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The Role of Plant Hormones as Modifiers of Sensitivity to Air Pollutants

By

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Summary

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The sensitivity of a plant to a particular pollutant depends upon the uptake capacity and the effectiveness of internal defence mechanisms. In this review we consider some of the ways in which plant hormones may be important in determining these qualities. Factors affecting the control of stomatal opening by ABA, and the manner in which pollutants might disrupt this regulation are discussed in the light of recent findings. Other hormones, e.g. volatile organic compounds such as ethylene, can enhance the injury potential of oxidising pollutants by directly reacting with them to form more harmful products.

Introduction

The responses of plants to external stimuli are mediated to a large extent by hormones. A plant hormone can be defined as a naturally occurring organic substance which is capable of influencing physiological processes at low concentrations (DAVIES 1995). This definition includes substances such as auxins and absciscic acid, which are transported from their site of synthesis to active sites elsewhere in the plant, as well as compounds such as ethylene which are effective at their site of synthesis and, through their volatile nature, may even affect other nearby plants.

Air pollutants (e.g. O₃, SO₂, NO_x) and other stresses such as drought, low temperature and nutrient shortage can cause disturbance to all stages of plant development and metabolism. Stress-related changes in, for example, photosynthesis,

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water-use-efficiency, growth, flowering, leaf abscission and senescence are well documented. All these processes are under some hormonal control, yet surprisingly little is known of the role of hormones in plant response to pollutants, or of the way in which hormones and their mechanisms of action are affected by pollutants.

The sensitivity of a plant to a particular air pollutant depends upon the uptake capacity for the pollutant and the effectiveness of internal defence mechanisms such as antioxidants. These factors are influenced by external conditions (light, temperature, wind, water and nutrients) and by the age and phenology of the plant. Here we shall identify ways in which the actions of plant hormones are able to modify the effect of pollutants, both indirectly by influencing plant metabolism and behaviour and more directly by their reactions with the pollutants themselves.

Importance of hormonal control in determining pollutant uptake

Since the primary route of entry of gaseous pollutants into the plant is through the stomata, the control of stomatal opening during pollution events is very important in determining the effective dose which the plant receives. It has been shown that stomatal closure can protect plants against O₃ injury (TINGEY & HOGSETT 1985) and that water-stressed plants, in which the stomata are closed, are less susceptible to pollutant damage (TELEWSKI 1992). When pollutant exposure interferes with the process of stomatal control, excessive water loss may occur so that the plant effectively suffers from drought.

Since the atmospheric conditions which give rise to high concentrations of O₃ frequently coincide with periods of drought, it is important to understand how the mechanisms which prevent drought stress in plants suffering from mild water deficit are affected by O₃. Soil drying results in the production of abscisic acid (ABA) by the roots, which is transported in the xylem to the leaves, providing the signal to the guard cells which results in stomatal closure. This root to shoot communication may be used by plants as a measure of soil water status (MANSFIELD & ATKINSON 1990). Stomatal behaviour is tightly linked to the concentration of ABA in the apoplast. As this increases, binding of ABA to the outside of the guard cell plasmalemma induces a rise in cytosolic Ca²⁺, resulting in stomatal closure (MCANISH & al.1991). Calcium is considered to be a secondary messenger in the process of stomatal closure and the control of Ca²⁺ levels in the apoplast and in compartments within the guard cells is vital (RUIZ & MANSFIELD 1994).

There are several ways in which exposure to pollutants might interfere with the pathway of ABA and thereby disturb stomatal regulation. Work by FINK 1991 suggests that prolonged exposure to ozone at a concentration of 300 ppb can result in the uncontrolled influx of calcium to the cytosol of epidermal and guard cells of Norway spruce leading to extensive precipitation of calcium oxalate crystals within these cells. Although the mechanisms responsible for these events are unclear it is likely that exposure of the plasmalemma to ozone at such a high concentration has led to the oxidation of reactive sulphhydryl groups of membrane proteins (HEATH & CASTILLO 1988) resulting in the disruption or impairment of membrane transport. In addition, damage to lipids and proteins in the guard cell

membranes might interfere with the binding site of ABA. Uptake of ABA by leaf cells is influenced by the gradient of pH between the apoplast and cytosol (MANSFIELD & ATKINSON 1990) which could be altered by exposure to acidifying pollutants such as SO₂ or NO₂.

