# ORIGINS OF ADVENTITIOUS ROOTS

B. E. HAISSIG
USDA-Forest Service
North Central Forest Experiment Station
Institute of Forest Genetics, Rhinelander, Wisconsin 54501

(Received for publication 13 September 1973)

## ABSTRACT

The paper reviews and interprets selected literature concerning the locale of formation, time of development, histological origins, and histological and cytological changes that occur during adventitious root initiation and development in twigs and branches of gymnosperms and dicotyledons.

## INTRODUCTION

The locale of formation, time of development, histological origins, and histological and cytological changes that occur during adventitious root initiation and development have been studied for years, though the information derived from such investigations lacks review and interpretation. The present paper compiles results from, and interprets, selected literature concerning the origins of adventitious roots that arise in twigs and branches of gymnosperms and dicotyledons. The review avoids literature concerning modification of rooting by applied hormones, except as required in the interpretation of rooting of untreated material. In general, the review was limited to subject matter that relates well to physiological investigations of the fundamental processes underlying adventitious root initiation.

## TERMINOLOGY

"Adventitious" applies to roots that arise in twigs, branches, leaves, aerial stems, underground stems, and old roots, as opposed to roots that originate from the embryo, either directly or as branches of the primary root (Esau, 1953; Hayward, 1938). Adventitious roots of gymnosperms and dicotyledons arise either from preformed root primordia developed during branch or stem formation, or in attached twigs (layers) or severed twigs and leaves (cuttings) that would not have differentiated root primordia during normal development. The latter type of root primordium will be called "induced" (Girouard, 1967) to distinguish it from the preformed type.

In the present paper, "root primordium" refers to a cellular aggregation in its earliest stages of differentiation into an adventitious root (Esau, 1960). "Primordium initiation" refers to dedifferentiation that directly yields the root primordium initial cells;[1] "primordium development" refers to division of the initial cells, and of cells adjacent to the primordium that may dedifferentiate and begin division after the initial cells appear; "primordium differentiation" refers to morphological differentiation of daughter cells that were produced during primordium development, that is, to differentiation of cells produced by division of initial cells or cells adjacent to a developing primordium. "Dedifferentiation" and "initial" have been defined elsewhere (Esau, 1960).

Primordium development precedes morphological differentiation, and then occurs concurrently with it. Morphological differentiation may arbitrarily be defined to begin when ordered (rather than apparently random) planes of cell division occur such that the planes of division yield a characteristic dome-shaped cellular aggregate. Physiological differentiation probably occurs much earlier, possibly at the start of primordium development, but it cannot be as readily detected as morphological differentiation.

## LOCALE OF INITIATION

### *Induced Primordia*

Induced root primordia most commonly arise near the base of cuttings (Mahlstede and Watson, 1952; Mullan, 1931; Smith, 1936; Taylor, 1926) as the result of stimulation from auxin, e.g., indole-3-acetic acid (IAA), and other factors that migrate to the basal cut surfaces where polarity changed (Leopold, 1964; Went, 1929; 1934).[2] Such primordia have originated one-tenth to 3 millimeters above the cut surface (Carlson, 1929; Connard and Zimmerman, 1931; Stangler, 1956) or at somewhat greater heights (Smith, 1936; Stangler, 1956). Induced primordia also frequently develop in callus tissue formed from the base of cuttings (Satoo, 1956).

Bannan (1942b) has shown that naturally-layered branches of white and black spruce

---

[1] In the strictest sense, primordium initiation does not begin with cellular dedifferentiation that directly yields the primordium initials. Rather, cellular dedifferentiation constitutes an event that marks the conclusion of one developmental phase and the onset of another, divergent developmental phase. The concluded phase consists of normal ontogeny that yields the progenitors of the primordium initial cells, and all other cells that were not generated by division of the initials but which become part of the adventitious root. The divergent developmental course consists of the whole of development of the adventitious root.

Formation of the adventitious root assumes increasing complexity, in terms of describing phases of development, because the progenitors of the primordium initials may be either "immediate" or "distant." Immediate progenitors may be considered to exist in certain plants, such as those that develop preformed root primordia or whose cuttings readily initiate induced primordia. However, immediate progenitors apparently do not exist in, for example, some difficult-to-root cuttings (see Discussion). In such instances, immediate progenitors of the primordium initials may arise only in callus tissue developed after the pattern of normal ontogeny has been altered in preparation of the cutting or air-layer. Nonetheless, dedifferentiation of immediate progenitors apparently occurs, even if those immediate progenitors arose by a circuitous developmental mode from progenitors much more distant in terms of cellular type and time. Thus, dedifferentiation of immediate progenitors to yield the primordium initial forms a visible marker, and timing point, to and from which anatomical and physiological studies may be precisely keyed.

