Short-term effects of potassium fertilization on the hydraulic conductance of *Laurus nobilis* L.

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This study reports experimental evidence on the effect of short-term potassium fertilization on potassium uptake, tissue concentration and hydraulic conductance of pot-grown laurel plants. Potassium uptake and loading into the xylem of laurel seedlings increased within 24 h after fertilization. Potassium was not accumulated in roots and leaves, but the [K⁺] of xylem sap was 80% higher in fertilized plants (+K) than in potassium-starved plants (−K), as a likely result of recirculation between xylem and phloem. Increased xylem sap [K⁺] resulted in a 45% increase in transpiration rate, a 30% increase in plant hydraulic conductance (Kplant), and a 120% increase in leaf-specific conductivity of the shoot (kshoot). We suggest that this increase was due to ion-mediated up-regulation of xylem hydraulics, possibly caused by the interaction of potassium ions with the pectic matrix of intervessel pits. The enhancement of hydraulic conductance following short-term potassium fertilization is a phenomenon that can be of advantage to plants for maintaining cell turgor, stomatal aperture and gas exchange rates under moderate drought stress. Our data provide additional support for the important role of potassium nutrition in agriculture and forestry.

**Keywords**: hydraulic conductance, ionic effect, mineral nutrition, potassium, xylem sap.

Introduction

Long-distance water transport in plants occurs through the xylem, both axially within tracheids and vessels and radially through pits in the walls of adjacent conduits. For many years the major constraints to xylem hydraulics were attributed to anatomical features, like the number, length and diameter of conduits. More recently, it has been shown that the hydraulic conductance of xylem can be modulated by changes in the xylem sap cation concentration due to ion-mediated volume changes of pectins in pit membranes (Zimmermann 1978, Zwieniecki et al. 2001). Pectins form charged gels and behave like typical polyelectrolytes, swelling under dilute solutions and shrinking when cations (like potassium, K⁺) shield the negatively charged carboxylic groups. These volume changes are supposed to reversibly modify the dimensions of nanometre-sized pores in pit membranes, thus modulating the resistance to water flow through the pits and, hence, through the whole xylem network. In fact, intervessel pits build up a large fraction (up to 50%) of xylem hydraulic resistance (Wheeler et al. 2005).

This phenomenon, known as the ‘ionic effect’, has been repeatedly reported in excised stems under laboratory conditions (e.g., Zwieniecki et al. 2001, Boyce et al. 2004, Nardini et al. 2007, Aasamaa and Söber 2010, Cochard et al. 2010), and recent experimental evidence suggests that it plays important functional roles in planta (Zwieniecki et al. 2004, Trifilò et al. 2008, Nardini et al. 2010, Sellin et al. 2010). Conclusive evidence about the underlying mechanisms and the general occurrence of the ionic effect are still missing (Cochard et al. 2010), and the possibility that results obtained in excised segments are due to experimental artefacts has also been hypothesized (Van Ieperen 2007). However, recent experimental
results are consistent with the current interpretation of the ionic effect as a consequence of the inherent properties of intervessel pitting of the xylem conduit network (Jansen et al. 2011, Gortan et al. 2011).

Mineral nutrition is one of the factors affecting plant growth and water relations (Clarkson et al. 2000, Cramer et al. 2009), but the reported effects of different nutrient availabilities on xylem and plant hydraulic properties are somewhat contradictory. For example, nitrogen fertilization has been reported to influence either positively or negatively xylem vessel size, vulnerability to cavitation, hydraulic conductivity and water use efficiency in different species and growth conditions (e.g., Harvey and van den Driessche 1999, Ewers et al. 2000, Clearwater and Meinzer 2001, Trubat et al. 2006, Gorska et al. 2008, Atwell et al. 2009, Hacke et al. 2010). Phosphorus addition was found to decrease cavitation vulnerability in poplar (Harvey and van den Driessche 1997) and increase it in dwarf mangroves (Lovelock et al. 2006), whereas phosphorus deficiency decreased root hydraulic conductance in Pistacia lentiscus (Trubat et al. 2006).

