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Abscisic Acid Accumulation by Roots of *Xanthium strumarium* L. and *Lycopersicon esculentum* Mill. in Relation to Water Stress[1]

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KATRINA CORNISH[2] AND JAN A. D. ZEEVAART*
MSU-DOE Plant Research Laboratory, Michigan State University, East Lansing, Michigan 48824

ABSTRACT

Plants of *Xanthium strumarium* L. and *Lycopersicon esculentum* Mill. cv 'Rheinlands Ruhm' were grown in solution culture, and control and steam-girdled intact plants were stressed. Detached roots of both species were stressed to different extents in two ways: (a) either in warm air or, (b) in the osmoticum Aquacide III. The roots of both species produced and accumulated progressively more abscisic acid (ABA), the greater the stress inflicted by either method. ABA-glucose ester levels in *Xanthium* roots were not affected by water stress and were too low to be the source of the stress-induced ABA. The fact that ABA accumulated in detached roots and in roots of girdled plants proves that ABA was synthesized in the roots and not merely transported from the shoots.

Maximum ABA accumulation in detached roots occurred after 60 to 70% loss of fresh weight. In *Xanthium* roots, ABA levels continued to increase for at least 11 hours, and no catabolism was apparent when stressed roots were immersed in water, although the roots did stop accumulating ABA. When osmotically stressed, *Xanthium* roots reached a maximum ABA level after 2 hours, but ABA continued to rise in the medium.

Under optimal stress conditions, endogenous ABA levels increased 100 times over their prestress values in detached roots of *Xanthium*, and 15 times in *Lycopersicon* under nonoptimal stress, when endogenous ABA was expressed as concentrations based on tissue water content. These are much greater relative increases than observed in the leaves (15 times in *Xanthium*, 3 times in *Lycopersicon*), although the roots contain substantially less ABA than the leaves in all circumstances. The results suggest that the endogenous level of ABA in roots could rise appreciably prior to leaf wilt, and could modify the plant's water economy before the leaves become stressed.

There have been many investigations into stress-induced ABA accumulation in leaves, both on the intact plant (2, 3) and when excised (14, 23). It is now well established that endogenous ABA levels in leaves increase considerably when plants are water stressed (6, 22).

On the other hand, the response of roots to water stress is much less clearly understood (1). There have been very few studies of endogenous ABA levels in roots because of the relative difficulty of working with roots compared with leaves. Endogenous ABA levels are also much lower in root tissue than in leaves, anywhere from 30% (21) to 1% (20) of the leaf level. Nevertheless, there is some evidence that stressed roots *per se* produce ABA to several times their prestress level (12, 20, 21), although the results appear to vary from species to species. Osmotically stressed young maize roots also increased their endogenous ABA levels, and ABA was released into the surrounding medium (19).

In this paper, we present data on the effect of water stress inflicted by different methods on endogenous ABA levels in cocklebur and tomato roots.

MATERIALS AND METHODS

Culture of Plant Material. *Xanthium strumarium* L., Chicago strain, was grown in solution culture in two different ways. First, seedlings were suspended from perforated boards over trays containing a shallow layer of half-strength Hoagland nutrient solution without aeration. The plants were grown in a greenhouse under the conditions described previously (24) until sufficient roots had developed for experimentation. Second, seedlings were taken from the culture trays after 1 to 2 weeks and placed in a continuously draining solution culture apparatus. Each plant was suspended from a rubber stopper in the top of a tube 5 cm in diameter and 75 cm long. Half-strength Hoagland solution was automatically pumped into the 24 tubes until they were filled. To provide good aeration, the culture solution drained slowly from the base of the tubes until the roots were exposed to the air. The tubes were then refilled and the process repeated continually until the plants were removed for experimentation. The system was operated in a controlled environment chamber (24).

Lycopersicon esculentum Mill. cv 'Rheinlands Ruhm,' was grown in the same two ways as *Xanthium*, except that all the tomato plants were grown in the controlled environment chamber.

