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INTERRELATIONS IN THE EFFECTS OF BORON AND INDOLEACETIC ACID ON PLANT GROWTH

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(WITH ONE FIGURE)

Introduction

Some of the symptoms of plants deficient in boron are sufficiently similar to those expected in plants deficient in auxin as to suggest that the role of boron in plant nutrition is closely associated with the formation of auxin and possibly of other plant hormones. The experiments here reported show that indoleacetic acid added to nutrient solutions will partially replace boron.

Plants grown to maturity in sand cultures outdoors have yielded puzzling results in that, with boron concentrations averaging about 0.05 ppm in the nutrient solution, the growth of some fifteen species has been markedly at variance in succeeding summers. In some seasons growth was greatly depressed and there were pronounced deficiency symptoms, whereas in other seasons the same species were normal or nearly so. Analyses of the plant material showed similar concentrations of boron in the normal and deficient plants. Spectroscopic examinations of the plant material for other elements that might have been introduced as impurities replacing boron were negative, as were many culture experiments with elements such as aluminum, gallium, scandium, germanium, and indium, in addition to some of the elements previously tested by BRENCHLEY and WARINGTON (I).

Elongation of the stems, petioles, and roots of plants in minus-boron nutrient solutions is slow or may cease soon after the cotyledons have developed. The rate at which new nodes are formed is affected later. With the tendency for the terminal bud to abort or take on a fasciated appearance, similarly abnormal branches appear in the axils of the leaves. The leaves of cotton and other plants deficient in boron are small, become deeply cupped, and have a peculiarly patched sort of chlorotic mottling. Buckling of the mesophyll of boron-deficient leaves indicates a greater depression in the growth of vein structures than of mesophyll. The downward cupping of leaves, as suggested by Dr. H. E. HAYWARD, may reflect also a greater retardation of the growth of the phloem than the xylem elements. Growth of the marginal mesophyll is checked in advance of that adjacent to the main veins, and the formation of lobes of cotton leaves may be partially or wholly repressed. Boron-deficient leaves are usually thickened. Splitting open and corking of veins of boron-deficient plants is sometimes observed. The roots of such plants, as shown in the instance of the pea plant by SOMMER and SOROKIN (2), are short and stubby, and the secondary roots make little growth.

The effects of auxin deficiency on plant growth cannot be described very accurately, since conclusions in many instances must be drawn indirectly or by inference. WENT (4) states that while there is practically no evidence linking leaf-blade growth with auxin, there is considerable circumstantial evidence pointing to the conclusion that auxin specifically conditions petiole and vein growth. Auxin tends to inhibit the development of lateral branches. Root formation is induced by auxin but other hormones have been found essential to root growth.

Experimentation

In each of the experiments here discussed, Acala cotton plants were grown in Hoagland's solution (5, 5, 2, and 1 millimole per liter respectively of $Ca(NO_3)_2$, KNO_3, $MgSO_4$, and KH_2PO_4) in unaerated quart mason jars. To this solution, which contained less than 0.01 ppm of boron derived as an impurity in the chemicals, was added 0.1 ppm each of zinc and manganese, and sufficient iron citrate. Indoleacetic acid, when used, was added daily and cumulatively.

The first experiment was conducted in the spring, during a period when most of the days were overcast. There were two storms, each of several days" duration. In this experiment, as shown by table 1 and figure 1, the daily addition of 0.01 ppm of indoleacetic acid to minus-boron solutions resulted in greatly increased leaf development. At the time the measurements were made (the 28th day after transferring the seedlings to the culture solutions), 1 ppm of boron had been present in culture A for only 16 days, whereas indoleacetic acid had been added daily to cultures C, D, and E for **24** days. In other words, boron was added to a parallel untreated culture only after the first response in root growth from indoleacetic acid had been observed. The leaves on plants in culture E were nearly

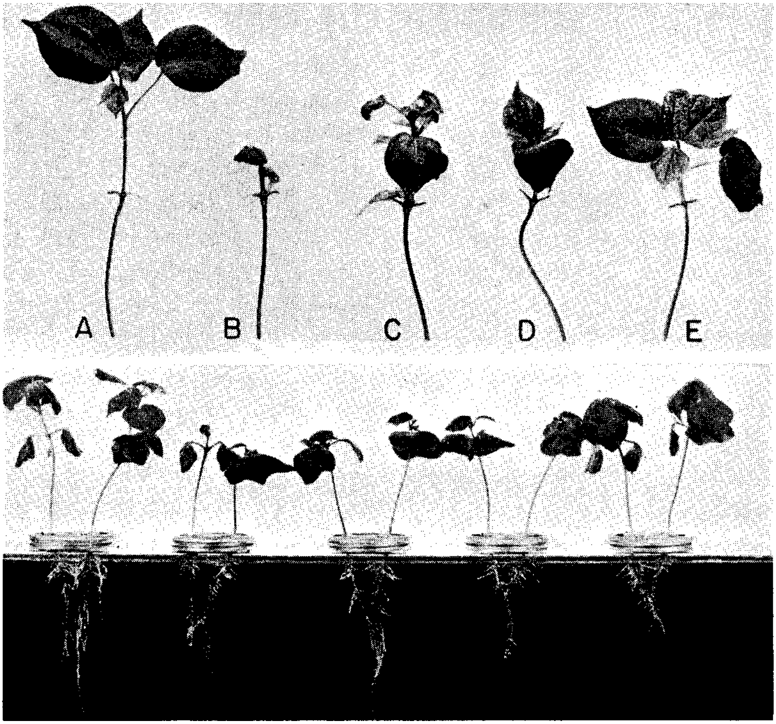

FIG. I.—Acala cotton plants grown in nutrient solutions. Above, single plant from each culture with cotyledons removed; below, the two remaining plants.

