement. *Ann Sci For* 48, 561-573
- Bazzaz FA (1979) The physiological ecology of plant succession. *Ann Rev Ecol Syst* 10, 351-371
- Bowes G (1993) Facing the inevitable: plants and increasing atmospheric CO<sub>2</sub>. *Ann Rev Physiol Plant Mol Biol* 44, 309-332
- Bunce JA (1992) Stomatal conductance, photosynthesis and respiration of temperate deciduous tree seedlings grown outdoors at an elevated concentration of carbon dioxide. *Plant Cell Environ* 15, 541-549
- Ceulemans R, Mousseau M (1994) Effects of elevated atmospheric CO<sub>2</sub> on woody plants. *Tansley Review* no 71. *New Phytol* 127, 425-446
- Curtis PS, Teeri JA (1992) Seasonal responses of leaf gas exchange to elevated carbon dioxide in *Populus grandidentata*. *Can J For Res* 22, 1320-1325
- Duff GA, Berryman CA, Eamus D (1994) Growth, biomass allocation and foliar nutrient contents of two *Eucalyptus* species of the wet-dry tropics of Aus-

- tralia grown under CO<sub>2</sub> enrichment. *Funct Ecol* 8, 502-508
- Eamus D, Jarvis PG (1989) The direct effects of increase in the global atmospheric CO<sub>2</sub> concentration on natural and commercial temperate trees and forests. *Adv Ecol Res* 19, 1-55
- El Kohen A, Venet L, Mousseau M (1993) Growth and photosynthesis of two deciduous forest species at elevated carbon dioxide. *Funct Ecol* 7, 480-486
- Evans JR, (1989) Photosynthesis and nitrogen relationships in leaves of C<sub>3</sub> plants. *Oecologia* 78, 9-19
- Field CB, Stuart Chapin F III, Matson PA, Mooney HA (1992) Responses of terrestrial ecosystems to the changing atmosphere. A resource-based approach. *Ann Rev Ecol Syst* 23, 201-235
- Gaudillère JP, Mousseau M (1989) Short term effect of CO<sub>2</sub> enrichment on leaf development and gas exchange of young poplars (*Populus euramericana* cv I ). *Acta Oecologia Oecol Plant* 10, 95-105
- Gordon DR, Rice KJ (1993) Competitive effects of grassland annuals on soil water and blue oak (*Quercus douglasii*) seedlings. *Ecology* 74, 68-82
- Griffin JR (1971) Oak regeneration in the upper valley, California. *Ecology* 52, 862-868
- Guehl JM, Picon C, Aussenac G, Gross P (1994) Interactive effects of elevated CO<sub>2</sub> and soil drought on growth and transpiration efficiency and its determinants in two European forest tree species. *Tree Physiol* 14, 707-724
- Idso SB, Kimball BA (1992) Seasonal fine-root biomass development of sour orange trees in atmosphere of ambient and elevated CO<sub>2</sub> concentration. *Plant Cell Environ* 15, 337-341
- Idso KE, Idso SB (1994) Plant responses to atmospheric CO<sub>2</sub> enrichment in the face of environmental constraints: a review of the past 10 years research. *Agric For Meteorol* 69, 153-203
- Idso SB, Kimball BA, Allen SG (1991) Net photosynthesis of sour orange trees maintained in atmosphere of ambient and elevated CO<sub>2</sub> concentration. *Agric For Meteorol* 54, 95-101
- Joffre R, Gillon D, Dardenne P, Agneessens R, Biston R (1992) The use of near-infrared spectroscopy in litter decomposition studies. *Ann Sci For* 49, 481-488
- Johnsen KH (1993) Growth and ecophysiological responses of black spruce seedlings to elevated CO<sub>2</sub> under varied water and nutrient additions. *Can J For Res* 23, 1033-1042
- Julkunen-Tiitto R, Tahvanainen J, Silvola J (1993) Increased CO<sub>2</sub> and nutrient status changes affect phytomass and the production of plant defensive secondary chemicals in *Salix myrsinifolia* (Salisb). *Oecologia* 95, 495-498
- Körner C, Miglietta F (1994) Long term effects of naturally elevated CO<sub>2</sub> on Mediterranean grassland and forest trees. *Oecologia* 99, 343-351
- Lindroth RL, Kinney KK, Platz CL (1993) Responses of deciduous trees to elevated atmospheric CO<sub>2</sub>: productivity, phytochemistry, and insect performance. *Ecology* 74, 763-777
- McCarthy JJ, Dawson JO (1990) Growth and water use efficiency of *Quercus alba*, *Q bicolor*, *Q imbricaria*, and *Q palustris* seedlings under conditions of reduced soil water availability and solar irradiance. *Trans Ill State Acad Sci* 83, 128-148
- McPherson GR (1993) Effects of herbivory and herb interference on oak establishment in a semi-arid temperate savanna. *J Veg Sci* 4, 687-692
- Mousseau M, Saugier B (1992) The direct effect of increased CO<sub>2</sub> on gas exchange and growth of forest tree species. *J Exp Bot* 43, 112 1-1130
- Norby RJ, Gunderson CA, Wullschlegel SD, O'Neill EG, McCracken MK (1992) Productivity and compensatory response of yellow poplar trees in elevated CO<sub>2</sub>. *Nature* 357, 322-324
- Olsvig-Whittaker LS, Naveh Z, Giskin M, Nevo E (1992) Microsite differentiation in a Mediterranean oak savanna. *J Veg Sci* 3, 209-216
- Pettersson R, McDonald AJS, Stadenberg I (1993) Response of small birch plants (*Betula pendula* Roth) to elevated CO<sub>2</sub> and nitrogen supply. *Plant Cell Environ* 16, 1115-1121
- Tenhunen JD, Beyshlag W, Lange OL, Harley PC (1987) Changes during summer drought in leaf CO<sub>2</sub> uptake rates in macchia shrubs growing in Portugal: limitations due to photosynthetic capacity, carboxylation efficiency and stomatal conductance In: *Plant Response to Stress. Functional Analysis in Mediterranean Ecosystems* (JD Tenhunen, FM Catarino, OL Lange, WC Oechel, eds), series G, *Ecological Science*, vol 15, Springer-Verlag, Berlin, 305-328