At present, we are not aware of any studies which have investigated direct effects of pollutants on the action of ABA. However, ATKINSON & al. 1994 demonstrated that excised leaves of barley which had been exposed to SO₂ and NO₂ failed to show a rapid reduction in their rate of water loss when ABA was added exogenously, suggesting that exposure to the pollutants had prevented the normal response of guard cells to ABA. Another recent study at Lancaster University (ROBINSON, pers. comm.) has provided evidence that ozone may reduce the sensitivity of guard cells to ABA, perhaps by interference with the membrane binding site. When ABA was applied to epidermal strips from leaves of *Aster tripolium* which had been exposed to ozone, only limited stomatal closure resulted, compared with plants grown in clean air.

Recent work has revealed that at low temperatures (10°C) ABA has only a weak effect on stomata and may even cause them to open. Their sensitivity to ABA increases with temperature above 15°C (HONOUR & al. 1995). These authors suggest that ABA has an important function in maximising the opportunity for CO₂ uptake in plants which are mildly water-stressed, by limiting stomatal opening at high temperatures when evapotranspiration is greatest, but allowing opening at low temperatures. This is consistent with the diurnal pattern of stomatal behaviour observed in plants adapted to warm climates and experiencing mild water stress so that the leaves contain sufficiently high levels of ABA to induce stomatal closure. High conductance rates early in the morning decline as the temperature rises and the stomata become more responsive to ABA, often resulting in a midday closure which enables plants to optimise water-use-efficiency. Such modifications of diurnal stomatal behaviour could have considerable relevance for the uptake of pollutants such as O₃ which, at least at lower altitudes, increases in concentration from early morning, reaching a maximum during mid-afternoon. In well-watered plants, stomatal conductance frequently peaks at around midday, often coinciding with the highest O₃ concentration. In the absence of a direct effect of O₃ causing stomatal closure, O₃ uptake will also be at a maximum at this time. For plants which exhibit midday closure, however, O₃ uptake will be reduced, since maximum stomatal conductance and O₃ concentration are no longer synchronised.

Ethylene and related compounds

The regulatory effects of endogenously produced ethylene (C₂H₄) on flowering and fruit ripening, and its association with the senescence process are well known. In addition, C₂H₄ is produced in response to a wide range of stresses, and has been shown to induce intracellular defence mechanisms, such as pathogenesis-related proteins and chitinase (reviewed in KANGASJÄRVI & al. 1994). In some studies the rate of C₂H₄ production has been closely related to pollutant exposure and plant injury, and it has been proposed as a possible bioindicator. This

has only limited potential, however, because it is a non-specific stress response, influenced by many environmental factors and by age and phenology of the plant (TELEWSKI 1992).

The emission of C_2H_4 by plants has been found not only to indicate stress, but also to play an important part in the mechanism by which oxidative pollutants cause injury. MEHLHORN & al. 1991 showed that if C_2H_4 synthesis was inhibited in pea plants, their sensitivity to O_3 was reduced. Individual plants, even from the same species, seem to differ in their inherent ability to produce C_2H_4 , and this may be an important factor in determining their sensitivity to pollutants. In the O_3 -sensitive tobacco line Bel W3, LANGEBARTELS & al. 1991 demonstrated O_3 -induced increases in C_2H_4 and its immediate precursor, aminooxyacetic acid (ACC), which were correlated with leaf injury. In contrast, a tolerant line, Bel B, which did not show enhanced ACC or C_2H_4 production, was uninjured. TELEWSKI 1992 studied C_2H_4 emission and needle damage in two species of *Pinus* growing in areas where O_3 damage was observed. In both species, needles from trees showing O_3 injury symptoms produced more C_2H_4 than those from undamaged trees.

