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Update on Long-Distance Signaling

How Do Chemical Signals Work in Plants that Grow in Drying Soil?[1]

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We have known for many years that the dehydration of plant cells can lead to accumulation of the plant growth regulator ABA. Application of this compound to well-watered plants mimics many of the effects of soil drying on gene expression, physiology, growth, and development, making this compound a strong candidate for a role in the droughted plant. Dehydration of leaves can result in massive accumulations of ABA, and roots also synthesize the compound in increased amounts as they are exposed to drier and drier soil.

Davies and Zhang (1991) argued that an important component of the drought responses of many plants can be an ABA signal moving from the roots to the shoots to regulate physiology and development as a function of soil water status/availability. Many recent reports show relationships between stomatal conductance and soil water status or xylem ABA concentration, which seem to support this view. Nevertheless, critical examination of the ABA-signaling hypothesis must show that enough extra ABA moves in the transpiration stream to the shoots to account for the changes in functioning that are recorded. Many other chemicals moving in the xylem to shoots can also provide shoots with "information" concerning root functioning, and we must consider the nature of such signals. We should also be concerned with the nature of the information that might be transmitted by a root signal (e.g. a measure of soil water status or soil water availability) and the form that such a chemical signal might take (e.g. the concentration of the signal molecule in the transpiration stream or the flux of signal molecules to the site of action in the leaf).

IS IT REALLY NECESSARY TO TAKE ACCOUNT OF CHEMICAL SIGNALING OF SOIL DRYING?

To provide firm evidence for root-to-shoot signaling of the effects of soil drying, it is necessary to artificially manipulate the plant to break the link between soil drying and reduced water uptake. Passioura (1987) has done this successfully using a pressure vessel placed around the roots of a plant growing in drying soil. As the soil dries, pressure is increased to balance the increase in soil suction. Pressurized plants show shoot water relations that are similar to those of well-watered plants, even though the roots are in contact with drying soil. Reductions in leaf growth rate and stomatal conductance (Passioura, 1988; Gollan et al., 1992) must, therefore, be attributed to an effect of soil drying that does not require a change in shoot water status.

In another experiment, Gowing et al. (1990) divided the roots of small apple trees into two containers. Soil drying in one container restricted leaf expansion and leaf initiation with no obvious effect on shoot water relations. When roots in contact with drying soil were severed from the plant, leaf growth rate recovered to that shown by well-watered plants. It seems unlikely that this treatment could make more water available to the shoots, and a more likely explanation for the restriction in shoot growth is the increased supply of an inhibitor originating in roots that have contact with drying soil, the supply of which is removed when the roots are removed.

Correlative evidence for the control of shoot growth and physiology by a root signal is provided by the increasing number of reports of a clear relationship between leaf conductance and soil water status and an apparent relationship between both of these variables and the concentration of ABA in the xylem (Tardieu et al., 1992a; Janssen and Markhart, 1993; Khalil and Grace, 1993). Experiments of many different kinds have demonstrated that ABA can have a powerful effect on the stomata of many species. Despite this, it is still necessary to establish that an apparent relationship between stomatal conductance and ABA concentration in the xylem is more than a correlation. Indeed, we must be able to show that any chemical signal is actually controlling stomata (rather than the converse), because we might expect that the concentration of any substance in the xylem stream would increase as stomatal closure decreased the transpiration flux.

IS ABA THE ONLY CHEMICAL SIGNAL? AND HOW MUCH IS NEEDED TO EXPLAIN THE RESPONSES THAT WE SEE?

