Drought resistance of *Ailanthus altissima*: root hydraulics and water relations

P. TRIFILÒ,¹ F. RAIMONDO,¹ A. NARDINI,¹,² M. A. LO GULLO³ and S. SALLEO¹

1 Dipartimento di Biologia, Università di Trieste, Via L. Giorgieri 10, 34127 Trieste, Italy
2 Author to whom correspondence should be addressed (nardini@univ.trieste.it)
3 Dipartimento di Scienze Botaniche, Università di Messina, Salita Sperone 31, 98166 Messina S. Agata, Italy

Received February 17, 2003; accepted June 29, 2003; published online December 1, 2003

Summary  Drought resistance of *Ailanthus altissima* (Mill.) Swingle is a major factor underlying the impressively wide expansion of this species in Europe and North America. We studied the specific mechanism used by *A. altissima* to withstand drought by subjecting potted seedlings to four irrigation regimes. At the end of the 13-week treatment period, soil water potential was –0.05 MPa for well-watered control seedlings (W) and –0.4, –0.8 and –1.7 MPa for drought-stressed seedlings (S) in irrigation regimes S1, S2 and S3, respectively. Root and shoot biomass production did not differ significantly among the four groups. A progressively marked stomatal closure was observed in drought-stressed seedlings, leading to homeostasis of leaf water potential, which was maintained well above the turgor loss point. Root and shoot hydraulics were measured with a high-pressure flow meter. When scaled by leaf surface area, shoot hydraulic conductance did not differ among the treated seedlings, whereas root hydraulic conductance decreased by about 20% in S1 and S2 seedlings and by about 70% in S3 seedlings, with respect to the well-watered control value. Similar differences were observed when root hydraulic conductance was scaled by root surface area, suggesting that roots had become less permeable to water. Anatomical observations of root cross sections revealed that S3 seedlings had shrunken cortical cells and a multilayer endodermal-like tissue that probably impaired soil-to-root stele water transport. We conclude that *A. altissima* seedlings are able to withstand drought by employing a highly effective water-saving mechanism that involves reduced water loss by leaves and reduced root hydraulic conductance. This water-saving mechanism helps explain how *A. altissima* successfully competes with native vegetation.

Keywords: hydraulic conductance, root anatomy, stomatal conductance, tree of heaven, weed.

Introduction  The invasion of natural habitats by alien plants is a serious threat to the conservation of biodiversity of ecosystems throughout the world (Loope et al. 1988, Hood and Naiman 2000). Among woody alien plants invading temperate and Mediterranean ecosystems, *Ailanthus altissima* (Mill.) Swingle (tree of heaven) is one of the most successful competitors with native vegetation. *Ailanthus altissima* is a deciduous tree native to China. Since its introduction into Europe during the second half of the eighteenth century, this species has greatly expanded its distribution range throughout both Europe and North America (Kowarik 1995, Knapp 2000), becoming an important weed. On the other hand, the well-known stress tolerance of *A. altissima* makes it an interesting candidate for the remediation of marginal or degraded areas, especially in the semi-arid Mediterranean regions where its use for industrial biomass production has been proposed (Tsao et al. 2002).

Despite the threat to natural biodiversity represented by *A. altissima* and its potential commercial value, our understanding of the physiological bases of competitiveness and stress tolerance of this species is limited. We are unaware of any published studies describing the mechanisms of drought resistance used by *A. altissima*. Generally, plant growth and productivity are largely dependent on water availability and plant responses to water shortage (Levitt 1980). Several morphological and physiological traits are involved in drought resistance, including rooting depth, stomatal control of transpiration and xylem vulnerability to cavitation. In recent years, increasing attention has focused on changes in water permeability of roots in response to drought (e.g., Facette et al. 1999, Steudle 2000, Tyree et al. 2002). For example, roots have been reported to be more vulnerable to cavitation compared with stems (Sperry and Ikeda 1997), and important morphological and anatomical changes have been reported to occur in roots of plants subjected to water shortage, leading to severe impairment of water uptake (Dubrovsky et al. 1998). Lo Gullo et al. (1998) reported that a substantial reduction in root hydraulic conductance ($K_r$) of *Olea oleaster* Hoffm. et Link seedlings occurred during drought stress; after soil rewetting, $K_r$ recovered only after the production of new roots. Thus, the hydraulics of the root system is an important determinant of the plant response to water stress (Nardini et al. 2002).

