

Temperature-Dependent Water and Ion Transport Properties of Barley and Sorghum Roots¹

I. Relationship to Leaf Growth

Hormoz BassiriRad², John W. Radin*, and Kaoru Matsuda

Department of Plant Sciences, University of Arizona, Tucson, Arizona 85721 (H.B., K.M.), and United States Department of Agriculture, Agricultural Research Service, Western Cotton Research Laboratory, Phoenix, Arizona 85040 (J.W.R.)

ABSTRACT

Root temperature strongly affects shoot growth, possibly via “nonhydraulic messengers” from root to shoot. In short-term studies with barley (*Hordeum vulgare* L.) and sorghum (*Sorghum bicolor* L.) seedlings, the optimum root temperatures for leaf expansion were 25° and 35°C, respectively. Hydraulic conductance (L_p) of both intact plants and detached exuding roots of barley increased with increasing root temperature to a high value at 25°C, remaining high with further warming. In sorghum, the L_p of intact plants and of detached roots peaked at 35°C. In both species, root temperature did not affect water potentials of the expanded leaf blade or the growing region despite marked changes in L_p . Extreme temperatures greatly decreased ion flux, particularly K^+ and NO_3^- , to the xylem of detached roots of both species. Removing external K^+ did not alter short-term K^+ flux to the xylem in sorghum but strongly inhibited flux at high temperature in barley, indicating differences in the sites of temperature effects. Leaf growth responses to root temperature, although apparently “uncoupled” from water transport properties, were correlated with ion fluxes. Studies of putative root messengers must take into account the possible role of ions.

Root zone temperature fluctuates both diurnally and seasonally, exerting diverse effects on plants. In many species, shoot growth responds strongly to changes in the temperature of the root environment (4–6, 18, 19, 27). In addition, root temperature significantly influences stomatal behavior (3, 18, 22), leaf water status (3, 22), and the expression of symptoms due to nutrient deficiencies and other environmental stresses (4, 22, 26). Despite these important consequences, the mechanism(s) coupling root temperature to shoot responses are poorly characterized. Root temperature is reported to affect both water and ion transport (10, 13), and either of these changes could alter shoot growth by limiting the supply of water and nutrients to the expanding tissue. More recently,

several reports have implicated nonhydraulic messengers (perhaps hormonal) from the root system in the control of shoot responses (18, 22, 27, 30). The existence of such messengers is inferred, in part, from the failure to find changes in shoot water status associated with changes in shoot behavior. Although negative evidence may allow inferences about the existence of messengers, it does not *per se* establish their nature. Further deductions about the involvement of hormones require more detailed knowledge of the possible alternative messengers functioning within a system.

Here we characterize the short-term responses of barley and sorghum to root temperatures from 15 to 40°C. These two species are acclimated to widely different temperature ranges during the growing season and were expected to be affected differently by root temperature. Root water transport properties (J_v^3 and L_p) were studied using both intact plants and excised roots. Fluxes of K^+ , NO_3^- , and PO_4^{3-} were studied with detached roots. Because ion influx into the root and release to the xylem may be differentially regulated (12, 21), an attempt was also made to separate these two processes and assess the effects of root temperature on each. All determinations of plant water status and root water and ion transport properties were carried out within 4 h after the commencement of root temperature treatments, so that some of the earliest processes controlling root temperature-induced changes in shoot growth might be identified.

MATERIALS AND METHODS

Growth Conditions

Seeds of barley (*Hordeum vulgare* L. cv ‘Arivat’) and sorghum (*Sorghum bicolor* L. cv ‘Funks’) were germinated in vermiculite and transferred to modified half-strength Hoagland solution (8) at 4 and 6 d of age, respectively. Before and after transplanting, seedlings were grown at $25 \pm 2^\circ\text{C}$ with 13

¹ This work was supported in part by Western Regional Project W-154 and is journal paper No. 7332 of the University of Arizona Agricultural Experiment Station.

² Present address: Department of Range Science, Utah State University, Logan, UT 84322.

³ Abbreviations and symbols: J_v , volume flux; ψ_w , water potential; ψ_{GR} , ψ_{EB} , ψ_r , ψ_x , ψ_o , water potentials of the growing region of the leaf, expanded blade, root, xylem, and medium, respectively; π , osmotic pressure; π_x , π_o , osmotic pressures of the xylem exudate and medium, respectively; L_p , hydraulic conductance; J_i , ion flux; C_i , ion concentration in the xylem exudate; σ , reflection coefficient.

h daily light (250 to 300 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD). In some experiments, the nutrient solution was modified to obtain a K^+ -deficient medium as described by Kurtz and McEwan (11). The π values of the two solutions were identical (measured by vapor pressure osmometry). The root medium was vigorously aerated throughout the experiments.

Root Temperature Treatments

Temperature control was obtained by immersing the nutrient solutions containing the plants in several water baths, each set at a different but constant temperature. In most cases, data from more than one experiment had to be combined to construct a complete response curve from 15 to 40°C root temperature.

