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Temperature effects on hydraulic conductance and water relations of *Quercus robur* L.

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Abstract

The effects of temperature on root and shoot hydraulic conductances (g_{shoot} and g_{root}) were investigated for *Quercus robur* L. saplings. In a first experiment, conductances were measured with a High Pressure Flow Meter on excised shoots and detopped root systems. The g_{root} and g_{shoot} increased considerably with temperature from 0–50 °C. Between 15 °C and 35 °C, g_{shoot} and g_{root} varied with water viscosity. In a second experiment, the impact of temperature-induced changes in g_{root} on sapling transpiration (E) and leaf water potential (Ψ_{leaf}) was assessed. Intact plants were placed in a growth cabinet with constant air and variable soil temperatures. E increased linearly with soil temperature but Ψ_{leaf} remained constant. As a consequence, a linear relationship was found between E and g_{plant}. The results illustrate the significance of g_{plant} for the stomatal control of transpiration and the significance of temperature for tree water transport.

Key words: Water relations, temperature, hydraulic conductance, stomata, oak, *Quercus robur* L., Fagaceae.

Introduction

In temperate woody species, stomata tend to close and leaf transpiration is reduced when soil water deficit increases (for a review see Hinckley and Braatne, 1994). Consequently, leaf water deficit is controlled and xylem embolism is minimized (Jones and Sutherland, 1991; Cochard *et al.*, 1996). The mechanism of stomatal closure is well documented (Hinckley and Braatne, 1994), but the mechanism by which stomata sense changes in soil dryness is not entirely understood. From a hydrodynamic point of view, a depletion in soil water content results in two kinds of constraints for the plant: one caused by a decrease in the soil water potential (Ψ_{soil}) and one caused by a decrease in the hydraulic conductance of the soil–plant continuum (g_{plant}). The first stress determines the leaf water potential (Ψ_{leaf}) when transpiration is null, for instance at predawn (Ψ_{leaf} equals Ψ_{soil} approximately). The second stress develops only when a water flow (E) occurs in the soil–plant continuum. For a given E, g_{plant} determines the drop in Ψ_{leaf} below Ψ_{soil} as:

$$\Psi_{\text{leaf}}=\Psi_{\text{soil}}-(E/g_{\text{plant}}) \tag{1}$$

Many studies have demonstrated that stomata respond to changes in Ψ_{soil} (Davies and Kozlowski, 1975; Bréda *et al.*, 1993; Lu *et al.*, 1995; Le Quéré *et al.*, 1998). However, the possibility also exists that stomata could directly respond to changes in g_{plant} (Whitehead, 1998). Indeed, for some species under soil drought conditions, a better correlation has been found between E and g_{plant} rather than E and Ψ_{soil}. This was the case for temperate oak species (Cochard *et al.*, 1996; Bréda *et al.*, 1993), spruce (Lu *et al.*, 1996) and five tropical species (Meinzer *et al.*, 1995). However, under soil drought conditions both Ψ_{soil} and g_{plant} are reduced, and it is then difficult to prove a direct response of stomata to a change in g_{plant}.

The aim of this study was to assess a possible direct impact of g_{plant} on stomatal function. An experiment was designed in which reversible changes in g_{plant} could be operated while Ψ_{soil} was kept constant. In a first experiment, the effects of temperature on root and shoot hydraulic conductances were measured. A direct method was used to assess g_{plant} independent of E which was necessary to separate the effect of g_{plant} on E. Then, in a second experiment, the temperature dependence of the root conductance (g_{root}) was used to alter g_{plant}. Stomatal closure following a chilling stress has been reported for

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many species (Ameglio *et al.*, 1990; Fennell and Markhart, 1998; Bassirirad *et al.*, 1993) and has usually been attributed to a decrease in g_{root}. Therefore, well-watered potted saplings were exposed to a range of soil temperatures and plant transpiration rates and leaf water potentials were measured.