The effect of potassium availability on plant water balance has mainly been studied in relation to turgor regulation of stomatal guard cells, but the results are contradictory (Fournier et al. 2005, Benlloch-González et al. 2008). There are a few reports on the effects of potassium on root hydraulic conductance, which was reduced by increased potassium availability in both sunflower (Quintero et al. 1998) and pepper plants (Cabañero and Carvajal 2007). A recent review by Römheld and Kirkby (2010) has highlighted the several benefits of adequate potassium nutrition for plant resistance to several biotic and abiotic stresses. Recent findings on the impact of cations on xylem hydraulics suggest a possible additional role for this nutrient in the modulation of plant hydraulic efficiency and water balance.

The aim of this study was to test whether plant hydraulic conductance is affected by short-term changes in soil potassium availability. Our hypothesis was that potassium fertilization should induce a rapid increase in [K+] in plant tissues and an enhancement of plant hydraulic conductance, possibly favouring higher gas exchange rates and photosynthesis, which are limited by whole-plant hydraulics (Nardini and Salleo 2000, Sperry 2000). To this end, the eventual effects of potassium fertilization on the hydraulic conductance of potted Laurus nobilis L. (laurel) plants were tested on both whole plants and excised shoots. Laurel was chosen as study species because the hydraulic conductance of stems of this species is known to be extremely responsive to changes in the ionic concentration of xylem sap (Zwieniecki et al. 2001, Gascó et al. 2007), as a likely consequence of high intervessel connectivity (Jansen et al. 2011) and pit membrane chemistry characterized by abundant acidic pectins (Gortan et al. 2011).

Materials and methods

Plant material and growth conditions

Experiments were conducted on 50 2-year-old laurel seedlings, grown in 2-l pots with a mixture of sand and garden soil (3:1). Plants were grown in a greenhouse at the Botanical Garden of the University of Palermo, Italy. Minimum and maximum average temperatures in the greenhouse were 20 and 38 °C, respectively; relative humidity ranged between 80 and 30%. Plants were grown under low potassium availability by irrigating them twice a week with tap water containing no more than 0.13 mM potassium and fertilizing every 2 weeks with modified half-strength Hoagland solution containing no potassium (pH 6.3; N 7.5 mM, P 0.5 mM, Ca 2.0 mM, Mg 1.0 mM, S 1.0 mM, B 23.0 µm, Mn 4.6 µm, Zn 0.38 µm, Cu 0.14 µm, Mo 0.05 µm and Fe 10.0 µm).

After ~5 months, plants had an average height of 30 cm and an average diameter at stem base of 0.6 cm. Plants were divided randomly into two groups: (i) potassium-starved plants (−K) grown as described above and (ii) plants to be irrigated with 25 mM KCl 24 h before data collection (+K). Measurements were carried out in the greenhouse and in the laboratory on sunny days in June and July 2009 (see below).

Measuring potassium content

Water-soluble potassium content in the soil was measured using a selective flat potassium electrode (Cardy K; Horiba Ltd, Kyoto, Japan). Soil samples were taken with a cork-borer at mid-depth of six pots per treatment, dried to constant weight at 60 °C and ground in a mortar and pestle. Samples were extracted in double-distilled water (1:5, w/v) for 5 min on a shaker and filtered through filter paper (Whatman no. 2). The potassium content of the extract was measured using the ion-selective electrode (see above).

Leaves and roots from six plants per treatment were carefully rinsed in distilled water, dried to constant weight at 60 °C and ground in a mortar with liquid nitrogen. Powdered material was extracted in distilled water (1:10, w/v) for 60 min on a shaker and centrifuged at 5000 rpm for 10 min. The potassium content of the supernatant was measured as described above.

Xylem sap was extracted between 10:00 and 12:00 h from six plants per treatment. Plants were rapidly defoliated with a razor blade and each pot was inserted in a large custom-made pressure chamber, with the base of the shoot fixed in a rubber gasket. The tip of the shoot was cut with a razor blade, a ring of bark was removed to avoid phloem contamination and the cut surface was rinsed with distilled water. The pressure in the chamber was gradually increased to 1.4 MPa until xylem sap flowed out from the excised tip. After discarding the first droplet, ~100 µl of sap was collected directly on the electrode surface for determination of xylem sap [K+].
Hydraulic measurements