Growth Rate and Water Status

All measurements were taken on seedlings or detached roots of 5-d-old barley and 8-d-old sorghum at the same time of day to avoid physiological variations due to diurnal changes. Preliminary data revealed maximum growth rates in barley and sorghum seedlings at these respective ages. The length of the youngest leaf was determined with a ruler 2 and 4 h after initiation of root temperature treatments, and elongation rate was expressed as the average during that 2-h period. The air temperature was constant at 25°C. Tissue ψ_w and π were measured psychometrically (14), and turgor was calculated as $\psi_w + \pi$. In barley, ψ_{GR} is substantially lower than ψ_{EB} (24); therefore, the water status of both regions was determined. Our preliminary observations showed no such differences in the youngest sorghum leaf; therefore, only ψ_{EB} was determined. For determinations of ψ_w , five 0.5 cm-long segments from the leaf (growing or expanded blade regions) or the root were excised and placed in the psychrometer chambers. Root segments were blotted with paper towels, excised 5 to 5.5 cm from the tip in each plant; the growing and expanded segments of the leaf were excised 0 to 0.5 and 5 to 5.5 cm from the meristematic region of the shoot, respectively.

Volume Flow and Root Hydraulic Conductance

Flow rate in intact seedlings was determined by gravimetric measurements of transpiration. The basal regions of 10 seedlings were wrapped in 25- \times -100-mm polyurethane foam, and the roots were inserted in 25-mL plastic centrifuge tubes containing the continuously aerated nutrient solution. Thermocouples were also placed underneath the foam to monitor the temperature of the growing region. Replicate tubes containing the seedlings were weighed and placed in several water baths, each maintaining a different but constant temperature. Air temperature was constant at 25°C. After approximately 4 h at the constant root temperature, tubes were weighed again and the roots were severed from the seedlings and blotted with paper towels for fresh weight determination. The total volume flow in intact seedlings was expressed in units of $\mu\text{L g}^{-1}$ fresh weight h^{-1} . Root L_p of these intact seedlings was determined as the ratio $J_v/\Delta\psi_w$. The effective $\Delta\psi$ was taken to be the difference between the ψ_r and ψ_o , because ψ_r was the most realistic representation of the ψ_x (see "Results").

In work with detached roots, a capillary pipet was fitted to the stump of the root with a flexible tygon tube and roots were placed in vigorously aerated temperature-controlled medium. Rates of exudation from detached roots were determined from changes in the level of fluid in the capillary tube. The π_x and π_o were determined with a Wescor model 5500 vapor pressure osmometer. Root hydraulic conductance was calculated from:

$$J_v = L_p \sigma (\pi_x - \pi_o) \quad (1)$$

in which σ was assumed to be unity. Ion concentrations of xylem exudate from detached roots were determined by ion chromatography for anions and atomic absorption and flame emission analysis for cations. Ion fluxes were calculated from the relationship:

$$J_i = J_v C_i \quad (2)$$

All measurements with excised roots were made under steady-state conditions. A steady state was usually reached within 0.5 h after excision and was maintained for at least 5 h before J_v began a gradual decline.

RESULTS

Plant Growth Response

Short-term leaf growth rate of both barley and sorghum seedlings depended strongly on root temperature. The maxi-

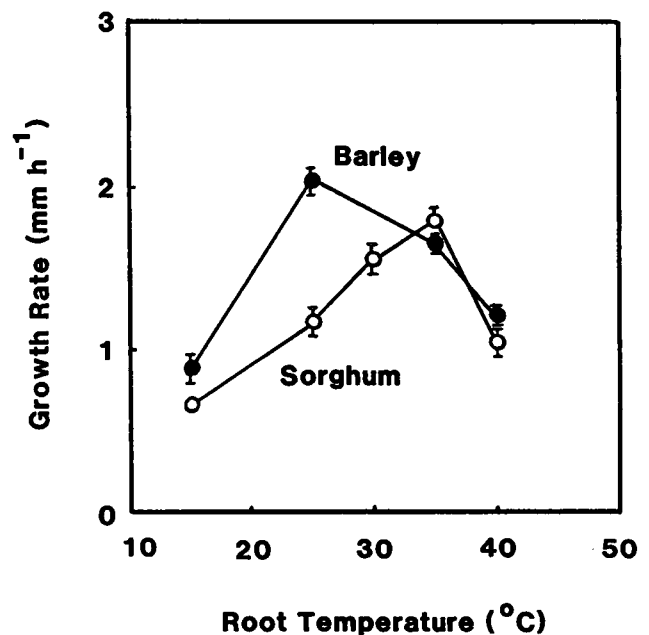


Figure 1. Short-term growth rates of leaves of barley and sorghum seedlings at different root temperatures. Growth was measured on the first leaf of 5-d-old barley and the second leaf of 8-d-old sorghum plants from 2 to 4 h after initiating the temperature treatments. Values are means \pm SE of 15 to 20 measurements. Error bars are not shown where they are smaller than the width of the symbol.

