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EFFECTS OF ABSCISIC ACID IN THE ROOT:  
COMMUNICATION BETWEEN SHOOT AND ROOT

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INTRODUCTION

The potential of abscisic acid to alter the water balance of plants during periods of water stress makes it a very interesting substance agronomically as well as from a fundamental scientific point of view. Because of its ability to stimulate stomatal closure the use of ABA as an antitranspirant was one of the first areas explored on an agronomic basis. In addition, reports of alterations in root permeability to water (hydraulic conductance) seemed to offer another avenue of approach to the problem of controlling, alleviating, or delaying potentially destructive water stresses in crops. Because of personal biases and experience we decided to concentrate our first efforts in the area of the effects on root conductance and as the reports in the literature varied and were at times contradictory we felt it best to conduct experiments of our own to resolve how ABA might affect our particular plant systems. Because there does not appear to be a consistent pattern of results in the literature we will make no attempt to reconcile our observations with others.

MATERIALS AND METHODS

*Phaseolus vulgaris* cv. Ouray plants were grown in nutrient solution in a greenhouse as described earlier (Fiscus, 1981). The experiments consisted of detopping the plants and monitoring the xylem sap exudation rate with or without various levels of applied pressure ranging to about 0.4 MPa. Details of the procedures are given elsewhere (Fiscus, 1981). At the appropriate time ( $\pm$ ) cis-trans ABA, dissolved in ethanol, was added to the root medium and the resultant changes in

volume flux and total ion flux, as determined by xylem sap electrical conductivity, were followed. The quantities of ABA added varied with the size of the plant and were calculated for a given dose based on the measured leaf area of the plant.

#### RESULTS AND DISCUSSION

We were able to trace the changes in volume flux as a result of ABA application to four distinct responses which are diagrammed in figure 1.

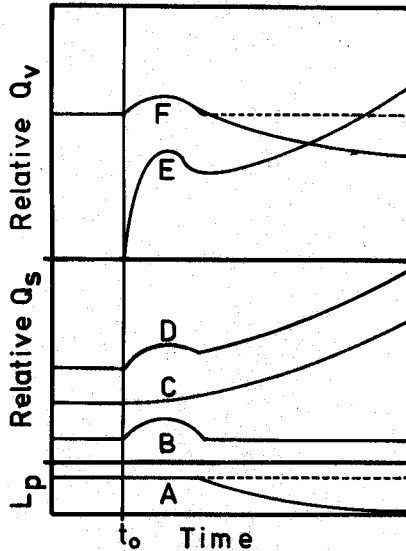


Fig. 1. Schematic representation of the events following ABA treatment at  $t_0$ . Curve A is hydraulic conductance; B, pulsed release of solutes; C, ABA-stimulated ion pump activity; D, B+C; E, volume flux in the absence of applied pressure; F, volume flux at high applied pressure. The dashed lines represent doses too low to reduce conductance (Reproduced from Fiscus, 1981).

Response 1 (curve B) is a release of solutes into the xylem sap which begins within 10 minutes of the application. Integration of the area under the solute transport curves (i.e. the area under the bulge in curve B) shows that the total quantity of ions released during this pulse is relatively unchanged between  $10^{-10}$  and  $10^{-7}$  mole  $\text{cm}^{-2}$  ABA (figure 2). The quantity of ions released increases sharply at doses greater than  $10^{-7}$  mole  $\text{cm}^{-2}$ . There seems to be no segregation of the data on the basis of applied pressure or

pre-ABA volume flux indicating that the ions are coming from a physiological pool of limited size.

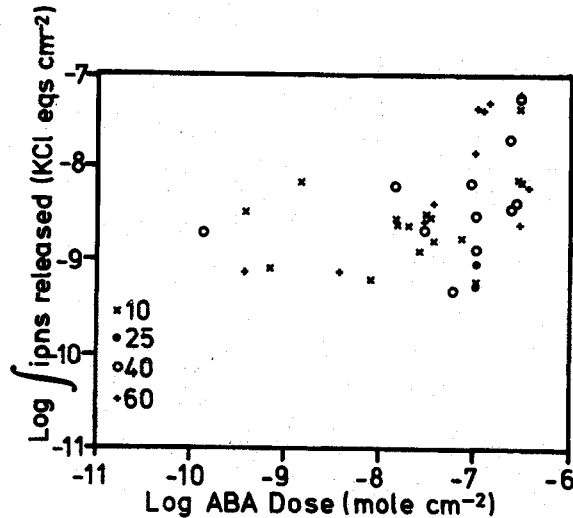


Fig. 2. Total quantity of ions released during the initial solute pulse caused by ABA. Numbers are the applied pressures on the systems in psig.