In the present study, we measured water relations parameters, including root and shoot hydraulics, of *A. altissima* seedlings subjected to increasing drought to characterize the physiological and anatomical bases of its resistance to drought. Specifically, we subjected seedlings to irrigation re-
gimes intended to simulate the gradually decreasing water availability during a typical Mediterranean spring. The Mediterranean-type climate is characterized by wet, mild winters and dry, hot summers. During spring, soil water storage progressively decreases so that water stress develops in plants in late April to May, when rainfall is greatly reduced and maximum air temperatures exceed 25 °C. Our protocol decreased water availability gradually to avoid the commonly used experimental design of abruptly depriving potted plants of irrigation and inducing unnatural responses that can lead to an overestimate of the actual water stress suffered by the plants.

Materials and methods

Plant material and growth conditions

Experiments were performed on 60 two-year-old seedlings of *A. altissima* collected from a natural stand along a roadside near the village of Basovizza, Trieste, northeastern Italy, in October 2001. Seedlings had a height of 0.60 ± 0.19 m and a trunk diameter of 6.0 ± 0.9 mm measured 20 mm above ground. Seedlings were carefully excavated to limit damage to the root system and planted in cylindrical pots (height = 0.7 m, diameter = 0.2 m) filled with a 1:1 (v/v) mixture of sand and loam. The potted seedlings remained outside at the Botanical Garden of the University of Trieste until bud break started (late March 2002). The seedlings were then transferred to a greenhouse where they were gradually adapted to environmental conditions simulating those occurring during a typical Mediterranean spring. Over a 10-day period, air temperatures were increased to 27 ± 1 °C during the day and 22 ± 1 °C during the night and air relative humidity was set at 60 ± 5%. The greenhouse was covered with shading net so that the maximum diurnal photosynthetically active radiation (PAR) was about 500 µmol m–2 s–1 (measured with an LI-190SA quantum sensor, Li-Cor, Lincoln, NE).

When first moved to the greenhouse, all seedlings were irrigated to field capacity. Seedlings were then randomly assigned to four groups (15 seedlings per group). The control group was well irrigated (W, Figure 1), whereas the other three groups of seedlings were water-stressed by progressively reducing the volumes of water supplied (S1, S2 and S3, Figure 1). From the seventh week to the end of the experiment, each W seedling received 1.0 l of water per week, whereas each of the S1, S2 and S3 seedlings received 0.25, 0.11 and 0.05 l of water per week, respectively. The treatment irrigation regimes were maintained for 13 weeks. Seedlings were irrigated twice per week and all measurements were performed 3 days after the last irrigation. At the end of this period, soil samples were collected from five pots from each group with a soil sampler at a depth of 0.3 m (i.e., at about half of pot height) and soil water potential (Ψₛₒₚ) was measured immediately with a WP4 Dewpoint PotentialMeter (Decagon Devices, Pullman, WA).

Leaf conductance to water vapor and water potential measurements

At the end of the 13-week treatment period, leaf conductance to water vapor (gₐ) and leaf water potential (Ψₐ) of W and S seedlings were measured. Measurements were performed between 1200 and 1400 h on two consecutive sunny days (PAR = 500 µmol m–2 s–1). Because *A. altissima* has odd-pinna leaves, gₛ and Ψₛ were measured on apical leaflets. We measured gₛ of at least 15 apical leaflets from different seedlings per group with a Li-Cor steady-state porometer (LI-1600) equipped with a 200-mm² leaf chamber. Each measurement took about 30 s. Leaf water potential was measured on at least seven apical leaflets from different seedlings per group with a pressure chamber (3005 Plant Water Status Console, Soil Moisture, Santa Barbara, CA). Leaves were detached from the seedling and wrapped in plastic film to prevent water loss, and Ψₛ of apical leaflets was measured immediately.

