The Plant Root and Its Environment

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edited by E. W. Carson

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Foreword

THE Southern Regional Education Board has been concerned with strengthening and expanding the opportunities in high-quality education in agriculture and its related sciences. This effort has been carried on through the Council on Higher Education in the Agricultural Sciences founded in 1956. The council has served effectively in formulating policy and providing general guidance for program development.

Currently, the council is guiding a five-year Southern Regional Education Board project supported by the W. K. Kellogg Foundation designed to advance land-grant institutions, agriculture, and agricultural sciences. To guide the planning activities involved in this project effectively, the council membership was organized into four subcommittees, with each assigned a particular area of responsibility. The council subcommittee no. 3, headed by Dr. Ben T. Lanham, Jr., Vice-President for Research, Auburn University, studied the needs and opportunities for advancing scientific knowledge in the land-grant institutions in the region.

The Institute on the Plant Root and Its Environment was a recommendation of this subcommittee, approved by the council for implementation. The concept of the institute was fully supported by the deans of agriculture and directors of the experiment stations of the region as an effective means of further developing faculty competence in an essential area of soil and plant agriculture. Scientists from twenty land-grant colleges of agriculture and the United States Department of Agriculture served as a planning committee to revise the proposed program prepared by Dr. Lanham's committee and plan this institute. This publication of the proceedings of the institute is being made available so that participants and other scientists in the region can use it to expand their programs of research and instruction.

T. J. HORNE, *Project Director*
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Preface

THE two-week institute from which this book resulted was intended to present the existing knowledge of the plant root, its functions and processes, and the many environmental factors that influence these functions. In addition, the institute was designed to assist individuals and institutions in evaluating their own research and educational efforts in these areas.

The large regional planning committee realized that even in a concentrated two-week program not all aspects of the root and its environment could be adequately covered. Therefore, the committee planned a program to cover those pertinent topics, e.g., *Rhizobia*, not already adequately covered by an institute, symposium, or publication. Nevertheless some duplication of material covered elsewhere was necessary to give the essential background and the cohesiveness to provide a self-contained program.

The presentations were before senior scientists and graduate students with very broad and diverse backgrounds of experiences and education. Thus, it is our hope that this publication will be useful in upper division and graduate courses in soils and plant nutrition where students of diverse training are found.

Not all that is desirable can be accomplished and often no more than is feasible. Nevertheless, we do regret the impossibility of including a complete transcript of all discussions and seminars. For example, informal seminars were conducted on Root–Root Interactions, Forest Pathology, Microbial Antagonisms in the Soil, Taxonomy and Morphology of the Genus *Endogone*, Root Exudations, Research Techniques, and Nutrient Supply. In addition, twenty hours of discussion were recorded, transcribed, and studied for use in these proceedings. One cannot convey the excitement of such informal sessions or do justice to the ideas presented and formulated in these discussions.

As with any undertaking of this magnitude, many individuals and agencies make significant contributions, and recognition of all involved is impossible. However, I would like to express appreciation to T.J. Horne of SREB, to the twenty-three members of the SREB Regional Planning Committee, and to the following from Virginia Polytechnic Institute and State University: M. E. Austin, Associate Professor of Horticulture, and W. H. Wills, Professor of Plant Pathology, for their service on the local planning committee; T. B. Hutcheson, Jr., Head, Agronomy Department, H. B. Couch, Head, Plant Pathology and Physiology Department, P. H. Massey, Associate Dean of Agronomic and Plant Science Division, and J. E. Martin, Dean of the College of Agriculture and Life Sciences, for their administrative support. I also wish to express my sincere thanks to my wife for her understanding and many hours of assistance throughout the institute and preparation of this publication.

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Abbreviations and Symbols

The most commonly used abbreviations and symbols are given here. Some may have other uses, and the less frequently used are described when they first appear in a chapter.

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a—activity coefficient
ads—adsorbed
Å—Angstrom
atm—atmosphere
ATP—adenosine triphosphate
avg.—average
C—Celsius, e.g., 10C = 10 degrees C
CEC—cation exchange capacity
coef—coefficient
cpm—counts per minute
df—degrees of freedom
deg—degree
diam—diameter
dry wt—dry weight
EDTA—ethylenediaminetetraacetic acid
eq—chemical equivalent, may be combined, e.g., meq
ft-c—foot-candle
g—gram
ha—hectare
hr—hour
HSD—honesty significant difference (Tukey's test)
kg—kilogram
l—liter
LSD—least significant difference
m—meter; mili-, 10^{-3}, may be combined
mm—millimeter
M—molar, moles/liter
meq—milliequivalent
ml—milliliter
mV—millivolt(s)
n—nano, 10^{-9}, may be combined
N—Newton (when not nitrogen)
N—normality
NAD—nicotinamide adinine dinucleotide
NADP—nicotinamide adinine dinucleotide phosphate
NAR—net assimilation rate ($mg \cdot dm^2$ leaves $\cdot$ unit $time^{-1}$)
ns—not significant
ODR—oxygen diffusion rate
OAA—oxaloactate
P—partial pressure; pressure; pressure potential
PEP—phosphoenol pyrurate
ppb—parts per billion
ppm—parts per million
r—radius
R—resistance
RGR—relative growth rate ($g \cdot 100g^{-1} \cdot$ unit $time^{-1}$)
S:R—shoot to root ratio
var.—variety
γ—surface tension
η—viscosity
Δ—difference
μ—micro-, 10^{-6}, micron, may be combined, e.g., μeq
ρ—density
σ—reflection coefficient
τ—matric potential
ψ—water potential
ω—osmotic potential

