Amer. J. Bot. 58(7): 665–671. 1971.

THE QUIESCENT CENTER IN CULTURED ROOTS OF CONVOLVULUS ARVENSIS L.[1]

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A B S T R A C T

Cultured roots of *Convolvulus arvensis* were incubated in 0.2–0.3 μc/ml methyl-^{3}H-thymidine for different intervals of time. In roots supplied with tritiated thymidine for 12 hr, 14 hr, 48 hr, or 14 hr followed by transfer to fresh medium for 24 hr, autoradiographs prepared of serial, longitudinal sections of the root tips showed the presence of a subterminal quiescent center in the root proper at the distal poles of the central cylinder and cortex. In addition, a zone of unlabelled cells in the columella, distal to the root cap initials, was present. In roots supplied continuously with tritiated thymidine for 64 hr, 96 hr, and 120 hr, the quiescent center was either reduced in size or was not present.

THE QUIESCENT CENTER, located subterminally in the apical meristem of elongating roots, was described by Clowes (1956a) as a population of cells which is metabolically inactive and which shows very low rates of cell division. Experiments following by autoradiography the incorporation of labelled precursors of deoxyribonucleic acid synthesis, protein synthesis, and the synthesis of insoluble polymers derived from the utilization of sucrose, have shown that quiescent centers are present in different types of roots at different developmental stages (Byrne and Heimsch, 1970; Clowes, 1956a, b, 1958a, b, 1961b; Fisher, 1968; Jensen, Kavaljian, and Martinot, 1960; Raju, Steeves, and Naylor, 1964; Riopel and Steeves, 1964; Thomas, 1967; Thompson and Clowes, 1968; Wilcox, 1962). Rabideau and Mericle (1953) studied the distribution of labelled compounds in the meristematic regions of the shoots and roots of corn seedlings by autoradiography after the seedlings had assimilated ^{14}C-carbon dioxide through the leaves for 24 hr. Rabideau and Mericle did not comment on the lack of labelling in the cells of the quiescent center and in the cells of the columella of the root cap, though this lack of labelling is clearly evident in their published autoradiographs. Although Alfieri and Evert (1968) and Miksche and Greenwood (1966) reported the presence of quiescent centers in initial roots of *Medicago sativa* L., *Trifolium pratense* L., and *Allium cepa* L. and in seedling roots of *Glycine max* Merr. respectively, their procedures for supplying tritiated thymidine for time periods which did not cover a significant portion of the cell cycle for cells of the apical meristem resulted in autoradiographs which did not sharply delimit the quiescent center. Wimber (1960), Raju et al. (1964), and Alfieri and Evert (1968) reported that roots formed from cuttings of *Tradescantia paludosa*, the lateral roots of *Euphorbia esula* L., and seedling roots of *Melilotus alba* Desr., respectively, do not contain quiescent centers. However, Clowes (1969) noted that roots of *Tradescantia* may, in fact, be shown to have a quiescent center consisting of approximately 120 cells. In addition, Clowes and Stewart (1967) and Clowes (1969) noted that the technique used by Raju et al. (1964), which involved handling the lateral roots of *Euphorbia*, activates the cells of the quiescent center into division. In the case of *Melilotus* tritiated thymidine was supplied to the roots for a relatively short period of time, namely 1–2 hr. Only those meristematic cells in which DNA was being synthesized were labelled, whereas other meristematic cells not synthesizing DNA, yet having a similar cell cycle, were unlabelled. If the labelled precursor had been available for a longer period of time, such as 12 hr, more cells would have been labelled and a more accurate and reliable delimitation of the quiescent center would have been possible.

The quiescent center may be operationally defined as comprising those cells of the apical meristem of the root proper which show, by the use of histoautoradiography, low rates of incorporation of appropriate precursors for the synthesis of DNA provided during a significant period of the average cell cycle time of the root tip itself. By this definition, quiescent centers occur in elongating seedling roots, lateral roots, and primary roots of mature plants. Quiescent centers are lacking in the initial stages of radicle growth of germinating seedlings and in the early stages of lateral root initiation before the organized meristem of the lateral root is formed (Clowes, 1958a).

As far as cultured roots are concerned, Street (1966), quoting an unpublished portion of the

[1] Received for publication 1 February 1971.