[2] Vöchtung (1884) introduced the concept of polarity, and Bloch (1943) defined it as: "Any internal asymmetrical axiate condition or any situation where two ends or surfaces in a living system react unequally or are substantially different."

and balsam fir develop root primordia in connection with dormant buds, whereas primordia in larch branches arise near dead dwarf shoots. Juniper branches, though not in contact with soil, sometimes develop root primordia on their undersides (Bannan, 1942a). These locations closely resemble those where preformed root primordia situate.

### *Preformed Primordia*

Esau (1953) stated that adventitious root primordia initiate in both nodes and internodes. Preformed primordia initiate most often in nodes (Datta and Majumdar, 1943), as exemplified by rockspray cotoneaster (Clark, 1933), Japanese honeysuckle (Sandison, 1934), and brittle willow (Carlson, 1938; Haissig, 1970a). Certain species, such as Lombardy poplar (Shapiro, 1958) depart from the nodal arrangement and initiate preformed primordia in longitudinal files between nodes.

Knight (1809) first described a peculiar type of "rough excrescence" on stems of apple trees. These growths proved to be clusters of preformed primordia or partially elongated roots that developed completely when covered with "mould". Borthwick (1905) located similar "papilla-like projections" in other tree species. The projections covered young and old shoots of Lawson false-cypress and giant arborvitae, and were arranged in irregular fashion on maple stems.

Swingle (1925) examined 500 varieties of apple, 180 of which contained the rough excrescences that Swingle termed "burr-knots". Apple burr-knots were found most frequently on the undersides of branches, near buds, or near branch bases (Swingle, 1925, 1926). The positioning of burr-knots, therefore, is akin to that of other preformed primordia and to induced primordia in naturally-layered branches. Burr-knots, however, contain from 1 to over 100 primordia or partially developed roots (Swingle, 1929). Other preformed root primordia occur singly, or in ranks or files, but not in clusters. Swingle did not speculate on why apple burr-knots might contain so many preformed root primordia, but it would be interesting to know what localized influence stimulated their formation, and whether it relates to the formation of dormant buds (Dermen, 1948; MacDaniels, 1953).

## TIME OF INITIATION

### *Induced Primordia*

It has been difficult to ascertain when induced primordia initiate and how long it takes for development, even in apparently uniform groups of cuttings, because these primordia usually do not initiate at the same time or at predictable sites. Thus, few workers have followed the course of induced primordia from dedifferentiation through differentiation. Use of acridine orange staining in conjunction with fluorescence microscopy (Gramberg, 1971) should markedly aid future studies of initiation and development.

Root primordia initiation has been known to take months (or not even occur) in some difficult-to-root woody cuttings, whereas it has begun within a few days in more easily rooted cuttings. Stangler (1956) traced primordia initiation in cuttings of clove pink carnation and bourbon tearose. In those species initials organized within 5 to 7 days after cuttings were planted. The first root tissues developed by or shortly after the twelfth day.

It remains unclear whether primordium initiation was delayed in all cuttings that required long rooting periods, or whether in some instances differentiation and, therefore, emergence were slow.

### *Preformed Primordia*

Initiation, development, and differentiation of preformed primordia have been easily studied because they occur with regularity in predictable locations. Trécul (1846) described preformed root primordia in yellowstem weeping willow as having initiated in 2- or rarely, in 1-year-old twigs. Vöchting (1884) thought preformed root primordia remarkable and was dismayed that Trécul's work, though somewhat inaccurate, had been ignored. Trécul erred with regard to the time at which preformed primordia initiated. In yellowstem weeping willow, Vöchting found primordia in 3- to 4-month-old twigs. He suggested that they might have initiated even earlier. Carlson (1938) has shown that, as Vöchting imagined, root primordia initiate in June within the lowest nodes of brittle willow shoots, and are present in each node except those near the twig apex by late autumn. Primordia initiate in the fourth node below the terminal leaf cluster of brittle willows grown in a controlled environment (Haissig, 1970a). In other species, such as Lombardy poplar (Shapiro, 1958), apple (Knight, 1809; Swingle, 1927), and bitter nightshade (Terras, 1900), primordia have initiated during the first or second year of twig growth. Development of primordia has depended greatly upon environment.

## HISTOLOGICAL ORIGINS

### *General Considerations*

De Bary (1884), Lemaire (1886), and Van Tieghem and Douliot (1888) described the histological origins and placement of root primordia. These authors placed primordia initiation near the vascular system, with initials located in the pericycle,[3] phloem parenchyma, or cambium, depending on stem age. More recently, Priestly and Swingle (1929) fixed the site of all primordium initiation near rays. Root primordia have initiated most often near developing vascular tissues, with primordia in young stems initiated at the edges of the vascular system, and those in old stems initiated from the cambium (Esau, 1953 and literature cited therein). Advancing age of tissues has for unknown reasons greatly decreased their ability to initiate roots (Hitchcock and Zimmerman, 1931, 1932; Hough, 1953; Zimmermann, 1926a, 1926b).

