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Plant hormones and water stress

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In recent years, the involvement of plant hormones has become a subject of interest in plant water relations. The interest was initially stimulated by research into leaf ageing and plant senescence and the role of cytokinins in these processes. Plant water stress and some other stresses enhance senescence. They also bring about reduction in the levels of endogenous cytokinins. Exogenous cytokinins retard leaf senescence and may stimulate stomatal opening. Later, interest in the subject gained momentum from the various observations of the role of abscisic acid in stomatal opening. Abscisic acid brings about rapid stomatal closure, and its endogenous levels in leaves increase rapidly when plants are subjected to water stress or several other stresses.

Hypotheses and data relevant to the possible role of hormones in plants subjected to environmental stresses are presented and discussed.

1. Introduction

In plant water relations research the plant is often considered as an aqueduct between the soil and the atmosphere. Water fluxes in the plant are determined and controlled by water potential differences within the system as well as changes in water permeability. A considerable effort has been made to make accurate measurements of water potentials. Water permeabilities are usually calculated rather than measured and the relation between water potentials and permeability is at times confusing (Weatherley 1975).

Changes which occur in water potentials or in permeability to water in plants are mediated at least in part via metabolic regulatory mechanisms. Changes in water potential may be affected through electrolyte transport, biochemical transformations, cell wall elasticity and other factors. Changes in tissue and membrane permeability can occur because of changes in membrane composition, spatial arrangement, changes in electrochemical potentials and ionic composition around membranes. Thus, it is reasonable to assume that both water potentials and membrane permeability may be modified and controlled through metabolic regulation. Therefore, the response of plants under conditions of water deficits may be metabolically regulated. This may result in quantitative departure of expectations made on the basis of physical aqueduct type models of the plant system (Weatherley 1975).

Plant growth in general is regulated through the intricate mechanisms of control which rest in the genome and respond to changes in the environment. It is known that various plant hormones play a role in this regulation. Photoperiodism, dormancy, flowering and senescence are good examples of processes that involve hormonal action.

It seems reasonable that hormones are also involved in the changes which occur in water potentials and membrane permeability. In accordance with this view, the response of plants to environmental water stress is associated with changes in levels and activity of various hormones in the plant. Such changes in turn may provide for an adaptation of the plant to varying environmental conditions.

2. Cytokinins

Cytokinins are apparently purine derivatives. There are many compounds known at present which possess cytokinin activity. Kinetin was the first of the cytokinins to be identified in hydrolysate of DNA (Miller, Skoog, van Seltza & Strong 1955). Since then, kinetin has been shown to be an active growth substance. Its best known activity is its ability to retard leaf ageing, apparently through retardation of proteolysis. The fact that cytokinins retard leaf ageing only in detached leaves suggests that cytokinins are root factors which are supplied to leaves from roots (Mothes 1964).

Kende (1965) has chromatographed xylem exudate of sunflower roots and bioassayed the chromatographic fractions for cytokinin activity. He provided sound evidence for the presence of cytokinins in the exudate as well as of possible origin of cytokinins in roots. Weiss & Vaadia (1965) have shown that root tip extracts of sunflower seedlings possess cytokinin activity. Extracts from sections just behind the tip did not possess such activity (see table 1).

Table 1. Kinetin-like activity in root tips and sections proximal to the root tip in sunflowers

(Weiss & Vaadia 1965)

part	R_f	callus mass mg	kinetin equivalents, parts/10^6 total activity	kinetin equivalents, parts/10^6 per gram fresh tissue
root tips	0–0.2	507.9	0.130	0.274
0–1 mm	0.5–0.8	570.5	0.170	0.358
proximal sections	0–0.2	32.1	0.001	0.001
1–3 mm	0.5–0.8	14.4	0.001	0.001

We have detected cytokinin activity in root exudate of banana, bean, tobacco, sunflower and tomato plants.

Sitton, Itai & Kende (1967) found that in sunflower plants at the time of flowering the amount of cytokinins transferred in the xylem sap from root to the shoot was drastically reduced. This reduction may be related to the cessation of root growth at the time of flowering.

3. Cytokinins and environmental stresses

Two of the more general qualitative responses of stressed plants are enhanced leaf senescence and proteolysis (Vaadia, Raney & Hagan 1961). These processes are known to be retarded by cytokinins (Kende 1971). Shah & Loomis (1965) demonstrated that cytokinins retarded senescence induced by drought in sugar beet leaves. Drought subjected plants responded to treatment with 6-benzylaminopurine, a synthetic cytokinin. The cytokinin treatment prevented the reduction in RNA levels as well as protein levels observed in the untreated plants.

