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Xylem-transported chemical signals and the regulation of plant growth and physiology

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SUMMARY

There is now a substantial body of evidence that shoot growth and physiology of plants rooted in drying soil may be regulated by chemical signals moving from the root to the shoot in the xylem stream. Although some evidence suggests that soil drying can reduce the supply of promoters of leaf growth and stomatal opening, there is now compelling evidence for an enhanced flux of inhibitors in the xylem stream of droughted plants. Some of this inhibitory activity is still to be identified but at least in some plants the bulk of activity can be explained by the enhanced concentration of the plant hormone abscisic acid (ABA).

A series of field experiments has now shown that ABA, moving as a signal from the roots to the leaves in the transpiration stream, can provide a measure of the access that the plant has to water in the soil in the rooting zone. We show here how this signal may be a variation in the concentration of ABA arriving at the sites of action in the leaf. The response to such a signal apparently varies as a function of the physiological state of the leaf. The basis of such variation in the sensitivity of response is also discussed. One other interpretation of the field data is that leaves respond to the amount of ABA arriving in the leaf, rather than the concentration. We show some evidence for this contention.

1. INTRODUCTION

The effects of soil drying on economic yield, leaf growth, gas exchange and other aspects of the physiology of plants are of much concern in many different environments. Although the effects themselves have been well-described, the mechanisms underlying these changes have been the subject of recent controversy (see Kramer 1988). There is no doubt that soil drying tends to reduce water uptake from the soil and result in a decrease in shoot water potential and turgor. In turn, these changes can affect shoot growth and physiology. Many recent papers have now shown that this sequence of events is not always seen in droughted plants and that physiological and developmental changes are not clearly attributable to effects on shoot water status. In this paper we examine the possibility that aspects of plant growth, development and physiology can be controlled by chemical signals generated in roots in contact with drying soil. We consider the nature of the signal and assess the type of information contained in a chemical signal moving from the root to the shoot.

2. EVIDENCE FOR A CHEMICAL SIGNAL GENERATED IN THE ROOTS OF DROUGHTED PLANTS

In an attempt to understand why shoot growth and physiology are influenced by soil drying under circumstances where shoot water relations are not affected, Passioura and colleagues (e.g. Gollan *et al.* 1986; Passioura 1988) have grown plants in drying soil in a pressure vessel, such that pressure applied to the root system exactly counteracts the increase in soil suction as the soil dries. This means that the shoot water relations of plants in drying soil can be sustained artificially at values close to those shown by well-watered plants. It is important to note that despite this manipulation, some interaction between roots and drying soil generates an influence that restricts leaf growth rate and leaf conductance.

Key evidence that this influence is a chemical inhibitor which moves from roots to shoots, probably in the transpiration stream, has been provided by Gowing *et al.* (1990). These authors divided the roots of individual plants between two separate rooting containers. The plant was allowed to dry the soil in one of these containers while the other was watered regularly. This treatment resulted in a restriction in leaf growth rate and a limitation in stomatal conductance even though the shoot water relations of these plants were not perturbed, compared to plants watered on both halves of the root system. Most importantly, when the portion of the root that had been in contact with drying soil was severed from the plants, leaf growth rates of these plants increased to the rates shown by the well-watered plants, even though no more water was made available to the remaining roots (figure 1). This result suggests that

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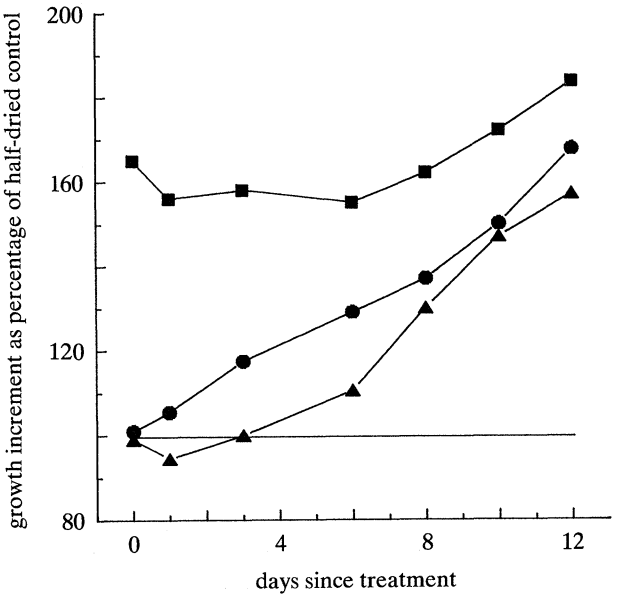

