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25 March 1957

Relationship between Auxin and Membrane-Integrity in Tissue Senescence and Abscission

Previous investigations have shown that the physiological aging and abscission of fruits and foliar organs attend a drop in the auxin level of these determinant organs (*1*). This report presents some experimental evidence of the probable role of auxin in such phenomena (*2*).

Segments of commercially grown Kentucky Wonder pole beans were prepared as described by Bonner and English (*3*). From 10 to 20 segments were placed, with all, part, or none of the exocarp removed, in petri dishes on filter papers, which were kept moist with distilled water or distilled water plux auxin [indole-3-acetic acid (IAA) or naphthalene acetic acid (NAA)] at concentrations of 4 to 50 ppm. The experiments were conducted both with and without asepsis. The dishes were stored in the dark at 25°C.

At the end of 2½ to 3 days, under aseptic conditions, the segments treated with 4 ppm auxin were plump and rigid, while the controls (water-treated) were soft and flaccid. Rigidity, however, was not directly related to the amount of water absorbed, for under some conditions the auxin-treated segments took up less water than did the control segments.

Hand sections made after 2½ to 3 days revealed that, in the segments treated with auxin, the intercellular spaces were filled with air (Fig. 1); this is a normal situation, as is shown by comparison with sections of fresh, whole beans. In contrast, sections of the controls showed that their intercellular spaces were filled with liquids (Fig. 2). Thus, it appears that the role of auxin in maintaining rigidity of the bean tissue is the result of an effect on membrane permeability; the auxin functions to maintain the selective permeability of the membranes, thereby preventing the exosmosis of cellular substances into the intercellular spaces. The latter process may be visualized as causal of disturbances in equilibria, which accelerate senescence.

Subsequent to liquid-logging of the intercellular spaces, there occurred a dissociation of cells, manifested by their separating at the middle lamella and rounding-up. The possibility that pectinases may be among the cellular substances liberated into the spaces is being investigated.

With concentrations of 4, 25, and 50 ppm auxin, membrane-integrity in the bean segments was maintained for 7, 11, and 17 days, respectively. In experiments performed without asepsis, the first sign of contamination appeared after the loss of membrane-integrity. Rapid bacterial decomposition followed as a result of the favorable substratum provided by the loss of cellular substances.

Auxin was most effective in maintenance of membrane-integrity when it was applied immediately. After 24 hours of water treatment it gave partial effects, and after 48 hours, no effects. This indicates that membrane-alteration begins during 24 hours, and is irreversible after 48 hours, of water treatment.

Sections of limp, whole beans showed that the effect of auxin on membrane-integrity is unrelated to the phenomenon of water loss that occurs as beans wilt, for the intercellular spaces were filled with air, although much water had been lost.

There was a differential response of tissues of the bean segments to loss of membrane-integrity. If such differential developments were to take place in selected tissues in other material, such as the abscission zone, the following hypothesis is suggested. The cells of the abscission zone are especially sensitive to a drop in auxin level. Below a critical level, the cells in this zone lose the integrity of their membranes; this permits the displacement of cellular fluids which affect the middle lamella, causing dissociation of cells, and the leaf abscises. Following are the results of some experiments on the effects of auxin on the abscission zone in *Coleus*.

A profusely branched stock of *Coleus* was used for the experimental work (*4*). Longitudinal hand sections show that the cells of the petiole are arranged in longitudinal rows, with conspicuous and continuous intercellular spaces oriented longitudinally and extending through the abscission zone. These spaces are normally filled with air, as is evidenced by their interference with transmission of light owing to reflection phenomena (Fig. 3).

Coleus shoots were spirally debladed from nodes 1 to 6, inclusive (*5*). Within 3 days the debladed petiolar stumps at nodes 3 to 6 had abscised, while petioles at the uppermost nodes 1 and 2 were intact. Hand sections of debladed petioles from node 1 showed that the air in the intercellular spaces had been displaced by cellular fluids only in the cell layers of the abscission zone (Fig. 4). Various stages in the liquid-logging of the spaces were observed by means of fresh sections of many debladed petioles from nodes 1 and 2. At each node the opposite, nondebladed petiole served as a control. The controls always showed intact air columns through the abscission zone.