Whole-plant transpiration (E) and hydraulic conductance \( K_{\text{plant}} \) were measured on 12 plants per treatment using the evaporative flux method (EFM) according to Tsuda and Tyree (2000). The day before measurements, all plants were irrigated to field capacity with either deionized water (–K plants) or a 25 mM KCl solution (+K plants). The following day each pot was tightly enclosed in a plastic bag to prevent evaporation from the soil, and plants were put on a technical balance under a combined sun + lamp illumination providing a photosynthetic photon flux density of \( \sim 600 \, \mu\text{mol m}^{-2} \text{s}^{-1} \) at the plant top. Average temperature and relative humidity during measurements were 38 °C and 40%, respectively. After 1 h (which was sufficient to reach quasi-steady-state conditions), \( E \) was calculated by recording the change in weight of each plant in a 35-min interval. Two leaves per plant were then detached and leaf water potential \( (\Psi_{\text{leaf}}) \) was measured using a pressure chamber (SKPM 1400; Skye Instruments Ltd, Powys, UK). Evaporative flux method measurements were performed between 10:00 and 12:00 h.

In order to estimate soil water potential \( (\Psi_{\text{soil}}) \) in the two groups of plants, three plants per treatment were enclosed overnight in a plastic bag to allow equilibration of \( \Psi_{\text{soil}} \) with \( \Psi_{\text{leaf}} \). Leaf water potential of three leaves was measured the following morning and related values were taken as estimates of \( \Psi_{\text{soil}} \). Whole-plant hydraulic conductance was then calculated as

\[
K_{\text{plant}} = \frac{E}{(\Psi_{\text{soil}} - \Psi_{\text{leaf}})}
\]

Shoot hydraulic conductance \( K_{\text{shoot}} \) was measured on 10 plants per treatment using the vacuum pressure method (VPM, Kolb et al. 1996), slightly modified according to Lo Gullo et al. (2005), using an 8-l PVC vacuum chamber. Shoots from plants treated as described above were excised under tap water and the stem base was connected to polyetheretherketone (PEEK) tubing ending in a beaker containing the perfusion fluid and placed on an analytical balance (AL 104; Mettler Toledo, Greifensee, Switzerland). A commercial mineral water roughly matching dilute xylem sap composition (Levissima; San Pellegrino SpA, Milano, Italy), with a potassium content of 0.05 mM, was filtered to 0.22 \( \mu \text{m} \) and used as perfusion fluid (Nardini et al. 2007). The excised shoot was placed in the chamber and a vacuum pump reduced the pressure in 0.02 MPa steps. At each pressure (from –0.08 to 0.00 MPa relative to atmospheric pressure), a computer recorded the weight of the beaker at 20 s intervals to calculate flow rate. Flow rates \( (F) \) were plotted versus the absolute pressures applied \( (P) \) and the hydraulic conductance was calculated from the slope of the \( F \) to \( P \) linear relationship (Lo Gullo et al. 2005). Air temperature during flow rate measurements was 27 ± 1 °C.

At the end of all measurements, leaf surface area was measured using a portable leaf area meter (AM100, Analytical Development Company, Hoddesdon, UK) and \( K_{\text{plant}} \) and \( K_{\text{shoot}} \) were scaled by leaf surface area. Leaf-specific shoot conductivity \( (K_{\text{shoot}}) \) was calculated as \( K_{\text{shoot}} \) multiplied by the length of the excised shoot segment. All values were corrected for the viscosity of water at 20 °C.

A parallel experiment was performed to estimate the actual potassium content of the perfusion fluid flowing through the shoot during the hydraulic conductance measurements. Shoots of –K or +K plants were excised and connected to PEEK tubing as described above. The beaker containing the perfusion fluid was placed in a pressure chamber (see above) and flow was driven by applying a pressure of 0.08 MPa. The tip of the shoot was cut with a razor blade, a ring of bark was removed to prevent phloem contamination, and the cut surface was rinsed with distilled water. The perfusion fluid was collected in an Eppendorf vial. Every 15 min the potassium content of the collected perfusion fluid was measured using the ion-selective electrode (see above).

Statistics

All data are presented as mean value ± standard deviation. Occasional extremely high or low values were deleted from the data set, using as a threshold the mean ± twice the standard deviation for each group. The significance of differences between treatments was tested with unpaired Student’s t-tests, at \( P < 0.05 \).