### *Induced Primordia*

Induced root primordia have initiated in a wide range of tissues. Buds (Sudds, 1934a, 1934b; Swartley, 1943), epidermis (McVeigh, 1938), epidermis and cortex (Wilson, 1927), pericycle (Carlson, 1929; McMartin, 1933; Stangler, 1956), phloem (Mahlstede and Watson, 1952; Satoo, 1952, 1955, 1956), cambium (Satoo, 1956; Smith, 1925, 1928, 1936; Taylor, 1926), xylem (Corbett, 1897), pith (Connard and Zimmerman, 1931), parenchyma (Naylor and Johnson, 1937; Naylor and Sperry, 1938; Smith, 1942), and other tissues contain cells (parenchyma or cambium) capable of dedifferentiation and, therefore, root primordia initiation. Cambium, phloem, and pericycle have most often been observed as the seats of primordia initiation, whereas cortex, pith, and xylem have been least important.

Root primordia, as indicated above, have most frequently been induced to initiate adjacent to or within vascular systems of twigs, petioles, and laminae. Such primordia

---

[3] Pericycle was often considered as a specific tissue located between the endodermis and vascular system; however, Esau (1943) showed that pericycle is the earliest primary phloem. Herein, the term pericycle is used as it was by the authors cited.

often initiate near or within rays (Bannan, 1941, 1942a, 1942b; Mahlstede and Watson, 1952; Satoo, 1954, 1956; Yim, 1962a, 1962b), especially at the edges of vascular bundles where fascicular cambium touches rays (Carlson, 1933; Hartsema, 1924; Smith, 1925, 1936). Induced root primordia have also initiated in association with leaf traces (Delisle, 1939; Naylor and Johnson, 1937; Satoo, 1952, 1956), and bud or branch traces (Satoo, 1956).

Priestly and Swingle (1929) indicated that root primordia frequently initiate near vascular elements because of the good available nutrient supply. Hormone supply may also determine favourable sites.

Root primordia also initiate in tissue developed at the wounded basal surfaces of cuttings and layers. Such "wound callus", or simply "callus" (Simon, 1907) was considered by Balfour (1913) as important in root initiation because its cells were "undifferentiated" and capable of division. Actually, callus development by cuttings has not assured root initiation.

Cuttings from woody plants, especially difficult-to-root species, have initiated most root primordia (when they did so) within basal callus tissue. Satoo (1956) studied 30 species of woody plants; roots initiated very often in callus developed by fir and spruce cuttings. Primordia also initiated frequently in callus of cuttings from species such as *Cryptomeria,* false-arbovitae, baldcypress, yew, and *Torreya.* In pine cuttings almost all primordia initiated within callus tissue (Satoo, 1952, 1955).

Satoo (1956) stated that in coniferous cuttings basal callus developed initially from cambial and phloem cells, and later was enlarged by divisions of pith and cortical cells. Xylem elements then differentiated within the callus in connection with stem xylem. Phloem cells initiated root primordia before cambium developed within the callus. A somewhat different pattern of callus development and root initiation in cuttings of a conifer, slash pine, has been described by Mergen and Simpson (1964). Callus originated from pith and enlarged by divisions of stem cambium and phloem. Cambium produced within the callus cut off xylem cells centripetally, and root primordia initiated within centrifugally developing phloem cells. Reines and McAlpine (1959), in having described similar callus development by slash pine cuttings, noted that massive callus contained disorientated vascular tissue and initiated no root primordia. Few other reports have dealt with the origins and vascularization of basal callus tissue from cuttings, or initiation of root primordia within it.

### *Preformed Primordia*

According to Swingle (1927), Van der Lek first noted that preformed root primordia often initiate near leaf traces, branch traces, and medullary rays. Indeed, a distinct relationship between placement of these primordia and those particular vascular structures has been shown. Bud (Clark, 1933; Wolfe, 1934) or branch gaps (Swingle, 1927), leaf gaps (Carlson, 1938; Swingle, 1927), and medullary rays (Borthwick, 1905) are frequently sites of initiation for preformed primordia. When such primordia initiate in medullary rays, they are often located where cambium passes across rays into adjacent vascular bundles (Datta and Majumdar, 1943; Terras, 1900) or, less frequently, where rays abut cambium (Borthwick, 1905).

As can be surmised from their sites of origin, preformed primordia have often initiated from cambial cells or ray parenchyma cells recently cut off from cambium. Other origins, such as pericycle (Sandison, 1934), have been less frequently reported.

Thus, preformed primordia seem to have shown less variation in sites of initiation than induced primordia. It is hazardous to make more precise statements about the origins of preformed primordia because few studies have concerned their initiation.

## INITIATION AND DEVELOPMENT

### *Induced Primordia*

Initiation and development of induced root primordia have been studied mostly in twigs, petioles, and laminae. For that reason, the following discussion does not include primordia initiated in callus tissue. Their initiation and development needs further description.

