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## *EFFECT OF THE ROOTS ON THE PRODUCTION OF AUXIN BY THE COLEOPTILE*

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Since it had been shown by Skoog (1936, 1937) that removal of the seed (endosperm and scutellum) of Avena seedlings greatly reduces the production of auxin in the coleoptile tip, the question arose whether removal of the root system would have any effect upon the auxin relations of the plant. This was the purpose of the present investigation.

From seedlings of "Victory oats" which were grown in physiological darkrooms under standard conditions (see, e.g., Went 1935), the root system was cut off with a sharp razor blade. At the same time the coleoptile was decapitated by severing 2 mm. of the tip. In order to allow water uptake the level of the water in the zinc trays, from which the plants ordinarily take up their water, was raised until the endosperm was half submerged. The level of the water of the trays in which the roots of the intact control plants were hanging was also raised to the same extent. The plants used were of the same age as required for the standard auxin tests. Three hours after the first decapitation the end of the coleoptiles was cut off again, the primary leaf pulled loose and agar blocks containing indole-3-acetic acid (hetero-auxin) were unilaterally applied to the top of the coleoptile. The resulting curvatures were photographed 110 minutes later. The results are given in table 1 from which it is clear that removal of the

roots, 3 hours before the application of auxin, does not change the response to auxin of the coleoptiles. However, if the period of time between the removal of the roots and the application of auxin was 15 to 20 hours instead of 3, the sensitivity was markedly increased in regard to plants with an intact root system. Table 2 shows that this increase in sensitivity may

TABLE 1

Auxin curvatures of plants with and without their root system. Roots removed 3 hours before the auxin was applied. Curvatures photographed 110 minutes after the auxin was applied. Average values of 12 plants.

| EXPERIMENT NUMBER | AUXIN CONCENTRATION | AUXIN CURVATURES WITH ROOTS | AUXIN CURVATURES WITHOUT ROOTS |
|---|---|---|---|
| 61105 | 0.374 mg. per l. | 10.2 | 12.1 |
| | | 10.3 | 10.6 |
| 61109 | 0.187 mg. per l. | 5.5 | 3.6 |
| | 0.374 mg. per l. | 10.3 | 11.9 |
| | 0.561 mg. per l. | 15.7 | 17.2 |

TABLE 2

Auxin curvatures of plants with and without their root system. Roots removed 15 hours before the auxin was applied. Curves photographed 90 minutes after the auxin application. Averages of 12 plants.

| EXPERIMENT NUMBER | AUXIN CONCENTRATION | AUXIN CURVATURES WITH ROOTS | AUXIN CURVATURES WITHOUT ROOTS |
|---|---|---|---|
| 61113 | 0.187 mg. per l. | 4.6 | 10.3 |
| | 0.374 mg. per l. | 12.8 | 18.7 |
| 61210 | 0.117 mg. per l. | 22.8 | 21.1 |
| | | 19.3 | 21.2 |
| | 0.059 mg. per l. | 7.1 | 11.2 |
| | | 8.9 | 11.4 |

be more than 100%. Especially if the curvatures are far below the maximum angle, this effect is prominent. Curvatures near the maximum angle (about 20°) do not show a difference between plants with and without their root system.

It has been pointed out repeatedly (Van der Wey 1931, van Overbeek 1936 and others) that the less auxin the coleoptiles contain the more sensitive they are to applied auxin. Hence, in order to explain the higher sensitivity of the plants from which the roots were removed, it was assumed that the production of growth hormone by the coleoptile tip was reduced as compared with plants with normal root systems. This was actually observed (Fig. 1). The tips of plants from which the roots had been removed for about 15 hours were placed on agar blocks. After the tips had been standing for 2 hours the hormone content of those blocks was determined in the usual way. The blocks on which the tips of intact

plants had been standing had a relative auxin content of 11.3° (Fig. 1), whereas the blocks on which the tips of plants from which the roots had been removed had been standing had only a concentration of 6.5°. In the same experiment the auxin production of plants from which the seed had been removed (roots intact) was determined, and also of plants from which both roots and seed were removed (cut off at the base of the mesocotyl). Figure 1 also shows the length of the plants of the various groups. It is clear that the more the production of auxin was inhibited the less the

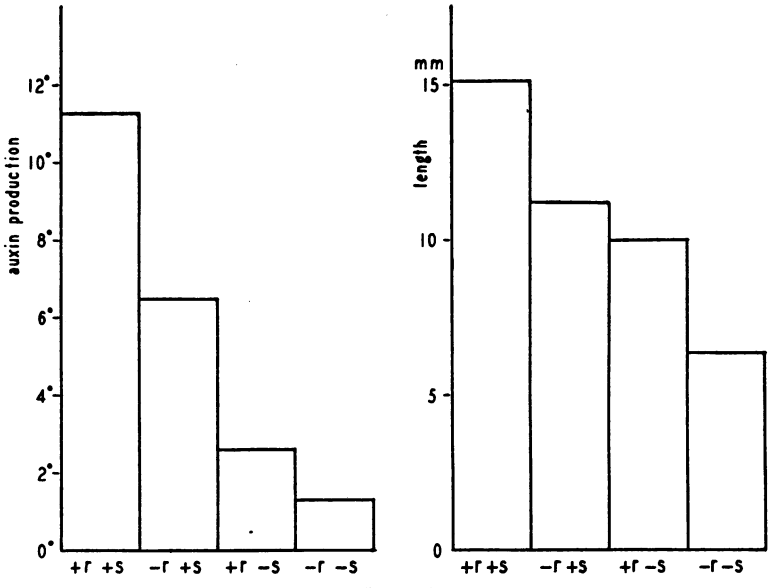


FIGURE 1

Auxin production and length of coleoptiles of Avena seedlings which were left intact (+ r + s) or from which the roots (− z + s), the seed (+ z − s) or both were removed. Removals were made 20 hours before the determination of the auxin production. The length represents that part of the coleoptile which sticks out above the glass holder. Experiment number 61222.

