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Chill-induced wilting and hydraulic recovery in mung bean plants

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Abstract. (1) The hydraulic conductance of roots of chilling-sensitive mung bean plants is reduced markedly at low temperatures. When roots are chilled suddenly under high irradiance, or when plants with roots chilled in the dark are exposed to a natural dawn, the stomata remain open for several hours. During this period the plants may wilt severely if the evaporative demand is sufficiently large. Under lower evaporative demand and less severe wilting, the plants may subsequently rehydrate.

(2) Following root chilling there is a rapid (< 30 min) initial change in root conductivity (3.2-fold).

(3) Within hours the hydraulic conductivity of the pathway from stem xylem to leaf tissue decreases dramatically.

(4) Within 1 d, the hydraulic conductivity of the roots decreases further (4.5-fold).

(5) Over 5 d these large resistances disappear and conductivity recovers to a value greater than at the start of chilling. This response and stomatal closure allow the plant to rehydrate to a condition similar to that of controls.

(6) There is no simple relation between this hydraulic recovery and the accumulation of abscisic acid in the roots.

Key-words: Vigna radiata; root chilling; hydraulic conductivity changes; wilting; abscisic acid.

Introduction

Temperatures between 0 and 12°C cause injury or death to many plants of subtropical and tropical origin. The actual temperature at which chilling injury occurs depends on the plant species, the length of time the plant is held at chilling temperatures, and the degree of prior 'chill hardening' (Stewart & Guinn, 1969). When the roots are chilled there may be rapid wilting (Kramer, 1942; Kuiper, 1964; McWilliam, Kramer & Musser, 1982) and it is this response which is studied in this paper.

On chilling the hydraulic conductance of roots decreases substantially (Markhart *et al.*, 1979a). Therefore, chilling the roots of plants may reduce the rate of water uptake and/or lower the water potential in the shoot (Slatyer, 1967). However, wilting depends on evaporative demand so that chilling injury can be prevented by maintaining a saturated atmosphere around the leaf (Wilson, 1976).

Chilling-sensitive plants have been observed to recover turgor after their roots have been 4 or 5 d at 5°C (Böhning & Lusandana, 1952; Gröbbelaar, 1963). An explanation of this response was not proposed but the pretreatment of seedlings with synthetic abscisic acid [(±)-ABA] prior to whole-plant chilling can reduce chilling-induced water-loss (Rikin & Richmond, 1976). Additionally, large concentrations of ABA accumulate when plants wilt (Wright, 1969; Milborrow, 1974). Thus, ABA may be involved in this hydraulic recovery (Glinka, 1977; Fiscus, 1981). Part of this protective effect of ABA against chilling is associated with stomatal closure (e.g., McWilliam *et al.*, 1982). However, direct effects of (±)-ABA on root conductance have also been demonstrated by Markhart *et al.* (1979b).

In this study we measure the changes over several days in the hydraulic properties and ABA concentrations in mung bean plants chilled under different evaporative conditions.

Materials and methods

Mung bean plants (*Vigna radiata* (L.) Wilczek cv. Berken) were grown to the five-leaf stage in phytotron glasshouses (Morse & Evans, 1962) at 21/16°C (day/night temperatures) in cylindrical pots 200 mm long and 50 mm in diameter, and containing vermiculite. These pots were supported in an ambient-temperature, aerated water-bath containing tap water. The plants were transferred every 3 d to another bath at the same temperature which contained Hoagland's solution and were returned to the water-bath after 8 h in nutrient solution.

Effect of irradiance on dehydration induced by chilling

The experimental procedure involved leaving 20 of 80 plants in the ambient water-bath and transferring the remaining plants to an aerated 5°C low-temperature bath at 2400 h. Air temperature was 21/16°C for all treatments. The three different irradiances to which plants with chilled roots were

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exposed were 0%, 25%, and 100% of full glasshouse irradiance. Shading was provided by Sarlon shade cloth, irradiance was measured with a Lambda Li 185B Radiometer with a Li 190 SEB sensor. Relative water content (r.w.c.) was determined using the method of Weatherley (1950). the main experiment was conducted in December, the month of highest irradiance in Canberra.

Measurement of root conductance. Prior to measuring root conductance, at least 1 dm^3 of tap water at either 5°C or 21°C was slowly poured into the pots to rinse out solutes so that the osmotic pressure of water in the pot was near zero. The shoots were then cut off with a razor blade immediately below the cotyledons and the leaf areas were measured on a planimeter (Lambda Li 3000). The pot was placed either at 5°C or 21 ± 1°C in a pressure chamber (Soil Moisture Equip. Corp. Model 3000) and a seal tightened around the stem. The chamber was pressurized with nitrogen and the sap exuded from the cut stem was collected in pre-weighed vials filled with surgical cotton. At any pressure, sap was collected in four vials over successive periods of 30 s to calculate the exudation rate. Even at the lowest exudation rates, the measured changes in vial weight were at least 20 times larger than the weighing errors or evaporative losses from the vials.