Materials and methods

Experiments were conducted on 6–9-month-old oak saplings (*Quercus robur* L.). Acorns were germinated in water and transplanted into 5 dm^3 plastic pots containing a natural soil from the Mondon forest, in the eastern part of France (soil texture was about 1:1 sand and loam). A slow releasing fertilizer (Nutricote T100) was added to the soil upon planting. Plants were grown at the INRA centre near Nancy (France) in a temperature-controlled greenhouse with daily maximum/minimum temperatures averaging 25/15 °C. Pots were automatically watered twice a day using deionized water.

Plants were used during June (experiment 1) and August 1998 (experiment 2), leaf area was *c.* 0.3 m^2 and shoots were *c.* 1.3 m long.

Experiment 1

The aim of the first experiment was to quantify the effects of temperature on root and shoot hydraulic conductances (g_{root} and g_{shoot}, mmol s^{-1} MPa^{-1} plant^{-1}). Plants were brought to the laboratory and cut a few cm above soil level. Shoots and potted roots were immersed in an aerated tap water bath whose temperature could be adjusted between +1 °C and +50 °C. The g_{shoot} and g_{root} were measured with a High Pressure Flow Meter (HPFM, Tyree *et al.*, 1993; Cochard *et al.*, 1997). In short, the technique consists of measuring the water flow entering root or shoot systems when applying a series of water pressures between 0.1 and 0.5 MPa. Conductances are then derived from the flow/pressure relationships. Sample temperature was measure by a thermocouple either appressed against the bark (shoots) or inserted near the centre of the pot (roots). Bath temperature was first set to 20 °C then decreased to *c.* 2 °C in 5 °C steps. Bath temperature was then increased to 50 °C in 5 °C or 10 °C steps. For each target temperature, conductances were measured at least 30 min after the temperature had stabilized. Measurements were conducted on five root and three shoot systems.

Experiment 2

The second experiment aimed at assessing the impact of temperature-induced changes in g_{root} on sapling transpiration (E, mmol s^{-1} plant^{-1}) and leaf water potential (Ψ_{leaf}, MPa). Intact potted plants were placed in a growth chamber where light (400 µmol m^{-2} s^{-1} at the top of the plant), air temperature (24 °C) and air vapour deficit (18 hPa) were maintained constant throughout the experiment. Pots were enclosed in an insulated box placed above the scale of an analytical balance (0.1 g resolution) inside the chamber. A copper coil, bypassing water from a thermostatted bath, refrigerated the air inside the box. Heat dissipation was effected by a little fan inside the box. The box was not touching the plant, the pot nor the balance in order to record plant transpiration accurately and continuously. Thermocouples were used to measure temperature of the soil, the air inside the box and of the air inside the chamber. Plants, watered to field capacity, were installed in the chamber with a target soil temperature set to 25 °C. After *c.* 12 h the soil was rewatered to field capacity. After a further 12 h, leaf water potentials were measured on three leaves with a pressure chamber. The same protocol was repeated on the same plant the following 5–6 d with different soil temperatures. The whole experiment was repeated for three plants. Soil temperature was adjusted between *c.* 7 °C and 40 °C in 10 °C steps following different pathways (increase then decrease or decrease then increase).

Whole plant hydraulic conductance (g_{plant}, mmol s^{-1} MPa^{-1} plant^{-1}) was computed as:

$$g_{\mathrm{plant}} = E/(\Psi_{\mathrm{soil}} - \Psi_{\mathrm{leaf}}) \tag{2}$$

The temperature dependence of the Ψ_{soil} has been analysed by Muromtsev (Muromtsev, 1981) and discussed by Kramer (Kramer, 1983). Because the soil was well-watered throughout the experiments, it can be concluded that temperature had virtually no effect on Ψ_{soil} and that $\Psi_{\mathrm{soil}} = 0$ MPa.

