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*Short Communication*

# Abscisic Acid Raises the Permeability of Plant Cells to Water

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A number of recent observations have indicated a role for abscisic acid in maintaining water balance. Treatment with ABA reduces the transpiration rate (3, 5), probably by bringing about stomatal closure (2, 4). Furthermore, water stress leads to a significant increase in ABA concentration in leaves (5, 7). On the other hand, ABA increases the rate of root exudation (6).

The present communication reports a marked effect of ABA on the permeability of plant tissues to water. The effect is observable both on $L_p$, the coefficient of hydraulic conductivity, and on $P_d$, the coefficient of diffusional permeability to water.

The effect on hydraulic conductivity was detected in experiments in which osmotic water flux between cells and medium was followed with time. The equations for net osmotic flux into or out of cells can be written as follows:

$$J_v \text{ (in)} = L_p(\sigma_i\pi_i - \sigma_e\pi_e - P) \quad (1)$$

$$J_v \text{ (out)} = L_p(-\sigma_i\pi_i + \sigma_e\pi_e + P) \quad (2)$$

where $J_v$ = volume flow of water; $\pi_i$ and $\pi_e$ are the osmotic values for the cell and for the external solution respectively; $\sigma_i$ and $\sigma_e$ are the average reflection coefficients for the internal and external solutes; and $P$ is the turgor pressure. Changes in water flux would thus follow from alterations in $L_p$, in $\pi_i$, in $P$, or in $\sigma$. We have earlier (1) defined conditions under which a change in $L_p$ may be distinguished from changes in the other parameters. Figure 1 shows the effect of ABA observed under these defined conditions. Discs excised from the xylem of root storage tissue of *Daucus carota* L. were washed in running tap water for about 16 hr. In the case of the efflux experiments, they were then immersed for 3 hr in 20 mg/liter ABA or in distilled water, after which they were transferred to 0.45 M mannitol. This concentration is hypotonic to the tissue. Net water efflux was determined by weighing the tissue at intervals. In the case of the influx experiments, the discs were first equilibrated for 3 hr in 0.45 M mannitol with or without 20 mg/liter ABA. They were then transferred to distilled water, and net influx was determined at intervals again by weighing. All experiments reported here were carried out at 27 C.

Figure 1 shows that ABA increased the flux of water both into and out of the tissue. This fact rules out the possibility that the change in flux was due to a change in $\pi_i$ or in $P$, since it is clear from the reversal of signs in equations 1 and 2 that if a factor affected flux via an alteration in either $\pi_i$ or $P$, the effect on influx would have to be the opposite of that on efflux. Moreover, the fact that efflux was measured into hypotonic solution excludes the possibility that ABA treatment was changing $\sigma$ (1). When ABA-treated tissue was transferred to water after measurement of efflux, it returned to its original fresh weight (as did the control), thus confirming the conclusion that $\pi_i$ and $\sigma$ had not been affected, *i.e.*, that solutes had not been lost from the tissue. It is, therefore, a valid deduction that the changes in flux shown in Figure 1 must be due to changes in $L_p$.

$P_d$, the coefficient of diffusional permeability to water, is also raised by ABA treatment. This was detected by measuring the flux of tritiated water between the tissue and the medium. In the experiment summarized in Figure 2, cylinders of carrot tissue were first equilibrated with tritiated water (specific activity 50 $\mu$c/ml) for 3 hr, with or without added ABA. Each cylinder was then sequentially transferred through a series of six test tubes containing 10 ml of $H_2O$ at time intervals as indicated in Figure 2. Samples from the test tubes were counted in a Packard Tricarb liquid scintillation counter.

Figure 2 shows that increasing concentrations of ABA progressively lowered the half-time for efflux of THO. The latter (*i.e.*, the point at which $A_t/A_0 = 0.5$ in Fig. 2) was 13.2, 10.1, and 7.5 min for $H_2O$, 10 mg/liter and 20 mg/liter ABA, respectively. No change in weight of the cylinders was observed during the experiment, indicating that full turgor was maintained for the entire period in both ABA-treated and control tissue.

Table I shows that the effect on $P_d$ was observable within 30 min of the start of ABA treatment. (The values for half-times given in this table, and in the tables following, were obtained from time curves plotted as in Fig. 2). Maximal effect was achieved after 3 hr.

The increase in $P_d$ brought about by ABA was reversible, but very slowly so. In the experiment summarized in Table II, the cylinders were treated for 3 hr with 20 mg/liter ABA or water and were then immersed in running tap water for a transition period of varying duration before efflux measurement. During the final 3 hr of the transition period, the cylinders were equilibrated with THO. Table II shows that $t_{\frac{1}{2}}$ remained low for many hours, only returning to its original value after 3 to 4 days in tap water.