The technique for routine measurement of root conductance was as follows: immediately following removal of the shoot, 0.6 MPa was applied and maintained; between 2 and 6 min later the exudation rate was measured over four periods of 30 s. So that plants of different sizes could be compared more easily we have determined the root conductivity as defined by Fiscus (1981), which is the ratio of root conductance to plant leaf area.

Effect of low root temperature on relative water content, transpiration, leaf conductance, root conductivity, and ABA content of mung bean plants

Experimental plants grown under the standard conditions were transferred to the aerated, low-temperature root-bath at 0900 h on 15 September 1981 for 6 d. Control plants were maintained in the ambient temperature bath during this period. Relative water content, irradiance, and root conductivity were measured as described earlier. Transpiration was assessed in subsets of six plants whose pots were surrounded by polyethylene bags that were sealed at the stem and whose weight loss was recorded every 2 h. To avoid anaerobic conditions individual pots were included in the transpiration reading for only 6 h. All pots were returned uncovered to their respective water-baths overnight. Leaf diffusive conductance was measured with a Lambda Li 60 diffusive resistance meter. ABA was measured using the methods outlined in King & Patrick (1982) involving high-performance liquid chromatography for purification of methylated ABA and electron capture detection on a gas-liquid chromatograph for quantification. Experimental and control leaf and root samples were taken from four or five plants at 1200 h on days 1, 2, 3, and 5. These samples were weighed fresh, then immediately frozen in liquid nitrogen and freeze-dried prior to dry weight and ABA determination. Root conductance was measured at 0930 on day 1 (that is, within 20 min of chilling), then at midday on days 1, 2, 3, and 5 for control and treated plants.

Rehydration of wilted shoots. To establish a range of values of shoot r.w.c., plants were transferred to the 5°C root-bath and removed after periods from 1 to 3 h. The shoots were excised under water just below the hypocotyls and left standing in flasks of water at 21°C and in a low-energy fluence rate ($\sim 30\ W\ m^{-2}$). Immediately and 30 min after excision the r.w.c. of the leaves was measured.

Osmotic pressure. Leaves from fully hydrated shoots were placed in test-tubes and plunged into liquid nitrogen and the tissue crushed with a pestle. Osmotic pressure of the expressed sap was measured using a thermocouple psychrometer (Wescor HR 337).

Leaf water potential. Single leaves from control plants and plants chilled for 5 d were enclosed in plastic bags and transferred to a pressure chamber where a plot of relative water content *v.* applied pressure was obtained. (No difference was discerned between control and chilled plants.) An averaged plot thus obtained was used to estimate leaf water potential from r.w.c. in whole plants. These results were used to produce the scale of approximate water potential in Fig. 4.

The effect of applied (±)-ABA on root conductance

Root conductance was measured in samples of standard five-leaf plants at the beginning and after 6 d of exposure of their roots to an aerated solution of (±)-ABA. Temperature was that of the glass-house (21/16°C, day/night). In the first experiment (±)-ABA concentrations were 2×10^{-3}, 2×10^{-4}, and 2×10^{-5} mol m^{-3} (each in 0.001% ethanol) and these were compared with two controls, one of 0.001% ethanol and the other of distilled water. A second experiment was conducted with only two (±)-ABA concentrations (2×10^{-3} and 2×10^{-2} mol m^{-3} in 0.01% ethanol) and controls of 0.01% ethanol and of distilled water.

Results

Measurement of root conductance

Figure 1 shows the cumulative weight of sap expressed from a cut stem by a pressure of 600 kPa

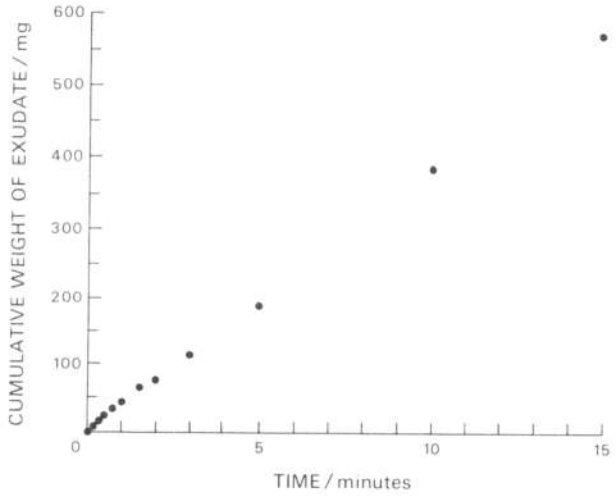

Figure 1. The cumulative weight of sap expressed from an excised root system is plotted against the time after the application of 0.6 MPa. Cumulative weighing errors and relative timing errors are negligible on this scale.