Results

Results from experiment 1 are shown in Fig. 1. Although the organs were perfused for several hours, the time-dependent changes in hydraulic conductance were negligible. When the temperature was decreased from 20 °C to 2 °C and returned to 20 °C after *c.* 4 h, only a 4.2% decrease in the hydraulic conductance was noticed. Because absolute values varied from plant to plant or between root and shoot (Fig. 1a), conductance values were divided, for each sample, by the conductance measured at 20 °C (Fig. 1b). Changes in organ temperature resulted in large variations in g_{root} and g_{shoot}. For example, from 20 °C to 2 °C, a *c.* 50% decrease in conductance was noticed. Between 15 °C and 35 °C, the variations in conductance could entirely be ascribed to variations in water viscosity (plain line in Fig. 1b; data from Lide, 1996). Below 15 °C, the decreases in g_{root} and g_{shoot} were *c.* 10% higher than the decrease in water fluidity. Above 35 °C, g_{root} and, mostly, g_{shoot} values increased much more than water fluidity.

Results from experiment 2 are shown in Fig. 2. Plant transpiration decreased linearly with decreasing soil temperature (Fig. 2a). From 40 °C to 7 °C, an 80% decrease in E was measured. However, leaf water potentials remained nearly constant (Fig. 2b). As a consequence, whole plant hydraulic conductance, g_{plant} increased with soil temperature (Fig. 2c) and g_{plant} was linearly correlated with E (not shown). Changes in water fluidity largely accounted for the variations in g_{plant} (thick plain line in Fig. 2c).

Discussion

The objective of this study was to assess the effect of plant hydraulic conductance (g_{plant}) on plant transpiration (E). g_{plant} was altered by changing the soil temperature and the impact on E was measured (experiment 2). However, the determination of g_{plant} in such experiments

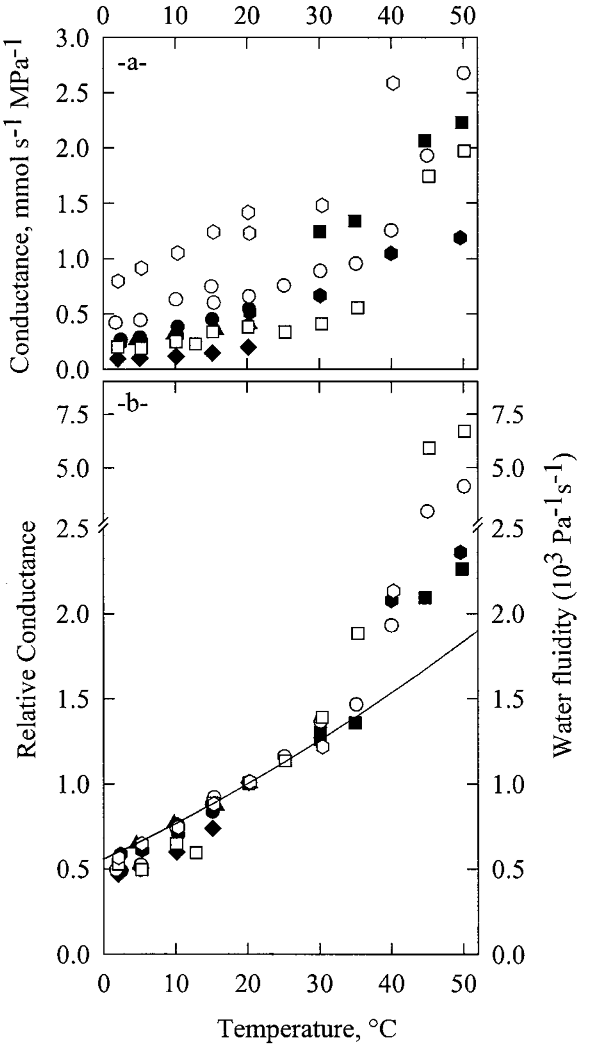

Fig. 1. Effect of temperature on root (closed symbols) and shoot (open symbols) hydraulic conductances of *Quercus robur* saplings. In (b) values have been normalized using the hydraulic conductance at 20 °C as the reference. Different symbols represent different trees. The straight line in (b) represents the temperature dependence of water fluidity (inverse of water viscosity).