Leaf water potential isotherm measurements

Leaf water potential isotherms of five apical leaflets from different seedlings per group were determined from pressure–volume (P–V) curves (Tyree and Hammel 1972) measured with a pressure chamber. On the evening preceding the experiments, leaves were detached from the seedling and placed in contact with water that had been filtered to 0.1 µm to prevent vessel clogging and embolism. The leaves were kept in the dark and allowed to rehydrate overnight. Leaf water potential at the turgor loss point (Ψₛₒₚ), osmotic potential at full turgor (πₒ) and bulk modulus of elasticity (εₒtₐₐ) were calculated from the P–V curves, thus providing information about the leaf turgor range as well as leaf osmoregulation.

Shoot and root hydraulic conductance measurements

Root (Kₛ) and shoot (Kₐ) hydraulic conductance of seven seedlings per group were measured with a high-pressure flow meter (HPFM, Tyree et al. 1995) in the transient mode (Bogeat-Triboulot et al. 2002). All soils were rehydrated to field capacity 15 min before measurements to avoid possible errors in the estimate of Kₛ of seedlings growing in very dry soil. This procedure was intended to reestablish the hydraulic continuity between roots and soil that might have been interrupted because of soil or root contraction, or both, during soil desiccation. The shoots were excised under filtered water at about 50 mm above the soil. This was achieved by excising shoots after enclosing the pots in plastic bags to prevent soil rehydration and then immersing them in water. During Kₛ measurements, the cut surfaces of the shoots remained immersed in water. The HPFM was first connected to the base of the excised root system. The pressure was increased from 0.03 to 0.50 MPa within 90 s, while recording flow (F) and pressure (P) every 3 s. Root hydraulic conductance was calculated from the slope of the linear region of the relationship between F and P. Five to seven transient measurements per seedling were performed. The base of the stem was then connected to the HPFM and Kₐ was measured as described.

After each experiment, the length of the current-year stem was recorded and total leaf surface area (Aₐ) was measured with a Li-Cor leaf area meter (LI-3000A equipped with an LI-3050A). To estimate the total surface area of fine roots (Aₛ), soil was carefully removed from the root system under a
gentle jet of water, and fine roots (< 2 mm diameter) were excised in 20-mm segments. Root surface area of 10 subsamples per group was calculated by placing the root segments in a glass box and covering them with a white plastic sheet to keep them in a fixed position while improving the contrast of the root images. The box was placed on a scanner connected to a computer. The BMP images were read with custom-made software, and $A_R$ was calculated by multiplying the projected area by $\pi$, assuming the root segments were cylindrical in shape. To determine root dry mass (RDM), root subsamples were dried at 70 °C for 3 days. A conversion factor between RDM and $A_R$ was obtained. All fine roots collected from the root system were oven-dried and total $A_R$ of each seedling was computed by multiplying total fine root dry mass by the RDM:$A_R$ ratio.

Both $K_R$ and $K_S$ were scaled by $A_L$, thus obtaining leaf-specific root ($K_{RL}$) and shoot ($K_{SL}$) hydraulic conductance. We also scaled $K_R$ by $A_R$ to obtain root-specific hydraulic conductance ($K_{RR}$), i.e., root hydraulic conductance per unit root surface area.

Anatomical measurements

Changes in the hydraulic conductance of roots might depend on changes in root anatomy in response to drought stress (Lo Gullo et al. 1998, Nardini et al. 1998). Therefore, we monitored changes in the fine root structure of W and S3 seedlings. The root systems were removed from the soil as previously described. Roots were excised at about 6 mm from the tip (near the root hair zone). Samples were washed repeatedly in distilled water, dried on filter paper and fixed in a solution of 50% water and 50% formalin:acetic acid:ethanol (1:1:1, v/v). Samples were then dehydrated in an ethanol series, stained with Fast Green and embedded in paraffin. At least two 10-µm-thick cross sections from five seedlings per group tested were observed with the aid of a light microscope. To observe suberized cell walls, an equal number of root cross sections were stained with Sudan III.

Statistics

Data were analyzed with the SigmaStat 2.0 (SPSS, Chicago, IL) statistics package. One-way ANOVA was used to test differences between experimental groups. We used Tukey’s test to make post-hoc pairwise comparisons between all means.