Figure 1. Daily increment in leaf area by apple trees with roots divided between two pots. Plants were supplied with water either to both halves of the root system (filled squares) or to one half of the root system only. Results are for plants that had received the above treatments for 24 d prior to the start of the measurements and are expressed as percentages of the growth of the plants that remained with half of their root system in dry soil (solid line). Other groups of plants were either rewatered (filled circles) or had the roots in dry soil excised (filled triangles). All points are 3-day pooled means ($n=6$). (From Gowing *et al.* 1990.)

this treatment removed the source of an inhibitor of leaf growth which was generated as a result of the association between roots and drying soil. Were leaf growth of droughted plants limited by the availability of a compound normally required for leaf functioning, then we would not expect that removal of roots in drying soil would result in a recovery of shoot growth.

3. HOW DOES THE INTERACTION BETWEEN ROOTS AND DRYING SOIL RESULT IN A MODIFICATION OF SHOOT GROWTH AND PHYSIOLOGY?

Much early literature has addressed the possibility that shoot functioning in droughted plants is influenced by a restricted supply of cytokinins from dehydrating roots (see e.g. Blackman & Davies 1985). While there can be little doubt that cell dehydration can reduce the synthesis of cytokinins and that reduced xylem transport of cytokinin to the leaves can be detected in droughted plants (e.g. Fussader *et al.* 1992), there must be some doubt about a central role for these compounds in the signalling process. Unless the roots dry very substantially, the reduction in the flux of cytokinins must be comparatively small. Published dose–response relationships for cytokinins seem to suggest that it is unlikely that shoots could detect and respond to anything but a substantial change in cytokinin supply. Nevertheless, Meinzer *et al.* (1991) have provided evidence for the involvement of cytokinins in root signalling in sugar cane growing in the field.

Drying the soil around the roots of a plant will eventually have very substantial effects on root growth and functioning. Many of these will contribute to changes in the chemical composition of the xylem sap. Elsewhere in this volume, Ruiz *et al.* have proposed a role for calcium in the xylem as a chemical signal. We know that calcium ions can interact with ABA to influence stomatal behaviour and growth and the same may be true of many other ions whose uptake will be restricted by soil drying. Radin *et al.* (1982) and Radin (1984) have shown how deficiencies of nitrogen and phosphorus can increase stomatal sensitivity to ABA and Gollan *et al.* (1992) and Schurr *et al.* (1992) note dramatic variation in the sensitivity of stomata to an ABA signal, as a function of variation in the ionic status in the xylem.

In an attempt to elucidate the importance of chemical signals in natural environments, Tardieu & Davies (1993) have modelled the stomatal behaviour of a field crop of maize. The variables included in this model are described elsewhere in this volume by Tardieu. It is important to note here that these authors were able to produce an effective description of the stomatal response to a decrease in soil water availability simply on the basis of changes in the fluxes of water and ABA through the plant as the soil dried. This is not to say that the effects of variation in cytokinin and ion content in the xylem are never important but it does perhaps argue for a central role for ABA in this process. Furthermore, the results of the split root experiment, described above, cannot be explained in terms of variation in cytokinin supply. An increase in the transport of cytokinins to the shoot would not be expected to result from the removal of dehydrating roots and hence cannot explain the increase in leaf growth. Rather, these data suggest that leaf growth of plants in drying soil is limited by the enhanced transport of an inhibitor from dehydrating roots and that removal of these roots removes the source of this inhibitor.

The plant growth regulator abscisic acid (ABA) is a well-documented inhibitor of both leaf growth and stomatal opening in droughted plants. It is now clear that ABA can be synthesised in roots (Cornish & Zeevaart 1985) and that roots in contact with drying soil contain increased amounts of ABA, even under circumstances where soil drying neither influences leaf water relations nor promotes extra ABA synthesis in leaves. Increased ABA concentrations are detected in the xylem of droughted plants and it has been suggested by Zhang & Davies (1989) that this ABA 'signal' can provide the shoot with a measure of the water availability in the soil (see also Tardieu, this volume).

