Reduced photosynthesis in old oak (Quercus robur): the impact of crown and hydraulic architecture

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Summary We tested the hypothesis that changes in crown architecture of old pedunculate oak trees (Quercus robur L. ssp. robur Kl. et Kr. et Rol.) reduce leaf specific hydraulic conductance of shoots, thereby limiting stomatal conductance and assimilation of affected shoots. At the end of summer 1999, hydraulic conductance and leaf specific hydraulic conductance, measured with a high-pressure flow meter in 0.5- to 1.5-m long shoots, were 27 and 39% lower, respectively, in shoots of low vigor compared with vigorously growing shoots in a 165-year-old stand in southeastern Germany. Two types of bottlenecks to water transport can be identified in shoots of old oak trees, namely nodes and abscission zones. The reduction in hydraulic conductance was especially severe in shoots with diameters of less than 2 mm. Maximum stomatal conductance and maximum net assimilation rate increased significantly with hydraulic conductance and leaf specific hydraulic conductance. Our data support the hypothesis that changes in shoot and consequently crown architecture observed in aging trees can limit photosynthesis by reducing shoot hydraulic conductance. Thus, in addition to increasing pathway length and lower conductivity of xylem in old trees, structural changes in shoot and crown architecture need to be considered when analyzing water relations and photosynthesis in mature and declining trees.

Keywords: assimilation, hydraulic conductance, hydraulic limitation, stomatal conductance.

Introduction

As trees age, height growth and wood production decline. The hydraulic limitation hypothesis attributes this reduction in productivity to hydraulic limitation of photosynthesis caused by increased resistance in the vascular systems of old trees (Yoder et al. 1994, Ryan and Yoder 1997, Hubbard et al. 1999). Yoder et al. (1994) postulated that increasing path length and the reduction in hydraulic conductance of the conducting tissue limit stomatal conductance in large old trees.

There is substantial experimental evidence that stomatal conductance is positively correlated with hydraulic conductance of the soil–root–leaf pathway in a wide range of plant species (Meinzer and Grantz 1990, Sperry and Pockman 1993, Bond and Kavanagh 1999, Meinzer et al. 1999). Above ground, the largest hydraulic resistance along this pathway resides in the smallest shoots of the crown (Yang and Tyree 1993). In old and declining trees, the smallest shoots are characterized by short internodes and a high frequency of nodes, and a decrease in shoot growth increment in these shoots is the first sign of reduced vigor (Roloff 1993). The formation of short shoot internodes reduces leaf specific conductance of these shoots (Rust and Hüttl 1999). Tausend et al. (2000) observed a pronounced impact of differences in crown architecture on gas exchange. Therefore, in addition to path length, developmental changes in crown architecture may also influence whole-plant conductance (Becker et al. 2000).

In pedunculate oak, the architecture of the crown is strongly influenced by the age and vigor of the tree (Roloff 1993, Sonesson 1999, Rust et al. 2000). In vigorous trees, the peripheral crown consists of a dense network of long shoots. Decreasing vigor results in reduced shoot growth increments and a characteristic modification of the branching pattern. Eventually, the declining crown can be described as consisting of brush-like leaf clusters. In old oak trees (more than 80–100 years old), cladoptosis (the active shedding of shoots) seems to be the main mechanism responsible for the transformation of crown architecture. It is enabled by a special abscission zone formed at branch junctions. These abscission zones, which are characterized by small conduits (Rust et al. 2000), may have an even larger impact on hydraulic conductance than the high frequency of nodes.

Our hypothesis was that modifications in crown architecture of old oak trees reduce leaf specific hydraulic conductance of shoots, thereby limiting stomatal conductance and assimilation of affected shoots. To test the hypothesis, we investigated gas exchange and hydraulic conductance of shoots differing in vigor.

Materials and methods

Field site and plant material

In August 1999, we conducted experiments on Quercus robur L. ssp. robur Kl. et Kr. et Rol. trees growing in a stand planted in 1835. The site was located near Dresden, southeastern Germany at 124 m a.s.l.
Thirty-five shoots were selected from four trees to cover a range of shoot structures. The investigated branches were classified on the basis of vigor classes (VC) as: VC 0 = mean shoot increment over the last 3 years exceeds 20 cm year\(^{-1}\); VC 1 = mean shoot increment over the last 3 years does not exceed 15 cm year\(^{-1}\); VC 2 = mean shoot increment over the last 3 years does not exceed 10 cm year\(^{-1}\); and VC 3 = mean shoot increment over the last 3 years does not exceed 5 cm year\(^{-1}\) (Roloff 1993).