Response 2, coincident with response 1, is a rapid transient peak in volume flux. The peak (for example curve E in figure 1) is likely the result of the release of solutes in response 1 and shows a similar sensitivity. Although there is a great deal of scatter in the data a sharp upturn in the response around  $10^{-7}$  mole  $\text{cm}^{-2}$  is evident. The transient peak is very strongly inversely related to the pre-ABA volume flux (Fiscus, 1981).

The half time necessary to reach the transient peak is relatively constant over several orders of magnitude (figure 3), showing significant increases only when the ABA dose drops to about  $10^{-9}$  mole  $\text{cm}^{-2}$ , at which time it becomes difficult to detect the fast peak with certainty. Increases in the half time are apparent even if we ignore the lonely data point at 180 minutes which may be suspect. It appears therefore that the increase in half times in this area of the curve may reflect a threshold value for the peak response and therefore the pulsed release of solutes (response 1).

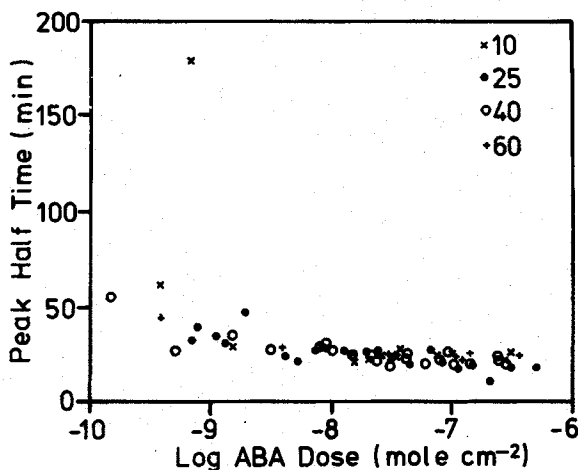


Fig. 3. Half times for the rapid transient peaks. Numbers indicate the applied pressure on the system in psig.

Response 3 is a much slower, gradual stimulation of ion transport into the root xylem from the medium which may not become apparent for 90 to 120 minutes after the ABA application. Finally, response 4, which occurs only at very high dosages, is a reduction in the root system hydraulic conductance.

That response 3 is persistent under conditions of the continued presence of ABA is shown by the diurnal patterns of root pressure exudation in the absence of applied pressure. This type of exudation depends entirely on the continued transport of solutes and any stimulating effect ABA might have on cellular ion pumps should manifest itself during this process. Figure 4 is an example of the very large stimulatory effect of ABA applied to the root medium on the exudation process. Interestingly enough the endogenous rhythm has a more powerful influence on the process than does the continued presence of ABA. However the result of the treatment was clear since the diurnal peaks produced by the relevant control plants were about the same or only slightly less than the peak on the first day. ABA stimulated diurnal peaks were as much as 700% of the controls at  $8 \times 10^{-9}$  mole  $\text{cm}^{-2}$ . The transient peak immediately following ABA application is also apparent in this figure.

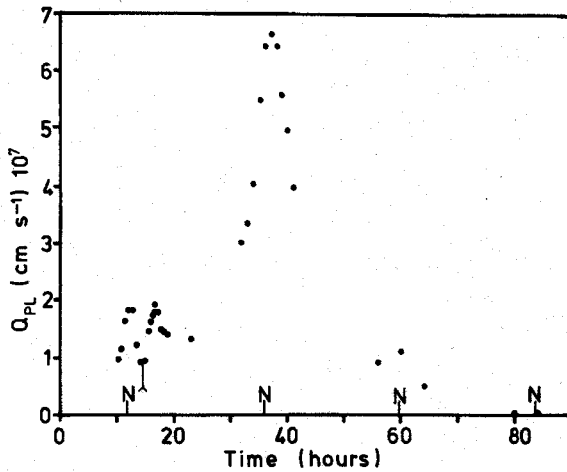


Fig. 4. Diurnal peak in root pressure exudation under the influence of applied ABA. The arrow indicates the time of addition and the letters N on the axis signify local noon.

The responses outlined above, with the exception of the decrease in root hydraulic conductance, are very similar to those which occur in the leaf under certain circumstances and I will attempt to tie them together and to speculate on how the root system might be involved in an ABA related response of the whole plant to water stress.

