

complete medium⁸ (containing both vitamin B₁ and nicotinic acid) are able to synthesize auxin. Details will be published later.

¹ Report on work carried out with the aid of assistants supplied by the Works Progress Administration, Official Project Number 665-07-3-83, Work Project L-9809.

² *Planta*, **19**, 354 (1933).

³ *Jour. Gen. Physiol.*, **18**, 23 (1934).

⁴ Nagao, M., *Sci. Rep. Tohoku Imp. Univ.*, **10**, 721 (1936); Boysen Jensen, P., *Det. Kgl. Danske Vidensk. Sels., Biol. Medd.*, **13**, 1 (1936); Van Raalte, M. H., *Rec. trav. bot. néerl.*, **34**, 278 (1937).

⁵ van Overbeek, J., and Bonner, J., *Proc. Nat. Acad. Sci.*, **24**, 260 (1938).

⁶ Went, F. W., and Thimann, K. V., *Phytohormones*, Macmillan, New York, 1937.

⁷ The amounts of auxin are expressed in degrees of curvature in the standard *Avena* test on the basis of 50 root tips and a volume of agar corresponding to 8 blocks (1120 mm.³). All tests were done in quadruplicate and at the same time in order to avoid errors due to variation in sensitivity of the plants. If root tips are placed on plain agar blocks no auxin is found in them. Ether extraction of such tips that had been transferred to fresh plain agar blocks for a total period of 20 hours, yielded $46.6^\circ \pm 1.6^\circ$.

⁸ Addicott, F. T., and Bonner, J., *Science*, **88**, 577-578 (1938).

CELL POLARITY AND THE DIFFERENTIATION OF ROOT HAIRS

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Communicated March 24, 1939

By means of a technique recently described by Sinnott¹ it is possible to observe the division and enlargement of cells in the living root tips of certain grasses, and to trace the history of these cells until differentiation is complete. In certain genera the cells which are to form root hairs (the trichoblasts) are sharply differentiated at the last cell division from those which are not, and the two develop very differently. In other genera differentiation of root hair cells is delayed for some time, and any cell, until rather late in its development, seems to have the capacity to form a root hair. A detailed comparison of these two types of differentiation throws light on the mechanism of root-hair determination. Root hair development was studied in *Phleum pratense*, *Poa trivialis*, *Chloris gayana* and *Sporobolus cryptandrus*.

In the genera *Phleum* and *Poa*, just before the last cell division (usually the fourth from the tip) in the surface layer or dermatogen, the apical end of the cell becomes more densely protoplasmic than the basal. The division which then follows is an unequal one, the apical (distal) daughter cell, which is the trichoblast and destined to produce a root hair, being

considerably smaller than the basal (proximal) one (Fig. 1, above). It also has denser contents, as may be seen in the living condition or by staining with Ruthenium Red or other agents. The new wall between the two cells is somewhat convex toward the proximal side, so that the cells differ more in the length of their side walls than in volume. The absolute and relative sizes of these apical and basal cells, measured along the side walls at the beginning of development and at maturity, are shown in table 1. *Phleum* has slightly larger cells, but the relative size of the two cell types is much the same as in *Poa*.

TABLE 1

	<i>Phleum</i>	<i>Poa</i>	<i>Chloris</i>	<i>Sporobolus</i>
MERISTEMATIC REGION				
Length of apical cell (micra)	4.68 ± 0.25	3.59 ± 0.23	6.60 ± 0.61	7.17 ± 0.21
Length of basal cell (micra)	10.33 ± 0.39	8.12 ± 0.30	9.00 ± 0.75	8.25 ± 0.26
Ratio, apical:basal	1.0 : 2.21	1.0 : 2.26	1.0 : 1.36	1.0 : 1.15
MATURE REGION				
Length of apical cell (micra)	98.3 ± 6.1	52.6 ± 4.4	95.0 ± 5.3	101.0 ± 5.2
Length of basal cell (micra)	244.8 ± 11.3	178.5 ± 8.5	137.0 ± 6.8	127.0 ± 6.8
Ratio, apical:basal	1.0 : 2.49	1.0 : 3.39	1.0 : 1.44	1.0 : 1.26
Percentage distance of root hair origin from apical end of cell.				
Per cent	14.0 ± 0.6	18.0 ± 0.5	23.9 ± 0.6	41.9 ± 1.1
Standard deviation	5.83 ± 0.40	5.25 ± 0.37	5.96 ± 0.43	9.84 ± 0.76