In view of these observations and the larger body of evidence from cytokinin effects on leaf senescence, it seems plausible that roots under stress provide reduced levels of cytokinins to the shoots. The shoots in turn behave as though their cytokinin supply is limited and exhibit enhanced protein degradation and other metabolic changes. Obviously this is a simplified view, for it neglects interactions of different plant hormones which may originate in roots and shoots. Yet it is of interest to evaluate the effect of environmental stresses on the supply of root cytokinins to shoots.

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4. Cytokinin levels in the exudate of stressed plants

Xylem exudate of plants which were briefly subjected to water deficits, salinity stress or osmotic stress, was assayed for cytokinin activity (Itai & Vaadia 1965). Water deficiency was imposed by withholding irrigation for a period of up to 5 days. In these treatments the plants exhibited temporary wilting. At the first signs of wilting, plants were rewatered, allowed to regain turgidity for a period of 2 h, then decapitated and exudate was collected from the cut root. Various salinity and osmotic stresses were imposed by different concentrations of sodium chloride and polyethylene glycol (Carbowax 6000) for two days. After two days of stress, these solutions were replaced by nutrient solution. Plants were decapitated and exudate was collected and assayed for cytokinin activity. In all the root stress cases studied, the detectable level of cytokinin activity in the root exudate was reduced. Only one example of data is presented here in table 2. However, the results obtained are similar for different types of stresses (Itai & Vaadia 1965).

Table 2. The influence of salinity on cytokinin activity in exudate of sunflower plants

treatment salt	exudate collected	callus mass	kinetin equivalent		% of
g/l	cm³	mg	μg/ml	μg	control
0	300	57.7	0.570	0.190	100
2.3	260	40.3	0.138	0.053	24.2
9.1	260	26.0	0.30	0.12	6.2

It should be noted that the amount of exudate collected is similar in all treatments, while the activity of cytokinins is reduced both on absolute basis as well as on concentration basis. The similar exudation rates observed are attributed to the fact that roots were not subjected to stress during the collection of exudate since plants were returned to nutrient solution before decapitation and thus the water potentials of the nutrient solutions were similar in all treatments.

The reduction in the levels of cytokinins in root exudates can be observed also when stress is applied to the shoots rather than to the roots. Itai & Vaadia (1971) examined the effect of water stress applied to tobacco shoots through enhanced evaporative demands. Plants were exposed for 30 min to an airstream which caused slight wilting of the leaves and then were allowed to recover turgor. This short period of water stress to the shoot resulted in a reduction of cytokinin activity to half that of the control. Again there was no difference between the amount of exudate collected in the treated and control plants. The cytokinin levels in the leaves themselves were reduced only slightly by this treatment. It is possible that their reduction, if significant, was due to chemical transformations of the cytokinins in the leaves rather than to reduced supply from the roots. That chemical transformations of ^{14}C kinetin may occur in water stressed leaves has been demonstrated (Itai & Vaadia 1971).

5. Stress cytokinins and leaf metabolism

Enhanced leaf senescence is associated with enhanced proteolysis. This can be demonstrated among other methods by the evaluation of the rate of incorporation of amino acids into protein in leaf disks. Enhanced ageing is associated with reduced incorporation, presumably because of enhanced proteolysis (Kende 1971).

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Drought pretreatment of tobacco plants resulted in reduced incorporation of L-leucine ^{14}C into protein of leaf disks as is shown in table 3 (Ben-Zioni, Aliza, Itai & Vaadia 1967). Plants were allowed to wilt, rewatered and allowed to recover turgor for 2 h at which time disks were excised for incubation in amino acid incorporation media. Similar procedure was followed when stress was administered by sodium chloride solutions (up to 0.1 M), mannitol (up to 0.16 M), or polyethylene glycol; stress solutions were replaced by nutrient solutions 2 h before excision of the leaf disks.

TABLE 3. INFLUENCE OF DROUGHT ON THE INCORPORATION CAPACITY OF L-LEUCINE ^{14}C INTO PROTEIN IN TOBACCO LEAF DISKS

		radioactive count/min	
treatment	disk mass mg	per disk	per 0.1 g fresh tissue
control	42.2	1840	4362
drought	43.9	1005	2286

The results of table 4 indicate that net incorporation into leaf disks was reduced also in salt or mannitol treatments.