applied to the wet roots in a pot in the pressure chamber. The exudation rate is very nearly constant between 1 and 15 min after the application of the pressure. (The initial rate is slightly higher and this difference is probably due to the transient volumetric response of the root system and suggests an apparent volumetric modulus for the roots of about 100 MPa. This value is much larger than the volumetric moduli of leaves—about 9 MPa in this study—but this is not unsurprising in view of the differences in anatomy.) Figure 2 shows a typical plot of exudation rate *v.* pressure. There is a small positive intercept on the exudation axis, and the relation is non-linear at pressures less than about 100 kPa. At pressures of 200 kPa or above, however, the relation is linear and may be extrapolated to an intercept very near the origin. Thus, for pressure differences of 200 kPa or more the roots behave under these conditions according to a simple resistance law, i.e. the flux is proportional to the applied pressure.

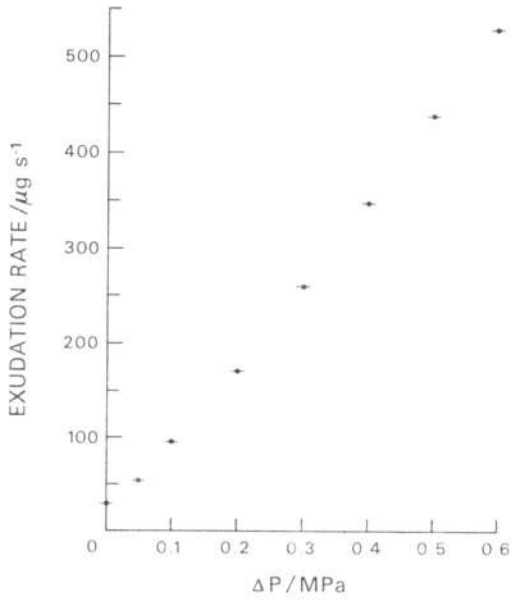

Figure 2. The exudation rate from an excised root system as a function of applied pressure. The bars are weighing errors and the nominal accuracy of the pressure meter.

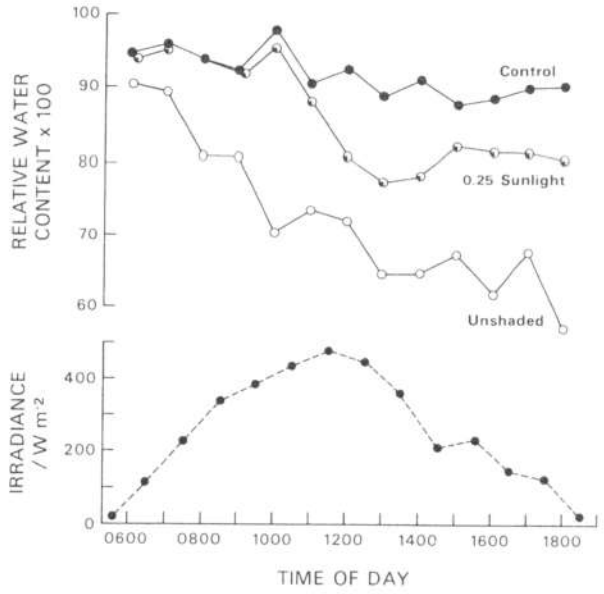

Figure 3. Relative water contents, transpiration rates, and root conductivities of mung bean plants whose roots were chilled at 5°C during a day. Roots of control plants were held at 21°C. Irradiance was full sunlight. Plants chilled but kept in darkness had r.w.c.'s indistinguishable from controls.

Effect of irradiance on dehydration induced by chilling

Figure 3 illustrates the effect of root chilling (5° *v.* 21°C) and irradiance on leaf relative water content (r.w.c.). For control plants in the ambient water bath (21/21°C shoot/root) the r.w.c. remained about 90% throughout the day. Chilled plants (21/5°C shoot/root) exposed to the highest irradiance (481 W m^{-2} PAR maximum) dehydrated rapidly after chilling and continued to dehydrate till the r.w.c. fell below 60% by 1800 h. The effect was less severe at the lower irradiance and plants in darkness, but with roots at 5°C, maintained r.w.c. similar to those of the control plants (data not included in Fig. 3). Similarly, plants transferred to a 5°C water-bath on a clear May day (269 W m^{-2}) and on an overcast July day (110 W m^{-2}) responded in the same manner as the 0.25 sunlight and zero sunlight treatments, respectively.

