The Organization of the Root Apex of *Glycine max*

C. E. Anderson and S. N. Postlethwait, Purdue University

The purpose of this paper is to compare the pattern of development in the apex of the soybean root with several theories on organization of root apices.

Hanstein (11, 12), in 1868, proposed a theory on apical organization called the Histogen theory. He suggested that the apex is composed of three cytogenerative regions: the plerome, which forms the cortex, the periblem which forms the stele, and the dermatogen, which forms the epidermis. Although these regions are easily distinguished in the roots of many species, some investigators disagree with Hanstein as to their nature. Hanstein proposed that cells, as they are formed at the apex, have had their final form determined. Esau (7) points out that there is no reason to assume that the destinies of different cells of the plant body are determined at their origin. Foster (9), in working with cytochimeras, found that histogenesis and organogenesis have no obligate relationship to the segmentation and layering of cells of the apical meristem. He further pointed out that gymnosperms and some angiosperms show no distinction between the plerome and the periblem.

These same regions were assigned a different name by Haberlandt (13). The stele, in his scheme, is derived from the procambium, the cortex from the ground meristem, and the outermost tissues from the protoderm. The root cap is formed by the calyptrogen. Those who use these terms are rather noncommittal about the origin of the tissues.

Guttenberg (10) advanced the theory that the initials for each region are derived from a single apical cell, with all tissues being ultimately referrable to its activity. In some cases it has been proposed that 2 or 3 apical cells serve as apical initials.

New research methods have enabled experimenters to approach the problem of apical organization in various ways. Clowes and Brumfield have employed some of these new procedures with interesting results.

Brumfield (1) used X-rays to alter the cells of the apex. He found that the resulting pattern of development was not always the same, but one of the more common patterns was a division into three distinct regions (fig. 2). This may indicate that 3 cells are responsible for all tissue formation. It also suggests that the derivatives of one cell may form all the different root tissues.

The validity of conclusions drawn from X-ray treatment has been questioned. Clowes (2) performed a series of experiments to determine the actual effect of X-rays on the root apex of *Zea*. He found that DNA synthesis can be lowered, that mitosis may be delayed, that chromosomes can be broken, at times so badly as to stop cell division altogether, and that disturbances caused by ionization may occur to change the rate of division and upset hormonal processes.

A recent concept of apical organization has suggested a quiescent center or a zone of limited cell division occupying a central position in the apical meristem. (Fig. 1) Clowes (3, 5, 6), by using radioactive tracers in various substances connected with cell division, has shown in *Zea* an area