Results

The experimental irrigation regimes applied to the seedlings (Figure 1) ranged between near field capacity and severe soil desiccation. Soil water potentials, measured 13 weeks after the beginning of the experiments, were –0.05 MPa for the well-watered treatment (W, Figure 1), compared with –0.42, –0.84 and –1.73 MPa for the S1, S2 and S3 treatments, respectively (Figure 1). Contrary to expectations, current-year stem length ($L_{cy}$), $A_L$ and $A_R$ were not statistically different among treatments at the end of the 13-week experiment (Table 1).

Table 1. Length of current-year twig growth ($L_{cy}$), total leaf surface area ($A_L$) and total surface area of fine roots ($A_R$) measured in well-watered (W) and in progressively drought-stressed (S1, S2 and S3, see Figure 1) $A. altissima$ seedlings after 13 weeks in different irrigation regimes. Values are means ± SD ($n = 15$). None of the treatment differences were significant for any parameter.

<table>
<thead>
<tr>
<th>Regime</th>
<th>$L_{cy}$ (m)</th>
<th>$A_L$ (m²)</th>
<th>$A_R$ (m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Well-watered (W)</td>
<td>0.059 ± 0.022</td>
<td>0.181 ± 0.089</td>
<td>0.042 ± 0.016</td>
</tr>
<tr>
<td>Mild stress (S1)</td>
<td>0.058 ± 0.015</td>
<td>0.149 ± 0.047</td>
<td>0.050 ± 0.016</td>
</tr>
<tr>
<td>Moderate stress (S2)</td>
<td>0.048 ± 0.010</td>
<td>0.140 ± 0.045</td>
<td>0.044 ± 0.013</td>
</tr>
<tr>
<td>Severe stress (S3)</td>
<td>0.059 ± 0.023</td>
<td>0.160 ± 0.060</td>
<td>0.040 ± 0.010</td>
</tr>
</tbody>
</table>

Figure 1. Irrigation regimes, expressed as liters of water per week, applied to potted $A. altissima$ seedlings. Soil water potentials ($\Psi_s$; MPa) measured at the end of the 13-week experimental period (see abscissa) are reported as means ± SD, $n = 7$. 
Seedlings reacted to increasing soil desiccation by marked stomatal closure as indicated by consistently decreasing \( \gamma_L \) (Figure 2A). Midday \( \gamma_L \) was about 230 mmol m\(^{-2}\) s\(^{-1}\) in W seedlings but decreased to about 100, 40 and 10 mmol m\(^{-2}\) s\(^{-1}\) in S1, S2 and S3 seedlings, respectively, with highly significant differences between treatments (\( P < 0.001 \)). Leaf water potential tended to decrease with increasing soil desiccation from about \(-1.1\) to \(-1.45\) MPa, but the differences between irrigation regimes were not statistically significant (Figure 2B).

We note that all midday \( \Psi_L \) values were well within the positive turgor region, because \( \Psi_{tlp} \) was much more negative than midday \( \Psi_L \) for all seedlings, including the most severely water-stressed seedlings in the S3 treatment (Figure 1). In S3 seedlings, \( \Psi_L \) was about \(-1.45\) MPa (Figure 2), whereas \( \Psi_{tlp} \) was as low as \(-2.5\) MPa (Figure 3A). Values of \( \Psi_{tlp} \) in W seedlings were about \(-1.8\) MPa (Figure 3A). Differences in \( \Psi_{tlp} \) between treatments were statistically significant (\( P < 0.001 \)). Because of the relative constancy of midday \( \Psi_L \) in seedlings in all of the irrigation regimes, \( \pi_0 \) (Figure 3A) was also similar (about \(-1.5\) MPa) among seedlings in all treatments. The treatments significantly affected \( \varepsilon_{max} \), and changes in \( \varepsilon_{max} \) (from about 23 MPa in W seedlings to about 34 MPa in S3 seedlings) paralleled changes in \( \Psi_{tlp} \) (Figure 3B).