This research was supported in part by research grant GM-08145 and a fellowship GM-41021 to H. L. P. from the National Institutes of Health, USPHS.

thesis of Abbott (1963), stated that cultured pea roots do not contain a quiescent center. Thomas (1967) reported the presence of a quiescent center in excised tomato roots maintained in culture for 6 days. The experiments reported here attempted to establish whether or not cultured roots of *Convolvulus arvensis* L. contained a quiescent center. Since roots grown in isolation in nutrient medium show normal root anatomy, it was important to know whether the quiescent center could be demonstrated. If cultured roots possess no quiescent center, then clearly the latter is of no importance in understanding root structure. In addition, since cultured roots can be maintained in a defined nutrient medium, they provide good experimental material for elucidating the function of the quiescent center in the development of the organized root.

MATERIALS AND METHODS—Cultured roots of *Convolvulus arvensis* L., obtained from a clone of roots maintained in a modified Bonner-Devirian medium (Torrey, 1954) over a period of 18 years by subculturing root tips and root segments, were used in these experiments. Roots were cultured in 125-ml Erlenmeyer flasks containing 50 ml of liquid Bonner-Devirian medium in the dark at 23 C. Cultures were agitated continuously on a horizontal rotary shaker at 80 rpm. Prior to use, root tips were transferred to fresh medium for 3–4 days to determine the approximate rate of elongation. Root tips elongating at a rate of 15–30 mm per day were used in the experiments to be described. Bonnett (1964) showed that the average rate of elongation for such roots of *Convolvulus* was 23.2 mm/day during 2 months without subculture.

The following procedures were used for the experimental treatments:

(1) Excised 15-mm root tips were transferred to modified Bonner-Devirian medium containing methyl-^{3}H-thymidine (specific activity 6.0 c/mM) at a concentration of 0.3 μc/ml for 12 and 48 hr before fixation.

(2) Elongating root tips of varying lengths were transferred to modified Bonner-Devirian medium containing methyl-^{3}H-thymidine (specific activity 6.7 c/mM) at a concentration of 0.2 μc/ml for 14, 64, 96, 120 hr before fixation or for 14 hr followed by transfer to fresh medium without tritiated thymidine for 24 hr.

Roots were fixed in 3 % glutaraldehyde in 0.025 M phosphate buffer (*p*H 6.8) for 2–2½ hr at room temperature and stored in 0.05 M phosphate buffer (*p*H 6.8) in the refrigerator until dehydration. The dehydration and embedding steps were performed at room temperature as follows: 5 min each in 15 %, 30 %, 50 %, 70 %, and 95 % aqueous acetone; 5 min in 100 % acetone; 10 min in fresh 100 % acetone; 10 min in 1:1 propylene oxide: 100 % acetone; 30 min in propylene oxide (3 changes every 10 min); 30 min in 3:1 propylene oxide: resin in capped vials; 1 hr in 2:1 propylene oxide: resin in capped vials; overnight in the same mixture in uncapped vials; 24 hr in resin; 15 min in fresh resin during evacuation at 80 C; and 2 days in an 80 C oven to harden the resin. The resin mixture was composed of Epon 812, Araldite 6005, and dodecenyl succinic anhydride (DDSA) in a ratio of 5:4:12 with 1.05 % DMP-30 (Rohm & Haas). These procedures for embedding with Epon-Araldite are standard procedures used in electron microscopy, and they provide easily obtainable serial sections. Sections 5 μ thick were used because this thickness is approximately half the width of a cell in the apical meristem. Therefore, the location of a nucleus of a cell would be within two serial sections. Sections were obtained using a Huxley Ultramicrotome with a dry glass knife and were then mounted on slides which were coated subsequently in the dark with Kodak Nuclear Track Emulsion NTB3 diluted 1:1 with distilled water. The dried slides were then stored in slide boxes with calcium chloride in complete darkness. After exposure periods ranging from 4–8 weeks, the slides were developed with chilled Amidol (4.5 g sodium sulphite, 1.1 g diaminophenol dihydrochloride, 2 ml 10 % potassium bromide, and 250 ml distilled water) under a Kodak Adjustable Safelight Lamp with a Kodak Wratten Series 2 filter. The sections were stained for 2–3 min with 0.05 % toluidine blue in phosphate buffer (*p*H 6.8) to which 1 % sodium borate was added. Measurements were made with the use of a calibrated ocular micrometer.