There are now two substantial field studies showing an apparent effect of xylem ABA on leaf conductance (Wartinger et al., 1990; Tardieu et al., 1992b) (Fig. 1). The relationship between these two variables suggests a sensitive effect of ABA on conductance and appears to be relatively robust and

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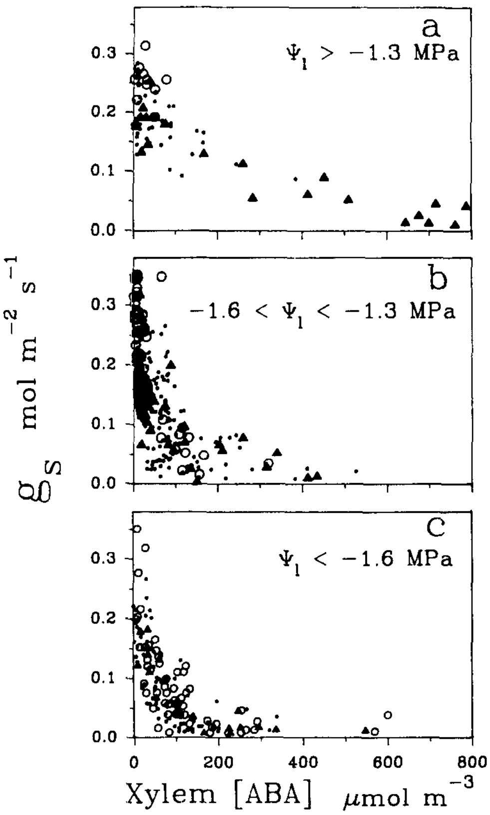

Figure 1. Leaf conductance (g_s) as a function of the concentration of ABA in the xylem sap of field-grown plants over three ranges of leaf water potential (Ψ). Relationships obtained by feeding field-grown plants artificial ABA are depicted by ▲. All other symbols show relationships between conductance and endogenously produced ABA. Variation is produced by a variety of treatments described by Tardieu et al. (1993).

to account for variation in stomatal conductance induced by different cultural treatments over a range of sampling dates. The potency of ABA in maize plants growing in the field has been confirmed by artificially augmenting the xylem ABA concentration by stem injection (Tardieu et al., 1993) (Fig. 1). The relationship between xylem ABA concentration and stomatal conductance in the manipulated plants shows good correspondence with that generated by soil drying. This result seems to suggest that extra ABA synthesized as a result of soil drying can account for most of the antitranspirant activity in the xylem sap of maize plants. A similar conclusion was reached by Zhang and Davies (1991), who removed most of the ABA from the xylem sap of laboratory-grown maize plants and found that most of the antitranspirant activity also disappeared.

These studies seem to provide quite compelling evidence for a central role for ABA in chemical signaling between roots and shoots and in the control of stomatal conductance in the field. There is evidence, however, that in some species substantial antitranspirant activity in the xylem stream cannot be attributed to ABA (Munns and King, 1988; Trejo and Davies, 1991). The concentration of ABA in the xylem stream is usually found to be a sensitive indicator of the water status of the soil around the roots of the plant, but in some studies it is clear that stomata start to close before changes in xylem ABA concentration can be detected. In other studies there may not be enough ABA to account for the responses that are seen, and in others removal of most of the ABA from the xylem sap has little effect on its antitranspirant activity or its capacity to restrict leaf growth (Munns, 1992). Munns et al. (1993) have increasing evidence that some changes in shoot functioning in droughted plants may be promoted by the accumulation of a large mol wt compound that may not normally be present in xylem sap but that may be formed in leaves as a result of a reaction that can be stimulated by soil drying. The most recent work by this group (Chandler et al., 1993) shows that filtering a compound with a large mol wt (not ABA) from xylem sap collected from droughted plants removed some of the capacity of that sap to induce production of dehydrins.

Part of the difficulty in assessing whether or not an observed change in shoot functioning can be explained entirely by a particular chemical signal is the problem of collecting a sample of xylem sap, the chemical composition of which reflects the composition of sap that was moving through the plant before the sample was taken. Ideally, sap should be sampled from "intact," transpiring plants, and this can be done using the root pressure device described earlier. Recently, however, Canny (1993) used x-ray microanalysis to probe the ion contents of small veins in flash-frozen leaves of *Helianthus*. These results suggest that even the root pressure vessel may yield sap in which the concentrations of certain inorganic ions are very substantially diluted. In most studies, the use of the root pressure vessel is not an option, and the Scholander pressure chamber is commonly used to force xylem sap from leaves, from segments of stem, or from root stumps. The assumption is made that the chemical composition of initial samples can reflect the composition of sap in the xylem before it was cut (Wartinger et al., 1990; Zhang and Davies, 1990), but there are now concerns about exactly what is sampled by the pressure chamber (Zimmermann et al., 1993) and whether wounding of tissue and failure to match flux through the cut stem with flux through the intact plant can cause substantial errors in the estimations of hormone concentrations. It is clear that in any investigation of chemical communication between roots and shoots, sampling methods for xylem sap should be fully validated.

