ROOT SYSTEM MORPHOGENESIS

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INTRODUCTION

In a paper of this length, only the briefest overview of the subject matter will be possible. Emphasis will be on coniferous root systems, as conifers predominate in planting programmes around the world. However, seemingly useful evidence or indications from a wider field will be drawn on.

A few general points need to be made at the outset. The simplest root system is a difficult subject for study: it is normally concealed by soil, and the population of which it forms part is typically variable. Few scientists are able to command the resources necessary to generate data that lend themselves to rigorous statistical analysis.

Once a root system has been exposed, there remains the problem of describing it usefully. Detailed morphological description of even a young root system is a formidable task (Russell, 1977).

A root system is part of a larger organism. The full value of any individual biological study, no matter how conclusive, cannot be realised except in the context of whole plant morphogenesis (Wardlaw, 1968; Torrey, 1976). Anything that affects shoot growth and development can hardly fail to affect root morphogenesis, and *vice versa.*

Genes and environment are inseparable in their effects on plants in general and on root systems in particular. Every trait is inherited in that it will always be produced in a specific environment. With some traits, the expression of the genetic constitution is essentially similar under a wide range of environments, while others, often said to be determined by environmental factors, may vary widely with nutrition, water supply, photoperiod, etc. (Sinnott, 1960). Both types of trait are, in fact, inherited, and both are environmentally determined. In the former type, the genetic constitution has a relatively meagre repertoire of response to changes in the environment, whereas in the latter it may be very wide (Sinnott, 1960).

Although organisation in plants reflects the precisely controlled genetic programme that determines development, precise growth patterns are disrupted by exogenous, environmental factors (Hallé *et al.,* 1978), more in some species than in others (cf. Köstler, 1962).

It must also be remembered that a root system is never completed. Throughout the life of a tree, the apical meristems of roots and shoots continue, when non-dormant, to grow and form new tissues (Torrey and Feldman, 1977). Also, within limits, a root system is always responding to the vicissitudes of the environment, including climatic variation. Climate is not stable (Rosenberg, 1978), and variations occur from year to year, over periods of hundreds of millions of years, and on every time scale in between (Kerr, 1978). Variations over a period of a few years are of particular significance to root system morphogenesis: a root system developed during a sequence of relatively dry years may, on certain sites, be totally unsuited to a subsequent sequence of relatively wet years (cf. Stone *et al.,* 1954). The dynamic aspect of root systems adds to the difficulty of description and experimentation.

Interpretation of the literature poses a problem also, because of the scarcity of environmentally-oriented anatomical investigations (Byrne, 1974).

Organic form develops by growth, a term that has been defined by biologists in various ways, but which, for morphogenesis has as its most important feature permanent increase in volume of an organ or organism (Sinnott, 1960).

"Morphogenesis" has come to be the preferred term for the biological science concerned with the dynamic and causal aspect of organic form: it differs from morphology, physiology, and embryology, although it includes elements of all three (Sinnott, 1960). Morphogenesis deals with some of the most elusive and intractable phenomena in science (Sinnott, 1960).

PRIMARY ELEMENTS OF ROOT SYSTEM FORM

It seems logical to begin a consideration of root system development with the seed. The primary root develops from the embryonic root apex which is usually quite well developed by the time the seed is ripe (Clowes, 1961). In the gymnosperms and dicotyledons, the root system consists of the primary root and its variously branched lateral roots (Essau, 1960), sometimes supplemented by adventitious roots, i.e., those arising outside normal organogenetic sequences either from roots or from other organs (Stone and Stone, 1943; Haissig, 1974a).

The early stages of germination are similar in all seed plants (Ching, 1963, 1966; Krugman *et al.,* 1974). Germination consists of three overlapping processes: imbibitional absorption of water, which causes swelling; concurrent enzymatic activity and increased respiration and assimilation rates, which signal the conversion of stored food and its translocation to growing regions; and cell enlargement and cell division (Evenari, 1957). The radicle, arising from the root promeristem or root apical meristem of the embryo (Esau, 1960), emerges and develops into the primary or tap root.

