



SHORT COMMUNICATION

Stem hydraulic conductance of European beech (*Fagus sylvatica* L.) and pedunculate oak (*Quercus robur* L.) grown in elevated CO₂

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Received 14 February 1997; Accepted 3 March 1997

Abstract

Over two seasons in c. 600 ppm CO₂, oak had lower stomatal conductance in CO₂-enriched compared to ambient air. Beech showed no response to CO₂ concentration on sunny days. Mirroring this pattern, exposure to elevated CO₂ reduced whole-shoot hydraulic conductance per unit leaf area in oak, but not in beech.

Key words: Climate change, Fagaceae, gas exchange, trees, water relations.

Introduction

Elevated atmospheric concentrations of CO₂ often reduce stomatal conductance (g_s), and hence leaf transpiration rate per unit leaf area (Curtis, 1996; Kerstiens *et al.*, 1995). Plant water use in response to elevated CO₂ has most commonly been estimated from discontinuous measurements of g_s carried out by steady-state porometry (Tyree and Alexander, 1993). The high-pressure flow meter offers a different, integrative approach, enabling the direct measurement of resistance to water transport in stems and roots (Tyree *et al.*, 1995). This provides valuable complementary information to porometry, since there are potential inaccuracies in the determination of g_s using cuvette systems, and estimation of the whole-plant transpiration rate is difficult. Leaf temperatures are often inaccurately measured, giving incorrect values of g_s (Tyree and Wilmot, 1990). Correct scaling-up requires knowledge of actual leaf temperatures and leaf boundary

layer resistances *in situ*. Whereas measurements of g_s apply only to specific times and sets of environmental conditions, measurement of stem hydraulic conductance can reveal the influence of CO₂ concentration on the development of hydraulic architecture (and by implication on maximum overall water consumption rate of the canopy) over the whole of a plant's life, which comes to an end with the measurement. In this study, we measured the hydraulic conductance of complete stem and branch systems in relation to the leaf area supplied, that is, leaf-specific conductance (K_L), was measured.

Materials and methods

Plants were grown from seed in the Solardomes (Townend, 1993) at Lancaster University receiving natural light and either ambient air or ambient air enriched by 250 ppm CO₂. Plants were kept well-watered throughout. Two concentrations of soil nutrients were used, supplied by a slow release fertilizer (1 or 4 g dm⁻³, Osmocote plus, 8–9 month formulation, Grace-Sierra UK Ltd, Nottingham, UK). They represented an adequate ('low N') and luxuriant ('high N') supply; the low nutrient treatment was not intended to result in deficiency, and this was confirmed by foliar nutrient concentrations (Heath and Kerstiens, 1997). The soil volume was 12 dm³ for oak (60 cm deep soil column) and 8 dm³ for beech (40 cm deep soil column). Full details are given in Heath and Kerstiens (1997).

K_L was measured in July/August of the third growing season using a high-pressure flow meter (Dynamax Inc., Houston, Texas) as described by Tyree *et al.* (1995). Whole shoots ($N=14$ per species and nutrient/CO₂ combination) were cut approximately 5 cm above the base, and immediately recut under water to avoid cavitation. After attachment of the stem base to the flow meter, the leaves were removed and kept for

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measurement of total area (Delta-T Devices, Burwell, Cambs., UK). Whole-stem hydraulic conductance was then measured by perfusing water through the stem under a pressure of approximately 500 kPa. Values of pressure and flow rate were recorded at intervals of 32 s, until the readings were stable (usually within 5 min). Hydraulic conductance was subsequently calculated from the stable readings of pressure and flow rate, and K_L obtained by division by total leaf area.

Measurements of g_s ($N=22\text{ d}^{-1}$, species and nutrient/ CO_2 combination) were taken on the same plants during their second season of growth *in situ* (at growing CO_2 concentrations in the Solardomes) using a portable infra-red gas analyser (LCA-3, ADC Ltd, Hoddesdon, Herts., UK) connected to a leaf chamber. Photosynthetic photon flux densities were between 1200 and 1600 $\mu\text{mol m}^{-2}\text{ s}^{-1}$ on the two days of measurement.

Results

K_L of oak was reduced by an average of 21% in elevated CO_2 ($P=0.016$) (Fig. 1a). This compared with an average reduction in g_s of 33% in elevated CO_2 on sunny days (Fig. 2a). In beech, K_L was unaffected by CO_2 concentration (Fig. 1b). Similarly, there were no significant reductions in g_s on sunny days (Fig. 2b). There were no significant effects of nutrient concentration on K_L in either species, nor were there any interactions between CO_2 and nutrients. In oak, the effects of both CO_2 and nutrient treatments on g_s were highly significant ($P=0.001$). In beech, the nutrient effect on g_s was significant ($P=0.001$). There were no interactions between CO_2 and nutrients on g_s in beech or oak.