At the other extreme of irradiance, when plants were transferred to the low-temperature bath at 1100 h during a period of high irradiance (>350 W m^{-2} PAR), wilting was rapid and r.w.c. dropped below 75% within 40 min. Chilling at high

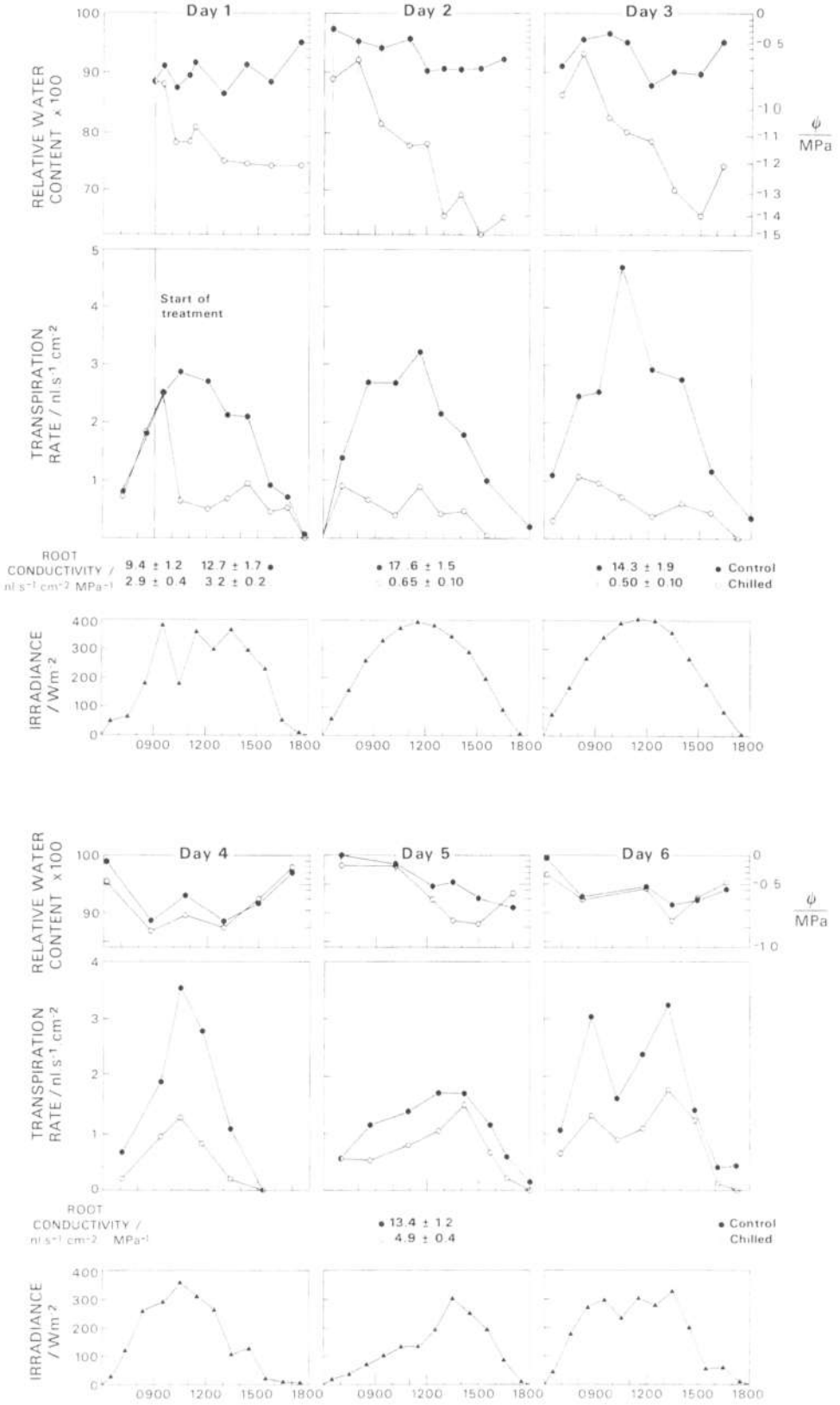

Figure 4. Against time over 6 d are presented (from the bottom) (i) irradiance; (ii) root conductivity (measured at 0930 h on day 1 and at midday on days 1, 2, 3, and 5); (iii) transpiration rate; and (iv) relative water content. Filled circles are controls and open circles chilled plants. The line at 0900 h on day 1 represents the start of chilling.

light-intensities produced a more rapid dehydration than during a natural dawn but the result in the afternoon was similar: i.e. r.w.c. fell to about 60% by 1800 h.

Effect of low root temperature on relative water content, transpiration, root conductivity, and ABA content of mung bean plants

The changes over 6 d in relative water content and transpiration following the chilling of mung bean plants are shown in Fig. 4. The treated plants were transferred to the low-temperature bath at 0900 h and had wilted within 1 h. Relative water content at this stage had dropped to 80% and by 1030 h transpiration had dropped to 30% of the control plant values.