Primary root

The primary root, which is generally strongly geotropic (Zimmerman and Brown, 1971; Coutts and Armstrong, 1976; Juniper, 1976), elongates rather rapidly, using reserves of energy and nutrients stored in the seed. Species vary in the strength of their initial tap root development (Toumey, 1929). Some species develop large woody tap roots that in suitable soils may penetrate to depths of several metres, providing support as well as a source of lateral roots: Lyford (1975) suggested that the short, weak tap roots developed in other species function primarily as a source of laterals. Toumey (1929) studied the development of several thousand individual seedling root systems of nearly 100 species in a variety of soil conditions during their first growing season and observed that for each species the initial root system followed a "definite course of development" and maintained a "characteristic form for a rather definite period". For example, the primary root of sugar pine (*Pinus lambertiana* Dougl.) seedlings penetrated nursery soil to depths of: from 10 cm to 15 cm before the cotyledons became free of the testa; from 30 cm to 45 cm in 70 days; and from 56 cm to 76 cm by the end of the first growing season, by which time a few weak laterals had developed, mostly 30 cm or more below the ground surface. In contrast, seedling bald cypress (*Taxodium distichum* Rich.) in the first growing season developed primary roots no more than 7.5 cm long and much-branched surface lateral roots up to 15 cm long. Toumey found that "tolerant species like hemlock and spruce" developed only short, superficial root systems in the first growing season, usually penetrating no more deeply than 7.5 cm to 12.5 cm. Place's (1952) data from experiments with white spruce (*Picea glauca* (Moench) Voss) and balsam fir (*Abies balsamea* (L.) Mill.) suggest that perhaps half of this first-year penetration is accomplished within a week or two after germination.

Root apex

The root apex, though not simple, is less complex than the shoot apex (Clowes, 1961; Romberger, 1963). Unlike the shoot apex, however, which produces leaves within a few hundred micrometres of the apical dome, lateral roots originate millimetres or centimetres behind the apex, so that their initiation does not complicate the structure of the apex itself (Torrey and Feldman, 1977). Differentiation of cells into tissues occurs in a continuous acropetal pattern, i.e., toward the root tip. Allen (1946, 1947a, b) has described in detail the development of the root apex in *Pseudotsuga* embryos. Extension growth of the root occurs in a short zone rarely exceeding 2 to 3 mm (Zimmerman and Brown, 1971).

Root cap

The root apex is terminated by a root cap whose cells are formed through the continuous division of the root-cap initials, a layer of dividing cells located just short of the apex along the junction between the root cap and the apical meristem (Torrey and Feldman, 1977).

The functions of the root cap were long considered to be protection of the apical meristem and assisting the growing root to penetrate the soil (cf. Esau, 1953), the mucilaginous nature of the cell walls on the periphery of the cap and those next to the main body of the root being an obvious feature of many actively growing root tips, though not in all environments (Esau, 1953, 1960). This mucigel, a mucopolysaccharide (Juniper and Roberts, 1965), may be important in promoting an active soil microflora (Barlow, 1975) that gives the rhizosphere its distinctive character (Rovira, 1962; Dangerfield, 1975). Barlow (1975) has suggested that mucigel may facilitate the development of mycorrhizal associations. At any rate, Clowes (1954a) showed that a root cap may persist even after an ectotrophic mycorrhizal sheath has been formed.