Table I. Influence of Root Temperature on Leaf and Root Water Status in Barley and Sorghum Seedlings

The ψ_w of the medium was constant at -0.08 to -0.10 MPa at all temperatures. Values are means \pm SE of four to five replicates.

Root Temperature °C	ψ_w		
	EB	GR	R
	MPa		
Barley			
15	-0.40 ± 0.04	-0.72 ± 0.05	-0.36 ± 0.03
25	-0.37 ± 0.03	-0.62 ± 0.05	-0.28 ± 0.05
35	-0.37 ± 0.02	-0.68 ± 0.04	-0.31 ± 0.03
Sorghum			
15	-0.62 ± 0.04		-0.30 ± 0.02
25	-0.54 ± 0.02	-0.54 ± 0.06	-0.28 ± 0.02
35	-0.62 ± 0.06		-0.30 ± 0.02
40	-0.61 ± 0.07		-0.31 ± 0.03

mum growth rate, measured within 4 h after beginning the treatments, occurred at 35°C in sorghum and 25°C in barley seedlings (Fig. 1). Growth rate of sorghum declined sharply at root temperatures above the optimum. Leaf temperature near the basal region was within $\pm 2^\circ\text{C}$ of the air temperature, indicating that differences in responses of the shoot were not due simply to warming or cooling of the leaf meristem. In other studies of barley seedlings (not shown), longer-term shoot growth responses were monitored at various root temperatures. At the end of the 4th d, 30, 50, and 65% of the plants had a new visible leaf in seedlings grown at 15, 25, and 35°C root temperatures, respectively. Thus, the inhibition of growth at high temperature did not indicate generally deleterious effects on all metabolic processes. In addition, effects of high temperature were rapidly reversible after more favorable conditions were restored (data not shown), indicating no long-lasting damage.

Seedling Water Status

The ψ_w of leaf and root were independent of root temperature within the range tested (Table I). Matsuda and Riazi (15) and Riazi *et al.* (25) demonstrated that in barley seedlings the ψ_{GR} was significantly lower than the ψ_{EB} and that short-

Table II. Effect of Root Temperature on Leaf ψ_{GR} , ψ_r , and ψ_p in Barley and Sorghum Seedlings

Values are means \pm SE of four to five replicates. In sorghum, ψ_{GR} was estimated from measured values of ψ_{EB} for reasons described in the text.

Root Temperature °C	ψ_{GR}	ψ_r	ψ_p
	MPa		
Barley			
15	-0.72 ± 0.07	-1.08 ± 0.02	0.36 ± 0.06
25	-0.62 ± 0.03	-0.95 ± 0.03	0.34 ± 0.04
35	-0.69 ± 0.04	-0.99 ± 0.02	0.30 ± 0.04
Sorghum			
25	-0.54 ± 0.06	-0.97 ± 0.02	0.42 ± 0.06
35	-0.58 ± 0.04	-0.94 ± 0.04	0.35 ± 0.04

term changes in leaf elongation rate were more closely associated with ψ_{GR} than with ψ_{EB} . Our results confirm the difference between ψ_{GR} and ψ_{EB} in barley, but root temperature did not alter the water status of either region (Table I) despite markedly altering elongation rate. In sorghum, leaf ψ_w determinations were made only in the expanded blade, because the ψ_{EB} was similar to ψ_{GR} in plants grown at 25°C root temperature (Table I), and the same relationship was assumed at other temperatures as well. Leaf ψ_w in sorghum was also unaffected by root temperature (Table I). The results show that short-term effects of root temperature on leaf growth were unrelated to tissue ψ_w . Cell turgor in the growing region was considered as a possible growth-limiting factor, but it also did not change significantly with root temperature (Table II).

J_v and L_p in Intact Seedlings

The flux of water through the seedlings depended strongly on root temperature. In intact sorghum seedlings, J_v increased up to 35°C and then declined at higher temperatures, whereas in barley, J_v increased with increasing root temperature up to 25°C and remained almost unchanged at 35°C (Fig. 2). Root L_p in intact seedlings was estimated from $J_v/\Delta\psi$. However, a major difficulty when using this ratio is to determine the effective driving force for root water transport. Often, the $\Delta\psi_w$ between the expanded leaf tissue and the medium has been

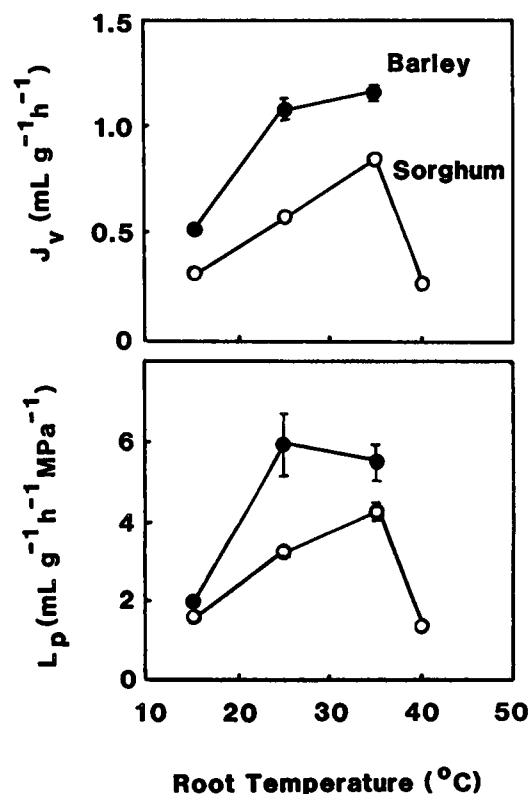


Figure 2. Influence of root temperature on J_v and root L_p in intact barley and sorghum seedlings. Values of J_v are means \pm SE of six measurements. Values of L_p are derived from mean J_v and from mean $\psi_o - \psi_r$, with ψ_r from Table I.