Hydraulic measurements revealed marked differences between \( K_{SL} \) and \( K_{RL} \) in seedlings subjected to increasing water stress (Figure 4). Values of \( K_{SL} \) were similar (about \( 4.0 \times 10^{-5} \) kg s\(^{-1}\) m\(^{-2}\) MPa\(^{-1}\)) in seedlings in all treatments, whereas \( K_{RL} \) decreased gradually with increasing water stress from about \( 6.4 \times 10^{-5} \) kg s\(^{-1}\) m\(^{-2}\) MPa\(^{-1}\) in W seedlings to less than \( 2.0 \times 10^{-5} \) kg s\(^{-1}\) m\(^{-2}\) MPa\(^{-1}\) in S3 seedlings. Roots were only moderately sensitive to the S1 and S2 treatments (corresponding to \( \Psi_{soil} = -0.42 \) and \(-0.84\) MPa, respectively, Figure 1) in that \( K_{RL} \) of S1 and S2 seedlings remained between 5.0 and \( 5.3 \times 10^{-5} \) kg s\(^{-1}\) m\(^{-2}\) MPa\(^{-1}\), i.e., only 20% less than \( K_{RL} \) of W seedlings.

When root hydraulic conductance was scaled by root surface area (\( K_{RR} \), Figure 5), highly significant differences between treatments (\( P < 0.01 \)) were noted. Thus, S1, S2 and S3
seedlings underwent reductions in $K_{RR}$ of 36, 44 and 70%, respectively ($K_{RR}$ decreased from $25.0 \times 10^{-5}$ kg s$^{-1}$ m$^{-2}$ MPa$^{-1}$ in W seedlings to about 16.0, 14.0 and $7.5 \times 10^{-5}$ kg s$^{-1}$ m$^{-2}$ MPa$^{-1}$ in S1, S2 and S3 seedlings, respectively).

Anatomical observations of cross sections of fine roots (Figure 6) revealed that, in S3 seedlings (Figure 6B), root cortical cells were consistently shrunken and a multilayer endodermal-like tissue with suberized walls was present (Figure 6C) with...
no visible root hairs. In contrast, roots of W seedlings had a single-layer endodermis, rounded cells in the cortex and several root hairs (Figure 6A). These anatomical differences between W and S3 seedlings indicate that the radial hydraulic conductance of water-stressed fine roots would likely be severely impaired by the suberized endodermal belt, which is relatively impermeable to water.

Both $K_{RL}$ and $K_{RR}$ correlated linearly with $\Psi_{soil}$ ($r^2 = 0.96$ and 0.89, respectively) (Figure 7A). When $g_L$ was plotted against $\Psi_{soil}$ or $K_{RL}$ (Figures 7B and 7C), $g_L$ was correlated with, and an exponential function of, both $\Psi_{soil}$ and $K_{RL}$. A $g_L$ value of less than 40 mmol m$^{-2}$ s$^{-1}$ is considered to reflect stomatal closure; this value was observed at a $\Psi_{soil}$ of about −1.0 MPa and a $K_{RL}$ of about 4.0 $\times$ 10$^{-5}$ kg s$^{-1}$ m$^{-2}$ MPa$^{-1}$.

**Discussion**

The irrigation regimes induced progressively more severe soil drying (Figure 1). In particular, S3 seedlings experienced severe soil desiccation, with $\Psi_{soil}$ reaching values as low as −1.73 MPa. Minimum annual predawn leaf water potentials ($\Psi_{pd}$, commonly considered to be an estimate of $\Psi_{soil}$) recorded for different species growing at the site from which our seedlings were collected were reported to be between −0.4 and −1.0 MPa for *Cotinus coggygria* Scop. and *Prunus mahaleb* L. but as low as −1.64 MPa for *Fraxinus ornus* L. (Nardini et al. 2003). Even more negative $\Psi_{soil}$ values have been estimated (on the basis of $\Psi_{pd}$) for degraded areas of the Mediterranean coastal area of Turkey (Vertovec et al. 2001) and in Sicily (Lo Gullo and Salleo 1988).