The cells of the root cap are living and often contain starch grains, and for more than a century the root cap has been regarded as the most likely site of gravity perception (Audus, 1975). The evidence is now overwhelming that in roots the site of perception of a gravitational stimulus lies in the core of the root cap (Juniper, 1976) or at least in amyloplasts (Barlow, 1974). Audus (1975) termed "reasonably conclusive" the evidence that the dense, sedimenting starch-laden amyloplasts are the organelles *directly* acted on by gravity and that their induced movement, or a change in the pressure exerted by them on some cell component, initiates the sequence of processes that culminates in the geotrophic response. Precision removal of the root cap of *Zea mays* L., leaving the meristem intact, deprived roots of their response to gravity but did not affect their rate of elongation (Juniper *et al.,* 1966).

There are also strong indications that the root cap is involved directly in growth regulator production (cf. Gibbons and Wilkins, 1970; Pilet, 1972; Torrey and Feldman, 1977).

The root cap is of far greater importance than its mass would suggest.

Quiescent centre (QC)

The region just proximal to the junction between the root cap and the rest of the root continues to be of intense interest to the morphogeneticist. Clowes (1945b, 1958, 1959, 1961, 1975), supported by the work of Byrne and Heimsch (1970), Phillips and

Torrey (1971, 1972), Webster and Langenauer (1973), Feldman (1975), Feldman and Torrey (1975, 1976), and others have shown that every investigated root apex has a quiescent centre (QC) of cells that divide much more slowly than the surrounding cells of the meristems. Romberger (1963) was reluctant to generalise about the occurrence of QCs in gymnosperm roots, although he acknowledged Chouinard's (1959) report, based on the distributional pattern of mitoses, of a QC in primary roots of jack pine (*Pinus banksiana* Lamb.), and referred to Wilcox's (1962a) confirmation of QC in roots of incense cedar (*Libocedrus decurrens* Torr.). The average cycle time for mitosis varies with species, of course, but on average the cells of the QC may take from about 150 to 500 hours to divide compared with about 12 to 13 hours for root cap cell initials and 20 to 22 hours for the cells immediately proximal to the QC (Torrey and Feldman, 1977).

Why, then, is there so much interest in these small tissues made up of inert cells? Torrey and Feldman (1977) give the answer: "The biconvex lens-shaped population of cells constituting the quiescent centre is important to the structural integrity of the developing root, in part because its surfaces determine and define the sites and shapes of the meristems — the distal meristem, which gives rise to root-cap cells, and the proximal meristem, which forms the cells of the root proper."

Depending on species, the QC of the primary root may be present in the dormant seed (Clowes, 1961) or it may appear a few days after germination (Clowes, 1958). In the case of lateral roots, the QC is usually initiated if not well developed by the time the lateral root breaks through the epidermis (Torrey and Feldman, 1977).

The number of cells comprising the QC (usually between several hundred and several thousand) seems to vary directly with both the size of the apex (Byrne, 1974) and the activity of root growth (Torrey and Feldman, 1977). The QC is not a homogeneous population of inert cells: "Rather, it is clear that within the [QC] cell population a gradient radiates outward from a more or less central point" (Torrey and Feldman, 1977).

Although the evidence also suggests that the QC is metabolically inactive (Byrne, 1974), there have been many suggestions that the QC is the site of synthesis or accumulation of plant growth regulators (Clowes, 1975). To date, the function of the QC remains obscure, but its greatest importance may be as a reservoir of cells relatively immune from perturbations that damage cycling cells (Clowes, 1975).

Proximal meristem

It seems clear that by cell division the proximal meristem gives rise to all the cells and tissues of the root proximal to the QC (Torrey and Feldman, 1977). The site of this meristem has only recently been fully recognised, and little is known as to how it functions.

Unlike the distal meristem, which is a rather precisely limited layer of cells, the proximal meristem is a "relatively wide band of cells arranged in arcs on the proximal face of the QC, averaging perhaps eight or more cell layers and varying in depth during changing activities of the root meristem" (Torrey and Feldman, 1977).

At various distances behind the proximal meristem, cells enlarge and develop specific characteristics according to the position of the cell in the root, i.e., cells become differentiated (Esau, 1960). Differentiation into the different elements does not take place synchronously. Apart from the somewhat elusive secretory cells (cf. Wilcox, 1954), the first tissues to differentiate are the phloem elements, with the xylem elements appearing later (Esau, 1953).