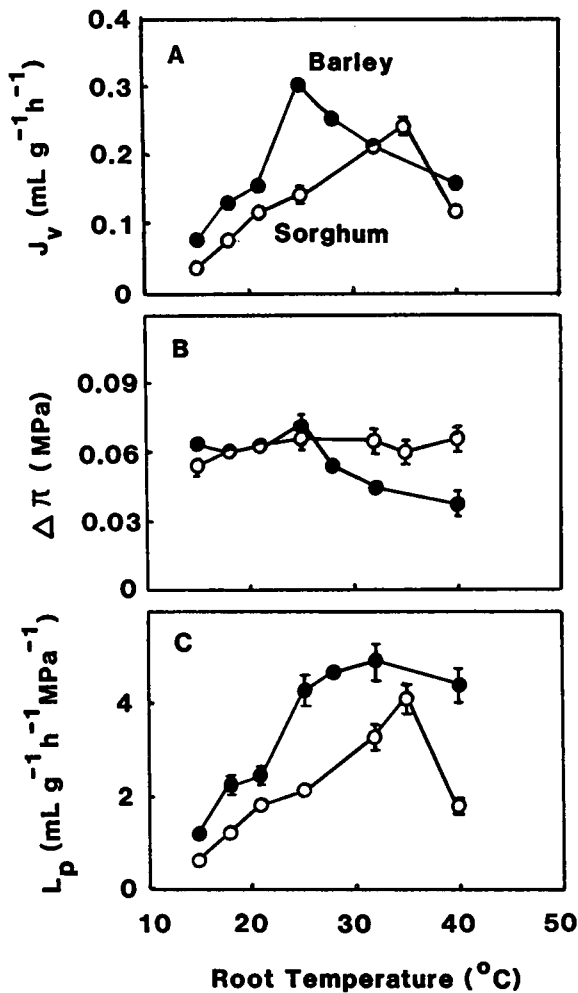


Figure 3. Influence of temperature on J_v , $\nabla\pi$, and L_p in excised roots of barley and sorghum seedlings. Measurements were made during steady-state flow within 4 h following excision. Values are means \pm SE of six measurements. Error bars are not shown where they are smaller than the width of the symbol.

used as the effective gradient to calculate root L_p , with the implicit assumption that, at steady state, the ψ_{EB} is a close approximation of ψ_x . This assumption is questionable for many cereals such as barley which exhibit nonuniform leaf water status. Rayan and Matsuda (24) and Rayan (23) used ^3H -labeled water to show that, in barley seedlings under steady state conditions, water in the growing region and expanded blade had not equilibrated with that in the xylem even after 5 h of root exposure. In contrast, water in the xylem of the basal portion of the root was fully equilibrated with root tissue water within 15 min. Rayan and Matsuda (24) concluded that neither ψ_{EB} nor ψ_{GR} adequately described ψ_x . On the other hand, the ready equilibration within the root indicates that ψ_r is more likely to approximate ψ_x and, as a result, would describe the effective gradient for radial water flow more accurately than would leaf ψ_w . Root hydraulic conductances were, therefore, estimated from $J_v/(\psi_o - \psi_r)$. In sorghum, L_p increased with increasing root temperature up to 35°C and

then declined when temperature was elevated above 35°C (Fig. 2). Similar responses were observed for L_p , J_v (Fig. 2), and shoot growth rate (Fig. 1). In barley, the L_p response to temperature also resembled that observed for J_v (Fig. 2). Increasing temperature stimulated both J_v and L_p in the 15 to 25°C range but had no further effect at 35°C, although the growth rate declined (Fig. 1). Because the differences in ψ_w between various tissues and organs remained constant with root temperature, the response of L_p to root temperature was essentially the same regardless of which $\Delta\psi$ was used to estimate it.

J_v and L_p of Detached Roots

In barley, exudation rates of excised roots increased almost linearly with root temperature from 15 to 25°C (Fig. 3A). Above 25°C, however, J_v decreased with increasing temperature. The inhibition of J_v at elevated temperatures was accompanied by a loss of the osmotic driving force $\Delta\pi$ (Fig. 3B) but not a decrease of L_p (Fig. 3C). These effects of high temperature were completely reversible when roots were returned to the optimum temperature (2).