In all experiments, roots were analyzed that had little secondary thickening. For experiments with isolated roots, the roots were detached from the plants, cut into approximately 2 cm lengths, and thoroughly mixed before placement into the appropriate treatments. The percentage dry weight of turgid detached roots was as follows: *Xanthium*, 3.8%; tomato, 6.6%. The percentage dry weight of turgid leaves (without petioles) was as follows: *Xanthium*, 18.7%; tomato, 15.7%.

Experiments with Intact Plants. Intact plants of either tomato or *Xanthium* were removed from the continuously draining solution culture apparatus; the roots were placed immediately into culture solution, and the shoot of each plant was enclosed in a plastic bag. The stems of half the plants were steam-girdled by directing a jet of steam for 3 min in a 1-cm band around the stem 0.5 cm above the root system. The roots of each plant were then blotted to remove excess culture solution and enclosed in plastic bags. The steam-girdled and control plants were then subdivided into two groups. One group was stressed in a stream of warm air (the root systems still enclosed in their plastic bags to prevent direct drying of the roots), until the intact plants had lost 15% of their fresh weight. The shoots were then replaced

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[2] Present address: Section of Plant Biology, Cornell University, Ithaca, NY 14853.

into their plastic bags. The stressed and turgid plants were incubated in darkness at room temperature for 6 h. After this time, the roots and leaves (without petioles) were harvested, frozen in liquid N_2, lyophilized, and weighed. The root samples were analyzed for ABA content (see below). The dried leaf samples were first ground by hand in plastic bags and thoroughly mixed; a small sample (10–40 mg) was then analyzed for ABA.

This experiment was repeated twice with tomato plants and each treatment was duplicated. The experiment was repeated 4× with *Xanthium*, 3× with duplicates, and once with four replicates. In this last experiment, the root and leaf samples were also analyzed for their ABA-GE[3] content (see below).

To confirm that the steam-girdles completely blocked phloem translocation, $^{14}CO_2$ labeling studies were carried out with two parallel sets of *Xanthium* and with one set of tomato plants. The plants were treated as described above until the steam-girdles were completed and the root systems were enclosed in plastic bags. One mature leaf of each intact plant (eight in each set) was then placed into a Plexiglas chamber (four at a time) and $^{14}CO_2$ was circulated through the chamber. The $^{14}CO_2$ was generated by adding lactic acid to 4 mg $Ba^{14}CO_3$ (53 mCi·mmol^{-1}) whereupon the leaves were illuminated (25). The $^{14}CO_2$ was circulated for 8 min. The shoot systems were then fastened into plastic bags. Separate bags for the roots and shoots were used to prevent the roots and shoots from sharing the same atmosphere and thus to preclude the possibility that the roots might assimilate respired $^{14}CO_2$. Plants to be stressed were dried in a stream of warm air as previously described. After the 6-h incubation period, the root systems of the labeled plants were detached. Each was placed between two sheets of cardboard held with rubber bands. These were frozen in liquid N_2 and lyophilized. The root systems were then placed under x-ray film (26) which was developed after 5 to 7 d.

Experiments with Air-Dried Detached Roots. Detached roots were thoroughly blotted and divided into equal quantities on a fresh weight basis, the amount depending upon the particular experiment. The roots were dried in a stream of warm air until the desired loss of fresh weight was achieved. *Xanthium* roots, for example, required a drying period of about 2 h to achieve a 70% loss of fresh weight. The roots were enclosed in plastic bags and incubated in darkness for the appropriate time period. They were then frozen in liquid N_2 and analyzed for ABA (see below). In every experiment, each treatment and incubation period was duplicated.

In one experiment, the water potential (ψ) of *Xanthium* roots was estimated after a 6-h incubation period. Roots (7–8 cm long) were coiled into sample chambers and their ψ was measured with a Wescor HR-33T dew point microvoltmeter equipped with C-52 sample chambers (Wescor) according to the methods of Nelsen *et al.* (13).