Relative water content in the treated plants recovered on all nights to approximately 90% or higher. After 0800 h on the second and third days, with increasing irradiance through the day, r.w.c. fell to about 65% and the leaf conductances were in the range 0.05–0.1 cm s^{-1}. During days 4, 5, and 6, r.w.c. in the treated plants was consistently above 85%, the plants regained turgor, and stomatal conductances and transpiration rates of the treated and control plants were more similar than in the first 3 d.

Root hydraulic conductivities* of plants sampled on days 1, 2, 3, and 5 are listed in Fig. 4. Immediately on chilling, conductivities were reduced 3.2-fold. This change was reversible: when roots were chilled for 15 min and then returned to 21°C their conductivity returned to equal that of the controls (data not shown). By days 2 or 3 conductivity had dropped a further 5-fold but by day 5 there was some recovery. Conductivity of the chilled roots was higher on day 5 than the value measured immediately following chilling. Changes in conductivity were measured in several independent experimental runs and their timing and order were reproduced in each run.

Relative to control plants, leaf and root ABA contents increased within 3 h of chilling (Table 1). Leaf ABA continued to increase over days 2 and 3, then there was a significant drop between days 3 and 5. Root ABA levels were significantly higher than control plant levels throughout the experiment although no trend was obvious. The changes in root conductivity after chilling do not correlate with changes in ABA in the plant. The 10-fold increase in ABA within 3 h of chilling was not matched by a change in conductivity.

We cannot resolve whether ABA in the roots was imported from the leaves and/or synthesized *in situ* (cf. Hartung & Abou-Mandour, 1980).

*We report conductivities in units of transpiration (nl s^{-1} cm^{-2}) and potential (MPa). We note that the conversion to SI units is 1 nl s^{-1} cm^{-2} $MPa^{-1} = 10^{-14}$ m^2 s^{-1} kg^{-1}.

Table 1. Abscisic acid content (μg kg^{-1} FWT) of leaves and roots of mung bean plants with roots either chilled (5°C) or held at ambient temperatures (21/16°C)

	Day 1	Day 2	Day 3	Day 5
Leaves 21°C	11.5±3.4	7.9±2.8	13.0±5.0	23.6±9.1
Roots 21°C	0.6±0.4	2.0±0.6	0.8±0.3	2.2±0.8
Leaves 21°C	100.8±12.0	136.5±6.0	228.8±66.0	45±7.1
Roots 5°C	9.5±3.3	10.2±1.8	3.7±2.4	14.1±2.7

All measurements made at 1200 h. Both low-temperature-treated roots and leaves significantly different from control roots and leaves. Values ±standard error, $n = 4$–6.

Effect of applied (±)-ABA on root conductivity

Root conductivity was measured after exposure for 6 d to (±)-ABA in the culture solution. There were no significant differences in root conductivities of treated and control plants, in two separate experimental runs. Neither ethanol at the concentration used in these experiments nor (±)-ABA affected root conductivity. The highest concentration of (±)-ABA applied in these experiments (10^{-2} mol m^{-3}) was 10- to 100-fold greater than in the leaves (approximately 10^{-3} mol m^{-3}) and roots (10^{-4} mol m^{-3}) after root-chilling (Table 1).

Differential rehydration following root-chilling

Plants stressed to various r.w.c.'s and then re-hydrated after root excision had differing rates of water uptake (Fig. 5). Plants with very low r.w.c. either rehydrate much more slowly than do plants with moderately high r.w.c. or else continue to dehydrate, i.e. lose water faster than they absorb through their petioles, when the plant stem is severed under water.

Leaf osmotic pressure

The osmotic pressure of leaf tissue from control plants was 0.84±0.03 MPa and that of leaf tissue

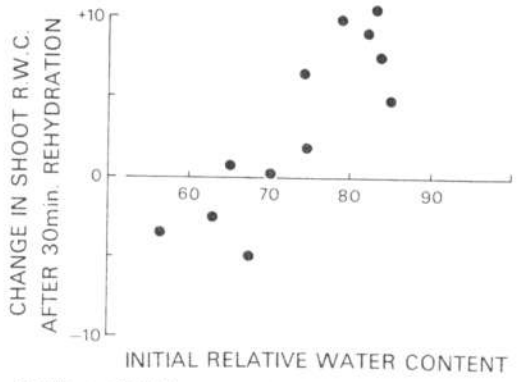

Figure 5. Effect of initial r.w.c. on the change in r.w.c. after 30 min rehydration of shoots. Plants were dehydrated to various extents by exposing their roots to 5°C for differing periods. The shoots were then cut under water and allowed to stand in water at 21°C. The r.w.c. was measured immediately and after 30 min.

from experimental plants after 6 d was 0.82 ± 0.02 MPa. Thus there was no significant osmotic adjustment involved in the regaining of turgor.