Temperature responses of excised sorghum roots differed from those of barley. In sorghum roots, J_v increased linearly with temperature from 15 to 35°C, but exudation decreased nearly one-half when the temperature was increased from 35 to 40°C. Because the osmotic gradient remained constant (Fig. 3B), the decrease in exudation at high temperature (Fig. 3A) can be attributed to a decrease in L_p (Fig. 3C) rather than a decrease in $\Delta\pi$, as was found for barley (Fig. 3B). As with barley roots, effects of changes in temperature were reversible (2).

It is important to note that, in both species, measurements of L_p of detached roots closely paralleled intact plant measurements of L_p despite the vast differences in methodology (Figs. 2 and 3).

Table III. Ionic Composition of Exudate from Barley and Sorghum Roots at 25 and 35°C

Samples were collected during steady-state exudation within 4 h after excision. Values are means \pm SE of six replicates.

Species	Ion Concentration			
	Barley		Sorghum	
	25°C	35°C	25°C	35°C
	<i>mm</i>			
Cations				
K ⁺	23.9 \pm 0.4	10.3 \pm 1.1	17.4 \pm 0.8	13.0 \pm 0.04
Na ⁺	2.6 \pm 0.1	2.2 \pm 0.2	1.8 \pm 0.1	1.3 \pm 0.04
Ca ²⁺	1.8 \pm 0.1	1.2 \pm 0.04	2.2 \pm 0.1	1.7 \pm 0.04
Mg ²⁺	2.2 \pm 0.1	0.8 \pm 0.1	1.9 \pm 0.1	1.6 \pm 0.1
Anions				
NO ₃ ⁻	23.0 \pm 0.3	10.3 \pm 0.5	19.2 \pm 1.2	13.1 \pm 0.6
Cl ⁻	3.9 \pm 0.5	3.3 \pm 0.3	3.1 \pm 1.0	3.3 \pm 0.3
PO ₄ ³⁻	4.5 \pm 0.2	3.8 \pm 0.4	3.8 \pm 0.7	4.3 \pm 0.2
Total	61.9	31.9	49.4	38.3

Ion Fluxes into the Xylem

The rate at which inorganic solutes are released into the xylem determines the rate of exudate production in excised roots, as well as the nutrient supply to the expanding tissues in intact plants. The major osmolytes in xylem exudate were NO_3^- and K^+ , which together accounted for about 70% of the total ions present in both sorghum and barley at either 25 or 35°C (Table III). The PO_4^{3-} and Cl^- ions each accounted for 10%, and Ca^{2+} , Mg^{2+} , and Na^+ together made up only 10% of the total ions. J_{NO_3} , J_{K} , and J_{PO_4} were determined because of both their predominance in the xylem and their importance as macronutrients affecting shoot growth. In both species J_{NO_3} and J_{K} , and consequently J_i , were enhanced by increased temperature in the 15 to 25°C range (Fig. 4). In this range, ion fluxes in barley were consistently higher than in sorghum. In barley between 25 and 35°C, J_i decreased by 50% (Fig. 4), a decline similar to those observed for $\Delta\pi$ and detached root J , (Fig. 3, A and B). In sorghum, these fluxes increased slightly or remained constant between 25 and 35°C (Fig. 4, A, B, and D). Ion fluxes in sorghum were severely inhibited when root temperature exceeded 35°C. Root temperature affected J_{PO_4} less than J_{NO_3} or J_{K} , but PO_4^{3-} concentration in the exudate was much lower than K^+ and NO_3^- concentrations.

Ion Uptake into the Root and Release into the Xylem

Ion flux may be largely regulated by symplastic release of ions into the xylem and by the rate of ion supply to the cytoplasm from either vacuoles or bathing medium (21). An

experiment was designed to identify the relative effects of temperature on these components of the transport pathway. Roots grown on half-strength Hoagland solution were excised and incubated at several temperatures in +K or -K nutrient solution. When K^+ is excluded from the medium (-K roots), J_{K} becomes primarily a function of ion release to the xylem supplied from internal sources, possibly the vacuoles (21). In barley roots, increasing temperature up to 25°C enhanced ion release to the xylem (Table IV). This response was independent of the K^+ status of the medium and, therefore, was almost entirely supplied by endogenous sources. At 35°C, J_{K} was decreased from the peak at 25°C, and inhibition was >60% greater in -K than +K roots (Table IV). The data imply that high-temperature injury to J_{K} involves inhibition of both ion influx to the root and transport to the xylem. In sorghum, J_{K} was unaffected by K^+ content of the medium at all temperatures tested (Table IV).

DISCUSSION

Root temperature has long been known to exert effects on shoot growth. Most early studies reported only long-term changes, without providing insights into mechanisms by which growth is affected (5, 19). Here we characterize changes in shoot water status and in water and ion transport through the root during the first 4 h after imposition of root temperature treatments. This allows the comparison of various temperature effects with leaf elongation rates early in the progression of symptoms, before secondary effects make interpretation more difficult.