In another experiment with *Xanthium* roots stressed to a 70% loss of fresh weight, some samples were immersed in double-distilled H_2O after 5 h of stress to investigate ABA accumulation during stress recovery. These samples were frozen in liquid N_2 after various time periods and the pooled roots and distilled H_2O were analyzed for ABA content.

Experiments on Detached Roots Stressed with the Osmoticum Aquacide III. Different concentrations of Aquacide III (Calbiochem-Behring Corp., La Jolla, CA) were made using half-strength Hoagland solution (the basal medium) as solvent. The solute potential (ψ_s) of the different solutions was measured using the Wescor apparatus described above.

In all experiments, detached roots of either tomato or *Xanthium* were blotted and divided into equal quantities as before. Root samples were then immersed in the appropriate media. Duplicate samples were aerated in darkness for the desired time periods. The roots were subsequently removed from the media, rinsed thoroughly twice with basal medium, and then frozen in liquid N_2. The rinses were pooled with the medium for each sample. Both roots and media were analyzed for their ABA content (see below).

Extraction and Purification Procedures. All samples of plant material were homogenized using a Polytron homogenizer (Brinkmann Instr., Westbury, NJ) and extracted with 80% acetone (acetone, 1% acetic acid, 0.01% 2,6-di-*tert*-butyl-*p*-cresol) in darkness at 4°C for at least 24 h. The samples were filtered and the tissue residue washed with acetone. The acetone was evaporated and the remaining aqueous fractions were frozen in liquid N_2 and lyophilized. Extracts of root samples that had been incubated in osmotica were partitioned twice, before being lyophilized, with ethyl acetate and back-washed with aqueous 1% acetic acid to remove the remaining Aquacide III. Media samples were acidified to 1% acetic acid and partitioned as described. All samples were then purified by semipreparative reverse phase HPLC as described (3), except that the samples were eluted by means of a convex gradient from 0 to 50% ethanol containing 1% acetic acid in 25 min (the percentage ethanol at any point in the gradient after t min = $50[1 - (1 - t/25)^{-2}]$). The ABA content (and the ABA-GE content where desired) of the samples was quantified using a Hewlett-Packard 5840A gas chromatograph equipped with a ^{63}Ni-electron capture detector as described (3). Small amounts of (±) − [^{3}H]ABA (16.0 Ci·mmol^{-1}), together with small amounts of (±) − [^{3}H]ABA-GE (145 mCi·mmol^{-1}) where appropriate, were added to the samples during extraction in order to determine losses during the purification procedures. Overall recovery of [^{3}H]ABA added to the samples was between 70 and 95% for all leaf and root material from experiments using percentage loss of fresh weight as the water stress; overall recovery of [^{3}H]ABA-GE was between 40 and 70%. Overall recovery of [^{3}H]ABA, from experiments using the osmoticum Aquacide III, was between 50 and 70% for tomato roots and 50 to 90% for their media, and between 40 and 70% for *Xanthium* roots and 40 to 80% for their media. All data have been corrected for losses. The results are expressed as ng ABA·g^{-1} dry weight. However, after incubation in Aquacide III, not all of the osmoticum could be rinsed from the roots and thus dry weight could not be determined accurately. In the experiments with Aquacide III, the amounts of ABA are therefore expressed on the basis of the original fresh weight (Figs. 6–8).

RESULTS AND DISCUSSION

Experiments on Intact Plants. Results from two experiments on intact plants of *Xanthium* and tomato are shown in Figures 1 and 2, respectively. In both species, the roots of the stressed control plants contained substantially more ABA than their turgid counterparts, although the relative contribution, if any, of ABA translocated from the leaves is unknown (25). Stress-induced ABA accumulated in the root systems of the control and steam-girdled plants to a similar degree over the turgid level. This ABA could not have been supplied by the leaves because of the steam girdles. In the experiments with $^{14}CO_2$, it was found that the steam girdles were completely effective in blocking downward translocation of radiolabeled assimilates. Every root system from the control plants contained radioactivity throughout as shown on the autoradiograms, whereas no trace of labeling was apparent in the roots of steam-girdled plants. All the experiments with *Xanthium* and tomato gave similar results, although the amount of ABA accumulated by the roots of stressed plants was somewhat variable. On average, roots of control *Xanthium* plants accumulated stress-induced ABA to 13× their turgid level, while a 10-fold increase was observed in the roots of the steam-

[3] Abbreviations: ABA-GE, β-D-glucopyranosyl abscisate; ψ, root water potential; ψ_s, solute potential.