The results so far discussed have concerned root tissue. ABA also alters the permeability of stem tissue to water and in the same direction. The half-time for efflux of THO from cylinders taken from the stem pith of *Pelargonium zonale* is lowered by ABA treatment to approximately the same extent as is observed for carrot cylinders (see first two values in Table III).

Since kinetin is known to be an antagonist of ABA with respect to its action on transpiration and stomatal opening (5, 6), it was of interest to examine its effect in the present system. Table III shows that kinetin does in fact have the opposite effect to that of ABA on diffusional permeability, both in carrot and in *Pelargonium* tissue. The half-time for THO efflux was raised by kinetin treatment by about 25% in both cases. When the tissues were treated with ABA in combination with kinetin, the effect of ABA predominated (Table III).

It seems paradoxical that a substance producing so marked an increase in the permeability of membranes to water as ABA

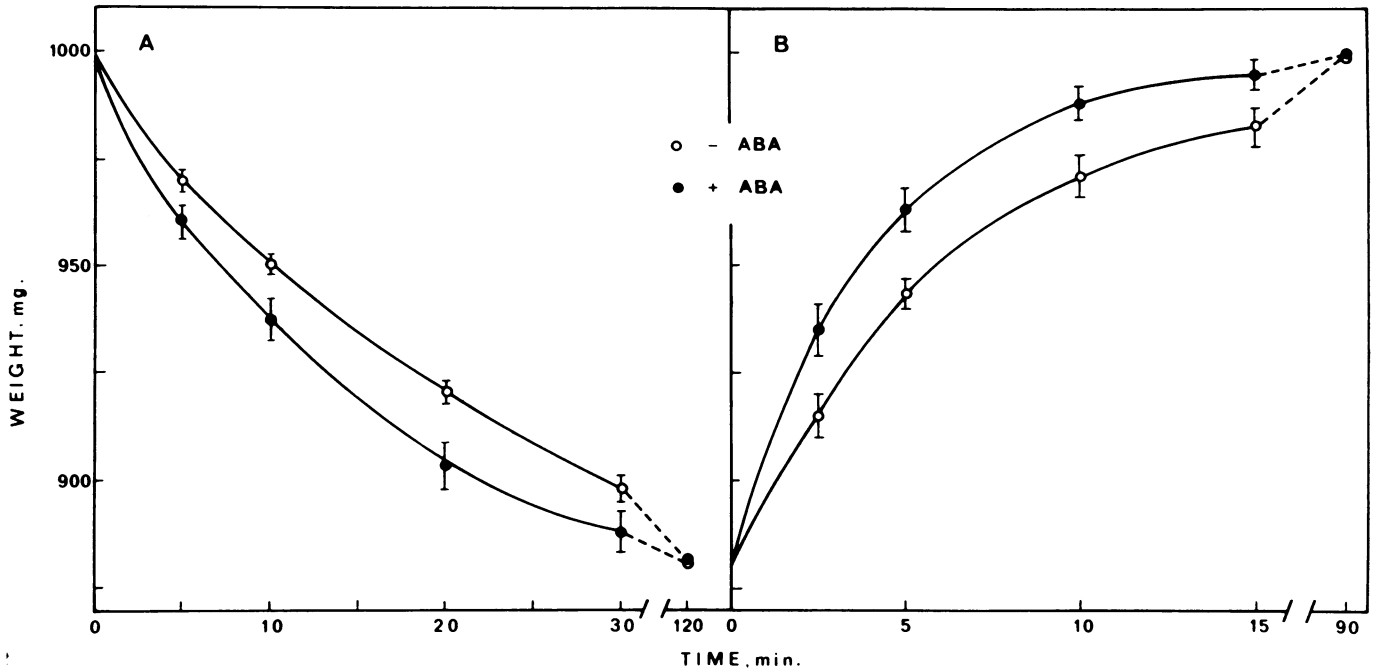


FIG. 1. The effect of ABA on the course of osmotic water flux out of and into carrot discs. A: Efflux. Samples of 16 discs (6 mm in diameter and 2 mm thick, combined fresh weight approximately 1 g) were transferred to 0.45 M mannitol after 3 hr in $H_2O$ or 20 mg/liter ABA. Efflux was then followed at the intervals indicated. B: Influx. Samples of 16 discs as above were equilibrated in 0.45 M mannitol with or without 20 mg/liter ABA. The equilibrium weight of each sample was approximately 880 mg. Influx was followed after transfer to water. Each point represents the mean of six determinations ± standard errors.