In one split root experiment (Saab & Sharp 1989), soil drying was found to affect leaf growth of maize plants but not stomatal conductance. We know that ABA is a potent regulator of stomatal behaviour and if we are to argue that a single root signal is modifying shoot growth and other aspects of shoot physiology,

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then it is necessary to explain why stomatal behaviour was not affected in this experiment. In a later section, we offer some explanations for variation in apparent stomatal sensitivity to an ABA signal but here we discuss the possibility that other inhibitors of shoot functioning may also be involved in root to shoot signalling.

Although increases in xylem ABA concentration correlate in time with a limitation in stomatal conductance induced by soil drying, it is by no means clear what is cause and what is effect. Stomatal closure will reduce transpiration flux and this might be expected to result in an increase in the concentration of solutes in the transpiration stream. Tardieu *et al.* (1992*a*) have noted that late in the day when evaporative demand and transpiration fluxes are high, xylem ABA concentration is reduced from values recorded during periods when water loss is restricted. The antitranspirant activity of xylem sap can be tested by collecting sap from transpiring plants and feeding this to detached leaves or to epidermal strips. Collection of xylem sap can itself be a problem since it is necessary to avoid the inevitable increase in solute concentrations that is likely to occur when plants are detopped and transpiration ceases. The pressure vessel described above (Passioura & Munns 1984) is the best means available for avoiding these problems but this cannot be used with large field-growth plants. We have argued that under these conditions, the composition of xylem sap extracted with low pressure from the midrib of large, detached and detipped maize leaves will approximate what was contained within the xylem before the leaf was cut (Zhang & Davies 1990; Tardieu *et al.* 1992*b*).

It is clear that xylem sap collected from droughted plants can contain substantial antitranspirant activity, but in some plants there may not be enough ABA in the sap to account for the restriction in transpiration caused by the sap. Munns & King (1988) have suggested that in wheat this discrepancy may be caused by a still unidentified compound with antitranspirant activity. They have substantiated this view by passing xylem sap through an immunoaffinity column to remove ABA and then retesting the sap for antitranspirant activity. Xylem sap from this species still retained the capacity to restrict transpiration, even though all ABA had been removed. Trejo & Davies (1991) were also unable to account for all the antitranspirant activity in *Phaseolus* sap but Zhang & Davies (1991) found that maize xylem sap with ABA removed retained very little capacity to close stomata, and that the ABA content of the sap caused a comparable degree of stomatal closure to an equivalent concentration of ABA made up in artificial xylem sap (figure 2).

It seems that in some plants (e.g. maize), there is no necessity to look for additional compounds with major antitranspirant activity. In other plants (wheat and *Phaseolus*), further work is necessary to identify the nature of extra antitranspirant activity. R. Munns (personal communication) has suggested that wheat xylem sap may contain a compound that can be polymerized in the leaf to a compound with substantial activity. The unpolymerized compound in the sap may not always be active. Munns has suggested that polymerization might be brought about by the very high solute concentrations recorded in the sumps in the leaf, which are described elsewhere in this volume by Canny.

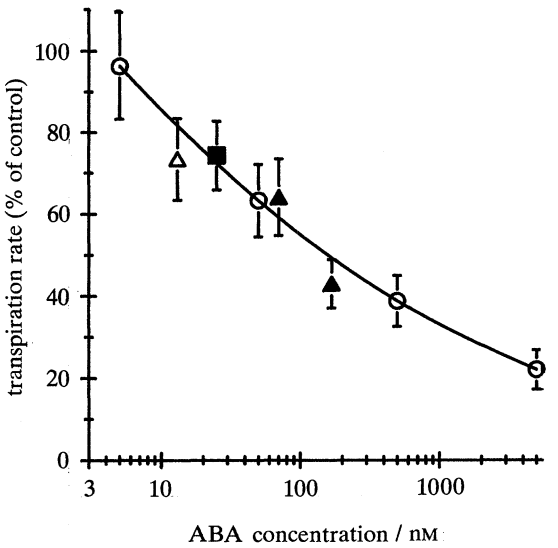

Figure 2. Transpiration of detached wheat leaves as a function of concentration of ABA in assay solutions. The solutions were synthetic ABA in artificial xylem sap (open circles), xylem sap from well-watered maize plants (filled squares), xylem sap from unwatered maize plants (filled triangles), and xylem sap from unwatered maize plants but with ABA removed by immunoaffinity column (open triangles) (from Zhang & Davies 1991). Data are expressed as percentages of the rate of water loss from control leaves fed with artificial xylem sap only (no ABA). Data are means of five observations. The bars are double standard deviations divided by the mean transpiration rate of the control leaves.