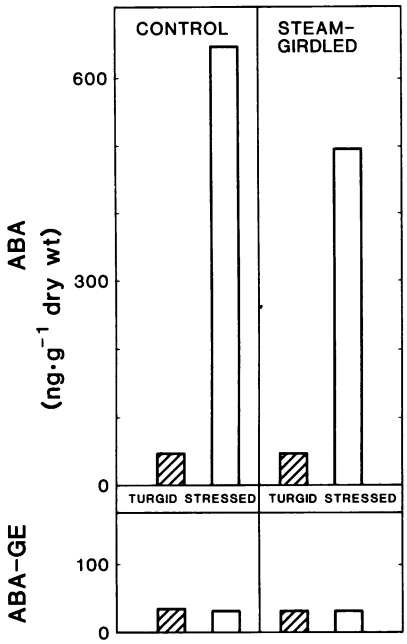

FIG. 1. ABA and ABA-GE levels in the roots of intact control and steam-girdled *Xanthium* plants. Stressed plants were dehydrated to a 15% loss of fresh weight and incubated for 6 h in darkness. Each value is the mean of four.

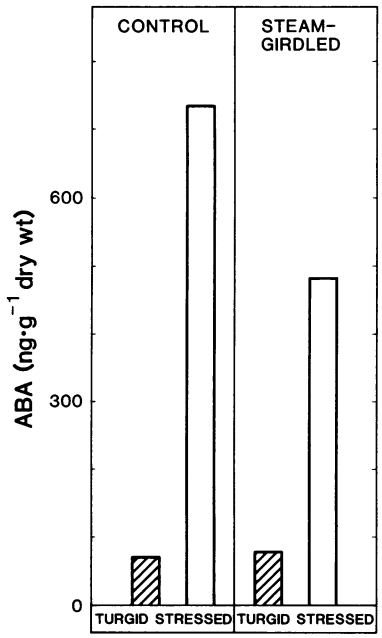

FIG. 2. ABA levels in the roots of intact control and steam-girdled tomato plants. Stressed plants were dehydrated to a 15% loss of fresh weight and incubated for 6 h in darkness. Each value is the mean of four from two experiments with duplicates.

girdled plants. In tomato, stress-induced ABA was accumulated, on average, in the control and steam-girdled plants, to 10× and 6× their turgid level, respectively. The level of ABA in the roots of the steam-girdled plants may indeed be an underestimate, as ABA could still pass into the shoots through the xylem during the incubation period. However, since the plants were incubated in plastic bags to restrict transpiration, transport of ABA from roots to shoots would be expected to be small. This is also suggested by the observation that the roots accumulated fairly similar amounts of stress-induced ABA in both the control and steam-girdled plants, despite the fact that the control roots were connected by the phloem to the considerably greater concentration of ABA in the leaves. The leaves of both steam-girdled and control plants contained typical ABA levels when turgid and stressed, *viz.*: turgid *Xanthium* leaves about 1.3 ng ABA·mg^{-1} dry weight, stressed leaves about 17 ng ABA·mg^{-1} dry weight (cf. 3); turgid tomato leaves about 3.0 ng ABA·mg^{-1} dry weight, stressed leaves about 7.6 ng ABA·mg^{-1} dry weight. *Xanthium* roots contained a low level of ABA-GE (Fig. 1), but unlike leaves (turgid leaves about 1.2 ng ABA-GE·mg^{-1} dry weight, stressed leaves about 1.8 ng ABA-GE·mg^{-1} dry weight) the ABA-GE content of the roots was unaffected by water stress (Fig. 1). The stress-induced ABA in the *Xanthium* roots was therefore not derived from the breakdown of a pre-existing pool of ABA-GE (Fig. 1), and probably arose from *de novo* synthesis, as occurs in stressed leaves (10, 12).