Hartsema (1924) observed strong movements of protoplasm before the first division of cells that were to become root initials. This action was accompanied by movement of the nucleus, formation of protoplasmic strands, and an increase in volume of protoplasm. Finally, the nuclei assumed central positions and cell division began. At other times, root initial cells have increased in size (Smith, 1942), nuclei have enlarged and assumed a central position (Carlson, 1929; Mahlstede and Watson, 1952; Stangler, 1956), nucleoli have become prominent (Carlson, 1929; Smith, 1925), and cytoplasm has increased in quantity or density (Carlson, 1929; Smith, 1925; Stangler, 1956). All or some of these changes are characteristic of future root initial cells prior to their first division.

These modifications have occurred, with a variable number of cells involved, within a few days after cuttings were planted (Stangler, 1956). From 1 to 3 cells divided first in some instances (Carlson, 1929; Naylor and Johnson, 1937; Stangler, 1956) and in others, groups of cells became root initials. The plane of these divisions has been radial or oblique (Carlson, 1929) or, more often, tangentially periclinal (Mahlstede and Watson, 1952; McVeigh, 1938; Smith, 1928; Stangler, 1956). Subsequent cell divisions have not seemed to follow any precise pattern.

Root primordia develop by division of the initial cells and their daughter cells, and by incorporation of adjacent cells. Pericycle and phloem cells (Carlson, 1929; Smith, 1936, 1942; Swartley, 1943), as well as recent cambial derivatives (Carlson, 1933; Stangler, 1956), have contributed to primordia by forming coverings over their advancing points (Stangler, 1956).

Advancing primordia may dispose of tissues blocking their path to the outside by either crushing or hydrolysis. Carlson (1929, 1933) found that endodermis was broken or hydrolyzed, whereas Smith (1928) stated that it was crushed. Cortex has also been hydrolyzed (Smith, 1936) or crushed (Bannan, 1941). Pond (1908) stated that emerging primordia are physically capable of crushing cortical cells, but he did not prove that crushing alone destroyed them.

Authors who considered that tissues ahead of primordia were hydrolyzed based their conclusions on the observations of pockets or cavities that surrounded apices of developing primordia. Smith (1942) felt that, because cavities developed well ahead of primordia, an enzyme could have been responsible for destruction of cortical cells. Bell and McCully (1970) have shown that cortical cells ahead of an advancing root tip separate (after enzymatic digestion of the middle lamella), collapse, and become devoid of proteins and nucleic acids. The foregoing hydrolytic activities require enzymes (pectinase, protease, nuclease, etc.). However, the complete enzymatic destruction of a cell requires one unique but undemonstrated process: hydrolysis of cellulose walls by a cellulase. Such cellulases probably exist (Bell and McCulley, 1970) but seem incapable of hydrolyzing collenchyma (Smith, 1936) or sclerenchyma (Mahlstede and Watson, 1952; Smith, 1928; Stangler, 1956). Thus, enzymic destruction of thin-walled cells probably occurs, but fibers and sclerids are more likely mechanically destroyed or displaced before substantial enzymic hydrolysis of cell contents occurs. Enzymes would seemingly hydrolyze cellular macromolecules, regardless of the method by which cell walls are disrupted, so that components of the macromolecules could be used to support development of the root or adjacent stem tissues.

Some research has suggested that bands of sclerenchyma in stems constitute so formidable an obstacle for emerging roots that the bands hinder root growth (Ciampi and Gellini, 1958, 1963; Goodin, 1965; Mahlstede and Watson, 1952). Indeed, it seems that sclerenchyma may physically hinder root emergence in some species or varieties of cuttings. However, the reduced root initiating potential of cuttings that contain large amounts of sclerenchyma bears investigation from a physiological perspective in order that it may be determined whether sclerenchyma, or patterns of development that lead to its formation, constitute a physiological rather than a physical barrier to root initiation, as appears likely in the majority of instances (Beakbane, 1961; Sachs, Loreti and De Bie, 1964). Such studies might indicate why advanced levels of differentiation in stems markedly decrease primordium initiating potential of the remaining meristematic or potentially meristematic cells. Advanced levels of differentiation reduce total meristematic potential of a stem, but a disproportionately large reduction occurs in the particular type of meristematic activity leading to primordium initiation.

Tissues begin to differentiate as primordia grow through cortex. Differentiation of the central cylinder usually begins first (Smith, 1925, 1928; Swartley, 1943), with promeristem, rootcap, and part of the vascular cylinder and cortex (Esau, 1960) developing before roots emerge (Smith, 1936, 1942; Swartley, 1943; Taylor, 1926). Tissue differentiation within the primordium involves derivatives of the initial and adjacent cells (Connard and Zimmerman, 1931; Stangler, 1956), but has not been fully described. The origin of root apices in woody plants has been reviewed (Romberger, 1963), and that publication should be consulted for additional information.

Vascular connection between root and stem takes place before or after tissue differentiation begins (Carlson, 1933). De Bary (1884) stated that the vascular system of a root connects with the nearest vascular bundle or bundles. Recent evidence supports that viewpoint (Naylor and Johnson, 1937; Smith, 1928, 1936). The vascular bridge between root and stem develops from tissue adjacent to the proximal end of a young root (Esau, 1960). Cambium (Connard and Zimmerman, 1931; Smith, 1928), pericycle (Stangler, 1956), xylem and phloem (Smith, 1936), and cortex (Wilson, 1927) may form part of the bridge. Vascular connections are usually complete before root emergence (Carlson, 1929).