Discussion

A plant will wilt if evaporative demand is high, the stomatal conductance high, and if the root conductivity is low enough. At the same evaporative demand the plant will regain turgor if either stomatal conductance falls or the root conductivity rises sufficiently. Although stomata are in the most advantageous position to control the flow of water from soil to atmosphere (Jarvis & Morison, 1981), other changes in the conductance in the soil–plant–atmosphere continuum can be important. Our results highlight the importance of root and/or stem conductance in the control of transpiration for plants with their roots chilled.

Root conductivity and initial chilling response

In our experiments water flow through the roots was time-independent (Fig. 1) and proportional to the potential difference applied during measurement of root conductance for pressures above about 200 kPa (Fig. 2). Thus, the hydraulic properties of the roots can be described by a simple hydraulic conductance for typical daytime values. Provided that the water outside the roots has negligible osmotic pressure, as here, then this conductance can be calculated from one measurement of flow and pressure difference. This simplification greatly expedited routine measurement of root conductance.

Tissue water potential can be calculated at any transpiration rate from the various conductances and water fluxes (root, stem, leaf) as well as tissue water capacities (leaf hydration/dehydration). Root water content is unlikely to change so that the rate of water uptake by the roots equals the transpiration rate less the rate of shoot dehydration. In the control plants, the dehydration rate is less than *c.* 0.2 nl s^{-1} cm^{-2}, which is small compared with typical daytime transpiration rates of around 2–4 nl s^{-1} cm^{-2}, and thus the rate of water uptake is approximately equal to the transpiration rate. In the chilled plants, however, the transpiration loss may be much greater than the rate of water uptake, which leads to the rapid dehydrations observed in the mornings of days 1–3 (Fig. 4).

With typical control transpiration rates of 2–4 nl s^{-1} cm^{-2} and root conductivities of 10–15 nl s^{-1} cm^{-2} MPa^{-1} (Table 2), the xylem water potential at steady state is expected to be about -0.13 to -0.40 MPa (i.e. transpiration ÷ conductivity). The leaf tissue water potential may be lower than this due to internal hydraulic resistances in the leaf (discussed later) but provided that these are not large, the potential will be higher than the osmotic potential of the cells (0.8 MPa) and so the leaves remain turgid.

Immediately after a plant has been chilled (Fig. 4), the stomatal resistance is the same as that of the controls and so the transpiration rate (for the moment) is the same as the controls at 2.5 nl s^{-1} cm^{-2}. However the root conductivity is now reduced to 2.9 nl s^{-1} cm^{-2} MPa^{-1} (Table 2). To produce a water uptake equal to the transpiration rate would require a potential difference of 0.86 MPa across the roots which would imply a xylem potential of -0.86 MPa and a leaf tissue potential lower still (severe wilting would be inevitable). However, the potential is not expected to fall instantaneously as the shoot has a finite volumetric modulus (about 9 MPa at high hydration) and so the tissue potential falls gradually as the plant dehydrates.

At 0930 on day 1, the chilled plants experienced their greatest rate of dehydration: 15% per hour or 1.0 nl s^{-1} cm^{-2}. Since the transpiration rate is 2.5 nl s^{-1} cm^{-2}, the rate of water uptake by the roots must be about 1.5 nl s^{-1} cm^{-2}. Using the root conductivity of 2.9 nl s^{-1} cm^{-2} MPa^{-1}, this implies a xylem water potential of -0.52 MPa and a somewhat lower leaf tissue water potential. (Using the approximate potential scale on Fig. 4, the leaf tissue water potential is estimated to fall from -0.8 to -1.2 MPa between 0900 and 1000 h in the chilled plants.)

Conductance changes over several days

The chilled plants wilted more severely on days 2 and 3 than they did on day 1 (Fig. 4). On each of these days the r.w.c. of the shoots fell from greater than 90% to rather less than 70% between 0800 and 1500 h. The average dehydration rate of about 0.3 nl s^{-1} cm^{-2} is half the average transpiration rate over this period—about 0.6 nl s^{-1} cm^{-2}. Thus, water uptake by the roots is only 0.3 nl s^{-1} cm^{-2} but the potential drop is large (-0.5 MPa) because between 1200 h on day 1 and 1200 h on day 2 the root conductivity in the chilled plants has dropped 4.5-fold to 0.6 nl s^{-1} cm^{-2} MPa^{-1}. Since the leaf tissue water potential falls well below -0.5 MPa, the xylem-leaf conductivity is again very low (< 1 nl s^{-1} cm^{-2} MPa^{-1}). The cause of this large decrease in root conductivity is not known but mechanical damage or cavitation caused by low water potentials are possible explanations. Whatever the cause, it is this secondary hydraulic response to chilling of roots which prevents the plants' rapid recovery of turgor. If the root conductivity in the chilled plants remained at its value measured 3 h after chilling, then the stomatal closure and reduced transpiration which are observed would be sufficient to allow the plant to rehydrate to an r.w.c. similar to controls within a few hours of chilling, as observed in experiments run under winter light-intensities (data not shown).