The distribution of ABA through the plant will be greatly influenced by the pH of the various plant compartments. Hartung and Slovik (1991) have shown how soil drying can cause a redistribution of ABA as a result of the increasing pH of the xylem sap, and they have emphasized that these changes can explain rapid and substantial changes in shoot functioning. As well as measuring changes in ABA concentration in the xylem, it is clearly important to measure xylem sap pH and to try to quantify other changes in the chemical composition of the xylem sap that can contribute to changes in pH and to the chemical control of shoot function.

DROUGHT EFFECTS ON THE CHEMICAL COMPOSITION OF XYLEM SAP

In a recent paper, Gollan et al. (1992) noted very large differences between individual *Helianthus* plants in the concentrations of inorganic ions in the xylem sap. These differences appear to result in substantial variation in the sensitivity of guard cells to the ABA signal, albeit over a rather restricted range in leaf conductance (Schurr et al., 1992). The authors show substantial effects of soil drying on the ionic content of xylem sap, and it seems likely that such changes could sensitize stomata to very low concentrations of ABA. We need to be aware of possible changes of this kind because a drought-induced increase in sensitivity to ABA of the magnitude reported by Schurr et al. (1992) could lead us to conclude that xylem sap containing very little ABA contains extra "unidentified" antitranspirant activity. It is clear that a full quantification of the effects of soil drying on ionic balance as well as effects on the hormone balance of xylem sap will be necessary to enable us to fully evaluate the chemical control of shoot functioning.

Additional evidence that several chemical components may be involved in chemical signaling comes from recent work by Augé and Duan (1991) concerning the influence of mycorrhizal symbiosis on nonhydraulic root signaling of the effects of soil drying. It is well known that mycorrhizal associations will influence the ion balance and the hormone balance of plants, and there is interest in the interacting effects of ABA and cytokinins on growth and stomatal behavior of mycorrhizal plants (Druger and Schonbeck, 1992). Much other work suggests that reduced supply of cytokinins and perhaps other promoters from roots in drying soil will contribute to the signaling processes (Meinzer et al., 1991). Unfortunately, there are no reports of studies in which the flux of cytokinins has been effectively quantified and compared to changes in growth and physiology induced by drought. More information is required before we can assign a clear role to cytokinins in the short-term regulation of gas exchange or in the long-term regulation of development of droughted plants.

HOW DOES THE SIGNALING WORK AND WHAT IS THE MESSAGE?

Our considerations so far have given us a general understanding that an increasing degree of soil drying leads to the increased production of the chemical signal and an increased suppression of shoot activity. Tardieu et al. (1992a) have been able to relate the concentration of ABA in the xylem of nontranspiring maize plants to the predawn water potential of the plant and the water available in the soil immediately before dawn. This suggests that the ABA signal can provide some measure of soil water availability that might be used to regulate development. During the day, these relationships are affected by the flux of water into the roots, which will be a function of the structure as well as of the water status of the soil. As a result, plants in compacted soil show generally higher ABA concentrations in the xylem during the day, and it is necessary to argue that xylem ABA concentration and, therefore, stomatal behavior are a reflection of the access that the roots have to soil water rather than a reflection of the soil water status alone.