As indicated earlier responses 1 and 2 are probably causally related in that the peak increase in volume flux is due to the pulsed release of ions. The mechanisms involved in the ion release process are not apparent from these experiments but the speed of the response supports the view that it may be a direct result of the ABA challenge to the membranes which control solute and volume fluxes through the system. The initial response probably involves binding of ABA to the membranes (Hocking, *et al.*, 1978) followed perhaps by hyperpolarization of the membranes (Hartung, *et al.*, 1980) which appears to occur in two phases, the first of which has a half time close to those for the transient peak responses we observe in *Phaseolus* roots. In any case the peak in volume flux and stomatal closure in leaves treated with ABA, either as a foliar spray or via petiolar feeding, may be manifestations of the same reaction. The sudden appearance of ABA in the leaf tissue may result in a sudden release of solutes leading to a loss of turgor and stomatal closure. Certainly the time course for these events is

appropriate. We have calculated half times for ABA stimulated stomatal closure from several randomly selected papers (Mansfield, 1976; Davies, 1978; Milborrow, 1980) and find them all to be about 25 min, which is very close to the average shown in figure 3 for the higher dosages.

This response to ABA however would be transient in nature and caused by the rapidity with which ABA is built up in the tissues during experimentation. For this reason it may or may not bear any relationship to conditions with which plants might ordinarily be confronted.

The slow buildup of ion transport activity (response 3) however is a response that takes some time to develop and therefore is consistent with the concept of induction or synthesis of some protein which may act to mediate the transport of ions across membranes. The usefulness of such a mechanism in the leaf is difficult to see since the levels of nutrients in the apoplastic spaces of the leaf are quite small anyway. The only way to increase the level of ions available to the leaf tissues is to move more up from the roots. It is here that the role of ABA response 3 might be found.

Osmotic adjustment is one way that plants have of dealing with increasingly adverse conditions so that any mechanism which aided this adaptation might have survival value. A possible sequence of events might involve increases of ABA in the leaf tissue which is subsequently transported via the phloem to the root system where it increases the ion uptake capacity of the roots thus aiding in the osmotic adjustment process. It is worth noting at this time that unpublished data indicates that the stimulation of the ion pumps is much more sensitive to low dosages of ABA than are any of the other responses discussed here. The transport of individual ions which may be important in this process ( $K^+$ ,  $Na^+$ ,  $Cl^-$ ) has been shown to increase dramatically after treatment with ABA (Karmoker and Van Steveninck, 1978).

Alternatively the ABA produced in the leaves need not be transported to the roots in order for the message to be conveyed. The tension in the xylem could do that job much more quickly and efficiently. A leaf water potential sufficiently low to cause loss of turgor would be hydraulically transmitted to the roots where it would be just as capable of causing turgor reductions in the root tissues.

We know that the roots are capable of synthesizing ABA and that root ABA content can rise under stress conditions (for example see the general reviews by Milborrow, 1974; Torrey, 1976; Walton, 1980). The increased levels of ABA might elicit the increase in ion transport activity. Any

regulatory communication between the root and the shoot may involve nothing more complex than an increased transport of ions to the shoot which may aid in the osmotic adjustment process. Osmotic adjustment then allows the stomata to remain open to lower water potential thus increasing CO<sub>2</sub> fixation over what one might expect from an unadjusted plant.

Any ABA synthesized in the roots could easily be transported to the leaves via the normal transpiration stream but it is unclear what purpose this could serve as ABA production in the leaf tends to continue until the stress is relieved. When the stress is relieved and any ABA built up in the root xylem sap may be transported to the leaves, the presumed need for it has disappeared.

### CONCLUSIONS

There are at least 4 responses of root systems to ABA treatment. First is the fast release of solutes from the root tissues which results in the second, a rapid increase in the volume flux through the roots. Third, and probably most important, is the slower buildup of ion transport activity and fourth is a decrease in the hydraulic conductance which occurs at very high dosages.

The fast release of solutes may be similar to what occurs in the leaf when suddenly challenged with ABA in the transpiration stream. I feel it is doubtful that naturally occurring conditions which might elicit this response would be common. The usual situation would probably involve a relatively slow drying process where ABA production was built up gradually and the ion transport processes built up even more gradually. It is even possible to speculate, especially in the light of some recent work indicating a relationship between ABA production and stomatal closure (Pierce and Raschke, 1980; Radin and Ackerson, 1981), whether or not a loss of turgor is involved, that in leaves ABA production is the result and not the cause of stomatal closure.

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