Our interpretations are based on the assumption that $\sigma =$

Figure 4. Effect of temperature on fluxes of major ions (J_i) in excised roots of barley and sorghum seedlings. Total J_i at 25° and 35°C (D) is calculated from ion concentrations reported in Table I. At other temperatures, total J_i is estimated assuming that measured J_{K} , J_{NO_3} , and J_{PO_4} together represent 80% of the total. In A to C, all values are means \pm SE of six measurements; error bars are not shown where they are smaller than the width of the symbol. In D, calculated total J_i is shown without error estimates.

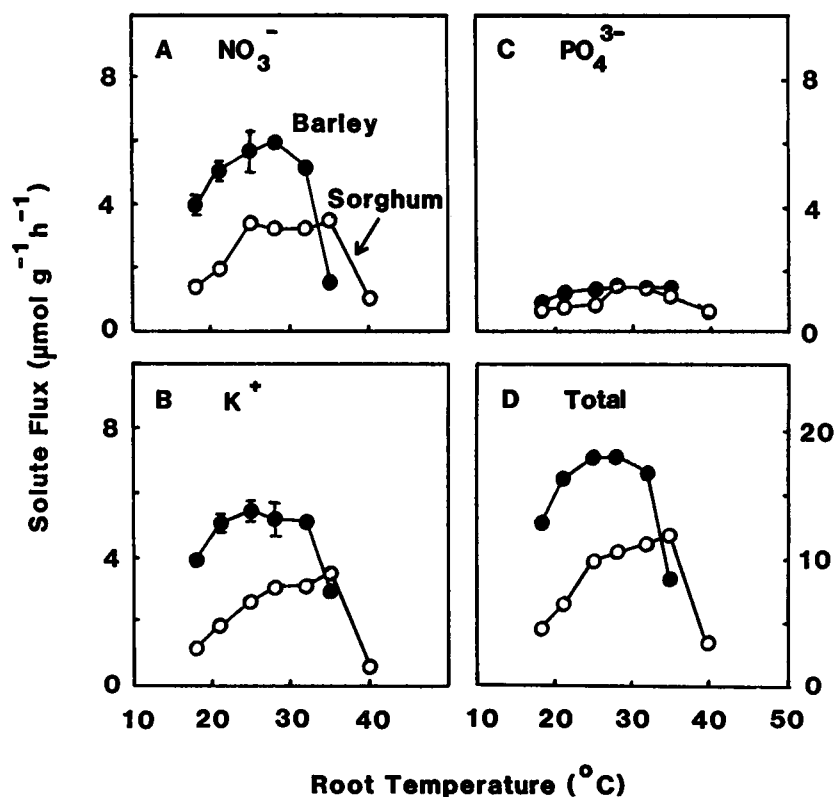


Table IV. Effect of Temperature and External K⁺ Supply on K⁺ Flux to the Xylem in Excised Barley and Sorghum RootsValues are means \pm SE of three to six replicates.

Root Temperature	K ⁺ Flux			
	Barley		Sorghum	
	+K	-K	+K	-K
$^{\circ}\text{C}$	$\mu\text{mol g}^{-1} \text{h}^{-1}$			
15	2.0 \pm 0.2	2.0 \pm 0.3		
20	3.5 \pm 0.5	3.2 \pm 0.5	0.9 \pm 0.0	0.9 \pm 0.1
25	4.4 \pm 0.5	4.1 \pm 0.4	1.8 \pm 0.2	2.0 \pm 0.2
35	2.8 \pm 0.5	1.1 \pm 0.3	2.0 \pm 0.1	1.7 \pm 0.1
40			0.9 \pm 0.3	0.9 \pm 0.3

l at all temperatures. Calculated values of L_p for excised roots could be erroneous if $\sigma \ll 1$, as might occur at extreme temperatures. Values of L_p derived from intact transpiring plants do not depend on σ , however, because in this case water flux is much less dependent on ion flux. The similarity of results with the two systems implies that changes in σ may not account for the temperature effects.

Regardless of whether L_p was determined in intact transpiring seedlings (Fig. 2) or excised roots (Fig. 3), the values of L_p followed the same pattern, and the two methods even produced quantitatively similar results. This finding indicates that properties of excised sorghum and barley roots realistically mimic those of roots of intact plants and that L_p can be determined accurately at low volume flow rates in excised roots (at least at this early stage of development). In this respect our results differ from those reported elsewhere, which suggest that high-flow methods should be used to measure L_p (7, 13). It is worth noting that, at these early stages of growth, transpirational flow through intact seedlings only moderately exceeded flow through exuding excised roots (approximately a 3:1 ratio; cf. Figs. 2 and 3). This relatively small difference may have contributed to the similarity of properties of intact and excised roots (2). BassiriRad (2) also found that a "reverse-flow" osmotic method led to similar values of L_p as those reported here but that pressurization of excised roots to increase the flow rate enhanced L_p by more than fourfold. The values derived from pressurized roots were considerably greater than those of intact plants, perhaps because pressurization may have altered the pathway of the water movement (20, 28).