4. WHAT IS AN APPROPRIATE DOSE OF ABA FOR THE CONTROL OF LEAF PROCESSES?

If we are to argue that ABA in the xylem can act as a measure of the availability of water in the soil, then it is necessary to assess the nature of the information contained within the ABA signal. In non-transpiring maize plants, the concentration of ABA in the xylem provides a clear indication of the availability of water in the soil (Tardieu *et al.* 1992*a*) (figure 3). In transpiring plants, however, the situation is not as clear. Tardieu describes elsewhere in this volume how the physical properties of the soil can influence the water flux through the plant so that there is no unique relationship between soil water availability and xylem ABA concentration. Rather, the ABA concentration signal reflects both the ABA synthesized as a function of soil drying and the flux of water through the system.

This raises the potential problem that under hot and dry conditions when fluxes of water can be very high,

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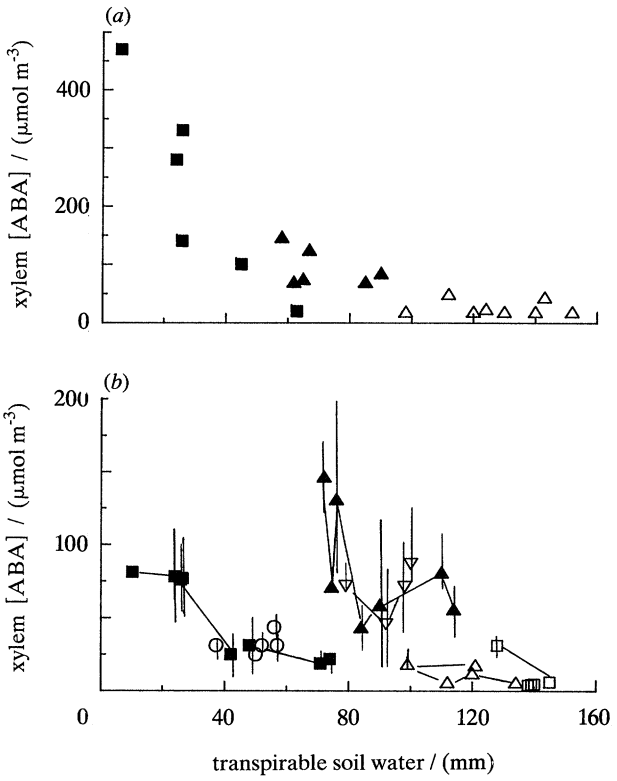

Figure 3. ABA concentration in the xylem sap of field-grown maize plants plotted against the transpirable soil water at (*a*) predawn and (*b*) during the day. Values in (*b*) correspond to the median, bars: quartiles (non-symmetrical with respect to the mean value). Symbols show different cultural treatments. (From Tardieu *et al.* 1992*b*.)