Contents

Part I

Biological Aspects of the Root and Its Environment

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1. Root Morphology

John M. Byrne

THE purpose of this presentation is not to review in detail the field of root anatomy. It is my intention to place our current knowledge or lack of it into a historical perspective, to point out controversies concerning the organization and function of the root meristem, and to emphasize from a plant anatomist's point of view problems concerning root growth and development that await solution.

I. ANGIOSPERM ROOT APEX, 1868–1900

Hanstein (1868, 1870) and his protégé Reinke (1871) were the first to investigate the apical organization of angiosperm roots. Both men realized that the meristem of the angiosperm root was multicellular rather than a single apical cell as Nageli (1858) had described for vascular cryptograms. After intense investigations of both shoot and root meristems, in which he used extremely crude histological methods, Hanstein (1869, 1870) proposed the histogen theory of apical organization. Early workers in the field of plant anatomy utilized this theory exclusively, although it was based on the misconception that an obligate histogenic relationship exists between the initial layers (histogens) and the mature tissue in shoot and root apices. As recently as the 1950's several workers in both the United States and Europe were using the histogen theory for the interpretation of root organization, even though the concept had been discredited for the shoot apex (Schmidt, 1924).

Hanstein's (1868, 1870) and Reinke's (1871) publications stimulated a great deal of interest in the structural aspects of the root apex. From 1874 to 1900 a massive research effort was made on the angiosperm root apex (Fleisher, 1874; Hegelmaier, 1874; Janczewski, 1874; Eriksson, 1876;

Holle, 1876; Traub, 1876; Flahault, 1878; Schwendener, 1882). Many of these studies were broad surveys of plant taxa; their major goals were to describe the apical organization in many taxa and to classify each species into structural types. Five types of apical organization were described for angiosperm roots:

1. Four groups of initials (histogens), one each for the central cylinder, cortex, rootcap, and epidermis; e.g., *Hydrocharis*, *Pistia*
2. Three groups of initials (histogens), one each for the central cylinder and the rootcap and a common group for the cortex and the epidermis; e.g., most monocotyledons
3. Three groups of initials (histogens), one each for the central cylinder and the cortex and a common group for the rootcap and the epidermis; e.g., most dicotyledons
4. Two groups of initials (histogens), one for the central cylinder and a common group of initials for the cortex, epidermis, and rootcap; e.g., *Gossypium* and *Hibiscus*
5. One group of ill-defined initials (histogens), the transversal type with all tissues sharing a common origin; e.g., Fabaceae.

These early studies, reviewed by Kroll (1912) and Schüepp (1926), account for the bulk of information available on the structure of root apices. It should be noted that none of the authors cited above included growth conditions in their papers.

II. ANGIOSPERM ROOT APEX, 1900–1971

The structural aspects of the root apex have received relatively little attention in the past 70 years. Instead of broad surveys, most of the more recent anatomical investigations have been intense developmental studies of one or only a few species. Also, many of the more recent investigations have focused on tissue differentiation rather than apical organization of the root (Young, 1933; Hayward, 1938; Esau, 1940, 1943a; Guttenberg, 1940; Cheadle, 1944; Goodwin and Stepka, 1945; Williams, 1947; Heimsch, 1951; Popham, 1955; Peterson, 1967). In the United States, because of the influence of Esau—who, in turn, was probably influenced by Soueges (1934–39)—the histogen terminology and rationale became less popular. Esau prefers a topographic approach in describing the apical organization of roots; i.e., she proposes that the *promeristem* (1953), or *protomeristem* (1967), be defined as the initials and their most recent derivatives. The difference between these two terms is not conceptual but lexicographical (Jackson, 1953). Also, she names each initial group of tiers or initials according to the mature tissue derived from the group. It will be pointed out later that recent data have placed limitations on this approach to the structure and function of the root apex.