Subsequent to the loss of selective permeability of the cell membranes in the abscission zone (evidenced by liquid-logging of the spaces) there was apparent a dissociation of cells, manifested by

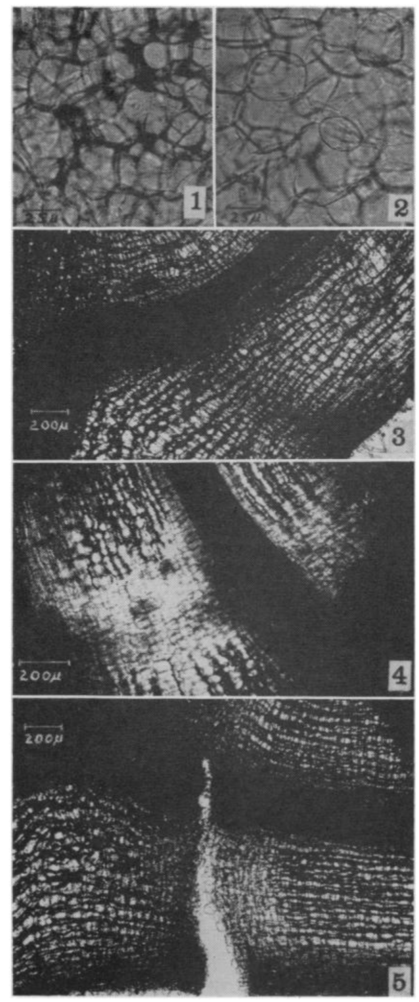

Fig. 1. Fresh section of bean segment after 3 + days of auxin treatment, showing air-filled intercellular spaces (they appear black, owing to reflection phenomena). Fig. 2. Fresh section of bean segment after 3 days of water treatment. Intercellular spaces are filled with liquid as a result of loss of membrane-integrity. Fig. 3. Longisection of control petiole (with blade intact) of *Coleus*. Note the air-filled intercellular spaces traversing abscission zone. Fig. 4. Longisection of petiolar stump (node 1), 3 days after deblading. Intercellular spaces in abscission zone are filled with liquid, owing to loss of membrane-integrity. Fig. 5. Longisection of petiolar stump (node 2), 3 days after deblading. Note centripetal progression of abscission, owing to dissolution of middle lamella.

their separating and assuming a spherical shape. This is illustrated in Fig. 5—a stage where complete dissolution of the middle lamella had occurred, resulting in the centripetal progression of abscission.

The hypothesis that auxin inhibits abscission through its effect on the maintenance of membrane-integrity was further supported by experiments in which 1 percent IAA in lanolin-water emulsion was applied distally on debladed petiolar stumps. Hand sections of these petioles, 3, 5, and 10 days after deblading, revealed a continuity of air in the intercellular spaces traversing the abscission zone.

A similar mechanism may be operative, attending a drop in auxin level, during tissue senescence in certain fleshy fruits as well as in abscission of determinant organs in other plants.

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25 March 1957

Differential Responses to Population Pressures by Normal and Dwarf Lines of Maize

Dwarf or semidwarf variants in such species as sorghums, apples, beans, and peas are of economic importance. Suggestions have been made that one of the numerous, genetically different, semidwarf mutants of maize might also be useful agriculturally. The rationale has been that the shortened stalk of such dwarf types would markedly reduce the incidence of stalk breakage and root lodging which make machine harvesting difficult. Therefore, these types would be acceptable if their yield were equal to or only slightly below normal. Leng (*1*) recently reported that single crosses made from inbreds which had been converted to the recessive mutant *brachytic* 2 were satisfactory in yield.

Field observations in our laboratory of dwarf types had indicated that they might actually possess yielding ability beyond their normal counterparts. These observations motivated the start of a testing program in 1954 designed to characterize the response of both dwarf and normal types to population pressures at high levels of fertility and with adequate water available. Work during the past 3 years has shown that at least one recessive semidwarf mutant *compact* (*ct*) has a significantly different response to population pressures from the normal inbred Hy or two other semidwarf mutants *reduced* and *brachytic* 2 (*2*).