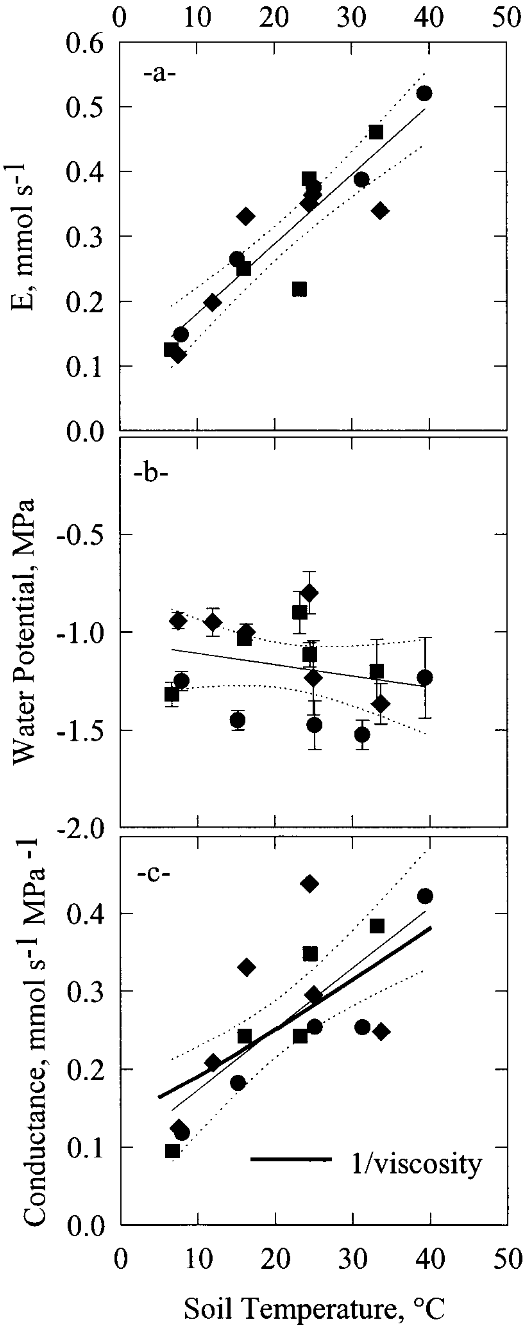

Fig. 2. Effect of soil temperature on plant transpiration rate (a), leaf water potential (b) and whole plant hydraulic conductance (c). Different symbols represent different trees. Error bars in (b) represent standard deviation ($n=3$). Thin lines are first order regressions with 95% confidence intervals. The thick line in (c) represents the theoretical dependence of conductance with water fluidity.

is mathematically linked to E (see equation 2). It was therefore necessary to determine the dependence of g_{plant} on temperature independently of E (experiment 1). This assumes that the HPFM technique correctly estimated g_{root} and g_{shoot}. Although this assumption may be questionable because, with the HPFM technique, positive pressures are applied which fill the intercellular spaces (Tyree *et al.*, 1999), there is evidence from the literature that this problem is minor and that the HPFM yields correct values (Yang and Grantz, 1996; Tsuda and Tyree, 1997). The comparison of the g_{plant} values obtained during the two experiments of this study gives further credit to the HPFM technique. Indeed, the mean g_{plant} derived from E and Ψ_{leaf} was 0.24 ± 0.03 SE ($n=3$) mmol s^{-1} MPa^{-1} at 20 °C, little different of the g_{plant} value measured with the HPFM (0.236 mmol s^{-1} MPa^{-1} resulting from $g_{\mathrm{root}}=0.38 \pm 0.12$ SE ($n=5$) and $g_{\mathrm{shoot}}=0.61 \pm 0.25$ SE ($n=3$) mmol s^{-1} MPa^{-1}). The two experiments were therefore relevant to distinguish the effects of changes in plant conductance on transpiration.

Temperature greatly affected root and shoot hydraulic conductances of *Quercus robur*. In the literature, changes in g_{root} with temperature have been attributed to changes in membrane fluidity and permeability (Améglio *et al.*, 1990; Carvajal *et al.*, 1996), or changes in water viscosity (Lopez and Nobel, 1991; Hertel and Steudle, 1997). Water viscosity was mostly responsible for the variation of g_{root} in this study. However, for temperature below 15 °C and above 35 °C, g_{root} varied more than water viscosity itself. This would suggest that a modification of membrane fluidity might have occurred at such temperatures.