plants had grown. So it seems that the auxin production, in these four groups of plants, determines their growth in length. Auxin curvatures of intact Avena plants increase with time until about $1^1/_2$ to 2 hours after the application of auxin. Then they decrease gradually, which is shown to be connected with new formation of auxin ("regeneration") by the decapitated plant (see Skoog 1937). Skoog showed that deseeded plants almost lack this power to produce auxin after decapitation. Hence, the auxin curvature of such plants increases over a much longer period of time. Plants from which the root system had been removed showed regeneration as is shown in table 3. Here it can be seen that, 5 hours after the auxin

blocks had been put on, the curvatures in the plants without roots are smaller than they were $3^1/_2$ hours before. This going back of the curvatures shows that regeneration takes place. The plants without seed but with roots also show some regeneration but at a later stage than the intact or the rootless plants. The plants which have been cut off at their base and placed on wet cotton do not show any sign of regeneration; their curvature

TABLE 3

Auxin curvatures of plants from which either the seed, the root system or both were removed, at various times after auxin application. Removals were made 15 hours before the auxin was applied. Averages of 24 plants. Auxin concentration 0.059 mg. per l. Experiment 61222.

| | TIME AFTER AUXIN APPLICATION: | | |
|---|---|---|---|
| | 90 MINUTES | 5 HOURS | 8 HOURS |
| Seed and roots present | 10.3 | 5.3 | straight |
| Roots removed | 14.9 | 11.2 | gone back |
| Seed removed | 8.7 | 16.4 | gone back |
| Seed and roots removed | 6.7 | 19.7 | about 30° curvature |

increases steadily. So it seems that such plants are even more suited to measure minute amounts of auxin than the deseeded plants of a test developed by Skoog.

*Conclusions.*—The fact that deseeded plants do not produce as much auxin as intact plants do, has been explained by Skoog by assuming that removal of the seed also removes the source from which the precursor of auxin is coming. A similar explanation may hold for the plants which were cut off at their base. According to Skoog this inactive precursor is present in the seed and is polarly transported in apical direction, principally in the same way as auxin is transported in basal direction. In derooted plants, however, the endosperm is retained, so the precursor may go up into the shoot and there be activated into auxin. The fact that regeneration takes place in derooted plants (with their auxin source intact) and practically not in deseeded plants is in agreement with the above view. If, however, all the active auxin in the shoot should derive from the precursor only and this precursor should be transported only by a mechanism of polar transport as described above, it is hard to see why the auxin production of the derooted plants is so much less than that of the intact plants.[1] The root system, which is the only factor by which the derooted and the intact plants differ, must have a part in the apical transport of auxin or its precursor.

It has been shown by Kögl, Erxleben and Haagen Smit (1934), Laibach and Meyer (1935) and others that germinating seeds contain active auxin. Hitchcock and Zimmerman (1935) showed that auxin when taken up by the roots can be transported toward the shoot by the transpiration stream. So Avery and Burkholder (1936) assumed that the active auxin may move upward from the seed through the vascular bundles to the coleoptile tip

from where it is dispersed downward. This conclusion first seemed unacceptable in the light of Van der Wey's investigations which showed that in *sections* of coleoptiles the auxin can be transported in basal direction and not in apical direction. However, if in the Avena seedling the roots are actively engaged in the upward transport of auxin as the experiments presented in this paper seem to indicate, Avery and Burkholder's opinion is not necessarily in conflict with Van der Wey's experiments.

As a tentative mechanism of the upward transport of auxin in the Avena seedling I would suggest combining the above-mentioned opinions in the following way. Auxin is present in the seed in two forms: the active form and the inactive precursor. Both forms may be transported from the seed toward the apex of the shoot, but the active form goes up only with the transpiration- or root-pressure stream.

*Summary.*—Removal of the root system for a period of 15 to 20 hours reduces the auxin production of the coleoptile tip of Avena seedlings markedly. This reduced production causes a decreased growth, but at the same time an increased sensitivity for auxin. This increase in sensitivity may be as high as 100%. New formation of auxin after decapitation takes place in plants from which the roots have been removed.

Plants from which both roots and seed have been removed have a lower initial sensitivity but they do not "regenerate," hence their curvatures do not decrease but increase steadily. This makes such plants even more useful to detect small amounts of auxin than the deseeded plants.

It is suggested that there are two ways by which the auxin from the seed reaches the apex of the shoot, viz., as inactive precursor which may be transported without the presence of the root system, and as active auxin which may go up with the transpiration- or root-pressure stream.

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