Adventitious roots usually emerge at right angles to the long axis of a stem (Taylor, 1926) and then turn downward (Carlson, 1933), but some have emerged through the base of cuttings (Mahlstede and Watson, 1952). Roots that exit through the base of cuttings may do so because their horizontal course is physically blocked. However, physical obstacles are not a universal cause for deviation. Purslane roots turned downward after they penetrated about one-half of the cortex, and then followed a course through the base of cuttings (Connard and Zimmerman, 1931). No physical obstacles blocked their course; therefore, some chemical influence may have directed the path of emergence, as indicated by the latter authors' findings that purslane roots grew toward decaying pith, rather than away from or parallel with it as in normal emergence.

### *Preformed Primordia*

The first stages of preformed root primordia development parallel those of induced primordia. However, preformed primordia are subject to engulfment and crushing by radially-expanding adjacent tissue. These primordia remain abreast of surrounding tissue by elongating radially. In brittle willow, cambium adds cells to primordia at the same rate that secondary phloem expands (Carlson, 1950), and in cotoneaster, division and expansion of cells within the primordia causes elongation (Clark, 1933).

Differentiation may be very slow in preformed primordia in attached twigs. In some instances it has gone uncompleted for many years (Carlson, 1950), and usually requires at least 2 or 3 years (Shapiro, 1958; Swingle, 1927). Tissues have been shown to differentiate and unite with the main vascular system as do those of induced primordia (Terras, 1900), but little detailed study has been given this phase of preformed root differentiation. Even the youngest and least differentiated preformed primordia develop into roots under favorable conditions (Carlson, 1938, 1950; Clark, 1933). The process by which they emerge from the stem resembles that of roots developed from induced primordia (Carlson, 1950; Wolfe, 1934).

It has not been shown what mechanisms so effectively prevent or impede differentiation of preformed primordia and, on the other hand, what stimuli fully activate primordia under favorable conditions. Light, darkness, dormancy phenomena, and auxins play some but unclear roles (Shapiro, 1958).

## DISCUSSION

Several areas concerning anatomical aspects of primordium initiation, development, and differentiation require further study, as noted above. Of these areas, the following deserve special attention: 1) The entire process of root formation in callus tissue produced by cuttings, including origin of the callus, vascularization, and cambium formation; and primordium initiation, development, and differentiation; and 2) preformed root primordium initiation.

Root formation from callus tissue needs special attention because callus tissue appears to constitute the major source of potential root initial cells in cuttings obtained from many difficult-to-root species. Preformed primordia deserve more attention because they constitute a nearly ideal system for physiological investigations of adventitious root initiation (Haissig, 1970a, 1970b, 1971, 1972).

Much of the literature cited in this review indicates that adventitious roots most frequently, and most readily, initiate from cells immediately adjacent to immature xylem. The relation seems to apply even for those initials originated in callus tissue because vascularization of callus apparently occurs prior to or concomitant with primordium initiation. As a hypothesis, I interpret the anatomical relation between immature xylem and primordium initiation as follows.

Primordium initiation and development depends in part upon an auxin, such as IAA (Haissig, 1970b, 1971, 1972). Recent evidence suggests that living xylem either synthesizes auxin (Sheldrake, 1971) or transports auxin from the stem apex (Morris and

Kadir, 1972) or both. Thus, auxin supply probably accounts in part for the location of initials near immature xylem, as long as suitable cells occupy the sites adjacent to living xylem, and as long as the sites themselves exist.

The most suitable sites (areas in medullary rays immediately adjacent to vascular bundles) and cells (interfascicular parenchyma or cambium) disappear in woody stems during secondary tissue development. Normal development of the stem produces a vascular cylinder that engulfs vascular bundles and closes medullary rays. The only favorable sites that remain adjacent to immature xylem are occupied by the parenchyma in leaf gaps, which frequently give rise to root initials in stems that have undergone secondary tissue development.

Stem cambium also occupies a position adjacent to immature xylem, but observation indicates that stem cambium does not constitute a favorable site for primordium initiation. First, the high degree of differentiation of these cambial cells, and whatever factors maintain that degree of differentiation, may preclude the type of dedifferentiation necessary to produce initials. In any event, the formation of an initial by cambial cells involves a circuitous route of redifferentiation because initials usually form from isodiametric cells. Second, cambial cells are probably subject to precise regulation of auxin supply by a system that insures normal development of secondary xylem and phloem (Sheldrake, 1971 and references therein). In that instance, the proximity of cambium to immature xylem would not necessarily enhance prospects for initial formation in the cambium, and, in addition, the cambium may act as a physiological barrier for auxin transport from immature xylem to phloem and cortical cells. Indeed a distinct auxin gradient exists from immature xylem to cortex (Sheldrake, 1971), and tissues exterior to the stem cambium apparently do not constitute ideal sites for initial formation. Moreover, the probability for primordium initiation decreases with increasing distance of cells from immature xylem. Early investigators thus termed root primordium initiation an "endogenous" process.

