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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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 (gₛ), 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 gₛ 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 gₛ using cuvette systems, and estimation of the whole-plant transpiration rate is difficult. Leaf temperatures are often inaccurately measured, giving incorrect values of gₛ (Tyree and Wilmot, 1990). Correct scaling-up requires knowledge of actual leaf temperatures and leaf boundary layer resistances in situ. Whereas measurements of gₛ 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 (KL), 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).

KL 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 $g_s$ ($N=22$ 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 μmol m$^{-2}$ 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.

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, 1983).
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 CO$_2$ response of $K_t$ 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 CO$_2$-grown plants which possess a much larger leaf area (Heath and Kerstiens, 1997). This implies that CO$_2$-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 CO$_2$ concentration on stomata exists (Mansfield et al., 1990; Morison, 1985; Mott, 1990), and the reduction in $K_t$ 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 CO$_2$ have major implications for drought tolerance, and, consequently, for forest regeneration and composition (Tschapinski et al., 1995). The lack of reduction of $g_s$ in beech grown in elevated CO$_2$ 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 CO$_2$, especially during those periods when demand 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 CO$_2$. On cooler, cloudy days, the stomatal conductance of beech was significantly reduced in elevated CO$_2$, 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 CO$_2$ 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 $K_t$ in line with the increase in whole-plant maximum transpiration rate in elevated CO$_2$ should keep the risk of xylem embolism constant for a given maximum rate of water supply from the roots.

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References