The important effect of transpiration flux on ABA concentration in the xylem is also clear from sequential measurements of ABA concentration made from early morning to late evening. One might expect that ABA concentration would increase as the day progresses and the soil dries. In fact, xylem ABA concentration is rather stable and may even decrease as evaporative demand and transpiration flux increase in the afternoon hours (Tardieu et al., 1992a). During these hours there is an increasing limitation of stomatal conductance that cannot, therefore, be explained by a concentration effect alone. Tardieu and Davies (1992) and Trejo and Davies (1994) have shown that stomatal sensitivity to an ABA signal can increase as the leaf water potential decreases (Figs. 1 and 2). This suggests, therefore, that high conductances of droughted plants early in the day can be explained by low stomatal sensitivity to what can be a substantial ABA signal. As leaf water potential declines to a minimum value at approximately midday (that need be no lower than the value exhibited by a well-watered plant), stomata are sensitized to the ABA signal.

A KEY ROLE FOR SENSITIVITY VARIATION IN THE SIGNALING PROCESS?

We have reported above that the sensitivity of stomata to an ABA signal can be modified by the chemical composition and pH of the xylem sap and by the water relations of the leaf. Other recent reports show that the limitations in stomatal opening imposed by high concentrations of ABA can be rapidly and completely reversed by lowering the leaf temperature (Rodriguez and Davies, 1982; Cornic and Ghashghaie, 1991), and there are also clear interactions between the effects of ABA and CO_2 on stomata (Raschke, 1977; Snaith and Mansfield, 1982). The influence of ABA on

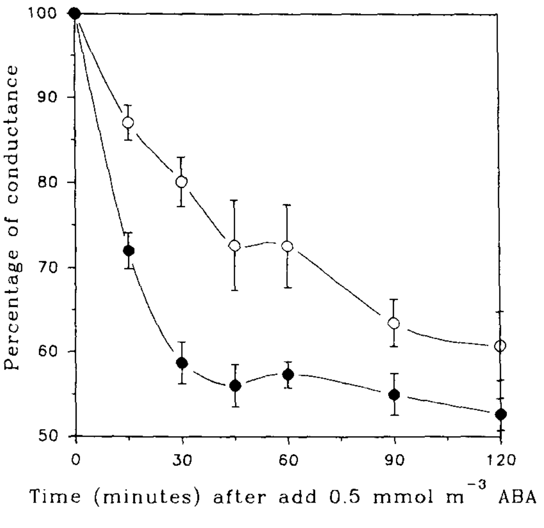

Figure 2. The response of leaf conductance of *Phaseolus* to a 1 μM solution of ABA fed through the petiole starting at time 0. Data are calculated from gravimetric measurements of water loss from detached leaves placed in small vials containing ABA solution. Responses are shown for leaves with (●) and without (○) a resistance added to restrict water uptake. The result of this treatment (see text) is a reduction of leaf water potential of approximately 0.3 MPa at the start of the experiment. As the result of stomatal closure, this difference in water potential is reduced as the experiment progresses. Modified from Trejo and Davies (1994).

cell growth can also be modified with variation in tissue water status (Saab et al., 1990).

There has been much discussion about the nature of variation in hormonal sensitivity (Weyers et al., 1987), but only limited progress can be made in this area until we know more about the binding of ABA at sites of action. There are difficulties in defining effective concentrations at the sites of action of the hormone and in the differentiation between real and apparent variation in sensitivity. Despite these uncertainties, observations of the kind described above allow us to suggest that an important component of the signal transduction chain between environmental perturbation and any modification in plant growth and physiology may be a modulation in the extent of the response to the hormonal signal.

The climatic variables that have important effects on ABA sensitivity of stomata can vary substantially over short periods. It seems possible, therefore, that variation in the ABA supply to the leaves in conjunction with variation in the sensitivity of the leaf's response to the ABA could allow the plant to integrate the different effects of climatic and edaphic perturbation. The relatively stable root signal might provide the basis for the regulation of the long-term development as a function of the access of the plant to soil water. The dynamic responses of stomata to climatic variation, which are necessary to regulate shoot water relations, can be determined by short-term variation in the sensitivity of the response to the chemical message as a result of interaction with factors such as evaporative demand, intercellular CO_2 concentration, and temperature. The implication of this hypothesis is that ABA is an integral part of stomatal responses to variation in $[CO_2]$, vapor pressure deficit, and temperature, as well as the response to variation in soil water availability. There is some evidence in the literature for this contention (Grantz, 1990), and further evidence is provided by the model described below.