After 5 d the chilled plants have recovered to r.w.c.'s similar to the controls. This is the result of a significant ($P = 98\%$) increase in root conductivity in combination with the already reduced stomatal conductance. The regaining of turgor by the chilled plants does not involve a change in the osmotic pressure in the cells, since the osmotic potentials of controls and chilled plants were not significantly different after 5 d.

Other changes in hydraulic conductivity

By calculating the ratio of water uptake rate to the xylem-leaf difference in potential it can be seen (Table 2) that the conductivity of the shoot pathway has decreased substantially (11-fold) from its value just after chilling. Furthermore, a measurable decrease in shoot conductivity after chilling the roots could also be seen in excised shoots. Figure 5 shows the extent of shoot rehydration varied with the degree of initial dehydration prior to detaching the shoot. Since the stems were cut under water, the water potential of all stems is zero at the cut end. Had the hydraulic conductivities been equal, the shoots with the lowest r.w.c. should then have rehydrated most quickly, since in these the potential difference driving water uptake is greatest. The contrary behaviour is reported in Fig. 5. Shoots with r.w.c. between 75% and 85% took up enough water to increase their r.w.c. considerably. Those with r.w.c. below 75%, however, took up water more slowly than they transpired and so their r.w.c. either fell or remained constant. Clearly, once shoots dehydrate below about 75% r.w.c., the hydraulic conductance of the pathway between shoot xylem and leaf tissue falls suddenly (a factor of about 11 in Table 2). Thus, while dehydrations to r.w.c.'s greater than about 75% are readily reversed under favourable hydraulic conditions, dehydrations below this r.w.c. are not readily reversible.

This abrupt and large variation in conductivity explains the varied response to chilling under different irradiance (Fig. 3). If the evaporative demand is sufficiently high the resultant transpiration causes the shoot to dehydrate to an r.w.c. below 75% and the hydraulic conductivity decreases suddenly. The stomata close and this lowers transpiration, but the extra resistance keeps water uptake even lower and so no rehydration occurs. For lower evaporative demands the r.w.c. never falls low enough to cause the sudden increase in resistance and stomatal closure leads to rehydration.

The large decrease in hydraulic conductivity could be the result of cavitation in xylem vessels which occurs at sufficiently negative potentials (around -1.2 MPa), or mechanical damage to these vessels (perhaps their collapse) resulting from the large geometrical changes in the tissue incurred during large contractions (about 25% in volume). We have been unable to distinguish between these explanations, but see Milburn (1973).

Possible involvement of ABA

ABA has been variously reported to increase, to decrease, or to have no effect on root conductance. Glinka (1977, 1980) reported that ABA increased conductance of sunflower stumps at low flow rates. Similarly, Tal & Imber (1971) concluded that ABA increased conductivity in decapitated tomato plants. Several studies have found that ABA does not affect root conductivity (Cram & Pitman, 1972; Erlandsson, Petersson & Svensson, 1978; Karmoker & van Steveninck, 1978) whilst Markhart *et al.* (1979b) and Fiscus (1981) found a decrease in hydraulic conductivity following ABA application. At physiological concentrations, applied (±)-ABA did not change conductivity in this study. Also, although with chilling there was a significant rise in ABA level there was no correlation between root conductivity and endogenous ABA levels in the root (Table 1). It appears unlikely, therefore, that endogenous levels of ABA control root hydraulic conductivity.

Acknowledgments

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Table 2. Relationship between tissue water potential and internal hydraulic resistance in leaf stem and root of mung bean plants following root chilling at 0900 h on day 1. Transpiration and root conductivities were measured, and from these values, the xylem water potential calculated using the Ohm's law analogy. The leaf tissue water potential was deduced from measured leaf r.w.c.'s

	Transpiration rate ($nl\ s^{-1}\ cm^{-2}$)	Root conductivity ($nl\ s^{-1}\ cm^{-2}\ MPa^{-1}$)	Calculated xylem water potential (MPa)	Leaf tissue water potential (MPa)	Effective xylem-leaf tissue conductivity ($nl\ s^{-1}\ cm^{-2}\ MPa^{-1}$)
0930 h day 1					
Controls	2.5	9.5	−0.26	~ −0.6	~7
Chilled	2.5	2.9	−0.86	~ −1.2	~7
1200 h day 1					
Controls	2.7	12.7	−0.21	~ −0.7	~6
Chilled	0.5	3.2	−0.15	~1.2	~0.5

References

Böhning, R.J. & Lusandana, B. (1952) A comparative study of gradual and abrupt changes in root temperature on water absorption. *Plant Physiology*, **27**, 475–488.