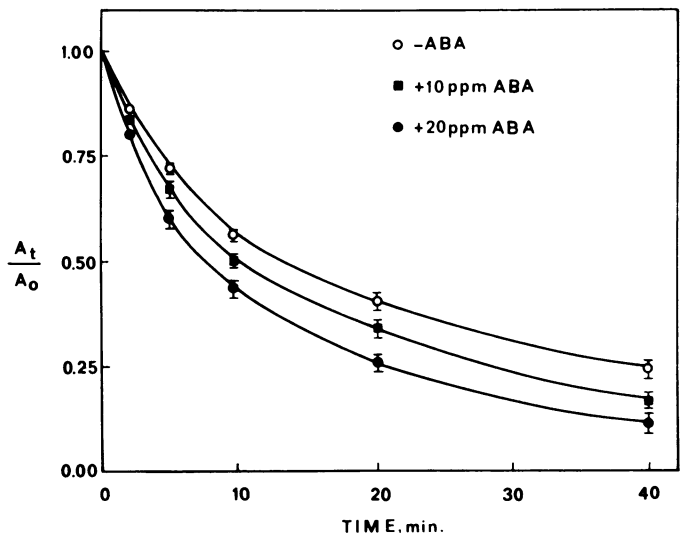


FIG. 2. The effect of ABA at two concentrations on the course of labeled water efflux from cylinders of carrot storage tissue. The cylinders, 6 mm in diameter and 20 mm in length, had first been equilibrated in THO with or without the addition of ABA. $A_0$ equals total radioactivity in the cylinder at the end of the equilibration period. $A_t$ equals radioactivity remaining in the tissue at a given time. Each point represents the mean of six determinations ± standard errors.

should bring about the closure of stomata. This fact perhaps deserves consideration.

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Table I. *The Effect of Increasing Duration of ABA Treatment on the Half-Time for Tritiated Water Efflux from Carrot Cylinders*

ABA concentration was 20 mg/liter.

| Duration of Treatment | $t_{1/2}$ |
|---|---|
| *min* | *min* |
| 0 | 12.2 ± 0.6[1] |
| 30 | 9.8 ± 0.8 |
| 90 | 8.4 ± 0.5 |
| 180 | 6.8 ± 0.6 |
| 300 | 7.3 ± 0.4 |

[1] Means ± standard errors of six determinations.

Table II. *Reversibility of the Effect of ABA on the Half-Time for Tritiated Water Efflux from Carrot Cylinders*

| Transition Period[1] | $t_{1/2}$ | |
|---|---|---|
| | −ABA | +ABA |
| *hr* | *min* | |
| 0 | 11.8 ± 0.6[2] | 7.4 ± 0.5 |
| 24 | 12.0 ± 0.8 | 7.2 ± 0.7 |
| 48 | 11.7 ± 0.4 | 8.4 ± 0.8 |
| 72 | 12.2 ± 0.8 | 9.5 ± 1.4 |
| 96 | 11.8 ± 1.0 | 10.6 ± 1.2 |

[1] Transition period was between ABA treatment and efflux measurement.

[2] Means ± standard errors of six determinations.

Table III. *Effects of ABA and Kinetin on the Half-Time for Tritiated Water Efflux from Cylinders of Carrot Root Storage Tissue and Pelargonium Stem Pith*

The cylinders were 6 mm in diameter and 20 mm in length.

| Treatment | $t_{1/2}$ | |
|---|---|---|
| | Carrot | *Pelargonium* |
| | *min* | |
| $H_2O$ | 11.0 ± 0.6[1] | 12.0 ± 0.4 |
| ABA, 20 mg/liter | 7.8 ± 0.4 | 8.0 ± 0.5 |
| Kinetin, 12 mg/liter | 13.2 ± 1.2 | 15.5 ± 1.4 |
| ABA, 20 mg/liter + kinetin, 12 mg/liter | 8.4 ± 0.9 | 7.6 ± 1.2 |

[1] Means ± standard errors of six determinations.

## LITERATURE CITED


1. Glinka, Z. and L. Reinhold. 1964. Reversible changes in the hydraulic permeability of plant cell membranes. Plant Physiol. 39: 1043-1050.
2. Jones, R. J. and T. A. Mansfield. 1970. Suppression of stomatal opening in leaves treated with abscisic acid. J. Exp. Bot. 21: 714-719.
3. Little, C. H. A. and D. C. Eidt. 1968. Effects of abscisic acid on budbreak and transpiration in woody species. Nature 220: 498-499.
4. Mittelheuser, C. J. and R. F. M. Van Steveninck. 1969. Stomatal closure and inhibition of transpiration induced by (RS)-abscisic acid. Nature 221: 281-282.
5. Mizrahi, Y., A. Blumenfeld, and A. E. Richmond. 1970. Abscisic acid and transpiration in leaves in relation to osmotic root stress. Plant Physiol. 46: 169-171.
6. Tal, M. and D. Imber. 1971. Abnormal stomatal behavior and hormonal imbalance in *flacca*, a wilty mutant of tomato. III. Hormonal effects on the water status in the plant. Plant Physiol. In press.
7. Wright, S. T. C. and R. W. P. Hiron. 1969. (+)—Abscisic acid, the growth inhibitor induced to detached wheat leaves by a period of wilting. Nature 224: 719-720.