Results

Soil and plant potassium concentration

The water-soluble potassium content of the soil was 10.0 ± 3.5 mg kg\(^{-1}\) dry weight (DW) for –K plants, while 24 h after irrigation with 25 mM KCl the potassium content of the soil increased to 96.0 ± 27.5 mg kg\(^{-1}\) DW. Even though no potassium was added to the nutrient solution during cultivation, plants did not show apparent symptoms of potassium deficiency, such as leaf chlorosis or necrosis.

Short-term fertilization with KCl had no effect on root or leaf potassium content, which was not significantly different between treatments, at least 24 h after fertilization (Figure 1a). Root potassium content of –K and +K plants was ~10.2 mg g\(^{-1}\) DW, while leaves of both –K and +K plants had <50% of the potassium content of roots, i.e., ~4.5 mg g\(^{-1}\) DW. In contrast, irrigation with 25 mM KCl had a strong effect on the potassium content of xylem sap (Figure 1b), which was 80% higher in +K plants, increasing from 3.5 ± 0.4 mM (–K plants) to 6.3 ± 1.4 mM.

Hydraulic measurements

Whole-plant transpiration rate increased substantially in plants treated with 25 mM KCl compared with potassium-starved
plants (Figure 2a). The transpiration rate measured for +K plants was $2.3 \pm 0.4 \text{ mmol m}^{-2} \text{s}^{-1}$, while that for −K plants was $1.6 \pm 0.3 \text{ mmol m}^{-2} \text{s}^{-1}$. In other words, plants with higher potassium availability increased their transpiration rate by ~45%. In contrast, adding 25 mM KCl did not significantly affect $\Psi_{\text{leaf}}$, which was $-1.5 \pm 0.2 \text{ MPa}$ in +K plants and $-1.3 \pm 0.4 \text{ MPa}$ in −K plants (Figure 2b), this difference being likely due to osmotic effects in the soil. In fact, $\Psi_{\text{soil}}$ turned out to be $-0.08$ and $-0.15 \text{ MPa}$ in −K and +K plants, respectively.

Transpiration rate and water potential values were used to calculate whole-plant hydraulic conductance on the basis of the EFM technique. $K_{\text{plant}}$ was 30% higher in +K plants than in −K plants, increasing from $0.70 \pm 0.21$ to $0.94 \pm 0.12 \text{ mmol m}^{-2} \text{s}^{-1} \text{ MPa}^{-1}$ (Figure 3a).

When shoot hydraulic conductance was measured in the laboratory using the VPM, this variable was found to be larger in +K plants than in −K ones, although $K_{\text{shoot}}$ was measured using the same reference solutions in the two groups. Because the shoots used for measurements in the vacuum chamber were not perfectly homogeneous in length, leaf-specific hydraulic conductivity ($k_{\text{shoot}}$) was considered to be a more suitable parameter to compare results (Figure 3b). In +K plants, $k_{\text{shoot}}$
was 2.0 ± 0.6 mmol s⁻¹ m⁻¹ MPa⁻¹, i.e., ~120% higher than that measured in −K plants (0.9 ± 0.5 mmol s⁻¹ m⁻¹ MPa⁻¹).

The potassium content of the perfusion fluid collected at regular time intervals after flowing through the shoots of −K and +K plants is shown in Figure 4. In both −K and +K shoots, the potassium content decreased gradually during measurements, but the perfusion fluid was always greatly enriched in potassium while flowing through the shoot, in that the lowest value measured was ~20 times higher than that of the mineral water used for perfusion. Thirty minutes after starting the perfusion experiments, the potassium content of the collected fluid was close to that of native xylem sap for both −K (1.6 mM) and +K shoots (4.7 mM). After 2 h, the potassium content had decreased to ~1.0 and 2.0 mM for −K and +K shoots, respectively. The amount of potassium in the perfusion fluid samples collected from +K shoots was always two- to threefold higher than that of the −K shoots.