*Ailanthus altissima* seedlings subjected to $\Psi_{soil}$ values comparable with field values suffered no reduction in growth compared with seedlings that were kept well irrigated (Table 1). This finding suggests that *A. altissima* is well equipped to cope with dry soil. We note, however, that our $\Psi_{soil}$ values were recorded only at the end of the experiment. Before the treatments began, all seedlings were irrigated to field capacity and water supply was gradually reduced during the next 6 weeks. It is therefore possible that most growth occurred during the first 2 to 3 weeks of the experiment, and this might have masked eventual differences between treatments. This does not invalidate our experimental design, however, because a mechanism for coping with summer drought that consists of completing most growth within the early spring period is a common feature of species growing in the Mediterranean Basin region (Lo Gullo and Salleo 1988).

Even under mild water stress conditions ($\Psi_{soil} = −0.4$ and −0.8 MPa in the S1 and S2 irrigation regimes, respectively), *A. altissima* seedlings reacted to water shortage by closing their stomata (Figure 2A), thus effectively reducing water loss. We found that, compared with W seedlings, $g_L$ was reduced by about 60% in S1 seedlings and by about 90% in S2 and S3 seedlings (Figure 2A). This suggests that *A. altissima* adopted a drought avoidance strategy based on water conservation, as defined by Levitt (1980). Stomatal closure proved to be effective, because $\Psi_{L}$ measured in water-stressed seedlings was not significantly different from that in the well-irrigated controls (Figure 2B), although a general trend toward slightly more negative values was observed. We note that, in every case, $\Psi_{tp}$ was 0.7–0.9 MPa more negative than $\Psi_{L}$ (Figure 3A), indicating that the leaves retained a large fraction of their turgor. Moreover, $\Psi_{tp}$ decreased substantially from W to S3 seedlings (Figure 3A). This was not a result of osmoregulation ($\pi_0$ was not statistically different among treatments, Figure 3A) but of changes in cell elasticity. Changes in $\varepsilon_{max}$ paralleled variations in $\Psi_{tp}$, with leaf cells becoming more rigid at decreasing soil
water availabilities. This behavior has already been reported for other species (e.g., Marsal and Girona 1997) and might help to explain the similar growth recorded in all our seedlings regardless of irrigation treatment.

Many studies have reported effective stomatal control of embolism in different woody and herbaceous plants (Jones and Sutherland 1991, Nardini and Salleo 2000, Cochard 2002). This refers to control of transpiration by stomatal closure, resulting in buffering of xylem water potential within the threshold value inducing xylem cavitation (Tyree and Sperry 1989). We did not measure vulnerability to cavitation, but we note that $\Psi_L$ of our seedlings was buffered between $-1.1$ and $-1.5 \, \text{MPa}$ (Figure 2), which has been reported as a common threshold value for xylem cavitation in many temperate and Mediterranean woody plants (Harvey and van den Driessche 1997, Nardini and Salleo 2000, Lemoine et al. 2002). Therefore, it is possible that stomatal closure in our water-stressed A. altissima seedlings prevented xylem cavitation and consequent impairment of water transport from roots to leaves. We observed a relative constancy of shoot hydraulic conductance (Figure 4), suggesting that stems and leaves of water-stressed seedlings had hydraulic efficiencies similar to those of well-irrigated seedlings. We note, however, that we measured $K_{SL}$ by the HPFM technique, which is not suitable for measuring embolism-induced loss of conductance because the high pressures applied during measurements (up to 0.5 MPa) are likely to dissolve any gas bubbles present in xylem elements. Therefore, the constancy of $K_{SL}$ recorded in our seedlings subjected to different degrees of water stress indicates that: (1) control and water-stressed seedlings did not differ in terms of total amount of conductive tissue; (2) water-stressed seedlings did not undergo any net permanent blockage of xylem conduits by solid bodies like tyloses or gums; and (3) no significant change in water permeability occurred in the leaf extra-vascular pathway where most shoot hydraulic resistance resides (Morillon and Chrispeels 2001, Tirey et al. 2001).