As far as is known, direct temperature effects on whole shoots hydraulic conductance have not yet been reported. Temperature effects were as large in shoots as in roots are were also mostly related to water viscosity. The drastic increase in g_{shoot} at high temperatures were irreversible (data not shown) and might have been caused by membrane degradations in the leaf blade.

Direct measurements of the temperature effects on hydraulic conductances were relevant to whole plant response to temperature, as shown by the second experiment. Changes in g_{plant} were also explained by changes in water viscosity, as expected from the dependence of g_{plant} and g_{root} on temperature (Fig. 1).

Results from the second experiment also validated the hypotheses that, in *Quercus*, stomata can close in response to the sole decrease in g_{root} and g_{plant}, without the need for a decrease in Ψ_{soil}. Plant transpiration responded linearly to temperature-induced changes in g_{plant}. Under drought soil conditions, a linear relationship has also been found between g_{plant} and E in *Quercus* (Cochard *et al.*, 1996). Other evidence for a coupling between g_{plant} and E can be found in the literature. For instance, Sperry and Pockman demonstrated that, in *Betula*, stomata were closing when shoot hydraulic conductance was reduced by xylem embolism (Sperry and Pockman, 1993). Using partial defoliation, Meinzer and Grantz have also shown a co-ordination between stomatal and hydraulic conductances in sugarcane (Meinzer and Grantz, 1990). Altogether, these experiments demonstrate that stomata can respond to changes in g_{plant}, independently of the way g_{plant} is altered (temperature, drought, xylem embolism or defoliation). The significance of g_{plant} for the understanding of tree water relations has probably been underestimated, especially on studies dealing with stomatal regulation. The results also raise the issue of the mechanism by which stomata could sense changes in g_{plant}. It has been proposed that a possible effect of g_{plant} is on ABA production in sugarcane (Meinzer and Grantz, 1991). ABA may also have triggered stomatal closure in our experiment because there is evidence for an increase in ABA production in freeze-stressed trees (Bertrand *et al.*, 1994, 1997). However, in *Quercus robur*, Triboulot *et al.* (Triboulot *et al.*, 1996) and Fort *et al.* (Fort *et al.*, 1997) found no evidence for an increase in xylem sap [ABA] when g_{plant} was reduced by drought, so for this species ABA might not be produced in response to a cooling stress as well. Another hypothesis is that E might have been regulated by an hydraulic signal, i.e. by Ψ_{leaf}. The constancy of the bulk leaf water potential is an argument against a direct effect of Ψ_{leaf} on g_{s}. Ψ_{leaf} was nearly constant in this experiment, but, as g_{plant} varied, Ψ_{xylem} must have changed. The possibility exists that changes in Ψ_{xylem} in the leaf blade may trigger the release of ABA in the leaves (Whitehead, 1998). Indeed, Tardieu and Davies developed a model for stomatal response to soil drought that combines hydraulic and chemical signals (Tardieu and Davies, 1993). The possibility also exists that a drop in g_{plant} may induce a transient drop Ψ_{leaf} which would promote a stomatal closure. Direct Ψ measurements in the leaf xylem and the leaf mesophyll with the pressure probe technique (Tomos and Leigh, 1999) may validate these hypotheses.

These data also illustrate the significance of temperature for plant water relations. Wood temperature can fluctuate considerably within a day or from day to day under field conditions. For instance, these fluctuations reached 20 °C in beech branches measured in eastern France during the 1997 growing season (personal observations). Root and soil temperatures were more buffered. Little attention has been paid to the impact of such temperatures on plant hydraulic conductances. However, when the temperature increases from 15 °C to 35 °C, g_{shoot} doubles (Fig. 1). The impact on g_{plant} is lower and depends on the ratio between g_{root} and g_{shoot}. The impact on tree transpiration is less predictable because air vapour pressure deficit also changes with temperature, but is certainly not negligible and should be considered.

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