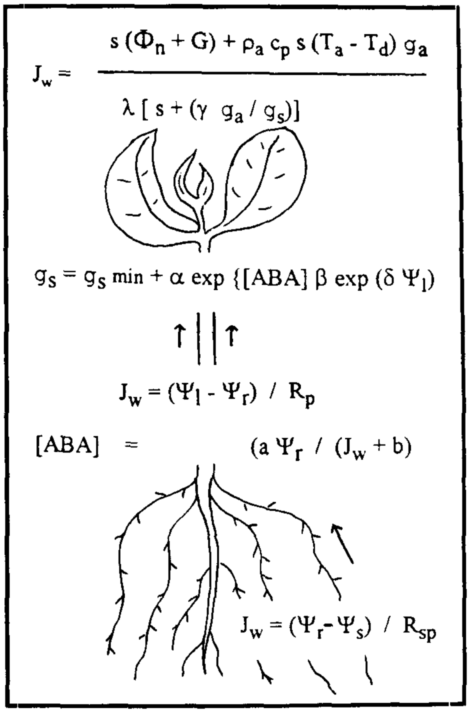

Figure 3. Representation of variables and equations of control in an interactive model describing water flux through maize plants (model described by Tardieu and Davies, 1993). Input variables are: Φ_n, net radiation; T_a and T_d, air and dew point temperatures, respectively; Ψ_s, soil water potential. R_p and R_{sp} are the plant and the soil-plant resistance to water flux, respectively. Unknowns are: g_s, stomatal conductance; Ψ_r and Ψ_l, root and leaf water potentials, respectively; J_w, water flux; [ABA], concentration of ABA in the xylem. Other symbols are constants (Tardieu and Davies, 1993). Arrows symbolize transfers of water and/or ABA.

A MODEL AND SOME PREDICTIONS

Tardieu and Davies (1993) modeled one of the interactive systems described above (ABA/leaf water relations) using five simple equations (Fig. 3). There are five unknowns (stomatal conductance, water flux, xylem ABA concentration, and root and leaf water potential). Inputs are net radiation, the vapor pressure deficit of the air, the initial soil water potential, and the soil hydraulic properties. The solution suggests that the kind of interactive system described in Figure 3 can operate in the plant and can account for variation in stomatal conductance with variation in the soil water reserve (Fig. 4).

Simulations of daily variation in gas exchange, water relations, and ABA concentration show a characteristic nonsymmetrical pattern of variation in stomatal conductance when water supply is restricted (high conductance early in the morning followed by steady closure of stomata throughout the day) (Tardieu and Davies, 1993). This is linked to increased stomatal sensitivity to ABA with the daytime decrease in shoot water potential. As in much published experimental data, there is no simple relationship between stomatal conductance and shoot water potential. The system allows for a control of leaf water potential without the necessity for a threshold water potential causing stomatal closure. As in much experimental data, shoot water potential reaches a plateau during the afternoon hours, and this plateau changes little with the soil water reserve.

Tests of the interactive model against a model involving purely chemical control suggest that, without the increase in stomatal sensitivity with leaf water deficit that we have described above, the kinds of ABA concentrations that are routinely observed in droughted plants fail to control stomatal behavior (Tardieu, 1993). A purely physical model (no chemical signal) predicts the drought-induced limitation of conductance but also predicts reopening of stomata in the afternoon hours, which is usually not observed with plants in drying soil under natural conditions. The interactive model provides some control of shoot water relations and of the ABA concentration in the xylem, but comparison with a purely physical model (ABA rendered ineffective) confirms that a relationship between stomatal conductance and the concentration of any chemical in the xylem (in this case "ineffective ABA") can be obtained in the absence of any controlling effect of the chemical on stomata (Fig. 4). This result means that the existence of such a relationship cannot by itself be cited as unequivocal evidence of chemical control of stomatal behavior in droughted plants.