The use of excised exuding roots allowed studies of ion transport in relation to water transport and leaf growth. In sorghum, increasing root temperature greatly increased the root L_p between 15 and 35°C but sharply inhibited it above 35°C (Figs. 2 and 3). Within the range tested, root temperature exerted only moderate effects on ion transport rates except at the extremes, when inhibition was severe (Fig. 4). Depriving the roots of an external source of K⁺, thereby eliminating K⁺ influx to the roots, did not alter J_K over the short-term (Table IV). In this species, temperature-induced changes in J_K and perhaps other ion fluxes resulted from effects on ion release to the xylem rather than influx into the roots. Differential behavior of ion uptake and transport into the xylem has been reported before (12, 21).

Leaf growth and L_p in sorghum responded similarly to root temperature, with both showing a sharp optimum at 35°C (Figs. 1–3). Despite this relationship, there was no effect of root temperature on the water status of the leaf. Thus, it is unlikely that water transport limited the leaf growth rate. In this species, ψ_{GR} was estimated from ψ_{EB} , because the two did not differ, in contrast to the barley leaf (Table I). Similarity of ψ_{GR} and ψ_{EB} may arise from errors in determination of ψ_{GR} because of cell wall relaxation after excision (16), although in barley (14) and maize (29), measurements of ψ_{GR} were unaffected by whether the tissue was excised or *in situ*. A more likely possibility is that the lack of a "growth-induced water potential" may result from the use of transpiring plants. Westgate and Boyer (29) found that transpiration affects both ψ_{EB} and ψ_{GR} of maize but to different degrees. Although growth may be more closely related to turgor than to ψ_{GR} (1, 9), this possibility is also discounted (Table II). The data are not consistent with a role for leaf water status in coupling leaf growth to root temperature. Growth was also related to ion transport, however, and a role for ions has not been ruled out.

In barley, root L_p increased strongly with increasing temperature up to 25°C and then remained constant with further increases in root temperature (Figs. 2 and 3). As with sorghum, root temperature did not affect ψ_{GR} despite greatly altered L_p (Table I). In barley, however, L_p was not correlated with leaf growth rate, which declined by about one-half when the temperature was increased from 25 (optimum) to 35°C (Fig. 1). Ion transport also declined markedly in the supraoptimal temperature range (Fig. 4). Further studies showed that external K⁺ supply limited J_K only at supraoptimal temperatures, implying that high temperature affected both K⁺ uptake and transport to the xylem (Table IV). In barley as well as in sorghum, some of the effects of extreme root temperatures on leaf growth might be mediated by ion supply (again, not through effects on turgor [Table II]).

Despite the similarities between excised roots and roots of intact seedlings, there are also important differences. In excised roots, L_p exerted important effects on J_v and contributed directly to its response to temperature (Fig. 3). In intact seedlings, J_v (transpiration) is controlled by the stomata, and effects of L_p are necessarily indirect, through leaf ψ_w . The observation that changes in root L_p were not accompanied by changes in leaf ψ_w (Table I) indicates that stomatal conductance must have been coupled somehow to root L_p . Meinzer and Grantz (17) and Radin (22) reported similar results with sugarcane and nutrient-stressed cotton, respectively. The changes in stomatal conductance and in leaf growth, despite constant ψ_w , imply that nonhydraulic messages are transmitted to the guard cells in addition to the zone of expansion. To the extent that root temperature affects ion transport to the xylem, ions may serve as messengers to the guard cells as well as to the growing region.

Many workers have suggested nonhydraulic signals from the root to the shoot (3, 22, 27, 30). To some degree this conclusion relies on negative evidence, *i.e.* exclusion of water status as a factor influencing shoot behavior. Our evidence is similar (Table I). Such evidence, however, does not by itself allow deductions about the nature of the signal. K⁺ (or another ion) may be such a signal at either high or low root tempera-

tures. In other work, ABA has been implicated in root-shoot communication (18, 27, 30). The dependence of shoot behavior on root temperature may be a complex interaction, possibly depending on numerous coupling factors operating simultaneously.

Finally, the responses of the root properties to temperature have agronomic and ecological significance. Soil temperatures fluctuate widely seasonally and (near the soil surface) diurnally, and vertical temperature gradients usually occur (19). Thus, the effects on water and ion transport may be substantial. Unlike long-term changes (4), short-term responses of root properties to temperature may alter water and ion fluxes irrespective of shoot demand. Quantitative understanding of growth and water use in a fluctuating environment will require detailed knowledge of the sort reported here.

ACKNOWLEDGMENTS

We thank Dr. J.W. O'Leary for many helpful discussions throughout the course of this work and Dr. A.J. Bloom for his critical comments.