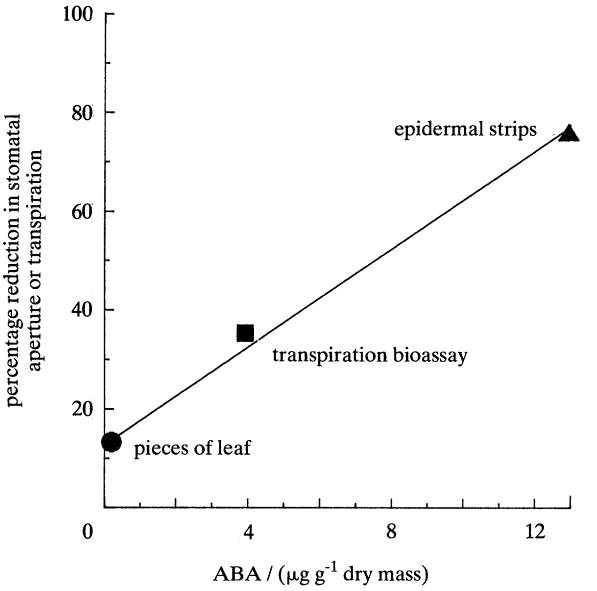

Figure 4. Reduction in stomatal aperture or transpiration as a function of the ABA concentration found in abaxial epidermis of *Commelina communis* L. after incubation in or feeding of ABA at 10^{-3} mol m^{-3} for 3 h. The treatments were: filled circles, leaf pieces floated on ABA solutions and stomatal apertures measured under the microscope; filled squares, shoots placed in ABA solutions for a gravimetric transpiration bioassay; and filled triangles, epidermis floated on ABA solutions and stomatal apertures measured under the microscope. (From Trejo *et al.* 1993.)

even though the synthesis of ABA may be substantial, concentrations of ABA will be low. Thus, under conditions where an ABA signal might be particularly beneficial initiating the processes necessary for turgor maintenance, the signal may be at its weakest. Under those conditions where the flux of water is at its highest, the plant apparently compensates for this dilution effect by an increase in stomatal sensitivity to a given concentration of the signal (Tardieu & Davies 1993). Apparent stomatal sensitivity to the ABA signal increases when the water potential of the leaf decreases as the day progresses. We have investigated the physiological basis of this change in sensitivity and have concluded that at least part of the observed variation can be attributed to a fundamental change in membrane properties (Tardieu & Davies 1992).

More recently, Trejo *et al.* (1993) have investigated the basis of variation in the sensitivity of stomata of *Commelina communis* to applied ABA. In this study, a given concentration of ABA was applied using three different techniques. Effects of ABA on stomatal aperture were investigated after incubation of isolated epidermis or leaf discs on solutions of ABA and effects on transpiration were investigated with a gravimetric bioassay. Stomata in isolated epidermis showed the greatest sensitivity to applied ABA while stomata in leaf discs incubated on the same solutions were virtually insensitive to the same concentrations. Trejo and co-workers were able to attribute differences in response to differences in the local concentrations of ABA in the epidermes of the leaves in the three situations. These were largely a result of very effective metabolism of applied ABA by *Commelina* mesophyll tissue, such that in leaf discs the concentration in the epidermis was much lower than that in the isolated epidermis, and varied as a function of the rate at which ABA was delivered to the epidermis (figure 4).

The results of this study suggest that the behaviour of stomata will depend on the balance between the amount of ABA arriving in the epidermis and the rate at which the hormone is removed from the site of action on the guard cells. Tardieu *et al.* (1993) failed to find a relationship between stomatal conductance and the flux of ABA into leaves in the field but this should not surprise us since we have no information on ABA partitioning or metabolism in these plants. Under many circumstances where transpiration rates, and perhaps also rates of metabolism, do not vary greatly, we would expect to find a correlation between xylem ABA concentration and stomatal behaviour, since the local concentration at the guard cells is dominated by the concentration of the arriving sap.

To investigate further the relative importance of the mass and concentration of ABA in the control of stomatal behaviour, Gowing *et al.* (1993) fed ABA in pulses to the petioles of detached cherry leaves. The degree of inhibition of leaf conductance was analysed with respect to the amount of ABA fed and to

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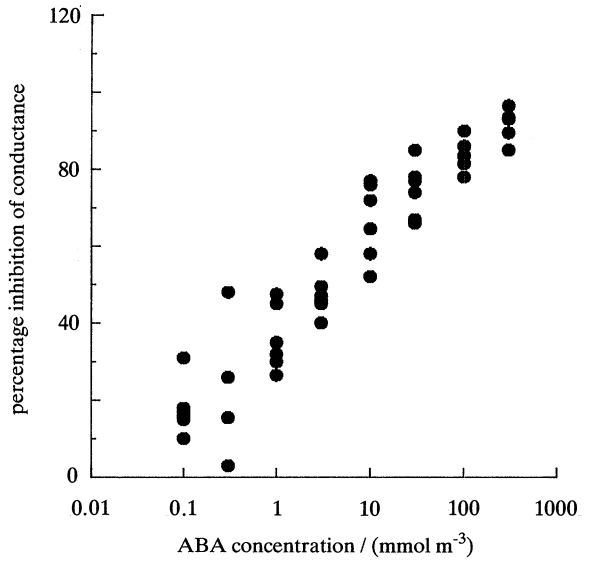

Figure 5. Inhibition of stomatal conductance of cherry leaves by a range of ABA solutions fed continuously to the cut petioles until the closing response was complete. Each point represents an individual leaf. (From Gowing *et al.* 1993.)