RESULTS—Examination after histoautoradiography of serial, longitudinal sections of 24 root tips supplied with tritiated thymidine for 12, 14, and 48 hr indicated that a quiescent center existed in all the roots in an almost hemispherical region located at the distal pole of the central cylinder and cortex, subterminal to the root cap (Fig. 1). As is shown in Fig. 1 and 2, incorporation of tritiated thymidine into the DNA of nuclei occurred in cells which form the stelar initials, the cortical initials, and the root cap initials. In addition, cells located in a single layer in the root proper between the quiescent center and the root cap initials were frequently labelled. About 5–6 % of cells within the quiescent center had labelled nuclei. No division figures were observed in cells of the quiescent center, though labelled division figures were evident in the cells of the root cap initials and in the cells at the proximal boundary of the quiescent center in the root proper. The distal boundary was stable. The proximal boundary fluctuated considerably over the surface of the quiescent center. In addition, the autoradiographs showed that the nuclei of cells in the columella, distal to the root cap initials, did not incorporate tritiated thymidine. Only cells of the root cap initials and cells in the root cap periphery had

labelled nuclei. Although no attempt was made to quantitate the incorporation of tritiated thymidine by silver grain counts, it was clear from the autoradiographs that the cells of the root cap periphery had higher levels of radioactivity than the root cap initial cells and the meristematic cells immediately proximal to the quiescent center.

In Table 1, the dimensions of the quiescent center and the width of the root at the level of