	A	B	C	D	E
Boron added 16 days before photographing, p.p.m.	1	0	0	0	0
Indoleacetic acid added daily for 24 days, p.p.m.	0	0	0.0001	0.001	0.01

normal in appearance, but it is to be noted that they were not supported in the same outward position from the petioles as those of culture A, which received boron. Internode and petiole elongation was promoted by indoleacetic acid, but in the highest concentration the total length of the internodes was only about half as great as in the plus-boron culture. Indoleacetic acid in a concentration of

0.0001 ppm added daily (culture C) induced root development which for a time appeared normal. Later, however, possibly because of accumulation of an unfavorable concentration of indoleacetic acid and because of retarded development of the leaves, the roots developing near the surface of the solution were shorter than in the plus-boron solution. In the higher indoleacetic acid concentrations (cultures D and E) the roots were short.

In a second experiment that included tomatoes and sunflowers as well as cotton, little or no response to indoleacetic acid resulted.

TABLE 1

LEAF DEVELOPMENT OF COTTON PLANTS IN SOLUTIONS WITH BORON AND WITH INDOLEACETIC ACID

	CULTURE				
	A*	B	C	D	E
Boron, ppm.	1	0	0	0	0
Indoleacetic acid added daily, ppm.	0	0	0.0001	0.001	0.01
Leaf areas (exclusive of cotyledons) sq. cm.:					
Plant 1	82	4	9	14	82
Plant 2	78	4	10	11	74

*In comparing leaf areas, account must be taken of the fact that boron was added to culture A 16 days before the measurement+ whereas cultures C, D, and E had been receiving indoleacetic acid for 24 days.

This test, conducted during a period of bright warm days, was discontinued after about the tenth day.

A third experiment was then set up with cotton plants, using four cultures for each treatment. Half of the cultures were placed in a brightly illuminated greenhouse and half in a muslin-covered lath house. The noonday light intensities in the lath house ranged from 500 to 1000 foot candles and in the greenhouse from 4000 to 7000 foot candles.

The plants in the lath house responded to indoleacetic acid in much the same way as they did in the first experiment. The internode elongation in the higher indoleacetic acid concentrations was somewhat better than in the first test, but it was not so good as in the cultures supplied with boron. Any advantages of indoleacetic acid for root development were uncertain or transitory in this experiment. The plants in the brightly illuminated greenhouse showed little response during the early period of the experiment. All the leaves were small and cupped, and no stimulation of root growth was observed. The greenhouse plants were maintained for a month longer than those in the lath house. At the end of this period each successively higher concentration of indoleacetic acid, including a pair of cultures receiving 0.1 ppm, had produced more and larger leaves than the next lower concentration. The total leaf area of the plants receiving 0.1 ppm indoleacetic acid was possibly eight or ten times as great as the plants in "o-boron o-indoleacetic acid" solutions, but none of the leaves were normal. The plants receiving boron were in all respects superior to any of the indoleacetic acid plants and had much greater leaf areas.

Because of the polar movement of indoleacetic acid, concentrations in the foregoing experiments that were sufficiently high to induce favorable responses in the growth of leaves and stems were injurious to the roots. Following a suggestion by Dr. E. J. KRAUS, a subsequent test was conducted in which indoleacetic acid was applied to the leaves and stems of cotton plants in solution with 1 per cent each of lanolin and sodium oleate as a spray three times per week. The concentrations used in this test were probably too low, since a substantial increase in the growth of stems and leaves resulted only from the highest concentration, which was 10 ppm.

Vitamin B_1 and yeast extracts were added, in other experiments, to minus-boron solutions alone and in conjunction with itidoleacetic acid. These substances did not improve growth nor lessen the severity of boron deficiency symptoms.

Discussion

These experiments provide evidence that boron as an element essential to the growth of plants can in some measure be replaced by indoleacetic acid. In no test, however, were the results obtained with indoleacetic acid equal to the responses that followed additions of boron to nutrient solutions. The findings point to the conclusion that at least one of the functions of boron in plant nutrition is intimately related to the formation of plant hormones. Any interpretation of the results must take into account the experimental difficulties associated with the movement of indoleacetic acid into the plant and to the active tissues in concentrations neither too high nor too low. Furthermore, possible distinctions must be recognized between the effects on plant growth of indoleacetic acid and auxin.

VAN OVERBEEK (3), by Avena coleoptile studies, has found that to some extent indoleacetic acid is inactivated by light, but to a lesser extent than is the case with auxin a. This fact may serve to account for some of the differences in responses of cotton plants under high and low illumination.

The inquiries on the comparative reactions of cotton plants to indoleacetic acid and boron had the work mentioned in the introduction as its background. Inasmuch as the evidence indicates some replaceability of boron by acetic acid and the importance of light and possibly of temperature in the reactions, a possible advance has been made in an understanding of the role of boron. A clue is thus provided as to why like amounts of available boron, both in culture solutions and it seems also in the field, may be effective to different degrees in different seasons with varied climatic conditions.

Summary

Experiments with young cotton plants show that indoleacetic acid will to some extent replace boron as an element essential to the growth of root, stem, leaf vein, and other leaf blade tissues. The results suggest that boron is essential to the formation of auxin in plants.

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