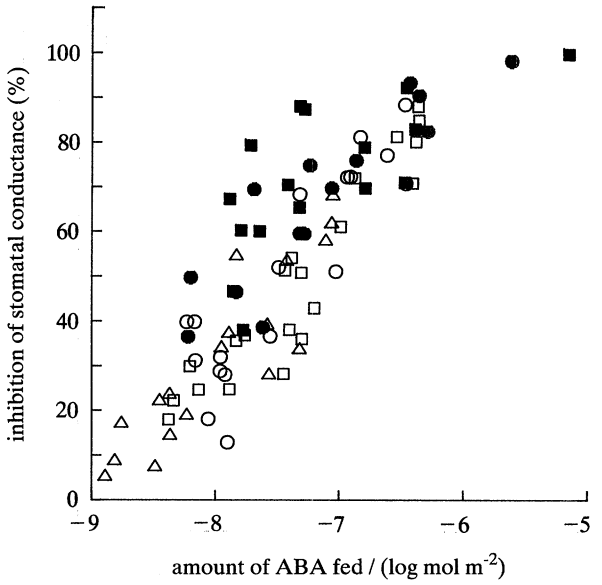

Figure 6. Inhibition of stomatal conductance by ABA in excised cherry leaves. Open symbols represent leaves fed with ABA concentrations in the range 100–300 mmol m^{-3} closed symbols represent ABA concentrations in the range 1–50 mmol m^{-3}. Variation in the mass of ABA delivered was a function of variation in the concentration of the feeding solution and variation in the length of the feeding pulse. (From Gowing *et al.* 1993.)

concentration of ABA in the feeding solution. Regression analysis of the data showed both variables to have a significant effect on leaf conductance (figures 5 and 6) but conductance was predominantly determined by the mass of ABA entering the leaf during the feeding pulse. The observation that the length of the feeding pulse had an influence on stomatal response suggests that either the stomata responded to a value of perceived ABA integrated over time, or to a local concentration which is a function of the rate of arrival and the rate of removal of ABA.

One argument against a stomatal response to an integrated signal is provided by a recent observation by MacRobbie (1990). A short exposure of epidermis of *Commelina communis* to a pulse of ABA resulted in a K^+ efflux from the guard cell, but the cell was then insensitive to a subsequent exposure to the hormone. It may be, therefore, that flux of ABA into the apoplast of the guard cell influences stomatal behaviour via the establishment of a local concentration which may differ substantially from the concentration measured some distance away in the xylem.

With the technology currently available to us, it is not possible to measure the local ABA concentration in the guard cell apoplast. Gowing *et al.* (1993) have used a simple model to predict the concentrations that might have been achieved in the apoplast under the conditions used in their experiment. Let this variable be called the 'apoplastic concentration' (C), which will reach its maximum value at the end of a feeding pulse. If the pulse were of x s duration, then at $t=x$, C_x will equal the integral of the ABA flux (F) from $t=0$ to $t=x$ less the amount of ABA removed from the apoplast, by partition into the symplast or by metabolism over the same period. Let us assume this removal of ABA is a first order process with respect to C, and that its rate is determined by the decay constant D. Therefore for a given volume of apoplast (V).

$$C_x = \frac{\int_0^x F\,\mathrm{d}t - \int_0^x D \cdot C\,\mathrm{d}t}{V}, \quad (1)$$

where,

$$D = \frac{\ln 2}{t_{1/2}}, \quad (2)$$

and $t_{1/2}$ is the half life of an ABA molecule in the apoplast.

Equation (1) can be solved to give

$$C_x = \frac{F}{D \cdot V}(1 - \mathrm{e}^{-Dx}). \quad (3)$$

If an ABA molecule in the apoplast was assigned a half life of between 15 and 30 min, then the explanatory power of a regression of the data in figure 6 against estimated maximum apoplastic concentration was greater than that of a plot of conductance against amount (81% versus 74%).

