CHANGES IN ELECTRICAL POLARITY IN THE AVENA COLEOPTILE AS AN ANTECEDENT TO HORMONE ACTION IN GEOTROPIC RESPONSE

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(WITH ONE FIGURE)

Introduction

The coleoptile of *Avena sativa* has been used extensively in the study of geotropic curvature (**1, 10**). When the coleoptile is placed in the horizontal position, it responds to the force of gravity as the stimulus by curving upward, by accumulating a greater quantity of growth hormones in the lower than remains in the upper half, and by establishing a transverse electrical polarity oriented so that the under side becomes electropositive to the upper side in the external circuit. Although there may be other concurrent responses, this paper is concerned only with these listed. It is generally accepted that the unequal hormone distribution is an essential precursor for the upward bending (**1, 10**), but these hormones must be *directed* to the under side by some orienting *force* (*polarity*). It has been suggested (**1, 10**), though it has not been proved, that the transverse electrical polarity might be the required orienting force. If the electrical polarity is to fulfill this requirement, then its establishment must chronologically precede the unequal growth hormone distribution. Consequently, an analysis of the experimental data on this point is in order.

Experimental

The curve in figure 1A is an average of 6 experiments showing the electrical responses of Avena coleoptiles when they are placed in the horizontal position. These electrical measurements were taken at points 2 millimeters below the apex. The contact on the upper side was connected to ground, and the contact on the under side was used as the variable. The details of the experimental procedure whereby these data were obtained have been reported elsewhere (**6, 7**). These experiments were performed on coleoptiles that were 32 (±) millimeters long at an average temperature of 21.8 (± 0.25) degrees Centigrade. Since the curve in figure 1A shows a transverse electrical polarity of 1.5 millivolts after 1 minute in the horizontal position, it reveals the fact that the appearance of this polarity can be detected within one minute or less. It is very probable that this electrical polarity could be demonstrated much sooner with an instrument of shorter period and greater sensitivity. The data in figure 1A are in agreement with the results of BRAUNER (**2**) and WILKS and LUND (**11**).

Data which have been published by DOLK (**3**) can conveniently be used for demonstrating the time required for an unequal distribution (in the upper and lower halves of the coleoptile) of growth hormones to occur as

the result of stimulation by gravity. DOLK placed coleoptiles in the horizontal position for a minimum of eleven minutes. At the end of this time the plants were decapitated and the tips placed on an apparatus on agar so that the upper and lower halves of the tips were separated by the edge of a razor blade. After leaving for a certain time on agar, the amount of growth substance was determined in the usual way (**1, 10**).

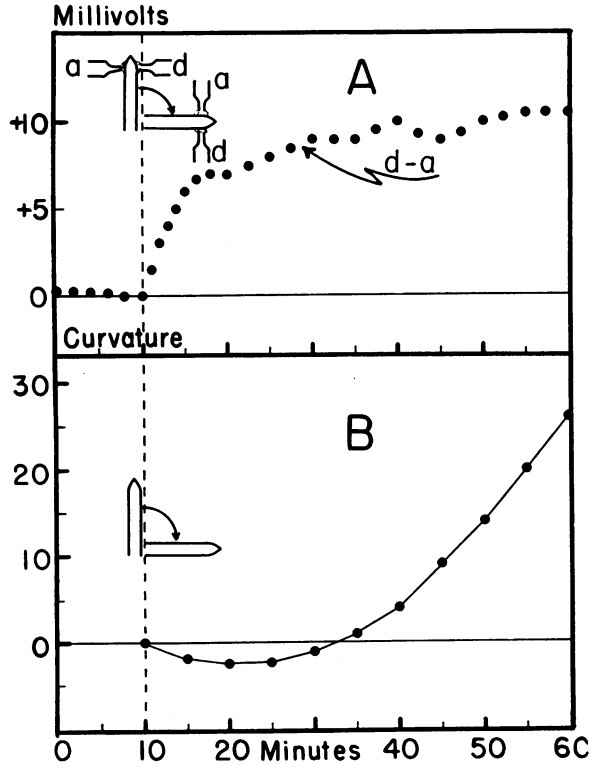

FIG. 1. A. Changes in the transverse E.M.F.'s in Avena coleoptiles when changed from vertical to horizontal positions. Contacts 2 mm. below apex. Curve represents average of 6 experiments.

B. Upward curvature of Avena coleoptiles in horizontal position measured in ocular scale division of 18 per millimeter. Average of 10 experiments.

The first line in DOLK'S (**3**) table IV indicates that the test blocks from the under side induced a curvature of 1 degree more than the test blocks from the upper side. A consideration of the experimental procedure used and a comparison of results obtained from identical experiments as shown in this table make it extremely doubtful whether a difference in curvature of 1 degree is significant.

The time that elapses before upward curvature begins can accurately be determined. Figure 1B shows the average geotropic curvature of 10 coleoptiles, each approximately 30 millimeters long. The curvature was measured by and is plotted in scale divisions (18 per millimeter) of an ocular microme-

ter. These experiments were performed at an average temperature of 25.2 (± 0.25) degrees Centigrade. This curve demonstrates that upward curvature can be detected after 22 minutes in the horizontal position. The initial sagging of the curve in figure 1B is probably due to the weight of the coleoptiles.

Discussion

As far as experimental measurements are concerned, as demonstrated by the data cited in this paper, the following sequence of responses of the Avena coleoptile to gravity has been conclusively settled: (1) Establishment of a transverse electrical polarity. (2) Unequal distribution of the growth hormones (**3**). (3) Upward curvature. However, the fact that a difference in hormone distribution has not been measured prior to eleven minutes in the horizontal position does not necessarily mean that a significant difference does not occur sooner. For this reason some relevant theoretical aspects should also be considered.

The growth hormones could not be transported from the upper to the lower side by simple diffusion; because, first of all, the required concentration gradient of growth hormones does not exist. Secondly, it has been shown that the velocity of hormone transportation is almost completely independent of temperature (**8, 9**). If diffusion were involved, this would not be true. The velocity of longitudinal hormone transport has been measured experimentally in the Avena coleoptile and is conceded to be about 10 millimeters per hour (**5, 8, 10**). If the minmum distance for the hormone to be transported in going from the upper to the lower side is assumed to be one millimeter,[1] then 6 minutes would be required for the hormones to reach the under side. Even if it were assumed that the growth hormones are transported a distance of 1 millimeter from the upper to the under side directly by protoplasmic streaming without hindrance by the cell walls, and the velocity of protoplasmic streaming is taken to be 10 microns per second (**4**), then 1.6 minutes would elapse before the hormones could reach the under side. From this study it becomes clear that the transverse electrical polarity is actually established in the Avena coleoptile *before* a difference in hormone concentration is considered possible. If a transverse electrical polarity is required for the lateral transport of growth hormones, then it obviously must be established previous to the unequal hormone distribution. The fact that the transverse electrical polarity is established prior to the unequal hormone distribution does not necessarily mean that it is the orienting force or polarity ["transverse polarization of the cells," *op. cit.* (**10**), p. 157] which is essential for lateral hormone transport. It means only that

[1] This assumption is well within reason because the transport of growth hormones from one side of the coleoptile to the other probably occurs in a basipetal diagonal direction rather than perpendicular to the longitudinal axis. The fact that the zone of curvature proceeds from the apex towards the base indicates that this concept of diagonal transport is correct.

the transverse electrical polarity fulfills the prime requirement of being established in the correct sequence.

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