HORMONAL RESPONSES TO ENVIRONMENTAL STRESS — A REVIEW

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ABSTRACT

Environmental stresses induce many changes in the growth and physiology of plants. These may include the cessation of growth, stomatal closure, progressive senescence of leaves and leaf and fruit abscission. In recent years there has been considerable interest in studying hormonal changes in response to stress. This paper will review recent work on plant growth hormones and consider the extent to which hormonal changes may account for the stress-modified growth and physiology.

In this paper I will review some recent work on plant growth hormones. Particular emphasis will be placed on changes in hormone levels in response to a number of environmental stresses and the extent to which these changes may be responsible for primary or secondary responses to stress. Levitt (1972) discussed plant responses to a wide range of stresses but placed little emphasis on hormonal changes. Responses to water stress have recently been extensively reviewed by Hsaio (1973). At the conference on "Mechanisms of Regulation of Plant Growth" held in Palmerston North in 1973 a number of papers were presented on stress physiology. Where possible references have been selected from the proceedings of this conference.

Five distinct classes of plant hormones are now recognised: (i) auxins (ii) gibberellins (iii) cytokinins (iv) abscisic acid (ABA) and related compounds (v) ethylene. All these hormone groups have been implicated in stress responses. Usually the first three classes are considered as promotors of growth and development whereas the latter two classes are considered to antagonise the effect of promotors. Whereas in many studies changes of only one hormone are followed, the ratio between various hormones is probably more important than the absolute level of a single hormone.

Usually the levels of hormones in tissues are measured following extraction in an organic solvent, although in some cases diffusates from tissues or xylem exudates are analysed. Diffusates and exudates probably give a more accurate measure of active hormone levels.

The methods used to measure hormone levels have, until recently, relied largely on bioassays in which at least two-fold changes in concentration were required for significance. Recently gas chromatographic assays with relatively specific detectors and gas chromatography-mass spectroscopy have been used to assay gibberellins, ABA and ethylene and to a lesser entent auxins and cytokinins. High pressure liquid chromatography systems hold considerable promise for rapid quantitative measurements of cytokinins in particular.

Auxins

Indoleacetic acid (IAA) has been recognised for 30 years as the principle auxin in plant tissue. In spite of a considerable amount of work, the factors controlling IAA levels in plant tissues are still poorly understood. IAA is produced in differentiating tissues particularly near a stem apex, in leaves and in developing fruit. It is known to be involved in apical dominance and root initiation and also, in high concentration, to induce ethylene production. IAA is basipetally transported in shoots and this transport is apparently inhibited by ethylene.

Gibberellins

More than 25 gibberellins have been identified in higher plants. Many of these gibberellins have little biological activity in growth assays but can often be converted to an active form by a simple chemical reaction in the plant. The most widely known gibberellin, gibberellic acid (GA_3), is readily available commercially.

Gibberellins promote stem elongation and gibberellin levels are highest in rapidly expanding tissues. They appear to be synthesised in young leaves, root apices and fruit and are transported throughout the plant. Systhesis can be inhibited by application of growth retardants such as Cycocel, Phosphon D and Amo 1618.

Cytokinins

These hormones were originally identified as cell division factors and are found in highest concentration in root meristems and developing fruit. They have been found to move readily in the xylem from the root tips to leaves and play a central role in the maintenance of protein synthesis in leaves and possibly in the direction of metabolite movement in the phloem. Zeatin, the first naturally occurring cytokinin to be identified, was extracted from maize kernels by a New Zealand group led by D.S. Letham in Auckland. A number of closely related compounds are known to be widely distributed in plants.

Abscisic Acid

This inhibitory hormone was identified almost simultaneously from three distinct sources: from cotton fruit, from sycamore leaves and from yellow lupin fruit. Although originally considered to be principally an abscision and dormancy hormone, there is now more interest in its role in plant responses to stress. Under a wide variety of stress situations, ABA levels have been shown to rise. Application of ABA to plants leads to rapid stomatal closure and increased water absorption by roots improving the water balance of water-stressed plants.