Experiments with Air-Dried Detached Roots. In *Xanthium*, the root ψ declined linearly with percentage loss of fresh weight, at least to a 30% loss (Fig. 3). The amount of stress-induced ABA accumulated by air-dried detached roots was found to be closely related to the actual amount of water lost by the roots. In tomato, maximum accumulation occurred at about a 60% loss of fresh weight (Fig. 4). Similar results were obtained for *Xanthium* roots, with a maximum accumulation at approximately 70% loss of fresh weight (data not shown); turgid *Xanthium* roots also had a higher water content (96.2%) than those of tomato (93.4%). This is a distinctly different pattern of ABA accumulation from that usually observed in leaf material during water stress. In leaves, no ABA accumulates until turgor is lost, com-

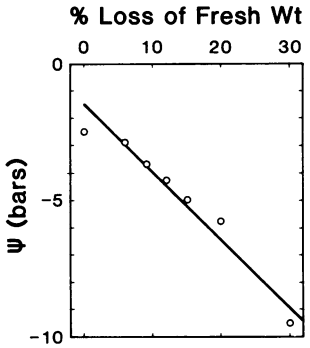

FIG. 3. Water potential (ψ) of detached *Xanthium* roots stressed to different extents and incubated for 6 h in darkness. Each value is the mean of two.

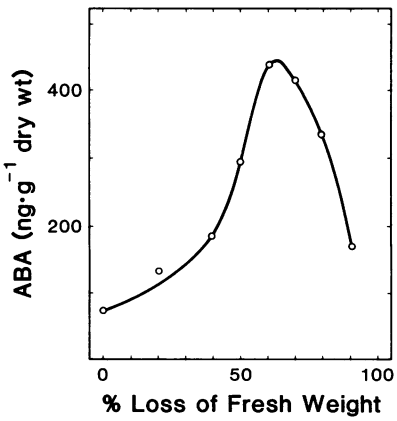

FIG. 4. ABA accumulation in detached tomato roots. Samples of 5 g fresh weight were stressed to different extents and incubated for 6 h in darkness. Each value is the mean of two.

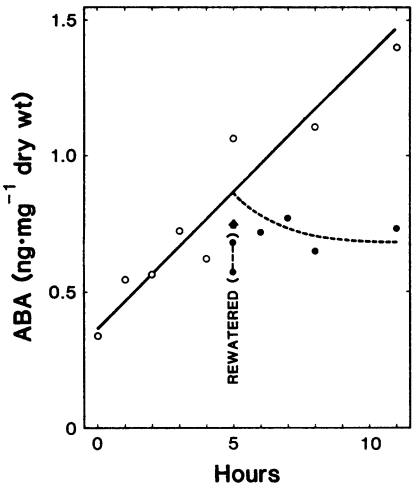

FIG. 5. ABA accumulation in detached *Xanthium* roots. Samples of 6 g fresh weight were dehydrated to a 70% loss of fresh weight achieved at 0 h. Stressed roots were incubated in darkness for different time periods. Some samples were immersed in 10 cm³ double-distilled H_2O after 5 h of stress, and incubated in darkness; the pooled roots and water were analyzed for ABA. Each value is the mean of two.

monly at about a 10% loss of fresh weight (5, 14, 15). In roots, it is difficult to determine turgor accurately by dewpoint psychrometry due to heterogeneity of the tissues and large amounts of apoplastic water. Hence, the threshold water loss for ABA accumulation was not determined. It is also striking that in roots the optimum degree of drying is so severe (60–70% loss of fresh weight) and that ABA still accumulates during stresses of at least an 80% loss of fresh weight in tomato (Fig. 4) and 85% in *Xanthium* roots (data not shown).