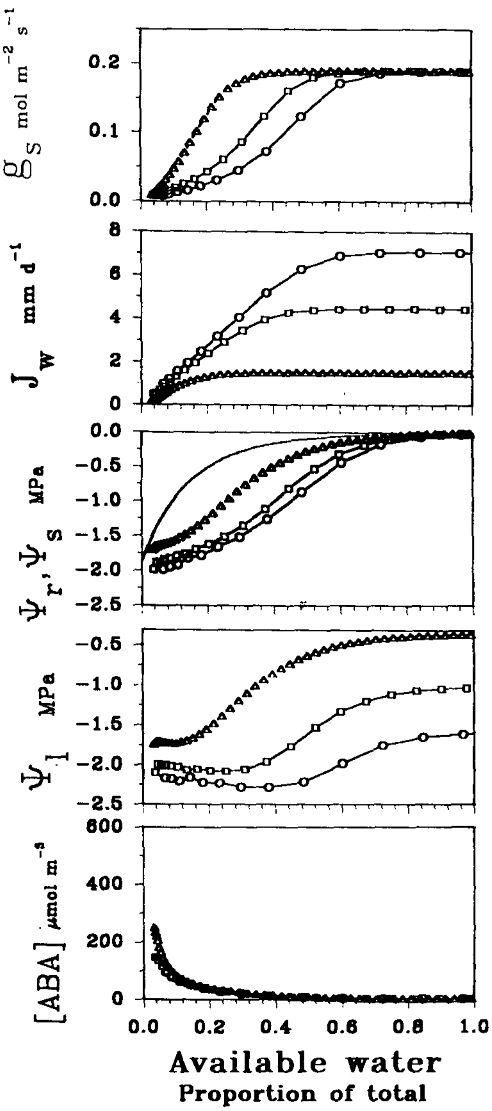

Figure 4. Simulated changes with time of stomatal conductance (g_s), water flux (J_w), soil and root water potentials (Ψ_s and Ψ_r, respectively), leaf water potential (Ψ_l), and xylem [ABA] plotted against available soil water during a drying period with three contrasting evaporative demands. The model used for the simulation is that described in Figure 3. The interval between two symbols represents 24 h. Solid line, Soil water potential. Symbols: Δ, 1.6 mm d^{-1} evaporative demand; □, 4.2 mm d^{-1} evaporative demand; O, 7 mm d^{-1} evaporative demand. Modified from Tardieu (1993).

Other important predictions from running the interactive model are (a) that increasing the capacity of a root system to synthesize ABA (perhaps by plant breeding [Quarrie, 1991]) would be expected to have little impact on stomatal conductance and on the rate of water use by the plant and (b) that the response of stomatal conductance to evaporative demand does not necessarily correspond to any special mechanism and can be explained by a model of stomatal control taking into account root messages and water flux (Fig. 4) (Tardieu, 1993).

THE FUTURE

Much of the evidence available to us suggests that chemical signals do have a role in the regulation of the physiology, growth, and development of droughted plants. We now have a framework for analysis of the performance of plants in the field, but this is based on the activity of only one chemical regulator, ABA, and there is still a considerable amount of uncertainty about some of its features. We need to know more about the sensitivity of various systems to the ABA signal, and we need more information about what appears to be very substantial variation in sensitivity in different situations. In nearly all of our work we relate leaf physiology or growth rate to the concentration of ABA in the xylem. We need some measure of hormone concentration at the site of action because it is clear that this variable can be influenced by the flux of the hormone into the apoplast of the guard cell as well as the concentration of the hormone in the transpiration stream (Gowing et al., 1993). Variations in flux may lead to variation in the apparent sensitivity of guard cells to a given ABA concentration. It also seems that variation in the rate of hormone metabolism and compartmentation can greatly influence concentration at the site of action and thus the apparent sensitivity of stomata to ABA arriving in the transpiration stream (Trejo et al., 1993). We have little information concerning these removal processes and whether they vary with environmental conditions and the physiological state of the leaf. Clearly, it is important to understand how the stomata actually "read" the ABA signal arriving in the leaf.