The above interpretation aids in an understanding of the positions assumed by root primordia within cuttings. It also helps to explain why the position of root primordia changes with age of a stem, and why cuttings from woody plants seem intrinsically more difficult-to-root than cuttings from other species. Of course, other factors than those discussed probably enter into the anatomical-physiological relations that determine root primordium initiating capacity. For example, factors other than auxin probably determine sites of primordium initiation because tissues near developing xylem (interfascicular parenchyma, interfascicular cambium, etc.) show a greater root forming response to applied auxins than do other tissues, such as epidermis, cortex, and pith (Hamner, 1938). As noted earlier, both inorganic and organic nutrition probably account for part of the predisposition of certain cells to initiate root primordia. Then, too, auxin synergists also modify the rooting response.

## REFERENCES

BALFOUR, I. M. 1913: Problems of propagation. **J. Roy. Hort. Soc. 38:** 447-60.

BANNAN, M. W. 1941: Vascular rays and adventitious root formation in **Thuja occidentalis** L. **Amer. J. Bot., 28:** 457-63.

——— 1942a: Wood structure of the native Ontario species of **Juniperus. Amer. J. Bot., 29:** 245-252.

——— 1942b: Notes on the origin of adventitious roots in the native Ontario conifers. **Amer. J. Bot., 29:** 593-8.

BEAKBANE, A. B. 1961: Structure of the plant stem in relation to adventitious rooting. **Nature, London 192:** 954-5.

BELL, J. K. and McCULLEY, M. E. 1970: A histological study of lateral root initiation and development in **Zea mays. Protoplasma, 70:** 179-205.

BLOCH, R. 1943: The problems of polarity in plant morphogenesis. **Chron. Bot. 7:** 297-9.

BORTHWICK, A. W. 1905: The production of adventitious roots and their relation to bird's-eye formation (Maserholz) in the wood of various trees. **Notes Roy. Bot. Garden, Edinb., 4:** 15-36.

CARLSON, M. C. 1929: Origins of adventitious roots in coleus cuttings. **Bot. Gaz., 87:** 119-26.

——— 1933: Comparative anatomical studies of Dorothy Perkins and American pillar roses. I. Anatomy of canes. II. Origin and development of adventitious roots in cuttings. **Contr. Boyce Thompson Inst. Pl. Res., 5:** 313-30.

——— 1938: The formation of nodal adventitious roots in **Salix cordata. Amer. J. Bot., 25:** 721-5.

——— 1950: Nodal adventitious roots in willow stems of different ages. **Amer. J. Bot. 37:** 555-61.

CIAMPI, C. and GELLINI, R. 1958: Studio anatomico sui rapporti tra struttura e capacita di radicazione in talee di olivo. **Nuovo G. bot. ital. 65:** 417-24.

——— 1963: Insorgenza e sviluppo delle radici avventizie in **Olea europaea** L.: Importanza della struttura anatomica agli effetti dello sviluppo delle radichette. **Nuovo G. bot. ital., 70:** 62-74.

CLARK, W. A. 1933: Vegetative propagation in cotoneaster. **Trans. Bot. Soc. Edinb., 31:** 256-61.

CONNARD, M. H. and ZIMMERMAN, P. W. 1931: The origins of adventitious roots in cuttings of **Portulaca oleracea** L. **Contr. Boyce Thompson Inst. Pl. Res., 3:** 337-46.

CORBETT, L. C. 1897: The development of roots from cuttings. **Meehans' Monthly, 7:** 32-4.

DATTA, A. and MAJUMDAR, G. P. 1943: Root initiation in the adult axes of a few dicotyledonous species. **Proc. Indian Acad. Sci., B18:** 109-18.

De BARRY, A. 1884: "Comparative Anatomy of Phanerogams and Ferns." English Translation by F. O. Bower and D. H. Scott, Clarendon Press, Oxford.

DELISLE, A. L. 1939: Histological and anatomical changes induced by indole-acetic acid in rooting cuttings of **Pinus strobus. Amer. J. Bot., 26:** 245.

DERMEN, H. 1948: Chimeral apple sports and their propagation through adventitious buds. **J. Hered., 39:** 235-42.

ESAU, K. 1943: Origin and development of primary vascular tissues in seed plants. **Bot. Rev., 9:** 125-206.

——— 1953: "Plant Anatomy." John Wiley and Sons, N.Y.

——— 1960: "Anatomy of Seed Plants." John Wiley and Sons, N.Y.

GIROUARD, R. M. 1967: Initiation and development of adventitious roots in stem cuttings of **Hedera helix**. Anatomical studies of the juvenile growth phase. **Canad. J. Bot., 45:** 1877-81.

GOODIN, J. R. 1965: Anatomical changes associated with juvenile to mature growth phase transition in **Hedera. Nature, London, 208:** 504-5.