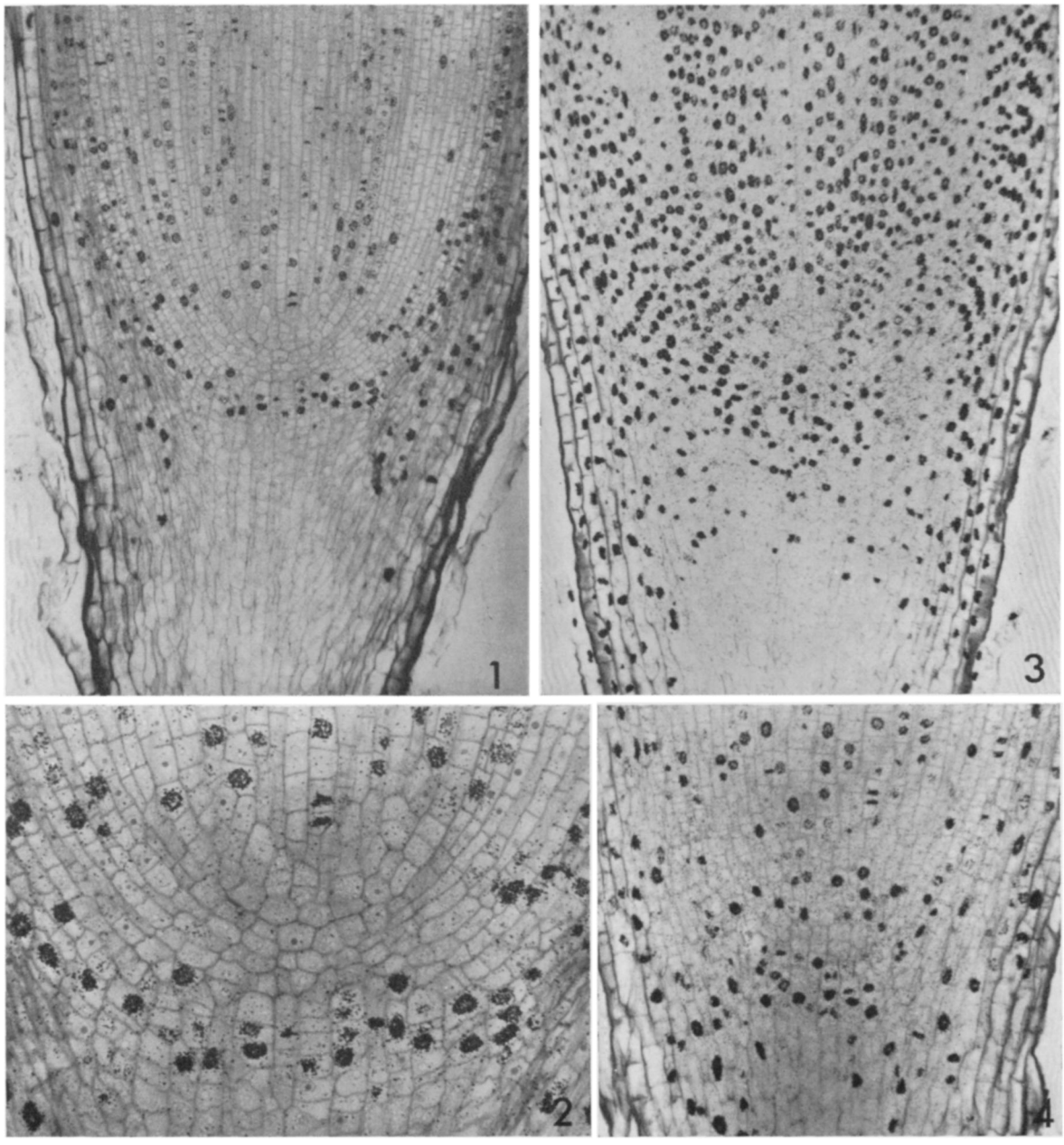

Fig. 1–4. Autoradiographs of longitudinal sections of root apices of *Convolvulus arvensis*.—Fig. 1. Median longitudinal section of a root apex provided tritiated thymidine for 12 hr, showing the incorporation into nuclei of cells of the stele, cortex, root cap initials, and root cap periphery. Note the lack of label in cells of the quiescent center in the root proper and in cells of the columella of the root cap. × 160.—Fig. 2. Enlarged view of Fig. 1 showing the distribution of labelled nuclei in cells of the root cap initials below the quiescent center and in initial cells of the stele and cortex bordering on unlabelled cells of the quiescent center. Stained nucleoli in unlabelled nuclei of cells of the quiescent center are evident. × 370.—Fig. 3. Median longitudinal section of a root apex supplied with tritiated thymidine for 64 hr. Note the smaller size of the quiescent center as compared to Fig. 1. × 160.—Fig. 4. Longitudinal section cut tangential to the quiescent center showing the lack of a clearly delimited region of unlabelled cells. × 190.

TABLE 1. *Measurements of the dimensions of the quiescent center and of the width of the root at the level of the quiescent center, taken from the most median longitudinal section*

Treatment[a]	Height of the quiescent center (μ)	Width of the quiescent center (μ)	Width of root (μ)	Width of quiescent center/ width of root
12–0	60–74	140	440	0.33
12–0	60–70	140	462	0.30
12–0	66–77	175	426	0.42
14–0	56	98	341	0.29
14–0	28–42	109	348	0.31
14–0	60–63	119	383	0.31
14–0	46	123	362	0.34
14–0	59	130	327	0.40
14–0	35–67	147	334	0.44
14–0	49–95	147	348	0.42
14–0	77–81	147	447	0.33
14–0	60–74	158	447	0.35
14–24	63–70	144	433	0.33
14–24	63–105	154	490	0.31
14–24	63–98	168	483	0.35
14–24	70–91	168	518	0.32
48–0	35–42	144	420	0.34
48–0	32–80	151	483	0.31
64–0	32–35	46	334	0.14
64–0	35–84	60	462	0.13
64–0	46–56	81	489	0.17
96–0	35–49	66	404	0.16
96–0	quiescent center lacking		419	—
120–0	quiescent center lacking		426	—

[a] Hours in tritiated thymidine followed by hr in fresh medium before fixation.

the quiescent center are listed for roots maintained in tritiated thymidine for various treatment periods. The ratio of the width of the quiescent center to the width of the root shows that the quiescent center spans 29–44 % of the width of the root for roots supplied tritiated thymidine for 12, 14, and 48 hr. For roots supplied tritiated thymidine for 64 and 96 hr, the quiescent center included only 13–17 % of the width of the root. The variation in height of the quiescent center for any given treatment resulted from the fact that the proximal boundary fluctuated over its surface. In the cultured roots maintained for 64 hr in tritiated thymidine, the quiescent center was markedly reduced (Fig. 3).

Of the two roots supplied tritiated thymidine for 96 hr, one had no distinct ouiescent center. Only a few scattered cells at the distal pole of the stele and cortex were unlabelled. The other root had a quiescent center comparable in size to that found in roots supplied with tritiated thymidine for 64 hr. In the one root which was supplied tritiated thymidine for 120 hr, all the cells of the quiescent center were labelled. The cellular patterns in these roots were not disrupted.