Discussion

Potassium nutritional status is known to be a key factor determining plant photosynthetic productivity and resistance to drought stress (Egilla et al. 2005, Pettigrew 2008). Our data suggest the following: (i) potassium uptake and loading into the xylem of laurel seedlings increased within 24 h after potassium fertilization; (ii) increased potassium content in xylem sap increased plant hydraulic conductance substantially, and hence it was likely to favour stomatal aperture, which in turn was a likely cause of the observed increase in transpiration rate. In spite of these effects, the water potential drop along the soil-to-leaf pathway did not change; (iii) enhanced xylem sap potassium concentration was a likely result of active potassium recirculation between xylem and phloem.

Growing young laurel plants for 4–6 months without specific potassium fertilization did not cause any onset of apparent deficiency symptoms. It is well known that mild K deficiency does not generally result in visible symptoms because of a high rate of redistribution of this nutrient between mature and developing tissues (Pujos and Morard 1997). Moreover, the initial level of potassium availability might have been adequate to
sustain plant growth for the whole study period. Hence, experiments reported in this manuscript have probably to be regarded more as additional potassium fertilization of plants with adequate levels of this nutrient, rather than as recovery from nutrient starvation conditions.

Despite apparently adequate potassium nutrition, irrigation of plants with 25 mM KCl solution induced important changes in plant water balance and hydraulics only 24 h later. Plant hydraulic conductance apparently increased by ~30%, allowing plants to sustain higher transpiration rates and stomatal aperture. In fact, leaf-to-air vapor pressure deficit conditions during EFM measurements were the same for both −K and +K plants. Despite increased water loss, the higher $K_{\text{plant}}$ of +K plants allowed them to maintain the same pressure drop between soil and transpiring leaves, which was ~1.3 MPa in both experimental groups.

Field crop nutrition studies have revealed that adequate levels of potassium availability are necessary for the maintenance of cell turgor and photosynthesis, especially under drought stress conditions (Mengel and Arneke 1982, Sen Gupta et al. 1989, Premachandra et al. 1993). This effect is at least partially due to the important role of potassium ions in the regulation of osmotic balance of plant cells. The finding that increased potassium availability enhances plant hydraulic conductance offers new possible interpretations for the role of this nutrient under drought stress conditions. In fact, water potential drop, and hence reduction in cell turgor pressure during transpiration, arises because of frictional resistances to water movement in the soil-to-leaf pathway. Under drought stress conditions, soil water potential decreases and frictional resistances increase as a result of cavitation-induced loss of xylem hydraulic conductance (Tyree and Sperry 1989, Salleo et al. 1996, Nardini et al. 2003), possibly leading to loss of turgor. The increase in $K_{\text{plant}}$ induced by increased soil potassium availability would reduce the soil-to-leaf water potential drop, thus allowing plants to maintain cell turgor even under drought stress conditions. Moreover, reduced pressure drop along the xylem would lower the risk of cavitation under high transpiration demand and low soil water availability. Even if xylem cavitation and embolism could not be avoided by drought-stressed plants, the enhanced xylem sap $[K^+]$ (see below) probably alleviated cavitation-induced loss of hydraulic conductance (Trifilio et al. 2008).

Several studies have shown that gas exchange rates, and hence photosynthesis, are limited by the hydraulic conductance of the liquid water pathway from the soil to the leaves (Nardini and Salleo 2000, Sperry 2000, Brodribb et al. 2005). The finding that enhanced $K_{\text{plant}}$ in +K plants translated into higher transpiration rates is consistent with the above studies and suggests that the positive effects of potassium availability on photosynthetic rates might be partially mediated by potassium-induced modulation of plant hydraulic properties.

Enhanced $K_{\text{plant}}$ in +K plants was accompanied by an increase in xylem sap potassium content compared with values recorded in −K plants. Although the composition of xylem sap samples may differ from that in intact plants due to changes in transpiration rates or in nutrient lateral exchange along the xylem (Schurr 1998), flux-controlled exudation remains a reliable method to compare xylem potassium content between different treatments. The hydraulic conductance of stem xylem of laurel has been reported to be very sensitive to changes in xylem sap potassium concentration (Gascó et al. 2006). Nardini et al. (2010) have reported a 30–60% increase in stem hydraulic conductance in this species for a change in xylem sap $[K^+]$ from 3 to 12 mM, a range similar to that observed in the present study, where xylem sap $[K^+]$ was 3.5 and 6.3 mM for −K and +K plants, respectively. Also the magnitude of the $K_{\text{plant}}$ increase recorded in the present study (+34%) was similar to that reported by Nardini et al. (2010) in the same species. Hence, it is reasonable to conclude that increased $K_{\text{plant}}$ in +K plants was due to ion-mediated up-regulation of xylem hydraulic conductance, possibly caused by the interaction of potassium ions with the pectic matrix of intervessel pits (Gortan et al. 2011) and consequent volume changes of these pit structures.