Eight to nine branches per tree were selected in the south-facing upper canopy (about 15 m above ground). One leaf per branch was labeled and gas exchange was measured several times throughout the day between 1000 and 1600 h. Stomatal conductance \((g_s)\) and net carbon assimilation rate \((A)\) were measured with a portable gas analyzer (HCM-1000, Walz, Effeltrich, Germany).

**Hydraulic architecture**

All the branches used for gas exchange measurements were enclosed in dark plastic bags with wet paper towels and immediately transported to the laboratory for further analysis.

Whole-shoot hydraulic conductance \((K_S; \text{kg s}^{-1} \text{MPa}^{-1})\) was measured with a custom-built, high-pressure flow meter (HPFM) as described by Tyree et al. (1993, 1994, 1995). In the laboratory, the bases of the shoots were recut under water to a basal diameter of 4–9 mm and connected to the HPFM. Branch temperatures were measured to account for changes in water viscosity and values were standardized to 20 °C. For the perfusion, we used degassed, filtered (pore size 0.2 µm) and acidified demineralized water. Leaves and petioles were removed by stripping them from current-year shoots. Shoots were infiltrated at a pressure of 0.1 MPa until water was dripping from the cut ends and water flow entering the shoot became constant.

We determined \(K_S\) by dividing the rate of water flow through the shoot measured with the HPFM \((F; \text{kg s}^{-1})\) by the pressure drop \((P; \text{MPa})\) from the base of the shoot to the apices with leaves removed (Yang and Tyree 1993). Leaf specific shoot conductance \((K_{LS})\) was calculated as \(K_S/A_L\), where \(A_L\) is leaf area, which was measured with a leaf area meter (Delta-T Devices, Cambridge, U.K.).

On another set of branches, hydraulic conductivity \((K_{10}; \text{kg s}^{-1} \text{m MPa}^{-1})\) and sapwood specific conductivity \((K_W)\) of excised segments with or without nodes were measured as described by Sperry et al. (1988). Briefly, a 5- to 10-cm long segment was excised under water to prevent air from entering the xylem. The segment was then connected to plastic tubing supplied with degassed, filtered and acidified demineralized water under a pressure of 0.006 MPa. Flow rates through segments were measured gravimetrically to determine \(K_{10}\).

**Statistical analysis**

Effects of vigor class on \(K_S, A_L\), and \(K_{LS}\) were subjected to analysis of variance with the branch basal diameter as covariate. All analyses were conducted with the general linear model in the SPSS software package (SPSS, Chicago, IL).

**Results**

Shoot leaf area was not correlated with vigor class but increased significantly with basal diameter. Mean leaf area of the shoots was 0.17 ± 0.05 m\(^2\).

Shoots of VC 0 and 1 (most vigorous shoots) had significantly higher \((P < 0.01)\) \(K_S\) than shoots of VC 2 and 3 (least vigorous shoots) (Figure 1A). Shoots of VC 0 had a significantly \((P < 0.01)\) higher \(K_{LS}\) than shoots in all other vigor classes (Figure 1B).

Sapwood specific conductivity of excised segments, \(K_W\), was reduced significantly \((P < 0.001)\) when a segment contained nodes (Figure 2); however, this effect was limited to segments with diameters of less than 2 mm. The smaller the diameter of the nodal segment, the larger the deviation in \(K_W\) from the value attained by internodes of similar diameter. Over the range of 1 to 5 mm in sapwood diameter, segments without nodes had a \(K_W\) of \(7.13 \times 10^{-6} \pm 0.2 \times 10^{-6} \text{kg s}^{-1} \text{m}^{-1} \text{MPa}^{-1}\), compared with a value of \(4.54 \times 10^{-6} \pm 0.3 \times 10^{-6} \text{kg s}^{-1} \text{m}^{-1} \text{MPa}^{-1}\) for segments with nodes.

Variation in \(g_s\) was closely associated with variation in \(K_{LS}\). Peak values of \(g_s\) initially rose sharply, then more gradually with increasing \(K_{LS}\) (Figure 3). The response of \(g_s\) to vapor pressure deficit did not differ significantly among vigor classes. Peak transpiration \((E_{\text{max}})\) increased linearly with \(K_{LS}\) (data not shown).

Peak net assimilation rates of individual shoots were significantly correlated with \(K_S\) and \(K_{LS}\). Net assimilation rate appeared to rise to a maximum \((A_{\text{max}})\) when plotted against \(K_S\) (Figure 4), and was linearly correlated with \(K_{LS}\) (Figure 5). The most vigorous shoots (VC 0) had significantly higher \((P < 0.01)\) peak assimilation rates than shoots in all other vigor classes.
A maximum than shoots in the other vigor classes (0.55 versus 5.97 ± 0.28 µmol m⁻² s⁻¹).