In these experiments, serial sections of each root were analyzed in order to avoid overlooking the presence of the quiescent center. Figure 4 shows a tangential section cut 100 μ away from the median section. Such a section may appear to be median longitudinal, yet this one clearly does not show a quiescent center. It was cut through the root proper and part of the root cap, and is characteristic of the region immediately tangential to the quiescent center with respect to the distribution of labelled nuclei. Serial sections enable one to examine the three-dimensional characteristics of the quiescent center which may not be otherwise obvious from studying merely one section.

DISCUSSION—In order to plan an experiment which will clearly demonstrate the presence of a quiescent center in a developing root, one must give careful consideration to the length of time a labelled precursor is available and the duration of cell cycles in the various regions of the apical meristem. Clowes (1961a, 1962, 1965), Clowes and Hall (1962), and Thompson and Clowes (1968) found that the average duration of the cell cycle in the central cylinder and cortex immediately proximal to the quiescent center in roots of *Zea mays*, *Sinapis alba*, *Vicia faba*, and *Allium sativum* ranged between 22–55 hr, whereas the average duration of the cycle for root cap initials ranged between 12–53 hr. Yet, the average duration of the cell cycle in the quiescent center of the same four species ranged between 165–520 hr. Since the quiescent center is defined as those cells of the apical meristem of the root proper which show low rates of incorporation of labelled precursors of DNA synthesis, the labelled precursor should be available long enough to allow these cells to be sharply delimited n autoradiographs. Therefore, providing the labelled precursor for 12–14 hr allows the precursor to be available to the cells located immediately proximal and distal to the quiescent center for a major portion of their cell cycle. At the same time, only a small percentage of the cells of the quiescent center would be labelled since the labelled precursor would be available for only a small portion of their cycle. Stein and Quastler (1964) reported that only a few of the cells in seedling roots of *Zea mays* were labelled after immersion in a tritiated thymidine solution for 4 hr. Their results indicated either that the uptake time for tritiated thymidine was considerably greater than 4 hr or that DNA synthesis was temporarily suppressed by the change in environment at the onset of the treatment. Therefore, experiments in which a labelled precursor is supplied for a short time will give results which are inconclusive and difficult to interpret.

Comparison of the dimensions of the quiescent center for roots maintained in tritiated thymidine for 12, 14, 48, and 64 hr shows that the apparent decrease in width was due to the incorporation of tritiated thymidine primarily by the cells located

adjacent to the cortical initials. This change might be caused by two factors. First, the nuclei of the cortical initials may have undergone β-radiation damage such that the cells of the quiescent center located adjacent to the cortical initials were subsequently activated into synthesizing DNA. Clowes (1961b) reported that roots of *Allium cepa*, supplied tritiated thymidine (1.9 c/mM) at a concentration of 20 μc/ml for 18 hr, underwent radiation damage, such that the cells of the quiescent center started synthesizing DNA 72 hr after the beginning of the treatment. Clowes (1961a, 1962) suggested that the sharp rise in the curve of labelled nuclei in the quiescent center at 36 hr for roots of *Zea mays* and *Sinapis alba* indicated that β-radiation damage was beginning to affect the cells. In our experiments, although the specific activity of the tritiated thymidine was higher, a much lower concentration of the isotope was used so that even with the extended exposure, damage by β-radiation should be minimized. In addition, the growth rate of the roots supplied with tritiated thymidine for 64 hr ranged between 20–30 mm per day, indicating that the tritiated thymidine did not adversely affect the growth of the roots for this treatment period.

The second factor involves the duration of the cell cycle in the various regions of the meristem. Cells located at the proximal boundaries of the quiescent center may have slightly different cycles than those located increasingly distant from the quiescent center or than those located within it. The manner in which the quiescent center was reduced—by the incorporation of tritiated thymidine into the nuclei of cells located adjacent to the cortical initials in the continued presence of a small, sharply delimited central region—indicated that the duration of cell cycles within it varied. There may be a gradient in the length of cell cycles such that progressively longer ones occur toward the central region of the quiescent center. Similar cell cycles within a specific region are not necessarily in phase. The few labeled cells in the central region of the quiescent center may be at a different stage of the cycle than adjacent ones, yet all may have cycles of similar duration.

