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DO PLANTS CRY?

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Do plants cry? Do plants have a centralized mechanism to notify them that something is wrong? The central alarm system in children can be set off by a large number of different stimuli. Do plants have a similar universal response, set off by a variety of trauma, to notify them that they have been subjected to some kind of environmental insult? A variety of stimuli--mechanical, chemical, disease, thermal, and irradiation--are known to cause the production of "wound" ethylene. Is it possible that a gas can take the place of tears, and if so, what function do these 'tears' serve?

Plants produce ethylene throughout their lives, and changes in the rate of production are associated with developmental phenomena, aging, and changes in the internal levels of IAA. Wound ethylene, as opposed to normally produced ethylene, is characterized by its rapid induction (frequently within minutes after the start of the stimulus) and its association with visible tissue damage. However, wound ethylene is produced only by partially disrupted cytoplasm; tissue which is completely destroyed fails to produce ethylene.

Mechanical induction. Increase rates of ethylene production have been shown to occur by bruising fruits and flowers (refs 1 to 6) or by cutting tissues (refs 7 to 18). But when tissue is homogenized completely, ethylene production stops (7) and can be replaced by the appearance of ethane instead (19).

The fact that wounding tissues increases ethylene production is the basis of the ancient technique of promoting fig ripening. This is the key to the question of Amos' employment in the Old Testament (20). Amos' job was to wound the fruit of the Egyptian sycamore fig with a knife and thereby to increase the rate of ethylene production. This was followed by an acceleration of fig fruit production.

Orchid flowers can remain fresh for months and do not fade until visited by pollinators (specialized insects or birds). Also removal of the pollinia (masses of pollen grains) has the same result. In either case, pollination or removal of pollinia increases the rate of ethylene evolution which terminates the life of the flower (21).

Goeschl et al (22) have shown that mechanical resistance to seedling growth caused an increase in ethylene production. They postulated this may have an effect on the ability of seedlings to force their way through the soil.

Jaffe (23) reported that physically shaking pea tendrils increases ethylene production; also unilateral application of ethylene caused rapid coiling of tendrils.

Chemical induction. A wide variety of chemicals provide a stimulus for ethylene production (2, 12, 18, 24, 26 to 29). [But excesses of certain chemicals (e.g., trichloroacetic acid and perchloric acid) which completely kill tissues prevent ethylene production (24)]. Also certain excretable metabolites of fungi increase ethylene production from bean plants (30, 31). Irrigation of citrus with water containing high levels of salts has been reported to induce leaf abscission; Rasmussen et al (25) have shown that an increase in ethylene production was responsible for the damage.

Cycloheximide, an antibiotic produced by Streptomyces, is a very potent ethylene-inducing chemical and is being developed as a fruit-releasing compound for citrus (32,33). Although compounds such as ascorbic acid (2, 34) have been

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examined as potential loosening agents, none is as effective on a mole basis as cycloheximide.

Ozone treatment of plant material increases the rate of ethylene evolution (Craker, personal communication).

Induction by disease. Viral diseases have been shown to induce ethylene production (18, 24, 35, 36). Neither the virus itself nor the biochemistry associated with replication was involved in ethylene evolution (18).

The ability of fungi to induce ethylene production and the fact that it is the plant and not the pathogen which produces the gas was first described by Williamson (37). Since that time, a large number of investigators have shown that plant tissue can respond to fungal infection by producing large quantities of ethylene (9, 28, 38, 39, 40, 41, 42). Bacterial infection also increases ethylene production (44).

Insect induction. Increased rates of ethylene production have been associated with insect damage to leaves (45). Insect-induced production probably has a role in insect-induced defoliation as well as fig ripening (20).

Temperature induction. Citrus leaf abscission has been correlated with injury following freezing temperatures (33). The freezing temperatures probably caused cell damage, since there was an immediate increase in the rates of electrolyte leakage, and ethylene production increased gradually over a 3 day period.

Induction by irradiation. A number of workers have hoped to utilize the sterilizing qualities of gamma radiation to preserve fruit. However, in a number of cases, the irradiation caused an increase in ripening, and it was learned subsequently that the irradiation caused an increase in the rate of ethylene production (46 to 49). The physiology of irradiation-induced ethylene production is obscure, and Maxie and coworkers (50) have shown that irradiation of fruit under nitrogen was less effective than irradiation in air.

Bitancourt (51) suggested that ethylene might be evolved directly from IAA; this suggestion was based on the observation that ethylene was formed when IAA was bombarded with electrons in a mass spectrometer.