An attempt to measure the half life of an ABA molecule in the leaf produced the results shown in figure 7. Here, tritiated ABA was fed to cherry leaves for 15 min, after which petioles were placed in buffer and allowed to transpire for periods ranging from 10 min to 7 h. After these periods, tritiated ABA and total tritium in the leaves were compared to estimate the percentage of tritiated ABA remaining unmodified. The decay constant to the line giving best fit to the data in figure 6 gave a half life of 36.2 ± 5.1 min. This suggests a very much higher turnover rate than

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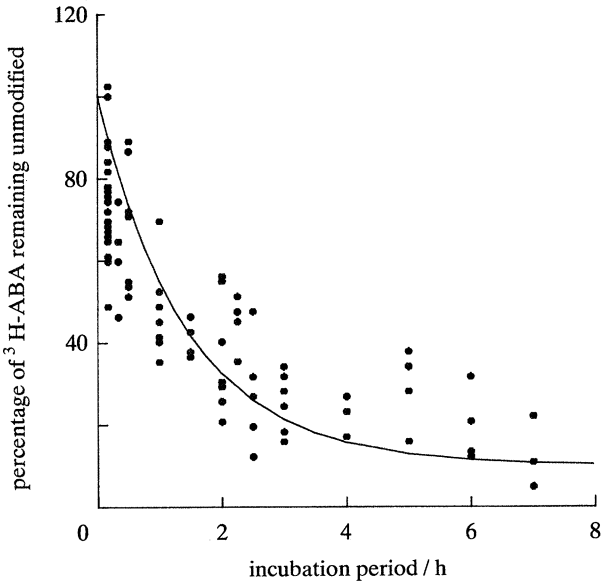

Figure 7. Rate of ABA catabolism by excised cherry leaves. The percentage of labelled ABA remaining unmodified over a timecourse of 8 h. Each point represents an individual leaf. (From Gowing *et al.* 1993.)

those recorded previously for several other species (e.g. Zeevaart 1980; Loveys 1984). One reason for this may be that xylem-derived ABA could be metabolised faster than intracellular ABA, much of which is within the guard cells (Hartung *et al.* 1980) and which may be shielded by the chloroplast envelope from the degradative enzymes in the cytoplasm.

The estimate of the turnover of ABA from the metabolism experiment (36 min) is of the same order as the optimal value for turnover calculated from the pulse-feeding experiment (15–30 min). The discrepancy between the two estimates could be a result of ABA leaving the active pool due to partitioning into cells (see Daeter *et al.*, this volume), at a slightly higher rate than that at which it is metabolized. The results suggest that at least in cherry leaves, the rate of ABA metabolism within the leaf is sufficient to prevent the accumulation of xylem-sourced ABA during the day and from day to day.

We have comparatively little information on the regulation of ABA metabolism in leaves. If its rate is affected by transpirational flux, or is promoted by some condition that also promotes transpirational flux, then the ABA concentration arriving at the guard cell could be strongly influenced by the prevailing xylem ABA concentration. Such a hypothesis would give a physiological basis to the results of Zhang & Davies (1989, 1990) and to the model of Tardieu & Davies (1993). Further experiments in which the ABA flux is modulated independently of concentration are needed to test this hypothesis.

CONCLUSIONS

As we have seen above, there are still many things that we do not understand about the mechanism of chemical signalling between roots and shoots. We know virtually nothing about the links between root conditions and the synthesis or redistribution of abscisic acid in roots, and we are only just beginning to get to grips with the interactions between the amount of ABA contributed to the transpiration stream and the flux of water through the plant. Most urgent perhaps is further elucidation of how the shoot actually 'reads' the chemical signal and translates this into a developmental or physiological response. Despite these and other shortcomings in our understanding, we can argue strongly that we already know enough to propose a framework of analysis to aid those interested in interpreting the drought responses of field grown plants. In the coming years, analysis of the cellular aspects of ABA production and response should move ahead in parallel with further investigation of the importance of chemical control of growth and development in the field. It seems likely that as a result of the types of studies described in this paper we will gradually modify our views both about what we should measure as a chemical signal and how we should measure it.

It is unthinkable that research into the effects of drought stress could be conducted without detailed measurement of water relations variables. Recent developments described here and in other chapters in this volume suggest that in many cases, such studies are equally incomplete without some consideration of chemical control of growth and development.

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