A. Ontogenetic Changes in the Root Apex

Recently, Guttenberg (1947, 1960, 1964) and his students (Guttenberg *et al.*, 1955) have revitalized interest in the root apex. Following a detailed investigation of the embryogeny and subsequent growth of the root in several species, they reported that ontogenetic changes occur in the apical organization of some roots such as *Anoda* and *Helianthus*. As described by Guttenberg, the dormant embryonic roots of these plants have a layered or "closed" pattern of apical organization. During growth, however, certain cells, which are histogenically related to the cortex, participate in rootcap formation. The result of this activity is that the apex becomes "open" during growth and resembles a transversal meristem.

In addition to reporting ontogenetic changes in some roots, Guttenberg has proposed that the promeristem (*urmeristem*) of a root consists of only one cell (*Zentralzelle*) or, at the most, a few cells (Guttenberg, 1947, 1960, 1964). According to his interpretation the *Zentralzelle* behaves like a formative center which may from time to time renew the initials (histogens) of mature tissues. Guttenberg's proposal of the existence of central cells was diametrically opposed to the view held by most plant anatomists and resulted in widespread criticism (Clowes, 1953, 1954, 1958, 1961).

Clowes (1950), working with *Fagus*, also reported histogenic involvement of the cortex with the rootcap in growing beech roots. However, Clowes's interpretation of the promeristem differed from that of Guttenberg. Making use of Schüepp's (1917) *Körper-Kappe* concept to analyze planes of divisions within the root apex, Clowes proposed that the promeristem of *Fagus* is quite large. Up to this time there had been little use made of the *Körper-Kappe* analysis. Schüepp's central idea was that the orientation of the T (or Y) divisions in the root apex could be used to determine the ontogenic relationship of root tissues. Basically, all tissues with the T divisions oriented toward the apex belong to the *Körper* (body), and tissues with T divisions oriented away from the apex are related to the *Kappe* (cap).

In two subsequent investigations Clowes (1953, 1954), utilizing both the *Körper-Kappe* analysis and surgical techniques, strengthened his contention that the promeristem in roots is quite large. Also, more importantly, Clowes (1954) suggested that cell divisions rarely occur within what he originally termed the *minimal construction center* of the root apex. He quickly investigated further the idea that a nonmeristematic group of cells exists within the meristem of the root.

B. Quiescent Center

Using both radioactive labels and more sophisticated staining techniques, Clowes (1956a, 1956b) presented direct evidence for the existence of a hemispherically shaped quiescent center in the roots of *Zea*, *Vicia*, and *Allium*. Other investigators (Rabideau and Mericle, 1953) had earlier published an autoradiograph of a corn root, which showed a zone of cells that did not assimilate $^{14}CO_2$; these investigators did not comment upon or point out the lack of label in their material. Clowes, unaware of the Rabideau and Mericle publication, was the first to recognize the significance of the unlabeled area and thus was the first to discover the quiescent center.

Initially many people were reluctant to accept the presence of a group of mitotically inactive cells in the root apex. This skepticism concerning the validity of the quiescent center was probably due to the fact that a similar region in the shoot apex, the *méristéme d'attent* (Buvat, 1952), had been discredited (Partanen and Gifford, 1958; Clowes, 1959b).

Clowes and his associates (Clowes, 1956a, 1956b, 1958, 1959a, 1959c, 1963, 1967; Clowes and Juniper, 1964; Hall, Lajtha, and Clowes, 1962; Thompson and Clowes, 1968) have demonstrated conclusively the presence of a quiescent center and, in some cases, have experimented with the region in *Sinapis*, *Pistia*, *Eichornia*, *Zea*, *Vicia*, and *Allium*. Other investigators have either discovered or confirmed the existence of a quiescent center in *Allium* and *Vicia* (Jensen, 1958); *Euphorbia* (Raju *et al.* 1964); *Glycine* (Miksche and Greenwood, 1966); cultured *Lycopersicon* (Thomas, 1967); cultured *Convolvulus* (Phillips and Torrey, 1970); *Abutilon* (Byrne, 1969); and *Malva* (Byrne and Heimsch, 1970b).

In view of the presence of the quiescent center in every angiosperm root thus far investigated, several basic questions, some of which remain unanswered, have arisen concerning quiescence.

First, when does the quiescent center appear in seedling roots? Depending upon the species, the quiescent center appears a few days after germination (Clowes, 1958) or is present in the dormant seed (Clowes, 1961; Byrne and Heimsch, 1970b). The latter is more difficult to prove because many nuclei in the dormant embryonic root apex may be at the 4C level of DNA synthesis (Avanzi *et al.*, 1963; Davidson, 1966).

Second, how big is the quiescent center? All the evidence suggests that several hundred cells may be quiescent and that the number is proportional to the size of the root apex. Clowes (1961) suggested that several thousand cells may be quiescent in very large apices; and Byrne and