Irradiation of vegetative tissue also has been shown to promote ethylene evolution. Wheat plants treated with ^{32}P formed large amounts of ethylene as well as propylene, isobutylene, and butylene (52). Irradiation with ^{60}Co also promotes the production of ethylene and other hydrocarbons from pea tissue (53), and Shah and Maxie (54) postulated that this was due to a stimulation of pathways normally elaborating the metabolite.

Biochemistry of ethylene production. Sakai et al (42) have shown that the pathway for ethylene production in diseased versus normal tissue is different. They concluded that the TCA cycle pathway is involved in ethylene production for diseased sweet potato tissue, but not for normal fresh tissue. Lund and Mapson (42) indicated that methionine is a probable source for ethylene in cauliflower tissue infected with Erwinia carotovora. The mechanism involved entails the production and release of pectate lyase and polygalacturonase by the bacterium into the cell wall of the host. This, in turn, was found to increase the solubility and activity of a glucose oxidase found in the cell walls of the cauliflower. The glucose oxidase, in turn, generated the production of H_2O_2, which apparently is a limiting factor in the synthesis of ethylene from 4-methylmercapto-2-oxobutyric acid via a cell wall localized peroxidase (Editor's Note: cf., What's New in Plant Physiology, September 1969). The source of the oxo acid was methionine and was synthesized via a transamination reaction. Methionine is known to be the source of ethylene in auxin-treated tissue and

ripening fruits. It is worth pointing out that in cases where the amino acid functions as a substrate, rates of gas production are high.

Function of wound ethylene. One function of wound ethylene would be to cause abscission, thereby terminating the life of unproductive organs, such as flowers and leaves damaged by stress factors. A second possible function of ethylene concerns its role in disease resistance mechanisms.

Chalutz and Stahmann (28) found that ethylene induced the formation of pisatin, a phytoalexin in pea pods. However, infection by Monilinia fructicola induced pisatin formation but not ethylene production. This means that the plant was able to respond to fungal invasion without the action of ethylene as an intermediate. Chalutz et al (41) reported that the ability of Ceratocystis fimbriata and Helmintoosporium carbonum to induce the formation of isocoumarin from carrot roots was directly related with their ability to increase ethylene production. But whether isocoumarin is actually a phytoalexin was questioned.

Stahmann et al (39) reported that ethylene increased resistance of sweet potato tissue to infection by Ceratocystis fimbriata. They also noted that the activity of peroxidase and other enzymes increased following ethylene treatment and suggested that the increase in disease resistance was associated with the increases in enzyme activity. However, the importance of these findings was dimmed by the subsequent report of Chalutz and Devay (9). They found that ethylene had no effect on disease development on sweet potato roots challenged with Ceratocystis.

However, there is still some reason to think that ethylene production and its ability to increase or induce enzyme synthesis can play a part in physiological defense mechanisms. Abeles et al (43) found that gassing bean plants with ethylene caused the induction of β-1,3-glucanase and chitinase until these proteins represent 10% of the protein content of the leaves. While the function of these enzymes can only be guessed, it appears strange that plants would form large quantities of hydrolytic enzymes for which the plant, so far as we know now, has no substrate. While β-1,3-glucans exist in the form of phloem callose, we are not aware of N-acetyl-D-glucose polymers in plants. On the other hand, the cells of fungi and bacteria contain both callose and chitin, and it would appear reasonable, at least superficially, to think that the β-1,3-glucanase and chitinase represent a means of destroying cell walls of susceptible fungi and bacteria. This would be analogous to the presence of lysozyme in tears which destroy the cell walls of certain bacteria. The only evidence in favor of this view was the observation that ethylene-treated bean plants challenged with Uromyces phaseoli (bean rust) developed the lesions of this disease less rapidly than controls (unpublished observations). However, the disease did go to completion eventually and apparently the ethylene treatment gave only partial relief. One problem with this experiment is the fact that Uromyces is normally a successful pathogen and possibly has already compensated against this kind of resistance mechanism.

While the title "Do Plants Cry" was set up primarily as an attention-getting device, it is obvious that ethylene plays some role in stress physiology and that understanding the mechanism of its production could have some economic implications. At present, the ability to harvest fruit mechanically depends on lowering the attachment force of fruit to stem tissue. Since one function of ethylene is to cause abscission, it would be useful to know ways to regulate ethylene evolution. Also, since diseases can cause increases in ethylene production, it would be valuable to learn if the gas acts as a signal in disease resistance mechanisms.

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