Ethylene

At the beginning of the century ethylene was recognised as the toxic principle in illuminating gas which induced stem swelling in peas. The role of ethylene in the respiration climacteric and ripening of fruit has been known since the 1930's. In recent years a close correlation between auxin level and ethylene production

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TABLE 1: Prinicpal roles of plant hormones

| HORMONE | | PRINCIPAL ROLES | | OTHER |
	Growth*	Senescence	Stomata	
Auxins	promotes	-	-	promotes apical dominance promotes root initiation
Gibberellins	promotes	delays	opens	increases amylase activity in leaves
Cytokinins	-	delays	opens	maintains protein systhesis in leaves
ABA	inhibits	promotes	closes	increases water absorption in roots
Ethylene	inhibits	promotes	-	induces epinastic curvature in leaves induces stem swelling

*Growth refers to elongation growth and excludes effects on lateral expansion

has been recognised and it has been found that ethylene inhibits auxin transport. Ethylene is now known to be involved in many physiological processes including abscision and sex determination of some flowers.

The principal roles of these hormones are summarised in Table 1.

Drought Stress

When plants are subjected to water stress the physiological responses include wilting, stomatal closure and, usually, enhanced rates of leaf senescence. The wilting is a direct effect of dehydration and loss of turgor (P) but the specific level of water potential (+) at which wilting occurs will depend on the osmotic potential (π) since, from the relationship

$$\Psi = \pi + P$$
Ψ will equal π when P is O

In maize a definite lag of 60-120 min has been demonstrated between the onset of stress and the elevation of ABA levels in leaf tissue (Beardsell and Cohen, 1975). It is possible, but not yet demonstrated, that the low levels of ABA present in unstressed leaves may move from the mesophyll to the guard cells in response to stress and thus induce stomatal closure.

Enchanced rates of leaf senescence have been noted in many plants subjected to stress and this can be measured by reduced levels of chlorophyll, protein or RNA. This phenonmenon should be regarded as a secondary rather than a primary response to stress. Evidence, mainly from the Arid Zone Research Institute in Israel, suggests that cytokinin transport from roots is much reduced by stress and this causes a reduction in cytokinin activity in leaves. A gradient of cytokinin-like activity is usually found in non-stressed plants with the greatest activity in the youngest leaves and low activity in old leaves. It has been proposed that reduction of these levels under stress, coupled with increased levels of ABA, account for the decreased protein and RNA synthesis and chlorophyll breakdown observed (Livne and Vaadia, 1972). This hypothesis is supported by experiments in which cytokinins were applied to stressed leaves. In these cases chlorophyll breakdown was innibited, protein systhesis enhanced and RNA loss reduced. (Itai & Ben Zioni, 1974. Shah and Loomis, 1965).

Water stress also stimulates ripening of fruit (Adato and Gazit, 1974) and abscision of cotton fruit and leaves. (McMichael et al., 1972). These effects appear to be mediated by enhanced ethylene production in the stressed tissue.

Waterlogging or Flooding

The responses of plants to flooding are complex and are induced by oxygen deficit. Root resistance to water flow increases and, if the plants are placed under high evaporative demand, water stress results. However, if the plants are under low evaporative conditions the symptoms of flooding are often leaf epinasty, leaf senescence, stem swelling, adventitious root formation and reduced plant height (Kawase, 1974).

The levels of cytokinins and gibberellins in xylem sap are much reduced by flooding. Gibberellin metabolism in roots and gibberellin levels in leaves are also reduced (Reid and Railton, 1974). ABA levels rise over a period of several days after plant roots are flooded (Wright, 1972). Ethylene is produced in the flooded zone and auxin levels also increase (Kawase, 1974).

All the flooding symptoms noted above can be attributed to hormonal changes. Thus leaf epinasty and stem swelling are typical ethylene responses; adventitious root formation arises from increased auxin levels; reduced plant height from reduced gibberellin and increased ABA levels; and finally enhanced leaf senescence from reduced cytokinin and increased ABA levels. There is some experimental evidence for these hormonal roles. Soil application of ethephon, an ethylene-releasing chemical, induced many symptoms characteristic of flooding (Kawase, 1974) and spraying plants with the cytokinin, benzyladenin overcame many of the damaging effects of flooding (Reid and Railton, 1974).