TABLE 4. INFLUENCE OF SALINITY AND MANNITOL IN THE ROOT MEDIUM ON INCORPORATION CAPACITY OF ^{14}C L-LEUCINE INTO PROTEIN OF TOBACCO LEAF DISKS

		radioactive count/min	
treatment	disk mass mg	per disk	per 0.1 g fresh tissue
control	33.9	12886	4370
NaCl	33.7	5863	1976
mannitol	40.4	7110	2870

The interaction between leaf age and stress is demonstrated in table 5. Here stressed and control leaf disks of different ages were used for incorporation studies in much the same manner as in tables 3 and 4. The results show that incorporation is reduced due to age as well as due to stress.

TABLE 5. INCORPORATION OF ^{14}C L-LEUCINE INTO PROTEIN IN TOBACCO LEAF DISKS OF DIFFERENT AGES AFTER MANNITOL AND SALT STRESSES

	radioactive incorporation count/min per 100 mg fresh tissue		
leaf age	mannitol	NaCl	control
young	1497	1976	4556
mature	1230	1029	2190
old	588	740	1460

Ben-Zioni *et al.* (1967) have studied the effect of addition of kinetin (5×10^{-5} M) to the incubation medium of control and stressed disks prior to measurement of incorporation of L-leucine ^{14}C. Kinetin pretreatment had no effect on incorporation in the control treatment. However, in prestressed disks kinetin pretreatment resulted in significantly higher rates of incorporation

than in the disks not pretreated with kinetin. These observations are consistent with the possibility that endogenous levels of cytokinins are reduced in stressed leaves.

The hypothesis that environmental stresses reduce cytokinin supply to the shoots from roots suggested to Livne & Vaadia (1965) to test whether cytokinins influence stomatal opening. The rationale, although oversimplified, was that stomatal closure may be associated with the reduction in cytokinin supply observed under stress. The addition of cytokinins to detached barley leaves indeed enhances transpiration rate. Detailed studies of stomatal opening showed that the effect is indeed on stomatal opening, that about 1 h is required to discern the effect and that it has a concentration optimum at about 3×10 M kinetin (Livne & Vaadia 1965). Several workers have confirmed these observations. However, it became apparent that cytokinins do not stimulate stomatal opening in all species tested nor are they effective in very young leaves. Gibberellic acid seems to interact with cytokinins in their effect on stomatal response and the effect of ABA on stomatal opening is more rapid, general and significant than the effect of cytokinins or gibberellins (Livne & Vaadia 1972; Hsiao 1973).

6. Abscisic acid, cytokinins, and transpiration

Tal (1966) described a tomato mutant, *flacca*, which wilts rapidly under water stress because of abnormal stomatal behaviour. The stomata of the mutant resist closure under conditions of darkness, wilting, plasmolysis of guard cells and treatment with phenylmercuric acetate. Such treatments all cause closure in the normal variety (*Rheinlands Ruhm*) from which the mutant was derived. Tal, Imber & Itai (1970) and Tal & Imber (1970, 1971 *a*, *b*) presented a detailed study of this mutant. The hormonal picture is indeed complex. However, the mutant contains higher levels of cytokinins and much lower levels of ABA than the control. Partial phenotypic reversion of the mutant to the control can be effected either by cross grafting on normal roots or by the addition of ABA by spray to the mutant. It is of interest that the phenotypic reversion with ABA spray was dependant on continued treatment. Treated mutant plants regained their wilty phenotype several days after spraying had ceased. This indicates that ABA undergoes a turnover in these plants.

It was further demonstrated (Tal & Imber 1971 *a*) that the addition of cytokinins to the root medium of tomato plants decreased root permeability to water and exudation rates over a 24 h period. The addition of ABA enhanced permeability and exudation rates. The effect of ABA was greater in *flacca*, the ABA deficient mutant. Thus, they concluded that kinetin should cause plant turgor to decrease and ABA should cause turgor to increase. This is because kinetin enhances stomatal opening and reduces root permeability while ABA brings about opposite effects.

Mizrahi, Blumenfeld & Richmond (1970) presented a demonstration of this effect in tobacco plants. Plants were stressed for 48 h in 6 g/l NaCl or 31 g/l mannitol. The control plants were grown in half strength nutrient solution. All plants were sprayed by either 5×10^{-5} M kinetin, 3.8×10^{-5} M ABA or water as control. Leaves were excised from the plants after 48 h and were allowed to transpire from water solutions. The results are given for mannitol stress in table 6. The results for salt stress are similar.