GRAMBERG, J. J. 1971: The first stages of the formation of adventitious roots in petioles of **Phaseolus vulgaris. Proc. K. ned. Akad. Wet., 74:** 42-5.

HAISSIG, B. E. 1970a: Preformed adventitious root initiation in brittle willows grown in a controlled environment. **Canad. J. Bot., 48:** 2309-12.

——— 1970b: Influences of indole-3-acetic acid on adventitious root primordia of brittle willow. **Planta, 95:** 27-35.

——— 1971: Influences of indole-3-acetic acid on incorporation of C-uridine by adventitious root primordia of brittle willow. **Bot. Gaz., 132:** 263-7.

——— 1972: Meristematic activity during adventitious root primordium development. Influences of endogenous auxin and applied gibberellic acid. **Plant Physiol., 49:** 886-92.

HAMNER, K. C. 1938: Histological responses of **Maribilis jalopa** to IAA. **Bot. Gaz. 99:** 912-54.

HAYWARD, H. E. 1938: "The Structure of Economic Plants." MacMillan Co., N.Y.

HARTSEMA, A. M. 1924: Anatomische und experimentella Untersuchungen über das Auftreten von Neubildungen an Blättern von **Begonia rex. Rec. Trav. Bot. ned., 23:** 305-61.

HITCHCOCK, A. E. and ZIMMERMAN, P. W. 1931: Rooting of greenwood cuttings as influenced by the age of tissue at the base. **Proc. Amer. Soc. hort. Sci., 27:** 136-8.

——— 1932: Relation of rooting response to age of tissue at the base of greenwood cuttings. **Contr. Boyce Thompson Inst. Pl. Res., 4:** 85-98.

HOUGH, W. S. 1953: Effects of parental age, location on the tree and age on rooting of Douglas-fir cuttings. **Univ. Brit. Col. For. Res. Cl. Res. Note 9.**

KNIGHT, T. A. 1809: On the origin and formation of roots. **Proc. Roy. Soc. Phil., Pt. 1,** pp. 169-76.

LEMAIRE, A. 1886: Recherches sur l'origine et le développement des racines latérales chez les dicotyledones. **Ann. Sci. nat. (Bot.), Series VII, 3:** 163-274.

LEOPOLD, A. C. 1964: The polarity of auxin transport. **Brookhaven Symposium in Biology, 16:** 218-34.

MacDANIELS, L. H. 1953: Anatomical basis of so-called adventitious buds in the apple. **N.Y. Agric. Exp. Sta. Mem. 325.**

MAHLSTEDE, J. P. and WATSON, D. P. 1952: An anatomical study of adventitious root development in stems of **Vaccinium corymbosum. Bot. Gaz., 113:** 279-85.

McMARTIN, A. 1933: Propagation from the leaf of **Acanthus. Trans. Bot. Soc. Edinb., 31:** 298-314.

McVEIGH, I. 1938: Regeneration in **Crassula multicava. Amer. J. Bot., 25:** 7-11.

MERGEN, F. and SIMPSON, B. A. 1964: Asexual propagation of **Pinus** by rooting needle fascicles. **Silvae Genet., 13:** 133-9.

MORRIS, D. A. and KADIR, G. C. 1972: Pathways of auxin transport in the intact pea seedling (**Pisum sativum** L.). **Planta, 107:** 171-82.

MULLAN, D. P. 1931: A note on the development of adventitious roots from the petioles of the leaves of some **Acanthaceae** and **Labiatae. J. Indian Bot. Soc., 10:** 167-8.

NAYLOR, E. and JOHNSON, B. 1937: A histological study of vegetative reproduction in **Saintpaulia ionantha. Amer. J. Bot. 24:** 673-8.

NAYLOR, E. and SPERRY, J. J. 1938: Vegetative reproduction in Chlorphytum elatum. **Amer. J. Bot., 25:** 695-9.

POND, R. H. 1908: Emergence of lateral roots. **Bot. Gaz. 46:** 410-21.

PRIESTLY, J. H. and SWINGLE, C. F. 1929: Vegetative propagation from the standpoint of plant anatomy. **U.S. Dept. Agric. Tech. Bull. 151.**

REINES, M. and McALPINE, R. G. 1959: The morphology of normal, callused, and rooted dwarf shoots of slash pine. **Bot. Gaz., 121:** 118-24.

ROMBERGER, J. A. 1963: Meristems, growth, and development in woody plants. **U.S. Dept. Agric. Tech. Bull. 1293.**

SACHS, R. M., LORETI, F., and DeBIE, J. 1964: Plant rooting studies indicate that sclerenchyma is not restricting factor. **Calif. Agric. 18:** 4-5.

SANDISON, S. 1934: Rooting of cuttings of **Lonicera japonica:** A preliminary account. **New Phytol., 33:** 211-7.

SATOO, S. 1952: Origin and development of adventitious roots in seedling cuttings of conifers. I. **Bull. Tokyo Univ. For., 43:** 59-81.