LITERATURE CITED

1. Acevedo E, Hsiao TC, Henderson DW (1971) Immediate and subsequent growth responses of maize leaves to changes in water status. *Plant Physiol* **48**: 631-636
2. BassiriRad H (1990) Influence of Temperature on Root Water and Ion Transport and the Subsequent Effect on Shoot Water Status and Growth of Barley and Sorghum Seedlings. Ph.D. dissertation, University of Arizona, Tucson, AZ
3. Benzioni A, Dunstone RL (1988) Effect of air and soil temperature on water balance of jojoba growing under controlled conditions. *Physiol Plant* **74**: 107-112
4. Clarkson DT, Hopper MJ, Jones LHP (1986) The effect of root temperature on the uptake of nitrogen and the relative size of the root system in *Lolium perenne*. I. Solutions containing both NH_4 and NO_3 . *Plant Cell Environ* **9**: 535-545
5. Cooper AJ (1973) Root temperature and plant growth. Res Rev No. 4, Commonwealth Bureau of Horticulture and Plantation Crops, East Malling, England
6. Cumbus IP, Nye PH (1985) Root zone temperature effects on growth and phosphate absorption in rape (*Brassica napus* cv Emerald). *J Exp Bot* **163**: 219-227
7. Fiscus EL (1975) Interaction between osmotic and pressure-induced water flow in plant roots. *Plant Physiol* **55**: 917-922
8. Hoagland DR, Arnon DR (1938) The Water Culture Method for Growing Plants without Soil. University of California Agricultural Experiment Station Circular 347, Berkeley, CA
9. Hsiao TC (1973) Plant response to water stress. *Annu Rev Plant Physiol* **24**: 519-570
10. Kennedy CD, Gonsalves FAN (1988) H^+ efflux and trans-root potential measured while increasing the temperature of solution bathing excised roots of *Zea mays*. *J Exp Bot* **39**: 37-49
11. Kurtz EB, McEwan AM (1960) Introductory Plant Physiology Laboratory Manual. Burgess Publishing Co, Minneapolis, MN
12. Läuchli A (1984) Mechanisms of nutrient fluxes at membranes of the root surface and their regulation in the whole plant. In SA Barber, DR Bouldin, eds, *Roots, Nutrient and Water Influx and Plant Growth*, special publication No. 49. American Society of Agronomy, Madison, WI, pp 1-25
13. Markhart AH III, Fiscus EL, Naylor AW, Kramer PJ (1979) The effect of abscisic acid on root hydraulic conductivity. *Plant Physiol* **64**: 611-614
14. Mason H, Matsuda K (1985) Polyribosome metabolism, growth and water status in the growing tissues of osmotically stressed plant seedlings. *Physiol Plant* **64**: 95-104
15. Matsuda K, Riazi, A (1981) Stress-induced osmotic adjustment in growing regions of barley leaves. *Plant Physiol* **68**: 571-576
16. Matyssek R, Maruyama S, Boyer JS (1988) Rapid wall relaxation in elongating tissue. *Plant Physiol* **86**: 1163-1167
17. Meinzer FC, Grantz DA (1990) Stomatal and hydraulic resistance in growing sugar cane: stomatal adjustment to water transport capacity. *Plant Cell Environ* **13**: 383-388
18. Milligan SP, Dale JE (1988) The effect of root treatment on growth of the primary leaves of *Phaseolus vulgaris* L: general features. *New Phytol* **108**: 27-35
19. Neilson KF (1974) Roots and root temperature. In EW Carson, ed, *The Plant Root and Its Environment*. University Press of Virginia, Charlottesville, VA, pp 293-295
20. Passioura JB (1988) Water transport in and to roots. *Annu Rev Plant Physiol* **39**: 245-265
21. Pitman MG (1982) Transport across plant roots. *Q Rev Biophys* **15**: 481-554
22. Radin JW (1990) Response of transpiration and hydraulic conductance to root temperature in nitrogen- and phosphorus-deficient cotton seedlings. *Plant Physiol* **92**: 855-857
23. Rayan AM (1989) The Elucidation of the Pathway of Water Movement in Barley (*Hordeum vulgare* L) Seedling using Anatomical, Cytological and Physiological Approaches. Ph.D. dissertation, University of Arizona, Tucson, AZ
24. Rayan AM, Matsuda K (1988) The relation of anatomy to water movement and cellular response in young barley leaves. *Plant Physiol* **87**: 853-858
25. Riazi A, Matsuda K, Arsalan A (1985) Water stress-induced changes in concentrations of proline and other solutes in growing regions of young barley leaves. *J Exp Bot* **36**: 1716-1725
26. Sheppard SC, Racz GJ, Martin L (1986) Critical concentration of tissue phosphorus when root temperature depresses growth. *J Exp Bot* **37**: 1265-1273
27. Smith PG, Dale JE (1988) The effects of root cooling and excision on growth of primary leaves of *Phaseolus vulgaris* L. *New Phytol* **110**: 293-300
28. Steudle E, Boyer JS (1985) Hydraulic resistance to radial water flow in growing hypocotyl of soybean measured by a new pressure-perfusion technique. *Planta* **164**: 189-200
29. Westgate ME, Boyer JS (1984) Transpiration- and growth-induced water potentials in maize. *Plant Physiol* **74**: 882-889
30. Zhang J, Davies WJ (1990) Changes in the concentration of ABA in xylem sap as a function of changing soil water status can account for changes in leaf conductance and growth. *Plant Cell Environ* **13**: 277-285