All the experimental evidence demonstrating the presence of a quiescent center in the root proper shows that the cells utilize specific precursors of DNA and protein synthesis at low levels or not at all. In addition, they do not utilize non-specific precursors, such as sucrose and compounds derived from the utilization of carbon dioxide by the leaves, which would be involved in the formation of a wide range of compounds and in respiration. The cells of the columella, distal to the root cap initials, also show a low level of utilization of precursors of protein synthesis and compounds derived from the utilization of carbon dioxide. Yet the cells of the columella differ from those of the quiescent center in that tritiated thymidine is not utilized at all.

The presence of a quiescent center has been correlated with changes in the growth of roots under different environmental conditions. By autoradiography Wilcox (1962) observed a group of relatively inactive cells in the apices of first-order lateral roots of incense cedar. He examined the differences in the size and appearance of the initials in dormant roots and concluded that these differences were probably related to the ability of the root to resume growth. He suggested that the quiescent initials are probably important in the periodic renewal of growth in the root and perhaps also in coordinating subsequent growth activity. Clowes and Stewart (1967) pointed out that the inactive cells described by Wilcox belonged to the quiescent center and were not, in fact, initials.

Clowes and Stewart (1967) followed the recovery from dormancy, induced by cold treatment, of seedling roots of *Zea mays* by observing changes in cell patterns, by the labelling of nuclei with tritiated thymidine, and by determining the rates of mitosis. Their results indicated that cells of the quiescent center divide after the cold treatment, whereas previously active cells of the root cap, the stele, and the cortex cease dividing. Cells of the quiescent center stimulated to divide subsequently regenerated a new meristem. Though Clowes and Stewart (1967) stated that the quiescent center serves in recovery from dormancy, they noted that this function is not particularly advantageous to the plant, since the plant can replace roots easily.

One possible function of the quiescent center would relate to its direct or indirect role in determining vascular pattern. Some experimental findings indicate that the control of vascular pattern resides in the apical meristem. In experiments with roots of *Vicia faba*, Clowes (1953) observed a reduction in the number of protoxylem poles formed in the root after wedges of tissue had been surgically removed from the region of the apical meristem. As a control he noted that removal of pieces of tissue just above the apical meristem had no effect on tissue pattern. He suggested that excisions in the apical meristem which produced a reduction in the number of vascular strands also produced a decrease in the size of the meristem. Torrey (1955) observed that 0.5-mm excised root tips of *Pisum sativum* grown in culture produced vascular patterns differing in complexity from the original root from which they were derived. In further studies with cultured, isolated pea roots, Torrey (1957) reported a direct correlation between the number of strands formed and the diameter of the procambial cylinder at the level of pattern initiation, indicating that perhaps factors controlling the latter dimension were important in determining

the vascular arrangement. Wilcox (1962) noted changes in the number of protoxylem poles in individual roots of incense cedar during periods of changing growth activity. These changes were apparently unrelated to fluctuations in the dimension of the zone of apical initials or to changes in the size of zones adjacent to the apical initials. He suggested that the geometry of these regions was not the critical factor in determining vascular pattern.

Although the actual site within the apical meristem for controlling the expression of the vascular pattern is still unknown, the quiescent center or meristematic cells immediately proximal to it are implicated. This control might be exerted by the production of auxins, gibberellins, or cytokinins within the quiescent center. That the root tip is rich in these hormones has been reported. Auxin concentrations are highest in the root tips of *Avena* (Thimann, 1934–35) and pea (van Overbeek, 1939). That root tips are rich in cytokinins has been shown in sunflower (Kende, 1965; Weiss and Vaadia, 1965) and pea (Short and Torrey, 1970). Jones and Phillips (1966) reported that diffusates and extractions of 3–4 mm root tips of *Helianthus annuus* contained gibberellin-like substances. In addition, Sitton, Richmond, and Vaadia (1967) reported that incubation of 3–5 mm root tips of *Helianthus annuus* with C^{14}-mevalonate yielded an intermediate in gibberellin biosynthesis. The suggestion that there is a gradient in the lengths of cell cycles within the quiescent center fits well with the idea that there is a center of synthesis for a cell-division factor which is supra-optimal in the quiescent center itself, diffuses outwardly to an optimal concentration for stimulating cell division in the apical initials and then becomes limiting. Changing the effective levels of these hormones within the apical meristem of cultured roots, such that alterations in the structure and activity, or both, of the quiescent center occur, would be one method by which the function of the quiescent center could be studied.

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