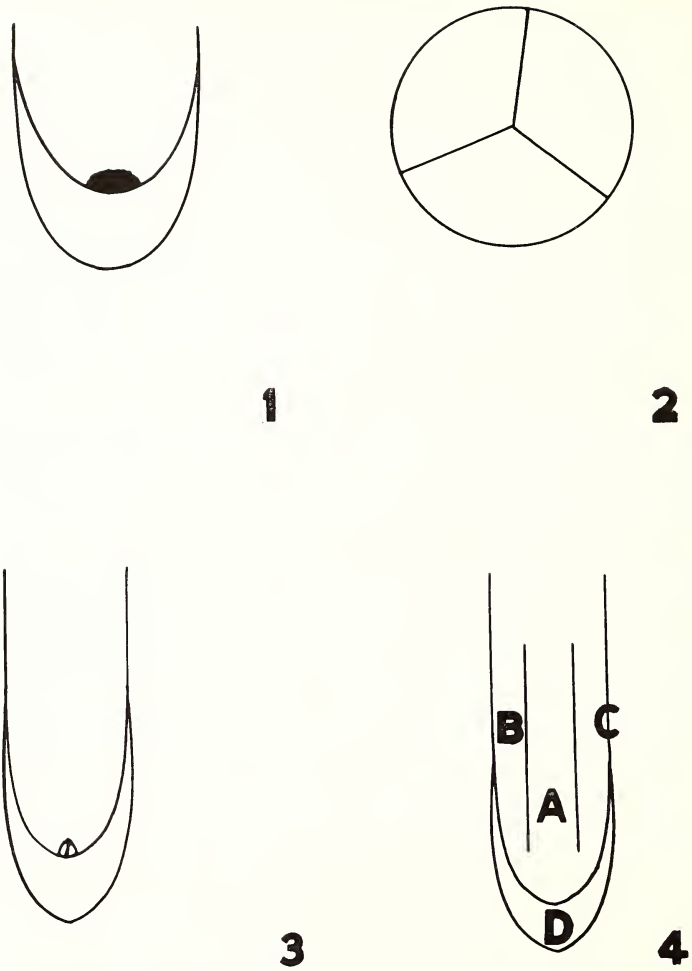

Plate 1. Figure 1. Root diagram showing quiescent center. Figure 2. Chimeral arrangement of root tissues after X-ray treatment by Brumfield. Figure 3. Root diagram showing apical cell as proposed by Guttenberg. Figure 4. In Hanstein's Histogen theory A—periblem B—plerome C—dermatogen. In Haberlandt's theory A—procambium B—ground meristem C—protoderm D—calyptrogen.

in the center of the apex which carries on little or no cell division. The area of peak cell division encircles this inactive center. Support has been offered to this theory by Miller (17) in his study of *Humulus lupulus*, and by Jensen and Kavajian (15) in their study of *Allium*.

The soybean root has in its organizational pattern a stele, cortex, epidermis and root cap. An organized meristem is responsible for the formation of the tissue of the root. The meristem displays some discreet regions of activity, however, in some areas cell division may be somewhat

irregularly distributed. The age of the root and the tissue type causes dissimilarity in the location and number of cell divisions.

Most of the cortex is produced by a single layer of cells which can be distinguished early in the organization of the apex. This layer of cells undergoes a series of periclinal divisions resulting in a radial alignment of its derivatives. The outer layers of cortex, having been derived directly from the periphery of the meristem, do not display this radial alignment. The cortex also shows concentric layering, which Heimsch (14), in studying tomato, considered to result from unison division in the initiating layer. The division in this layer is primarily responsible for the sudden increase in root diameter.

As activity begins in the inner cortical layer, the cells of the stele still appear rather large and inactive. This inactive area is often 6 to 8 cells wide and varies notably in its persistence basipetally. Further study may clarify the extent of this region. The termination of this area is delimited by an increase in cell activity, smaller cells, and ultimately differentiation of primary phloem.

The epidermis of the soybean root arises with the cortical tissue at the periphery of the apical meristem. In its early ontogeny the epidermis is indistinguishable from the cortical tissue. The first modification occurs as the epidermal tissue undergoes a series of anticlinal divisions to form a layer of radially elongated cells. This early elongated shape is not maintained. As the root expands the epidermal cells grow and attain a more isodiametric shape.

The origin of the root cap is somewhat more obscure. Part of the root cap forms from a series of periclinal and anticlinal divisions of tissue located acropetally to the cortical and epidermal initials. The central portion of the root cap, sometimes called columella, appears to have a separate point of initiation. Mann (16) has described the columellar organization in garlic roots as follows: "The root cap has a column of

Plate 2. Photomicrograph of 4-day old soybean root apex showing its apical organization. The magnification is 192 times.

8 to 10 longitudinal rows of cells. At the edges these divide periclinally, extending the cap laterally. The shape and position of the initial cells seem to provide no evidence that these groups of initials are distinct from one another." Clowes (4) found in autoradiographs of *Allium* and *Zea* that the columella is produced by a thin line of initiating cells directly beneath the inactive center of the apex.

The organizational concepts of Hanstein and Haberlandt are represented by figure 4. The corresponding regions can be observed in the soybean root apex as shown in figure 5. While either set of names could be applied to the regions observed in the soybean root, the mere coincidence of patterns does not preclude other more plausable and satisfactory explanations of organization.

In the soybean apex there is no evidence for a single apical cell or two or three apical initials as proposed by Guttenberg for dicotyledons (fig. 3).

The quiescent center as diagramed in figure 1 approaches most closely the organization of the soybean root apex. While this study has failed to define a minimal constructional area, observations of longitudinal and transverse sections of the soybean root apex show evidence of the presence of a quiescent center.

Further study is being conducted concerning the organization of the soybean root apex. It appears that no present theory on root apices is wholly acceptable. Esau (8) and Popham (18), studying pear and pea roots, found that organization varies some with the age of the root. For example in pea the tissue in the 5 day old root matured more slowly than in the 20 day old root. This change in rate of maturation means that mature tissues are found closer to the initiating cells in the older plants. With variation like this within species it is not unreasonable to expect differences between species.

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