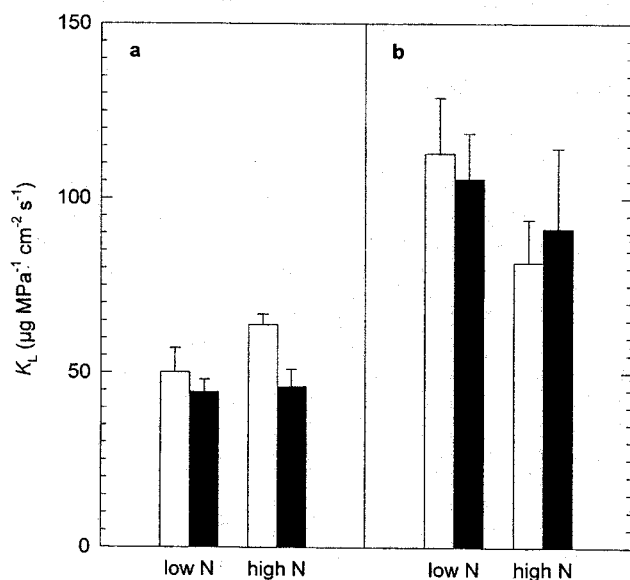


Fig. 1. Leaf-specific hydraulic conductance (K_L) of (a) oak and (b) beech seedlings during their third season of growth in elevated or ambient CO_2 . Open bars: ambient air, solid bars: elevated CO_2 ; low N: low nutrients, high N: high nutrients. Values are means ± 1 SE.

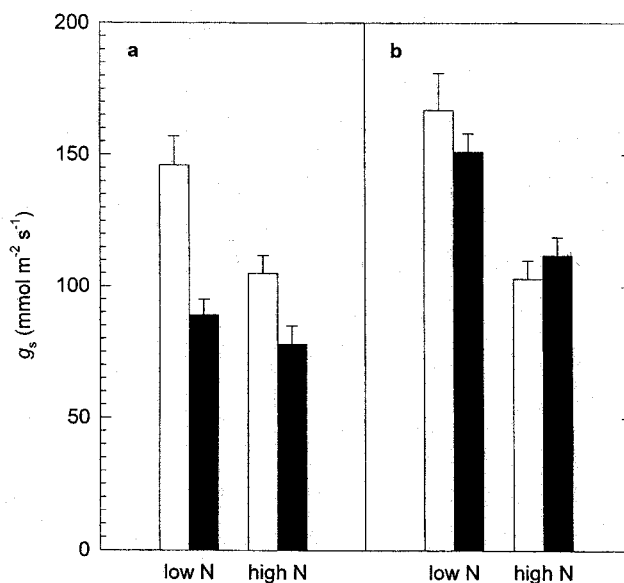


Fig. 2. Stomatal conductance (g_s) of (a) oak and (b) beech seedlings measured in bright sunshine. Open bars: ambient air, solid bars: elevated CO_2 ; low N: low nutrients, high N: high nutrients. Values are means ± 1 SE from 2 d in the second growing season.

Discussion

Interspecific differences in the response of stomatal conductance during periods of bright sunshine to CO_2 concentration were mirrored by interspecific differences in the CO_2 -response of whole-shoot hydraulic conductance per unit leaf area. This would appear to confirm the expectation that CO_2 -effects on plant water use (at least during periods of high transpirational demand) are reflected in K_L . The authors are not aware of any previous work involving direct measurement of the whole-shoot hydraulic conductance of trees in response to elevated CO_2 . Atkinson and Taylor (1996) measured the conductance of detached stem sections of *Quercus robur* and *Prunus avium* L. grown in elevated CO_2 . However, this does not answer the question of how the hydraulic architecture of the plant as a whole is affected.

Although there were no interactions between CO_2 and nutrient concentrations, the high nutrient treatment consistently reduced stomatal conductance in beech and oak (Fig. 2). In beech, this was mirrored by a decrease in K_L (Fig. 1b), although the effect was not significant ($P=0.147$). A possible explanation is the 25% reduction in root-to-shoot ratio that was found in beech grown with high nutrients (Heath and Kerstiens, 1997). In oak, there was no corresponding decrease in leaf-specific conductance with high nutrients (Fig. 1a). The authors could not explain this, except to say that the driving forces for the reductions in stomatal conductance in elevated CO_2 and with high nutrients would be different—the first, a direct response of the stomata to increased internal CO_2 concentration (Mansfield *et al.*, 1990; Morison, 1985; Mott,

1990), and the second probably a response to altered patterns of growth and carbon allocation to water-supplying and water-consuming organs.

The interspecific differences in the CO₂ response of K_L may be partly related to the characteristic differences in the development of conducting tissue. In oak, a ring-porous species, the production of wide xylem vessels is limited to the early season, whereas beech as a diffuse-porous species produces relatively wide vessels right through the summer. One could therefore argue that oak has a need for a more conservative risk-aversion strategy because once xylem embolism has occurred in the large vessels, its hydraulic conductance would be very limited for the rest of the season, whereas beech might be more opportunistic in this respect. Oak would therefore have to reduce g_s in the high CO₂-grown plants which possess a much larger leaf area (Heath and Kerstiens, 1997). This implies that CO₂-related changes in g_s in oak follow from an actual or anticipated limitation in water flow through the stem and branches. On the other hand, it is known that a direct effect of CO₂ concentration on stomata exists (Mansfield *et al.*, 1990; Morison, 1985; Mott, 1990), and the reduction in K_L in oak might simply follow the reduced demand per unit leaf area to be supplied. Whatever the mechanism, the co-ordination between whole-shoot hydraulic conductance and maximum transpiration rate is remarkable and confirms a similar finding for the ontogenetic development of sugarcane (Meinzer *et al.*, 1992).