The appearance and maturation of the first vascular elements are related to the growth of the root as a whole: the distance between the differentiated elements and the proximal meristem depends on the growth rate of the root and is also influenced by environmental conditions, by the type of root, by the developmental stage of the root (Esau, 1953), and by species.

The vascular system develops as longitudinal bundles or strands, and roots having two, three, four or more such bundles are termed diarch, triarch, tetrarch, or polyarch, respectively. Considerable variation has been reported in the patterns of vascular differentiation occurring in some species and even within a single root system (Torrey and Wallace, 1975). Preston (1943), for instance, found that the primary root of lodgepole pine (*Pinus contorta* Dougl.) was at first tetrach, then triarch, and finally diarch. The number of strands of primary xylem differentiated in a root affects root system morphology because lateral roots normally develop in rows adjacent to those strands (Fayle, 1975).

A remarkable variety of patterns of differentiation was obtained by Torrey (1963) in cultured roots of pea (*Pisum sativum* L.) by manipulation of the auxin and cytokinin levels in the roots. The growth regulators appeared to achieve their effect by influencing the time and place of cell divisions within the root. This variability contrasts with the stability of the diarch conditions reported by Noelle (1910) and Liese (1926) for *Pinus sylvestris* L. and by Wilcox (1964) for *P. resinosa* Ait. Wilcox, however, did not examine the primary root of the 1-year-old seedling, and Fayle (1975) found that although the diarch conditions predominated in this species, triarch and tetrarch states also occurred. The diarch condition is almost always present in other coniferous genera as well: *Araucaria, Cedrus, Picea, Pseudotsuga*, and *Tsuga* (Noelle, 1910). Torrey and Wallace (1975) observed that: "It is usually conceded that, in lateral roots, the vascular pattern remains the same as, or shows fewer numbers of vascular strands than, the main axis root to which they are attached and that diarch lateral roots are probably of most frequent occurrence."

The cortex and root cap are of common origin, and this account for the lack of clear demarcation between these tissues (Wilcox, 1954), although an approximate boundary becomes evident in the dormant root.

The endodermis differentiates from the inner layer of the cortex (Wilcox, 1954) to form a continuous sheath around the vascular stele. Development of the secondary condition of the endodermis, in which a continuous suberin lamella is laid down on all the walls, begins soon after the initial development of the endodermis has been completed (Wilcox, 1954). This was widely thought to prevent subsequent passage of water and nutrients into the vascular system. However, evidence produced by Addoms (1946), Kramer (1946), Clarkson and Robards (1975), and others strongly indicates that, even when mature and well developed, the endodermis remains permeable to some degree.

Cortical cells isolated by the secondary endodermis die and collapse. Thus the diameter of an actively growing root is typically greater in the young tip portion than at some distance further back where the primary cortex has collapsed.

Gymnosperms have no epidermis or specially differentiated dermal layer (von Guttenberg, 1941; Wilcox, 1954).

SECONDARY ELEMENTS OF ROOT SYSTEM FORM

Notwithstanding the strength of the expression of the inherent pattern of primary root development, Toumey (1929) found that the initial root habit in all one hundred tree species studied responded to different environmental conditions, and although the plasticity of the root system varied greatly with species, in all species this plasticity increased with time. This, of course, is because with very few exceptions the root system form is determined largely by highly plastic secondary elements.

Lateral roots

Very early during the development of a root system, the relative importance of the primary root begins to decline while that of lateral roots, sometimes supplemented or superceded by adventitious roots, increases rapidly. Although, in some strongly tap-rooted species growing in deep exploitable soil, the depth of penetration and persistence of the primary root are important factors in the development of the root system form, size, shape, and rate of change of a root system depend mainly on the lateral roots and their meristems.