As cell enlargement proceeds, these relative proportions are essentially maintained, although from the first the apical cell grows somewhat less rapidly than the basal so that the contrast between them increases until maturity. The partition wall loses its convex form and becomes straight. The basal cell soon becomes vacuolate but the apical one remains rather densely protoplasmic. As this cell reaches its final size, a root hair begins to develop from near the apical end, where more protoplasmic material is present. The nucleus usually occupies a position just below the young root hair. The point of origin of the hair, in terms of percentage distance along the cell from its apical to its basal end, is presented in table 1. This point, about 14% and 18% from the apical end, in these two genera, is relatively constant, showing a standard deviation of about 5.5%. The root hair itself is pointed forward at an angle of about 45° with the axis of the root.

In the genus *Sporobolus* (Fig. 1, below), on the other hand, there is no visible internal differentiation before the last division and the division itself is much more nearly an equal one, the two daughter cells usually being indistinguishable in size or contents, although there is a tendency for the apical one to be slightly smaller. As the cells expand to their final size, root hairs develop from some of them. Occasionally one finds alternating root-hair cells and hairless cells, as in the figure, but frequently there is a

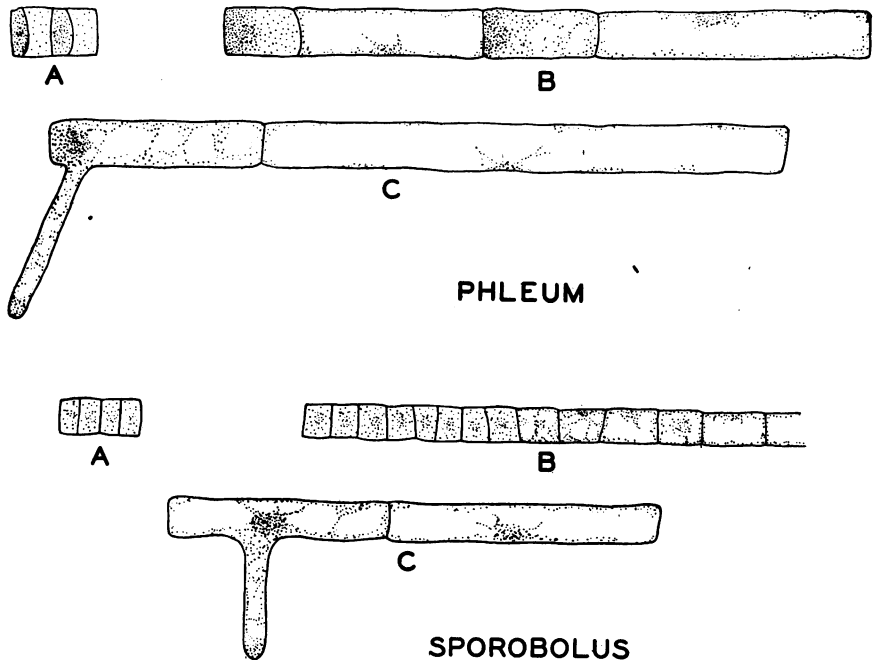


FIGURE 1

Above, *Phleum*: A, two pairs of cells in the meristematic region; B, the same cells during expansion; C, a root-hair cell and a hairless cell at maturity.

Below, *Sporobolus*: A, two pairs of cells in meristematic region; B, a series of cells during expansion; C, a root-hair cell and a hairless cell at maturity.

The apex of the root is toward the left.

continuous series of cells which develop hairs and then a group of several without them. The root hair originates near the middle of the cell, about 42% of the distance from the apical end (table 1). Its position is much more variable than in *Phleum* and *Poa*, however, the standard deviation being almost twice as great. The hair grows nearly straight out from the root at an angle of 90°.