Discussion

With increasing age, crown and consequently hydraulic architecture of trees undergo fundamental changes (Roloff 1993). In pedunculate oak, cladoptosis is the main mechanism responsible for the transformation of crown architecture. In stem junctions of juvenile oaks, the formation of regular xylem disables the abscission zone immediately after flushing, whereas in mature trees the frequency of active abscission zones increases with age and declining vigor. In addition, more and longer chains of short shoots are formed in aging trees. Because nodes (Figure 2; Rust and Hüttl 1999) and abscission zones (Rust et al. 2000) reduce hydraulic conductance, their occurrence may partially explain the results of Tyree et al. (1993), who found a 1.5- to 2-fold higher resistance in shoots of pedunculate oak than in sessile oak (*Quercus robur* L. ssp. *petraea* Kl. et Kr. et Rol.), which has a lower rate of abscission.

In shoots of VC 3, *K₅* was 27% lower than in shoots of VC 0 (Figure 1A). Because lower *K₅* is not offset by lower leaf areas, *K₇₅* was 39% lower in VC 3 shoots than in VC 0 shoots (Figure 1B). Two types of bottlenecks to water transport can be identified in shoots of old oak trees, namely nodes and abscission zones. The reduction in *Kₙ* was especially evident in shoots with diameters of less than 2 mm (Figure 2). Nodal constriction zones, which have been reported previously (Zimmermann 1978, Salleo et al. 1982, Tyree et al. 1983, Salleo and LoGullo 1986), are characterized by low vessel diameter and a high frequency of vessel ends (Zimmermann 1983). Because older segments tend to be wider than younger segments (regression *r* = 0.57, *P* < 0.001), our data indicate that, within a nodal zone, anatomical differences between nodal and inter-nodal wood decrease as the branch ages.

There is substantial evidence from modeling studies (Jones and Sutherland 1992) and experimental data that *gₛ* is at least partially limited by the hydraulic conductance of the soil-root-leaf pathway in a wide range of plant species (Meinzer and Grantz 1990, Sperry and Pockman 1993, Bond and Kavanagh 1999, Meinzer et al. 1999). In contrast to other studies of the hydraulic limitation hypothesis, where reduced hydraulic conductance of shoots in old trees was deduced from leaf gas exchange data, xylem sap flow and leaf water potentials (Yoder et al. 1994, Ryan and Yoder 1997, Hubbard et al. 1999, Tausend et al. 2000), we measured conductance with an HPFM, a technique that is independent of gas exchange data.
We found that maximum $g_s$ and $A$ increased significantly with $K_t$ and $K_{15}$ (Figures 3–5). Compared with other oak species, shoots of pedunculate oak contain a higher proportion of total aboveground resistance (Tyree et al. 1993). In addition, this species is more vulnerable to embolism than other oak species (Cochard et al. 1992). It seems likely that $g_s$ is adjusted to maintain xylem water potential above the critical point where runaway embolism (Tyree and Sperry 1988) would occur. Similar relationships between hydraulic conductance and gas exchange have been reported for intact plants by Meinzer et al. (1995) and Andrade et al. (1998) and for experimentally manipulated seedlings of ponderosa pine (Pinus ponderosa Dougl. ex Laws.) by Hubbard et al. (2001). Tausend et al. (2000) have shown that differences in crown architecture can significantly influence plant gas exchange. Similar effects could be expected from declining oak crowns, because in addition to changes in shoot structure, the crown becomes more open. These developmental changes in crown architecture might contribute more to the age-related reduction in wood production and height growth than does tree height (Becker et al. 2000).

The cause–effect relationship between plant vigor and crown hydraulic architecture deserves further study. Ryan and Yoder (1997) suggested that age-related changes in the conductance of boles and large branches could control crown architecture, leading to reduced branch tip lengths and gnarled branches. However, many studies of forest decline in Europe and North America have shown that changes in crown architecture are more closely related to tree vigor than tree height (Flückiger et al. 1989, Innes 1993, Roloff 1993). Thus, we conclude that changes in crown architecture are the consequence of several years of reduced branch increment (cf. Woodcock et al. 1995), and hence trees with gnarled branches are usually not as tall as trees with regular branching at the same site.

Our data support the hypothesis that age-related changes in shoot and consequently crown architecture of old trees can reduce leaf-specific hydraulic conductance of shoots and that these reductions can limit stomatal conductance and photosynthesis. Our data indicate that, in addition to increasing pathway length and lower conductivity of xylem in old trees, structural changes in shoot architecture need to be considered when analyzing water relations and photosynthesis of mature and declining trees.

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References