ABA accumulation by the roots has other dissimilarities when compared with leaves. *Xanthium* leaves, for example, began to accumulate ABA about 50 min after turgor loss and then reached a plateau after about 4 h (23). *Xanthium* roots, on the other hand, stressed to a 70% loss of fresh weight (Fig. 5), showed little evidence of a lag before accumulation began, accumulated ABA in a linear fashion, and had not reached a steady state level after 11 h of stress. Furthermore, when stressed roots were immersed in double-distilled H_2O (Fig. 5), the roots stopped accumulating ABA, but the ABA level did not decline. In the comparable experiment with detached *Xanthium* leaves (23), the ABA was rapidly catabolized and prestress levels were reached after approximately 4 h.

Turgid *Xanthium* roots commonly contain about 50 ng ABA·g^{-1} dry weight (*e.g.* Fig. 1). The samples analyzed at 0 h in Figure 5 contained 6× this amount. However, the samples frozen at 0 h were harvested on reaching a 70% loss of fresh weight after a drying period of approximately 2 h. If ABA accumulation began as the dry-down period commenced, by extrapolation, the roots would have contained about 150 ng ABA·g^{-1} dry weight. This value is closer to the normal level for turgid roots and supports the hypothesis that there is little delay before stress-induced ABA starts to accumulate in roots. After 6 h of stress (Fig. 5) the roots contained nearly twice the values for stressed roots in Figure 1. This is as expected, since the 70% loss of fresh weight provided an optimal stress for ABA accumulation (see above). The roots of the intact plants were not dried to this extent. When tomato plants were stressed to a 15% loss of fresh weight overall before incubation, the roots had lost 40% of their fresh weight after 6 h, whereas the leaves had lost only 11% at harvest.

Experiments on Detached Roots Stressed with the Osmoticum Aquacide III. Roots of tomato were also found to accumulate progressively more ABA the greater the stress when incubated in

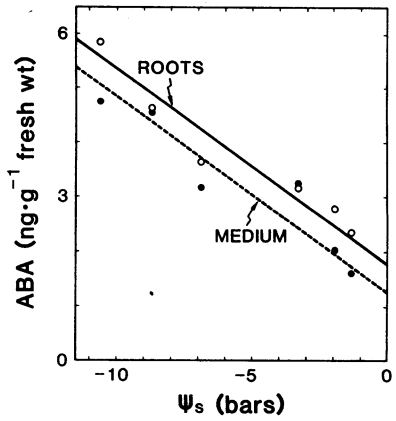

FIG. 6. ABA accumulation in detached tomato roots and in the surrounding medium. Samples of 3.5 g fresh weight were aerated in 15 cm³ of medium for 6 h in darkness. The media consisted of different concentrations of Aquacide III in half-Hoagland solution. Each value is the mean of two.

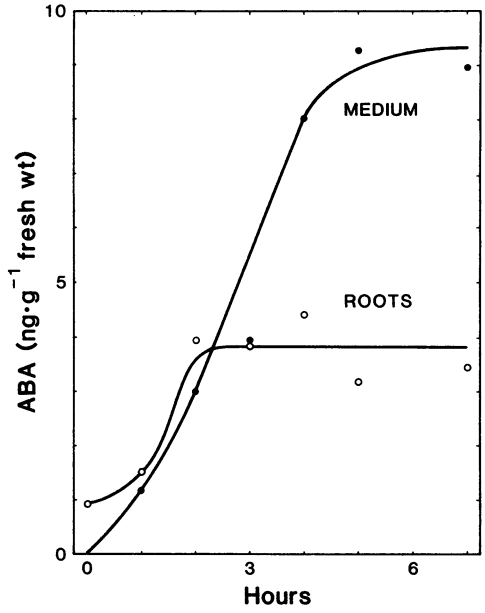

FIG. 7. ABA accumulation in detached *Xanthium* roots, and in the surrounding medium. Samples of 6 g fresh weight were aerated in 15 cm³ of Aquacide III and half-Hoagland solution ($\psi_s = -10.8$ bars) in darkness for different time periods. Each value is the mean of two.