It will be important to test the predictions resulting from the interactive model described above, particularly if breeding programs for drought resistance are to involve selection or genetic manipulation for production of (or sensitivity to) ABA. Finally, we need to define the nature of any unidentified antitranspirant and growth-limiting activity in the xylem sap. If activity is attributable to a particular compound, this may be of considerable practical significance.

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LITERATURE CITED

Augé RM, Duan X (1991) Mycorrhizal and non-hydraulic root signals of soil drying. Plant Physiol **97:** 821–824

Canny MJ (1993) The transpiration stream in the leaf apoplast: water and solutes. Philos Trans R Soc Lond-Biol Sci **341:** 87–100

Chandler PM, Munns R, Robertson M (1993) Regulation of dehydrin expression. *In* TJ Close, EA Bray, eds, Plant Responses to Cellular Dehydration during Environmental Stress. American Society of Plant Physiologists, Rockville, MD, pp 159–166

Cornic G, Ghashghaie J (1991) Effect of temperature on net CO_2 assimilation and photosystem II quantum yield of electron transfer of French bean (*Phaseolus vulgaris* L.) leaves. Plant Physiol **185:** 255–260

Davies WJ, Zhang J (1991) Root signals and the regulation of growth and development of plants in drying soil. Annu Rev Plant Physiol Plant Mol Biol **42:** 55–76

Druger U, Schonbeck F (1992) Effect of vesicular arbuscular mycorrhizal infection on transpiration, photosynthesis and growth of flax (*Linum usitatissimum* L.) in relation to cytokinin levels. J Plant Physiol **141:** 40–48

Gollan T, Schurr U, Schulze E-D (1992) Stomatal response to drying soil in relation to changes in the xylem sap composition of *Helianthus annuus.* 1. The concentration of cations, anions and amino acids in, and pH of the xylem sap. Plant Cell Environ **15:** 551–559

Gowing DJG, Davies WJ, Jones HG (1990) A positive root-sourced signal as an indicator of soil drying in apple, *Malus* × *domestica* Borkh. J Exp Bot **41:** 1535–1540

Gowing DJG, Jones HG, Davies WJ (1993) Xylem-transported ABA—the relative importance of its mass and its concentration in the control of stomatal aperture. Plant Cell Environ **16:** 453–459

Grantz DA (1990) Plant responses to atmospheric humidity. Plant Cell Environ **13:** 667–679

Hartung W, Slovik S (1991) Physicochemical properties of plant growth regulators and plant tissues determine their distribution and redistribution: stomatal regulation by abscisic acid in leaves. New Phytol **119:** 361–382

Janssen MG, Markhart AH III (1993) Gradual soil drying promotes stomatal closure and xylem ABA increase in common and tepary bean (abstract No. 878). Plant Physiol **102:** S-153

Khalil AAM, Grace J (1993) Does xylem ABA control the stomatal behaviour of water-stressed sycamore (*Acer pseudoplatanus* L.) seedlings? J Exp Bot **44:** 1127–1134

Meinzer FC, Grantz DG, Smit B (1991) Root signals mediate coordination of stomatal and hydraulic conductance in growing sugarcane. Aust J Plant Physiol **18:** 329–338

Munns R (1992) A leaf elongation assay detects an unknown growth inhibitor in xylem sap from wheat and barley. Aust J Plant Physiol **19:** 127–135

Munns R, King RW (1988) Abscisic acid is not the only stomatal inhibitor in the transpiration stream. Plant Physiol **88:** 703–708

Munns R, Passioura JB, Milborrow BV, James RA, Close TJ (1993) Stored xylem sap from wheat and barley in drying soil contains a transpiration inhibitor with a large molecular size. Plant Cell Environ **16:** 867–872

Passioura JB (1987) The use of the pressure chamber for continuously monitoring and controlling the pressure in the xylem sap of the shoot of intact transpiring plants. *In* Proceedings of the International Conference on Measurement of Soil and Plant Water Status. University Press, Logan, UT, pp 31–34