Cram, W.J. & Pitman, M.G. (1972) The action of abscisic acid on ion uptake and water flow in plant roots. *Australian Journal of Biological Sciences*, **25**, 1125–1132.

Erlandsson, G.S., Petersson, S. & Svensson, S. (1978) Rapid effects on ion uptake in sunflower roots. *Physiologia Plantarum*, **43**, 380–384.

Fiscus, E.C. (1981) Effects of abscisic acid on the hydraulic conductance of and the total ion transport through *Phaseolus* root systems. *Plant Physiology*, **68**, 169–174.

Glinka, Z. (1977) Effect of abscisic acid and hydrostatic pressure gradients on water movement through excised sunflower roots. *Plant Physiology*, **59**, 933–935.

Glinka, Z. (1980) Abscisic acid promotes both volume flow and ion release to the xylem in sunflower roots. *Plant Physiology*, **65**, 537–540.

Gröbbelaar, W.P. (1963) Responses of young maize plants to root temperatures. *Mededelingen van de Landbouwhogeschool te Wageningen*, **63**, 1–71.

Hartung, W. & Abou-Mandour, A.A. (1980) Abscisic acid in root cultures of *Phaseolus coccineus* L. *Zeitschrift für Pflanzenphysiologie*, **97**, 265–269.

Jarvis, P.G. & Morison, J.I.L. (1981) The control of transpiration and photosynthesis by the stomata. In *Stomatal Physiology* (eds P.G. Jarvis & T.A. Mansfield), pp. 247–279. University Press, Cambridge.

Karmoker, V.L. & van Steveninck, R.F.M. (1978) Stimulation of volume flow and ion flux by abscisic acid in excised root systems of *Phaseolus vulgaris* L. cv. Redland Pioneer. *Planta*, **141**, 37–43.

King, R.W. & Patrick, J.W. (1982) Control of assimilate movement in wheat. Is abscisic acid involved? *Zeitschrift für Pflanzenphysiologie*, **106**, 375–380.

Kramer, P.J. (1942) Species differences with respect to water absorption at low soil temperatures. *American Journal of Botany*, **29**, 828–832.

Kuiper, P.J.C. (1964) Water uptake of higher plants as affected by root temperature. *Mededelingen van de Landbouwhogeschool te Wageningen*, **64**, 1–11.

McWilliam, J.R., Kramer, P.J. & Musser, R.L. (1982) Temperature-induced water stress in chilling-sensitive plants. *Australian Journal of Plant Physiology*, **9**, 343–352.

Markhart, A.H., Fiscus, E.L., Naylor, A.W. & Kramer, P.J. (1979a) Effect of temperature on water and ion transport in soybean and broccoli systems. *Plant Physiology*, **64**, 83–87.

Markhart, A.H., Fiscus, E.L., Naylor, A.W. & Kramer, P.J. (1979b) Effect of abscisic acid on root hydraulic conductivity. *Plant Physiology*, **64**, 611–614.

Milborrow, B.V. (1974) The chemistry and physiology of abscisic acid. *Annual Review of Plant Physiology*, **25**, 259–307.

Milburn, J.A. (1973) Cavitation studies on whole *Ricinus* plants by acoustic detection. *Planta*, **112**, 333–342.

Morse, R.N. & Evans, L.T. (1962) Design and development of Ceres—an Australian phytotron. *Journal of Agricultural Engineering Research*, **7**, 128–140.

Rikin, A. & Richmond, A.E. (1976) Amelioration of chilling injuries in cucumber seedlings by abscisic acid. *Physiologia Plantarum*, **38**, 95–97.

Slatyer, R.O. (1967) *Plant-Water Relationships*. Academic Press, New York and London.

Stewart, J.M. & Guinn, G. (1969) Chilling injury and changes in the adenosine triphosphate of cotton seedlings. *Plant Physiology*, **44**, 605–608.

Tal, M. & Imber, D. (1971) Abnormal stomatal behavior and hormonal imbalance in *Flacca*, a wilty mutant of tomato. *Plant Physiology*, **47**, 849–850.

Weatherley, P.E. (1950) Studies in the water relations of the cotton plant. I. The field measurements of water deficits in leaves. *New Phytologist*, **49**, 81–87.

Wilson, J.M. (1976) The mechanism of chill- and drought hardening of *Phaseolus vulgaris* leaves. *New Phytologist*, **76**, 257–270.

Wright, S.T.C. (1969) An increase in the 'Inhibitor-β' content of detached wheat leaves following a period of wilting. *Planta*, **86**, 10–20.