solutions of Aquacide III (Fig. 6). ABA levels rose, in both the roots and the media, in a linear manner and a parallel relationship was maintained (Fig. 6). A similar pattern was observed when *Xanthium* roots were incubated, although in this case more ABA diffused into the medium than was retained by the roots (data not shown). However, when the time course of ABA accumulation at a single concentration of Aquacide III was investigated, *Xanthium* roots quite rapidly reached a maximum ABA content, while ABA continued to increase in the external medium (Fig. 7). Under these experimental conditions the total ABA produced by the roots reached a steady state after about 6 h. As discussed earlier, a steady ABA level was not reached in 11 h when the roots were stressed in warm air to a 70% loss of fresh weight (Fig. 5). In a single concentration then, the *Xanthium* roots behaved in a similar way to spinach leaf slices which also reached a maximum level of ABA in the tissue within 3 h, while ABA levels continued to increase in the medium (0.6 M mannitol)

(5). ABA levels have also been found to rise in young maize roots and in the surrounding medium when the roots were stressed in a range of sorbitol concentrations (19). More ABA accumulated in the medium than was retained by the tissues in *Xanthium* roots (Fig. 7), spinach leaves (5), and in young maize roots (19). On the basis of the model for cellular compartmentation of ABA (4, 5), it can be calculated that most of the ABA will be found in the medium. However, this is not invariably the case, as the tomato roots clearly retained more ABA than they released into the medium (Fig. 8). Thus, ABA efflux is not simply a passive process. Release of ABA into the liquid medium may have important implications under field conditions. There would probably be less release of ABA from roots into a dry soil than into a wet soil. Therefore, rain or irrigation might hasten the decline in root ABA content after relief of stress, particularly since rehydration of roots did not result in rapid ABA degradation (Fig. 5).

Comparison of the Effects of Different Types of Stress. *Xanthium* roots from the stressed steam-girdled plants (Fig. 1) contained 490 ng ABA·g^{-1} dry weight. If these roots are assumed to have lost 40% of their fresh weight, as was the case for tomato, then according to Figure 3 their ψ had dropped to −11.5 bars. When *Xanthium* roots were stressed with an osmoticum (ψ_s −10.8 bars, Fig. 7), they produced ABA in the roots and medium equivalent to 370 ng ABA·g^{-1} dry weight. Unstressed *Xanthium* roots have a ψ of −1.5 bars (Fig. 3). The osmoticum (ψ_s −10.8 bars) can then be assumed to exert a stress of −9.3 bars. This may be considered equivalent to a 31% loss of fresh weight (Fig. 3). In tomato (Fig. 4), a 40 to 31% loss of fresh weight corresponded to a 22% reduction in endogenous ABA. Again, assuming a similar behavior in *Xanthium* roots, the roots on the steam-girdled plants would contain 380 ng ABA·g^{-1} dry weight if stressed to a 31% loss of fresh weight instead of the 40% loss that actually occurred. This value is very close to the 370 ng ABA·g^{-1} dry weight produced by the roots incubated in the osmoticum. Thus, the roots apparently produce similar amounts of ABA in response to a single level of stress, regardless of the type of stress applied.

Comparison of ABA Levels in Roots and Leaves. Turgid *Xanthium* roots and leaves contained less ABA than the corresponding tissues in tomato (Table I). However, stressed detached *Xanthium* roots and leaves accumulated 28× and 13× their prestress ABA levels, respectively, which is considerably more than the corresponding stress-induced increases of 5.5× (8.3× under optimal stress) and 2.5× in the roots and leaves of tomato

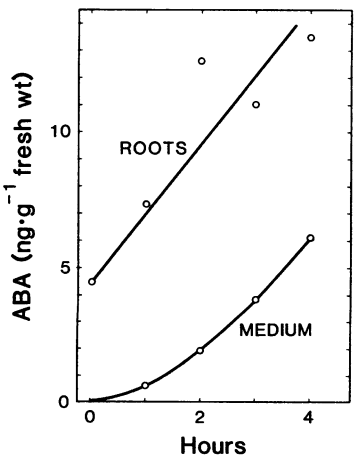

FIG. 8. ABA accumulation in detached tomato roots, and in the surrounding medium. Samples of 4 g fresh weight were aerated in 15 cm^3 of Aquacide III and half-Hoagland solution (ψ_s = −10.8 bars) in darkness for different time periods. Each value is the mean of two.