Lateral roots arising in normal sequence from a primary root are termed first order laterals; lateral roots arising in normal sequence from a first order lateral are termed second order laterals; and so on (Stone and Stone, 1943).

Whether arising on primary, lateral, or adventitious roots, the lateral roots of both gymnosperms and angiosperms are endogenous in origin, arising most commonly in the pericycle at the periphery of the vascular cylinder, i.e., in the ground tissue of the stele located between the phloem and the endodermis (Esau, 1960).

The dividing cells of the developing lateral root form a protrusion, the root primordium, which increases in length and penetrates the cortex (Esau, 1953, 1960). Before emergence, some lateral roots, e.g., those of *Zea mays* L., form a well developed root cap complete with statolith-containing cells (McCully, 1975). Other laterals may lack root caps, for, according to Kramer (1949) and Kramer and Kozlowski (1960), the short laterals of "pine" have either no root caps or very weakly developed ones, and Laing (1932) stated that root caps are absent from mycorrhizal roots in the Coniferae. However, it now seems that a root cap may be maintained within an ectotrophic fungal sheath to the development of which it may contribute (Clowes, 1954a).

In favourable rooting media, lateral roots emerge from the parent root in two, three, four, or more longitudinal rows associated with the position of the vascular groups within the stele (Büsgen and Münch, 1929). According to Esau (1960): "The position of the lateral root varies in relation to the vascular pattern of the parent root but is stable in a root with a given pattern. In a diarch root, the lateral root arises between the phloem and the xylem, in a triarch, tetrarch, etc., root opposite the xylem; in a polyarch root opposite the phloem." Thus, lateral roots develop with some predictability as to position, for in general they arise in acropetal order (i.e., the roots nearer the tip of the parent root are younger than those further from the tip) in some definite relation to the internal vascular pattern of the parent root (McCully, 1975). These relationships are no more than general, however, and much remains to be discovered about sequential emergence in intact as opposed to excised lateral roots.

When the vascular elements differentiate in the lateral root, they connect with the equivalent elements in the parent root (Esau, 1960).

As in the phenomenon of apical dominance in shoots, the main root axis meristem appears to inhibit lateral root initiation and growth in its immediate vicinity (Street, 1969), and the faster the growth rate of a root, the greater the distance between its apex and the nearest lateral root (Wilcox, 1954, 1968). The apical unbranched portion of an elongating lateral root, termed "root tip" by Lyford (1975), may be several centimetres long, e.g., more than 6 cm in jack pine (Kaufman, 1945); whereas in a dormant root of noble fir (*Abies procera* Rehd.) lateral roots may arise within 1 mm of the apical initials (Wilcox, 1954).

Control of meristematic activity in roots, including root initiation, involves interactions between growth regulators and certain nutrients (Street, 1969).

It has long been known that fertile soil promotes proliferation of lateral roots (cf. Knight, 1811). As Wiersum (1958) stated: "If the root system is studied in its relation to characteristics of the soil profile, the largest amount of roots per unit volume of soil is generally found in the most fertile layers or spots. This ... holds for both ... herbs ... and woody plants." In particular, a positive correlation has been reported between root branchiness and colloid-rich horizons and pockets in soils otherwise low in fertility (cr. Sutton, 1969).

Fertility, however, is governed by many factors, including pH, moisture, aeration, and soil structure, as well as by levels of nutrients, notwithstanding the fact that many workers have more strictly related the occurrence of dense branching of roots to high levels of nutrients (Wiersum, 1958). The difficulty in much of this work is that it is not possible to distinguish between the effects due to levels of adsorbed nutrients and those due to the not necessarily directly related concentrations in the soil solution.

For more than a century, solution culture experiments (cf. Nobbe, 1862, 1875; Leyton, 1952, etc.) have been used to investigate the influence of nutrient concentration on root branching. Although somewhat equivocal, the results of such studies reflect relationships generally comparable to those observed in soils of differential fertility: in dilute solutions, roots tend to be long, thin, and sparsely branched, whereas in more concentrated solutions, they tend to be short, stubby, and branchy.