The *compact* mutant arose by spontaneous mutation in a stock of Hy2 and has previously been designated as Hy2 (*dwarf*). It has been compared for 3 years in replicated yield tests to the normal Hy inbred, for 2 years to a Hy conversion to *reduced*, and for 1 year to a Hy conversion to *brachytic* 2. Thus all types under test were inbreds which had roughly comparable genotypes except for the loci conditioning plant height. Data on grain and stover yields, leaf areas, mineral content of the leaves, flowering dates, and ear characteristics were collected for each strain at various population levels. Figure 1 shows the yield in bushels per acre at four populations for 1956, the only year in which all four genetic strains were compared. Note the attainment of a yield optimum at 26,000 plants per acre by the *compact* strain and only slight decreases in yield at the higher populations; this is in marked contrast to the other types tested. Note, too, that at 26,000 plants per acre, the *compact* strain yields more than the normal strain yields at 13,000 plants per acre. Such a superiority in yield for the *compact* strain at higher populations over the normal strain at any population tested was also noted in the 1954 and 1955 tests.

The test reported here was made with inbred material, Hy, and various semidwarf mutants inserted into a Hy background. It would be unwarranted to extrapolate from the responses of inbreds to population pressures to the responses of hybrids. Other tests have shown, however, that normal hybrids with Hy as one parent react similarly to Hy with regard to population increases. Further, *reduced* hybrids respond in much the same manner as *reduced* Hy while *brachytic* 2 hybrids are similar to *brachytic* 2 Hy.

The *compact* strain clearly has a different response to high populations from three other comparable strains carrying other genes affecting plant size. This response enables *compact* to yield slightly more at high populations than the normal type yields at any population tested. Further, inbreds and hybrids carrying the same dwarfing gene (either *rd* or *br2*) react similarly to population pressures. These findings suggest that yield increases over normal hybrids can be obtained by the use of hybrids converted to the *compact* gene. Preliminary tests of partially converted hybrids will be made in 1957 (*3*).

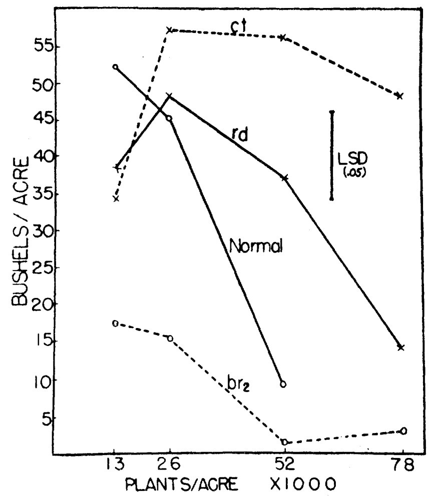

Fig. 1. Yields in bushels per acre for four inbreds which are genetically similar except for major genes that affect plant size (1956).

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2. We are indebted to W. R. Singleton for seed of the *reduced* types and to E. R. Leng for seed of the *brachytic* types.
3. This article is journal paper No. 1101 of the Purdue University Agricultural Experiment Station.

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Selective Blockade of Excitatory Synapses in the Cat Brain by γ-Aminobutyric Acid

γ-Aminobutyric acid (GABA) has been identified (*1*) as an active principle in the inhibitory substance (factor I) that can be extracted from the mammalian brain (*2*). Both the extract and the compound have been tested, chiefly on the crayfish stretch receptor (*1–3*), and both diminish the depolarizing electrogenesis caused by stretch of its mechano-sensitive dendrites. GABA also appears to augment the inhibitory postsynaptic potential of the receptor (*3*). On the dog brain, both "excitatory" and "inhibitory" effects by GABA and other amino acids have been reported (*4*).

The mode by which a synaptic drug exerts its overt effects in the central nervous system is often difficult to determine (*5, 6*). For example, although