It is evident that ABA reduces transpiration and cytokinins enhance transpiration in the control plants. In the stressed leaves a similar response is observed but transpiration rates are lower in all treatments.

Possible effects of root permeability on plant turgor cannot be deduced from the above

experiments. These experiments can be simply interpreted on the basis of the known effects of ABA and kinetin on stomatal opening. The former brings about stomatal closure while the latter brings about stomatal opening.

TABLE 6. THE INFLUENCE OF HORMONAL SPRAYS AND MANNITOL STRESS ON TRANSPIRATION RATES (g cm^{-2} h^{-1}) OF DETACHED TOBACCO LEAVES

	leaf sprays		
root medium pretreatment	water	ABA	kinetin
stress – mannitol 31 g/l	0.72	0.42	0.84
control – nutrient solution	0.92	0.66	1.26

Cessation of root aeration in tobacco plants growing in aerated nutrient solution often results in plant wilting. This is interpreted to be due to decreased root water permeability caused by the imposed oxygen tension (Kramer 1974). This would seem a good system to test the effect of pretreatment with cytokinins and ABA on plant water balance after cessation of aeration. Mizrahi (1972) conducted such experiments. Both kinetin and ABA were added to the culture solution of tobacco plants. These pretreatments greatly modified the response of the plants to cessation of aeration 48 h after the addition of the hormones. The results are given in table 7. Water saturation deficits of plant leaves are greatest with pretreatment with kinetin and smallest with pretreatment with ABA.

TABLE 7. THE EFFECT OF PRETREATMENT WITH ABA AND KINETIN ON WATER SATURATION DEFICITS (W.S.D.) OF TOBACCO LEAVES FOUR HOURS AFTER CESSATION OF ROOT AERATION

pretreatment	% w.s.d.	% of control
control	18	100
ABA 3.8×10^{-6} M	10.7	54.4
kinetin 5×10^{-6} M	27.4	152.2

Neither stomatal opening nor root permeability were measured in these experiments. They well might have been. However, the data do agree with the suggestion of Tal & Imber (1971 *a*) that kinetin reduces root permeability while ABA enhances root permeability in tomatoes and with the more generally known evidence that ABA induces stomatal closure while kinetin may enhance opening.

Mizrahi (1972) pursued further the adaptive response of tobacco plants to cessation of aeration conferred by ABA. He could show that stressed plants growing in nutrient solution which contains mannitol or sodium chloride have better water balance when the aeration of the solution culture is stopped. They do not wilt as the controls when aeration is stopped. In such plants the endogenous levels of ABA in the leaves increase. If such plants are returned to control culture solution the level of ABA in the leaves decreases and the plants do wilt if aeration is stopped. Resistance to wilting upon cessation of aeration can also be conferred simply by pretreating the plants with exogenous ABA as demonstrated in table 7. In further studies Mizrahi (1972) demonstrated that other stresses such as deficient nutrition also bring about enhanced leaf ABA content and resistance to wilting upon cessation of aeration.

It is now well known that ABA induces stomatal closure very rapidly (Raschke 1975). Minutes or even seconds depending on the plant species are sufficient to discern a response. With kinetin on the other hand the effects are not so clear cut. They are never as rapid and cannot

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be observed in all species. In fact ABA acts earlier than kinetin in response to an environmental stress. Yet the data presented here suggest that both hormones and possibly others effect and modify plant response to various environmental stresses.

8. ABA, KINETIN, AND ROOT PERMEABILITY

Root permeability to water has been measured in exuding roots by several workers. Collins & Kerrigan (1974) showed that kinetin reduced water permeability while ABA enhanced it in maize roots. These are similar results to those reported by Tal & Imber (1971*a*) but also involve rather long duration experiments of several hours. Short term effects on tissue permeability to water by ABA have been reported by Glinka (1973), including an enhanced root permeability to water after a 30 min pretreatment in ABA.