Since the stomatal control of transpiration is vitally important in preventing damage due to xylem embolism during drought (Cochard *et al.*, 1996), the contrasting responses of beech and oak to elevated CO₂ have major implications for drought tolerance, and, consequently, for forest regeneration and composition (Tschaplinski *et al.*, 1995). The lack of reduction of g_s in beech grown in elevated CO₂ during periods of high evaporative demand, in combination with greater total leaf area (Heath and Kerstiens, 1997), will cause a large increase in whole-plant water use in elevated CO₂, especially during those periods when damage due to excessive water loss would be most likely. In fact, during an imposed drought (Heath and Kerstiens, 1997) of 2-year-old beech seedlings during the hot summer of 1995, stomatal conductance was consistently higher in elevated CO₂. On cooler, cloudy days, the stomatal conductance of beech was significantly reduced in elevated CO₂, but the response was relatively weak compared to that of oak (Heath and Kerstiens, 1997). This pattern was consistent on a number of days over two seasons (Heath and Kerstiens, 1997). This means that during a dry spell, this behaviour will most probably exhaust soil water reserves earlier than it would have in pre-industrial CO₂ concentrations. Therefore, the probability of drought damage should increase for a given

annual precipitation pattern. On the other hand, as shown here, the ability to increase K_L in line with the increase in whole-plant maximum transpiration rate in elevated CO₂ should keep the risk of xylem embolism constant for a given maximum rate of water supply from the roots.

Acknowledgements

This work was funded by the UK Department of the Environment and the Forestry Authority. Our thanks also to TA Mansfield and PH Freer-Smith for much helpful advice.

References

- Atkinson CJ, Taylor JM. 1996. Effects of elevated CO₂ on stem growth, vessel area and hydraulic conductivity of oak and cherry seedlings. *New Phytologist* **133**, 617–26.
- Cochard H, Bréda N, Granier A. 1996. Whole tree hydraulic conductance and water loss regulation in *Quercus* during drought: evidence for stomatal control of embolism? *Annales des Sciences Forestières* **53**, 197–206.
- Curtis PS. 1996. A meta-analysis of leaf gas exchange and nitrogen in trees grown under elevated carbon dioxide. *Plant, Cell and Environment* **19**, 127–37.
- Heath J, Kerstiens G. 1997. Effects of elevated CO₂ on leaf gas exchange in beech and oak at two levels of nutrient supply: consequences for sensitivity to drought in beech. *Plant, Cell and Environment* **20**, 57–67.
- Kerstiens G, Townend J, Heath J, Mansfield TA. 1995. Effects of water and nutrient availability on physiological responses of woody species to elevated CO₂. *Forestry* **68**, 303–15.
- Mansfield TA, Hetherington AM, Atkinson CJ. 1990. Some current aspects of stomatal physiology. *Annual Review of Plant Physiology and Plant Molecular Biology* **41**, 55–75.
- Meinzer FC, Goldstein G, Neufeld HS, Grantz DA, Crisosto GM. 1992. Hydraulic architecture of sugarcane in relation to patterns of water use during plant development. *Plant, Cell and Environment* **15**, 471–7.
- Morison JIL. 1985. Sensitivity of stomata and water use efficiency to high CO₂. *Plant, Cell and Environment* **8**, 467–74.
- Mott KA. 1990. Sensing of atmospheric CO₂ by plants. *Plant, Cell and Environment* **13**, 731–7.
- Townend J. 1993. Effects of elevated carbon dioxide and drought on the growth and physiology of clonal Sitka spruce plants (*Picea sitchensis* (Bong.) Carr.). *Tree Physiology* **13**, 389–99.
- Tschaplinski TJ, Stewart DB, Norby RJ. 1995. Interactions between drought and elevated CO₂ on osmotic adjustment and solute concentrations of tree seedlings. *New Phytologist* **131**, 169–77.
- Tyree MT, Alexander JD. 1993. Plant water relations and the effects of elevated CO₂: a review and suggestions for future research. *Vegetatio* **104/105**, 47–62.
- Tyree MT, Patino S, Bennink J, Alexander J. 1995. Dynamic measurements of root hydraulic conductance using a high-pressure flowmeter in the laboratory and field. *Journal of Experimental Botany* **46**, 83–94.
- Tyree MT, Wilmot TR. 1990. Errors in the calculation of evaporation and leaf conductance in steady-state porometry: The importance of accurate measurements of leaf temperature. *Canadian Journal of Forest Research* **20**, 1031–5.