A mechanism by which C_2H_4 increases the susceptibility of plants to oxidative injury by pollutants was proposed by MEHLHORN & WELLBURN 1987. They showed that pea plants which were continuously exposed to O_3 after germination did not produce C_2H_4 or exhibit injury symptoms, whereas for plants grown in clean air, a sudden exposure to O_3 after 3 weeks promoted a rapid increase in C_2H_4 emission and severe foliar injury. A plausible explanation of the role of C_2H_4 and other hydrocarbons in pollutant injury is that their reaction with O_3 and other oxidising species entering the stomatal cavities produces free radicals. These react with components of the cell membranes, setting off a chain reaction in which further damaging molecular species are produced. Thus any stress which causes C_2H_4 production will increase the susceptibility of the plant to O_3 damage. It seems that some plants exposed to O_3 for long periods, such as the peas in the above mentioned experiment, are able to adapt by reducing their rates of C_2H_4 emission, and thus minimise their damage by O_3 . This hypothesis, put forward by MEHLHORN & al. 1991, may help to explain why plants are often more damaged by intermittent episodes of pollutant exposure, than by a continuous exposure, and this is an important consideration for experimental design. However, while stress-induced C_2H_4 synthesis in some non-woody plants has been shown to be transient, declining after a few hours (YIN & al. 1994), this is not always the case for woody species. Enhanced emissions from Norway spruce exposed to O_3 (WOLFENDEN, unpublished data) and from red spruce treated with acidic mist (CHEN & WELLBURN 1989) were maintained for several months after the end of the respective treatments.

Investigations into the biosynthesis of C_2H_4 and its regulation have provided further insight into its role in pollutant stress response. The synthesis of C_2H_4 is closely linked with that of polyamines, the two sharing a common precursor, S-adenosyl methionine (SAM). It has been suggested (LANGEBARTELS & al. 1991) that the differential production of either polyamines or C_2H_4 may determine whether a plant is protected or damaged by oxidising pollutants. Polyamines are major

scavengers of free radicals and are important in stabilising membranes by preventing processes such as lipid peroxidation. Increased polyamine synthesis following O_3 exposure has been shown in a number of species (LANGEBARTELS & al. 1991, ROWLAND-BAMFORD & al. 1989), and their antioxidant properties may be valuable in protecting plants against oxidising pollutants (BORS & al. 1989). The reaction of ACC to C_2H_4 is catalysed by oxygen free radicals, which may be scavenged by polyamines, thus inhibiting C_2H_4 production and indirectly reducing injury. During senescence the production of polyamines declines, increasing the availability of SAM for ACC synthesis. In the absence of polyamines, more free radicals are also available, allowing increased C_2H_4 production. Since premature senescence is a commonly observed feature of pollutant stress, the importance of the balance between polyamine and C_2H_4 synthesis in determining the plant's sensitivity is evident.

The importance of hydrocarbons of plant origin, other than C_2H_4 , in modifying plant damage by pollutants has received little attention. For example, isoprene is one of a number of non-methane hydrocarbons emitted by many plant species as well as from anthropogenic sources. Its production by plants seems to be linked to photosynthesis and is influenced by temperature and CO_2 concentration (MONSON & FALL 1989). No clear reason for isoprene emission has been identified, but it has been suggested as a way of dissipating excess energy during periods of high solar irradiation (SHARKEY & SINGSAAS 1995). However, TERRY & al. 1994 recently demonstrated that in four different species exposed to low concentrations of isoprene, flowering was advanced compared with controls. This observation provides strong evidence that isoprene may act as a signaling compound, modifying the timing of flowering. Although little is known of the effects of other environmental factors, especially air pollutants, on biogenic isoprene production, important implications arise from this finding. Isoprene is highly reactive in the gas phase and plays a major role in controlling the oxidising potential of the troposphere. (FEHSENFELD & al. 1992). Its decomposition in the atmosphere can result in the formation of significant quantities of O_3 . In a changing atmospheric environment, conditions which enhance isoprene emission rates may not only lead to increases in photooxidant concentrations, but might also affect flowering phenology in some species.

Conclusions

There is much scope for further work in this field. In this review our coverage has been limited to only a few plant hormones, which, through their influence on physiology and metabolism, have the potential to modify plant response to pollutants. Future research may reveal other important interactions between pollutant sensitivity and the regulatory functions of hormones. Although there is uncertainty as to whether polyamines and hydrocarbons such as isoprene should be classed as plant hormones, they undoubtedly have a regulatory effect on plant metabolism. With increasing knowledge of phytochemistry, especially of secondary metabolites, additional compounds may be revealed as important modifiers of plant stress reactions.

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