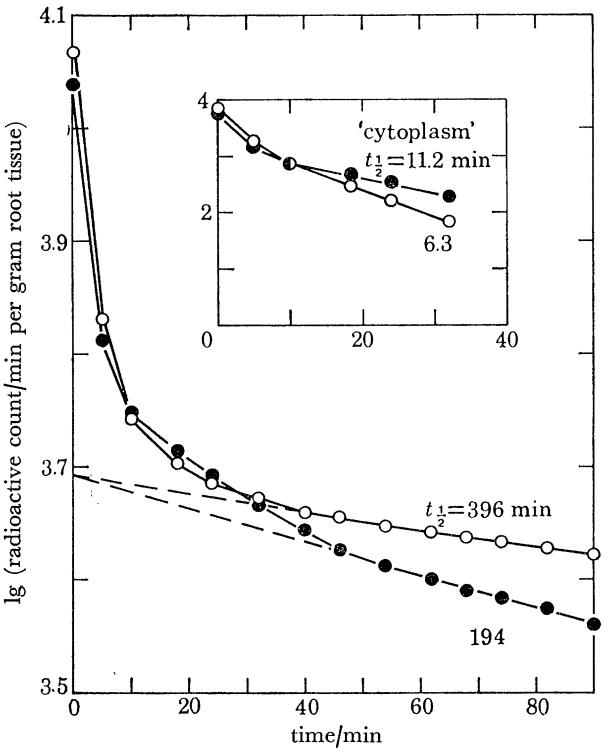

FIGURE 1. The course of the decrease in tissue ^{86}Rb in 1 cm sections of maize roots during wash with 10 mM KCl. Root sections were loaded for 4 h prior to the experiment in 10 mM KCl which included ^{86}Rb as tracer. There was no net flux of potassium into the tissue during the experiment. ○, ABA at 10^{-6} M was given to the root medium 16 h prior to the pretreatment and was included in the pretreatment and wash solutions; ●, no ABA. pH was maintained at 6. Plants were 12 days old and grown on half strength standard Hoagland nutrient solution.

The difference in time course of the effect of both ABA and kinetin on potassium permeability in maize root sections was studied by Vaadia & Wojciuch (1975). Compartmental analysis was made on 1 cm sections of maize roots which were pretreated in 10 mM KCl or K_2SO_4 containing ^{86}Rb tracer until no net flux of potassium could be observed. ABA or kinetin were added to the preload solutions for given periods. After the preload period, root sections were washed with similar but unlabelled solutions and aliquots were collected at frequent intervals. Aliquots were counted for radioactivity and data were plotted according to

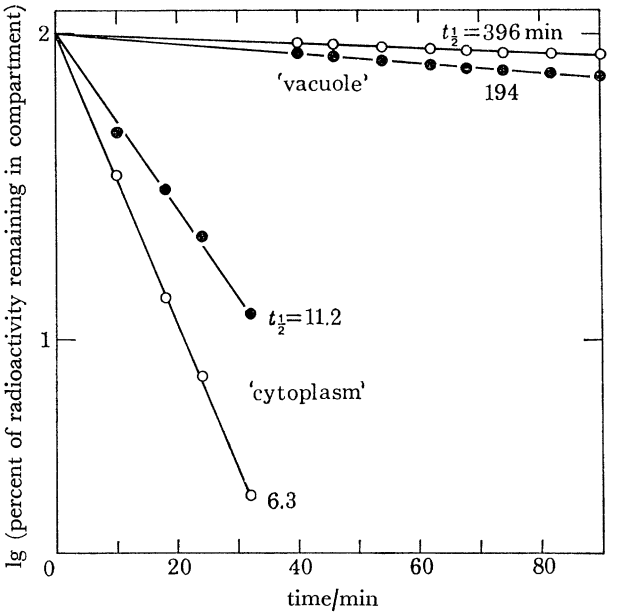

FIGURE 2. The course of the decrease in ^{86}Rb in maize roots during wash with 10 mM KCl. Data plotted as log percent of activity remaining in slow compartment ('vacuole') and in faster compartment ('cytoplasm') as obtained from the linear parts of the plot of figure 1.