In contrast to the relative constancy of $K_{SL}$, $K_R$ appeared to decrease in response to water limitation (Figures 4 and 5). When scaled by leaf surface area, however, $K_R$ was reduced by less than 20% in S2 and S3 seedlings compared with W seedlings (Figure 4), suggesting that A. altissima seedlings can maintain sufficiently high rates of water uptake per unit leaf surface area under moderate drought conditions. Substantial loss of $K_{SL}$ (over 70% with respect to controls) was observed, however, in S3 seedlings. Drought-induced loss of hydraulic conductance of the root system may depend on several alterations in root anatomy or physiology including xylem embolism (Sperry and Ikeda 1997), root shedding (Eissenstat et al. 1999), anatomical changes along the radial water pathway (Steedle 2000, Nardini et al. 2002) and aquaporin expression (Javot and Maurel 2002). We did not measure the cavitation-induced loss of conductance of root segments of A. altissima in response to drought; however, xylem embolism would have to be very severe to cause a significant reduction in total $K_R$ because the hydraulic resistance of the soil-to-root radial pathway is much higher than the axial hydraulic resistance in the root (Frensch and Steudle 1989). On the basis of the axial-to-radial hydraulic resistance ratio, we computed that a 50% reduction in axial conductance of a woody root segment can be expected to result in less than a 5% reduction in total $K_R$ (Nardini et al. 2002). Other effects of drought may, therefore, play a role in reducing $K_R$. In our seedlings, the root surface area, as estimated at the end of the experiments, did not differ between W and S seedlings (Table 1). Despite the errors associated with estimating $A_R$ of roots excavated from soil, our data suggest that no significant root shedding occurred as a consequence of drought. Thus, we conclude that reduced water supply to foliage was not a result of loss of water-absorbing root surface of water-stressed seedlings but was associated with the reduced water permeability of roots (Figure 5). In turn, the reduced water permeability of roots was likely caused by the production of multilayer endodermal-like tissue (Figure 6C) in fine roots of water-stressed seedlings, which can be expected to substantially increase the hydraulic resistance of the soil-to-root stele pathway. Similar drought-induced changes in root anatomy leading to comparable reductions in $K_R$ have been reported previously (e.g., Dubrovsky et al. 1998, Lo Gullo et al. 1998, Nardini et al. 1998).

Both $K_{RL}$ and $K_{RR}$ were linearly and positively related to $\Psi_{wil}$ (Figure 7A), suggesting that roots are sensitive to soil desiccation. A close relationship between $g_L$ and $\Psi_{wil}$, as depicted in Figure 7B, is often interpreted as evidence for chemical signals originating in the drying roots and transported to leaves, where they induce stomatal closure. We found a similarly close relationship between $g_L$ and $K_{SL}$, indicating that reduced $g_L$ in water-stressed A. altissima seedlings might be associated with hydraulic limitation of gas exchange (Nardini and Salleo 2000, Sperry 2000). Although the relative constancy of $\Psi_L$ in seedlings in all irrigation regimes as well as the large leaf turgor could be interpreted as evidence that chemical root-to-shoot signaling was triggered by soil desiccation (Tardieu and Davies 1993), the hydraulic limitation per se might have led to the stomatal response, as suggested by Sperry (2000). Our data strongly suggest that studies dealing with the effect of root drying on stomatal conductance should take into account the hydraulics of roots because these organs are sensitive to several abiotic stresses including drought.

The wide expansion of A. altissima in areas with pronounced summer droughts, as well as its successful competition with most Mediterranean species, is apparently associated with a highly effective water conserving mechanism that includes substantial reduction in water loss by leaves (reduced $g_L$) and a simultaneous reduction in root hydraulic conductance. This transient interruption of the hydraulic continuity with soil limits water loss to the soil. Such a mechanism allows plants to maintain high leaf water status (at all times, $\Psi_L$ was much higher, i.e., less negative, than $\Psi_{wil}$) thereby preserving the functional integrity of the photosynthetic apparatus. The observed maintenance of root biomass in water-stressed seedlings led to the conclusion that, after soil rewetting, the pericycle activity can produce new lateral roots without a large carbon investment. Even the S3 seedlings suffered no reduc-
tion in epigeal biomass during the experimental drought and grew as well as well-watered seedlings.

Our results provide an ecophysiological explanation for the high growth potential of *A. altissima* under water-stress conditions and indicate that the species has potential for commercial use in degraded or marginal areas of the Mediterranean Basin.

Acknowledgments

This study was funded by University of Trieste (Progetto Giovani Ricercatori 2001) and by Fondazione Cassa di Risparmio di Trieste.

References