Potassium fertilization had a smaller effect on $K_{\text{plant}}$ (+34%) than on $k_{\text{shoot}}$ (+120%), probably because plant hydraulics was dominated by root hydraulic resistance. In fact, roots make up an important fraction of plant hydraulic resistance in many woody plants (Nardini et al. 2006, Domec et al. 2009). At the root level, the main resistance to water flow is located in the radial soil-to-root stele extravascular pathway (Trifilio et al. 2004). Hydraulic conductance of the extravascular water pathway in the roots is known to respond to variations in nutritional status, as reported in sunflower for potassium (Quintero et al. 1998) and nitrate (Gloser et al. 2007). Further investigations are necessary to elucidate the role of potassium fertilization on the eventual up-regulation of root axial hydraulic conductance.

Despite increased $[K^+]$ in the xylem sap of +K plants, root and leaf potassium content remained unchanged in these plants when compared with −K ones, suggesting that potassium was not accumulated into these organs but eventually recirculated along the plant body through the stem. Phloem-to-xylem potassium recirculation is a well-known phenomenon and potassium is considered a fundamental osmolyte for phloem functioning (Cakmak 2005, Hermans et al. 2006). This interpretation is supported by the finding that $k_{\text{shoot}}$ was higher in +K than in −K plants, despite the fact that measurements were performed on excised shoots perfused with the same low-potassium-content perfusion solution. Similar low $[K^+]$ was expected to produce similar $k_{\text{shoot}}$ values, as observed in defoliated laurel stems (Gascó et al. 2006). In contrast, leafy shoots measured for hydraulic properties using a standard reference solution apparently modified the composition of the fluid flowing through stems. In fact, the reference solution with 0.05 mM K+ appeared to be enriched with potassium while flowing.
through the stem xylem. Within the typical time interval required for VPM measurements (i.e., 20–30 min), the outflow solutions showed an increase of [K+] to ~1.5 and 5 mM in −K and +K plants, respectively. Enhanced [K+] in the perfused solution was recordable even after 120 min, when [K+] was still significantly higher in +K than in −K plants. The persistently higher [K+] recorded in +K xylem sap explains why kshoo of these plants was higher than that of −K plants even when measured with the VPM technique, and suggests that xylem sap was continuously enriched with potassium ions probably originating from the phloem. Our findings are consistent with a recent report by Metzner et al. (2010) where experimental evidence has been provided for substantial up-regulation of potassium in the sap of transpiring bean plants and suggested that nutrient recirculation between xylem and phloem was responsible for the observed increase in xylem sap [K⁺]. When a 2.5 mM concentration of the isotope ⁴¹K⁺ was supplied to the xylem, the isotope tracer fraction in the conduit lumina turned out to be well below 30%, suggesting up-regulation of xylem sap [K⁺] to ~15 mM.

Our results are also consistent with a recent report by Sellin et al. (2010) revealing that significant differences in [K⁺] of xylem sap persisted in branches of silver birch, sampled from different heights, after 20 min perfusion of stems with deionized water under high pressure. This finding suggests that living tissues continued to enrich the xylem sap with potassium even after branch cutting. Moreover, phloem-borne potassium was found to regulate xylem hydraulic conductivity in maple branches (Zwieniecki et al. 2004).

In conclusion, our data show that fertilization with potassium enhances plant hydraulic conductance over the short term, a phenomenon that could be of advantage to plants for maintaining cell turgor, stomatal aperture and gas exchange rates under moderate drought stress. These findings provide additional support for the important role of potassium nutrition in agriculture and forestry and further highlight the potential risks associated with agro-forestry practices implying substantial impoverishment of soil potassium content (Smil 1999), as well as the need to develop specific strategies for potassium fertilization under scenarios of increasing drought stress events (Römheld and Kirkby 2010).

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