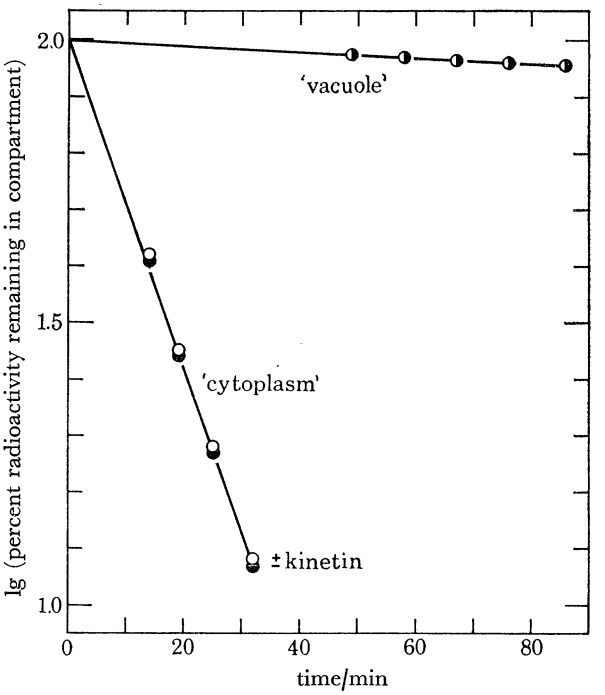

FIGURE 3. The course of the decrease in tissue ^{86}Rb in 1 cm sections of maize roots during wash with 10 mM KCl. Data plotted as log percent of activity remaining in slow compartment ('vacuole') and in faster compartment ('cytoplasm') as obtained from results of the type presented in figure 1. Conditions were similar to those given in figure 1 except that kinetin at 10^{-6} M replaced ABA.

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MacRobbie & Dainty (1958) as activity remaining in the tissue as a function of time. The compartmental analysis made on such data allows us to discern three linear portions to the curve (Cram 1968) which are commonly interpreted as 'vacuole', 'cytoplasm' and 'free space'. The slope of the line under the conditions of these experiments denotes the extent of the efflux of potassium through the membranes.

Figure 1 shows the results for control tissue and for tissue pretreated with 10^{-6} M ABA overnight prior to excision of the roots and during preloading and washing. ABA appears to slow down vacuolar efflux and enhance cytoplasmic efflux. In figure 2 these data are plotted as percent activity remaining in the 'cytoplasmic' and 'vacuolar' compartments separately. In figure 3 the effect of kinetin pretreatment is shown in a similar manner. It is shown that while ABA enhances 'cytoplasmic' efflux kinetin brings about a significant reduction in efflux. Kinetin, however, does not seem to have any effect on the 'vacuolar' fraction.

These results do not indicate much with respect to water permeability in roots. Yet they show that both hormones have an effect on potassium efflux in roots and have opposite effects on cytoplasmic efflux, just as is reported for their effects on water permeability. Further study is necessary here in order to evaluate whether the two responses are related. Could the efflux data with kinetin indicate a decrease of rates of water movement in the symplast?

The short term effect of both ABA and kinetin on potassium efflux have been reported (Vaadia & Wojciuch 1975).

9. Conclusions

Hsiao (1973; see also p. 479) has analysed the sensitivity of various plant parameters associated with stress to changes of water potential. He shows that plant or tissue turgor and cell enlargement are the most sensitive to stress and appear to be modified with minor changes in water potentials. However, during adaptation of plants to environmental stress a whole train of events is set in motion. Water potentials change, permeabilities are modified, growth is reduced, various metabolic reactions are slowed down or enhanced and hormonal levels are modified in roots and shoots.

It has been demonstrated in this paper that during water stress, osmotic stress or salinity stress, changes occur in the level of endogenous hormones. Root cytokinins generally decrease and leaf content of ABA increases. Other hormones are also modified (Livne & Vaadia 1972). It has been shown that the absence of ABA in a tomato mutant may bring about a lower level of turgor in the plant and that turgor is restorable by exogenous application of the hormone (Tal & Imber 1970, 1971*a*). Further it has been demonstrated that tobacco plants can become adapted to stress either by being subjected to stress or by being treated by exogenous ABA. During adaptation to stress the endogenous levels of ABA increase. Thus, ABA is able to modify the water relations of the plant without any associated environmental stimuli such as enhanced evaporation demands or reduced soil water potentials.

It should be noted further that similar changes in ABA levels in the plant occur in response to different environmental stresses. Nutritional deficiencies, lack of aeration, salt stress, osmotic stress, extreme root temperatures all result in qualitatively similar changes in endogenous hormonal levels (Mizrahi 1972).

Compartmental analysis of maize roots indicates that pretreatment of the roots with ABA or kinetin can influence potassium fluxes in these tissues where no net flux of potassium could be observed. This suggests that the hormones may modify membrane permeability.

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In conclusion, plant hormones are clearly involved in the response of plants to changes in environmental stresses. They are associated with modifications in root permeability, stomatal conductances and other plant responses to stress. The study of the nature of hormonal involvement in plant response to environmental stresses may yield relevant information for the understanding of plant behaviour under stress. It may also be of practical importance in the control of plant growth in specific circumstances of stress.

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