Low Temperature Stress

Temperatures around 5 to 10 C can prove very damaging to subtropical species, particularly in conjunction with high light intensity (Taylor et al., 1974). Evidence that hormones may also be involved in the chilling response comes from Drake and Raschke (1974) who showed that the stomata on chilled leaves were sensitised to CO_2, as are those on water stressed leaves. The common feature in both cases appears to be an elevated ABA level. In addition, it has been shown that application of GA_3 to the tropical grass **Digitaria decumbens** can reverse many of the effects of cool (10 C) nights (Karbassi et al., 1971).

High Temperature Stress

Under arid conditions leaf temperatures between 46-49 C may be reached and even very short periods (2 min) at these temperatures induce many responses in the plant. Although such temperatures are rarely, if ever, reached in New Zealand, it is interesting to note the comparison made by Itai and Benzioni (1974) of the

responses to high temperatures (2 min, 47C) and to water stress. In both cases cytokinin levels in xylem exudate and in leaves were reduced, ABA rose and metabolic processes such as protein synthesis, cellulose synthesis, respiration, cholorophyll degradation and ion movements were affected in a similar manner.

Hormonal Protection Against the Effects of Stress

Many of the responses to environmental stress appear to involve hormonal changes. This is not to suggest that other factors are not involved, undoubtedly they are, as for example in the case of mineral deficiencies, anaerobic conditions and dehydration. Hormones may only be the chemical signals indicating that part of the plant is under stress, thereby allowing other parts of the plant to adapt their metabolic activity. There have been suggestions that the application of hormones, or other chemicals, may protect the plant against the damaging effect of stress. In some cases this has been demonstrated. Thus, application of cytokinins has been shown to protect leaves against high temperature stress (Mothes 1964), the effects of flooding (Reid and Railton, 1974) and salinity stress (Benzioni et al., 1974). In these cases leaf senescence was retarded. However when applied to water stressed plants, kinetin has induced further desiccation and death of tissues (Kirkham et al., 1974, Mizrahi and Richmond, 1972). Similarly if waterlogged or salinated plants are placed under conditions of high evaporative demand they wilt rapidly and under these conditions kinetin would not have a "protective" role.

Gibberellins can reverse the growth inhibition induced by cool night temperatures on tropical grasses (Karbassi et al., 1971), but plants treated with gibberellin are more susceptible to freezing damage (Irving and Lanphear, 1968). On the other hand application of growth retardants such a CCC and Phosphon D which appear to reduce endogenous gibberellin levels, confer some drought resistance and frost tolerance on plants (Levitt, 1972. pp 164-166 and p 350).

Applications of ABA, to whole plants have been shown to reduce growth and transpiration. In pot experiments this has resulted in improved water use efficiency with enhanced survival (Misrahi et al., 1974). ABA, or an ABA-like chemical, would seem to have a number of desirable properties as an antitranspirant.

When tobacco plants growing in nutrient solution are stressed by adding NaCl or mannitol to the nutrient solution, by chilling the roots to 4 C, or by replacing the nutrient solution with distilled water, ABA levels have been shown to rise. In the case of nutrient deprivation this rise may take several days, in the other examples the rise can be measured within 3 hours. Such stressed plants exhibit resistance to cessation of root aeration. The same "hardening" can be conferred by ABA treatment and can be reversed by kinetin treatment (Mizrahi and Richmond, 1972).

Levitt (1972) has proposed that some of the adaptive responses to a particular stress may confer protection to the plant against other apparently unrelated stresses. From the above discussion it can be seen that the responses in common may be reduced cytokinin and gibberellin levels and increased levels of ABA and ethylene. It is possible that application of chemicals such as ABA or growth retardants may be of value in the field to protect plants against adverse environmental conditions.

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