Table I. *Typical ABA Levels in Roots and Leaves of Cocklebur and Tomato, Both Turgid and under Optimal Stress Conditions*

Data are expressed per unit dry weight and as nM concentrations based on the water content of the tissue in question. All values for stressed material may be considered maximal, except for stressed tomato roots (*). If it is assumed that optimal stress conditions are similar in both cocklebur (*i.e.* 70% loss of fresh weight, 11 h incubation in darkness) and tomato (*i.e.* 60% loss of fresh weight, 11 h incubation in darkness), then the tomato roots could accumulate a maximum of 1.5× the tabulated values (*).

Tissue	ABA Content			
	Turgid	Stressed	Turgid	Stressed
	ng·g^{-1} dry wt		*nM*	
Cocklebur				
Roots	50	1,400	7.5	771
Leaves	1,300	17,000	1,130	17,400
Tomato				
Roots	80	440*	21.4	329*
Leaves	3,000	7,600	2,120	6,250

(Table I). Under all conditions, the leaves of both species contained substantially more ABA than their roots (Table I), as has been reported for several other species (12, 20, 21). *Xanthium* leaves contained 26× more ABA (on a dry weight basis) than the roots when turgid and 12× more ABA than the roots after optimal water stress (Table I). Similarly, turgid leaves of tomato contained 38× more ABA than the roots, and 17× (12× under optimal root stress) more ABA after stress (Table I). It is possible that the ABA contents of the starting root material in the present experiments were especially low due to the leaching of ABA from the roots into the culture medium (1).

As discussed previously, the optimal degree of drying for stress-induced ABA accumulation is very different in leaves and roots. This means, in fact, that the actual increase in ABA concentration in the tissue during water stress is much greater in the roots than in the leaves. It can be calculated (Table I) that the ABA concentration in the roots of tomato and *Xanthium*, during optimal water stress, increased 23× and 103×, respectively, compared with concentration increases of 3× and 15× in the leaves. This represents an enormous increase of ABA in the roots (of *Xanthium* in particular) during optimal water stress. The optimal 60 to 70% loss of fresh weight in roots is probably a realistic dehydration level under field conditions. After all, a 15% loss of fresh weight by intact tomato plants resulted in only an 11% loss in the leaves after 6 h, but a 40% loss in the roots (see above). This degree of stress only produces a fairly mild leaf wilt; plants can survive much greater stresses. Under any stress of intact plants, the roots will undergo much greater dehydration than the leaves as a consequence of the water potential gradient that exists in all higher plants. In turgid *Xanthium* plants, for example, root ψ is about −1.5 bars (Fig. 3) compared with a leaf ψ of −5 bars (3). Therefore, during the early stages of drought, the effective concentration of ABA in the roots could increase considerably before leaf wilt occurs. This hypothesis is supported by preliminary data from mildly stressed intact plants incubated in darkness. After 6 h, the leaves had regained turgor, but the roots had lost up to 30% of their fresh weight and did accumulate stress-induced ABA (data not shown). ABA regulates the plant's water balance not only by its effects on stomata (17, 18), but also by altering the hydraulic conductance of the roots (8, 16), and ion flux into the stem (9, 16) via direct action on membranes (7, 11). Thus, stress-induced ABA production by roots could have considerable importance in intact plants by modifying the plant's water balance before the leaves have even detected a water

stress.

In conclusion, roots of both *Xanthium* and tomato produce and accumulate ABA under a variety of stress conditions. Unlike leaves, the root ABA level rises under mild stress and without much delay; the roots accumulate progressively more ABA the greater the stress up to an optimal degree of dehydration (60–70% loss of fresh weight), and they continue to accumulate ABA for at least 11 h.

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