The genus *Chloris* is somewhat intermediate between the two types just described. The last division appears to be slightly more unequal, the

apical cell being smaller than the basal, but this difference is by no means as great as in *Phleum* and *Poa*. As the cells enlarge, certain of them can be shown by appropriate staining to have more dense contents, and these are usually the smaller cells. They often alternate with somewhat larger ones, and are the cells from which root hairs develop. Frequently there may be a series of several successive root-hair cells. The hairs come out from about a fourth (23.9%) of the way back along the cell and are relatively constant in their position. They tend to bend forward apically somewhat.

In both *Sporobolus* and *Chloris*, roots which have been checked in their growth, because of age or for other reasons, tend to show a much more definite alternation of relatively small root-hair cells with relatively large hairless ones, and the hairs in such cases tend to originate nearer the apex of the cell than they do in fast-growing roots.

A comparison of these types of root-hair differentiation shows that early differentiation is associated with (1) denser cell contents at the apical end of the mother cell before its division into root-hair and hairless cells; (2) unequal division of this cell, the smaller daughter cell (which will produce the root hair) lying toward the apex and retaining denser cytoplasmic contents for a considerable time during subsequent extension; (3) an origin of the root hair near the apical end of the cell and in a relatively constant position; and (4) a forward growth of the root hair at an acute angle with the root axis. Conversely, where differentiation is late, the cell contents of the mother cell are of equal density throughout; the division of this cell is essentially equal so that there is less regular alternation of root-hair and hairless cells; the hair originates from near the middle of the cell but in a much more variable position, and the hair tends to grow directly out at right angles to the root axis.

These results can be explained by assuming that in *Phleum* and similar forms there is a strong apical tendency in the formation of root hairs, but very much weaker tendency in *Sporobolus* and its allies. This can perhaps best be pictured in terms of the distribution of materials under the influence of cell polarity. Where the cell is strongly polarized, the materials at one end will be markedly different from those at the other. Where polarization is weaker, distribution will be more nearly equal. If materials which stimulate root-hair formation move under the influence of strong polarity, they will accumulate at one end of the cell (the apical end in *Phleum* and its allies) from a very early stage and will cause the last division of the root hair mother cell to be unequal, the apical cell to be the root-hair cell, and the root hair itself to originate near the apical end of this cell in a constant and apically directed position. Conversely, the more equal distribution of these materials would tend to be associated with a division of the mother cell into cells essentially equal in size and in root-hair potency, and in the origin of an outward pointing root hair near the middle of the cell but more

variable in its position, exactly the situation which occurs in *Sporobolus*. In such cases of weak polarization it is probably differences in the internal or external environment rather than inherent differences in the cells themselves which determine whether a given cell will produce a root hair or not, and where it will be produced.

The material stimulating root-hair growth may be protoplasm itself or some more specific growth substance. In support of the former possibility is the fact that in *Phleum* and *Poa*, protoplasm and nucleus tend to move toward the apical end of the mother cell and of the root hair cell itself.

Aside from its effect on the distribution of stimulating materials, cell polarity might have an influence on root-hair production through differences in permeability at the two ends of the cell, through polar differences in the character of the cell wall, or through other factors affecting the form and development of the cell itself.

These pronounced and regular differences between cells in their capacity to form root hairs, and between related genera in the time and character of root-hair differentiation, should be taken into account in studies which deal with the factors responsible for root-hair development.

Whatever the causes may be for the facts here described, it is clear that in related genera of the grass family there are markedly different types of root-hair determination. In one, differentiation is early and strongly apical in character. In another it is late and but slightly or not at all apical. These forms evidently provide excellent material for experimental studies on some of the factors involved in differentiation, for they present a simple example of two sister cells which in some cases have the same fate throughout, in others become unlike only near the end of their growth, and in still others are differentiated, both in structure and function, very early in development.

¹ Sinnott, Edmund W., *Proc. Nat. Acad. Sci.*, 25, 55-58 (1939).

ON MODULAR AND p -ADIC REPRESENTATIONS OF ALGEBRAS

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Communicated March 17, 1939

1. In the usual treatment of the arithmetic of an algebra A , only maximal domains of integrity are considered. However, in the important case of the group ring belonging to a group G of finite order, a domain of integrity J which is not a maximal domain is defined in a natural manner. A basis of J is formed by the group elements. It is necessary for the in-