——— 1954: Origin and development of adventitious roots in cuttings of **Chamaecyparis obtusa. J. Jap. For. Soc., 36:** 355-9.

——— 1955: Origin and development of adventitious roots in seedling cuttings of conifers. II. **Bull. Tokyo Univ. For., 48:** 115-28.

——— 1956: Anatomical studies on the rooting of cuttings in coniferous species. **Bull. Tokyo Univ. For., 51:** 109-57.

SHAPIRO, S. 1958: The role of light in the growth of root primordia in the stems of lombardy poplar. pp. 445-65, **In** K. V. Thimann, (ed.), "Physiology of Forest Trees." Ronald Press Co., New York.

SHELDRAKE, A. R. 1971: Auxin in the cambium and its differentiating derivatives. **J. exp. Bot., 22:** 735-40.

SIMON, S. V. 1907: Experimentelle Untersuchungen über die Differenzierungsvorgänge im Callusgewebe von Holzpflanzen. **Jahrbuch für Wissenschaftliche Botanik. Berlin, 45:** 351-478.

SMITH, E. P. 1925: The origin of adventitious growths in coleus. **Trans. Bot. Soc. Edinb., 29:** 145-50.

——— 1928: A comparative study of the stem structure of the genus **Clematis**, with special reference to anatomical changes induced by vegetative propagation. **Trans. Roy. Soc. Edinb., 55:** 643-64.

SMITH, A. I. 1936: Adventitious roots in stem cuttings of **Begonia maculata** and **B. semperflorens**. **Amer. J. Bot., 23:** 511-15.

——— 1942: Adventitious roots in stem cuttings of **Tropaeolum majus** L. **Amer. J. Bot., 29:** 193-4.

STANGLER, B. B. 1956: Origin and development of adventitious roots in stem cuttings of chrysanthemum, carnation, and rose. **N.Y. Agric. Exp. Sta. Mem. 342.**

SUDDS, R. H. 1934a: A study of the morphological changes and the origin of roots in tip-layered cumberland black raspberry plants. **Proc. Amer. Soc. hort. Sci., 32:** 401-6.

——— 1934b: The origin of roots in several types of red and black raspberry stem cuttings. **Proc. Amer. Soc. hort. Sci., 33:** 380-85.

SWARTLEY, J. C. 1943: Adventitious root initiation in **Forsythia suspensa**. **Proc. Amer. Soc. hort. Sci., 43:** 301-6.

SWINGLE, C. F. 1925: Burr-knot of apple trees. Its relation to crowngall and to vegetative propagation. **J. Hered., 16:** 313-20.

——— 1926: The use of burr-knots in the vegetative propagation of apple varieties. **Proc. Amer. Soc. hort. Sci., 22:** 228-30.

——— 1927: Burrknot formations in relations to the vascular system of apple stem. **J. Agric. Res., 34:** 533-44.

——— 1929: A physiological study of rooting and callusing in apple and willow. **J. Agric. Res., 39:** 81-129.

TAYLOR, G. 1926: The origin of adventitious growths in **Acanthus montanus**. **Trans. Bot. Soc. Edinb., 29:** 291-6.

TERRAS, J. A. 1900: On the relation between lenticels and adventitious roots of **Solanum dulcamara**. **Trans. Bot. Soc. Edinb., 21:** 341-53.

TRÉCUL, A. 1846: Recherches sur l'origine des racines. **Ann. Sci. nat (Bot.), 6:** 303-45.

VAN TIEGHEM, P. and DOULIOT, H. 1888: Recherches comparatives sur l'origine des membres endogenes dans les plantes vasculaires. **Ann. Sci. nat. (Bot.), Series VII, 8:** 1-660.

VÔCHTING, H. von. 1884: "Über Organbildung im Pflanzenreich." Max Cohen and Son, Bonn.

WENT, F. W. 1929: On a substance causing root formation. **Proc. Ned. Acad. Wet., 32:** 35-9.

——— 1934: A test method for rhizocaline, the rootforming substances. **Proc. Ned. Acad. Wet, 37:** 445-55.

WILSON, C. L. 1927: Adventitious roots and shoots in an introduced weed. **Bull. Torrey Bot. Cl., 54:** 35-8.

WOLFE, F. 1934: Origin of adventitious roots in **Cotoneaster dammeri. Bot. Gaz. 95:** 686-94.

YIM, K. B. 1962a: On the rooting of the cuttings of two conifer species. **Korean For. J., 5:** 12-21.

——— 1962b: Physiological studies on rooting of pitch pine (**Pinus rigida** Mill.) cuttings. **Korean For. Exp. Sta. Res. Rep. 2:** 22-56.

ZIMMERMAN, P. W. 1926a: Vegetative plant propagation with special reference to cuttings. **Proc. Amer. Soc. hort. Sci., 1925:** 223-8.

——— 1926b: Important discoveries regarding root growth in cuttings. **Florists Exchange,** pp. 1357 and 1360.