Passioura JB (1988) Root signals control leaf expansion in wheat seedlings growing in drying soil. Aust J Plant Physiol **15:** 687–693

Quarrie SA (1991) Implications of genetic differences in ABA accumulation for crop production. *In* WJ Davies, HG Jones, eds, Abscisic Acid. Bios Scientific Press, Oxford, UK, pp 227–243

Raschke K (1977) The stomatal turgor mechanism and its responses to CO_2 and abscisic acid: observations and a hypothesis. *In* E Marre, O Ciferri, eds, Regulation of Cell Membrane Activities in Higher Plants. Elsevier Press, Amsterdam, pp 173–183

Rodriguez JL, Davies WJ (1982) The effects of temperature and ABA on stomata of *Zea mays* L. J Exp Bot **33:** 977–987

Saab I, Sharp RE, Pritchard J, Voetberg GS (1990) Increased endogenous ABA maintains primary root growth and inhibits shoot growth of maize seedlings at low water potential. Plant Physiol **93:** 1329–1336

Schurr U, Gollan T, Schulze E-D (1992) Stomatal responses to drying soil in relation to changes in the xylem sap composition of *Helianthus annuus.* II. Stomatal sensitivity to abscisic acid imported from the xylem sap. Plant Cell Environ **15:** 561–567

Snaith PJ, Mansfield TA (1982) Control of the CO_2 responses of stomata by indol-3-yl acetic acid and abscisic acid. J Exp Bot **33:** 360–365

Tardieu F (1993) Will increases in our understanding of soil-root relations and root signalling substantially alter water flux models? Philos Trans R Soc Lond-Biol Sci **341:** 57–66

Tardieu F, Davies WJ (1992) Stomatal response to abscisic acid is a function of current plant water status. Plant Physiol **98:** 540–545

Tardieu F, Davies WJ (1993) Integration of hydraulic and chemical signalling in the control of stomatal conductance and water status of droughted plants. Plant Cell Environ **16:** 341–349

Tardieu F, Zhang J, Davies WJ (1992a) What information is conveyed by an ABA signal from maize roots in drying field soil? Plant Cell Environ **15:** 185–191

Tardieu F, Zhang J, Gowing DJG (1993) A model of stomatal control by both ABA concentration in the xylem sap and leaf water status: test of the model and of alternative mechanisms for droughted and ABA-fed field-grown maize. Plant Cell Environ **16:** 413–420

Tardieu F, Zhang J, Katerji N, Bethenod O, Palmer S, Davies WJ (1992b) Xylem ABA controls the stomatal conductance of field-grown maize subjected to soil compaction or soil drying. Plant Cell Environ **15:** 185–191

Trejo CL, Davies WJ (1991) Drought-induced closure of *Phaseolus vulgaris* stomata precedes leaf water deficit and any increase in xylem ABA concentration. J Exp Bot **42:** 1507–1516

Trejo CL, Davies WJ (1994) Stomatal responses to water deficit and ABA. Aspects Appl Biol (in press)

Trejo CL, Davies WJ, Ruiz LMP (1993) Sensitivity of stomata to ABA: an effect of the mesophyll. Plant Physiol **102:** 497–502

Wartinger A, Heilmeier H, Hartung W, Schulze E-D (1990) Daily and seasonal courses of abscisic acid in the xylem sap of almond trees (*Prunus dulcis* M.) under desert conditions. New Phytol **116:** 581–587

Weyers JB, Paterson NW, Brook RA (1987) Towards a quantitative definition of plant hormone sensitivity. Plant Cell Environ **10:** 1–10

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:** 271–285

Zhang J, Davies WJ (1991) Antitranspirant activity in the xylem sap of maize plants. J Exp Bot **42:** 317–321

Zimmermann U, Haase A, Langbein D, Meinzer F (1993) Mechanisms of long-distance water transport in plants: a re-examination of some paradigms in the light of new evidence. Philos Trans R Soc Lond-Biol Sci **341:** 19–31