The localised nature of the response by roots to nitrate ions has been demonstrated by Hackett (1972) using an improvement of the ingenious technique devised by Wiersum (1958) to overcome some of the drawbacks of the conventional solution culture technique. Nitrate locally applied to roots of wheat (*Triticum aestivum* L. cv. Gabo) seedlings 4 to 5 days after germination effected an increase in the density and rate of extension only where nitrate was present externally. Whether the nitrate acted at the normal site of lateral initiation or introduced further laterals into a series already developing could not be determined. Hackett (1972) suggested that the nitrate increased the extension of only those lateral roots receiving it directly because they were reducing some of it *in situ* for their own growth, the root axis being anomalous "since it can evidently obtain the nitrogen it needs for growth whether or not nitrate is bathing its meristem."

Localisation of effect has also been reported by Coutts and Philipson (1976) in divided root systems of 2-year-old Sitka spruce (*Picea sitchensis* (Bong.) Carr.) seedlings, but root branching was not discussed.

In terms of their effects on root morphogenesis, nitrogen, and, to a lesser degree, phosphorus are usually regarded as the most influential nutrient elements (cf. Bosemark, 1954; Meagher and Armson, 1963; Philipson and Coutts, 1977, etc.).

Growth regulators and co-factors known to be involved in determining the rate, pattern, and distribution of plant growth include auxins, gibberellins, cytokinins, ethylene, vitamins, and some physiologically active cations. The role of these substances in controlling cell division and cell elongation in roots is much less understood than are their effects on shoots (Zimmerman and Brown, 1971). Hormonal inter-relationships between shoot and root are undoubtedly important (Lyr and Hoffmann, 1967) as are hormone ratios and hormone gradients (Torrey, 1976), both for shoot and root. Auxins seem to be synthesised mainly in the shoot, but have been found many times in roots, where their movement is polar towards the root tip (Zaerr, 1967; Torrey, 1976). Roots are a major site of synthesis of cytokinins and possibly also of gibberellins (Skene, 1975; Russell, 1977), although the evidence for the presence of gibberellins in roots (cf. Phillips and Jones, 1964) is largely indirect (Torrey, 1976).

Also, the position of existing lateral roots influences the location of any subsequent laterals, at least in several monocotyledonous species (Riopel, 1969) in which a three-dimensional zone of suppression was found in association with lateral root positions.

Secondary thickening in roots, discussed by Fayle (1968), is relatively unimportant in terms of root system morphogenesis excepting for its influence on the partition of assimilates between primary and secondary growth. The mechanism by which this partition is effected, however, is not known (Coutts and Philipson, 1976).

Rate of extension of lateral roots and their diameter have been found to be correlated in several plant species including conifers (cf. Wilcox, 1962a, b, 1967; Mason *et al.*, 1970) and a monocot (cf. Hackett, 1962).

(a) Heterorhizy

Considerable morphological variation occurs in the lateral roots of many plant species, including many trees. The term "Heterorhizie", coined by Tschirch (1905) to signify herbaceous species exhibiting more than one morphological root type, was soon applied to woody species by von Alten (1909) and Noelle (1910). Though not originally so intended, the term is now often applied in a more circumscribed sense to the long-and-short-root habit exemplified by the pines (cf. Aldrich-Blake, 1930; Hatch and Doak, 1933; Hatch, 1937; Wilcox, 1964) and other genera in the Pinaceae (Sutton, 1969) and the Betulaceae and Fagaceae (Wilcox, 1962a, b; Lyford and Wilson, 1964).

The concept is not uniformly applicable, however, even among conifers. *Libocedrus decurrens,* for instance, did not fit the long-and-short-root pattern (Wilcox, 1962b). Furthermore, the physiological roles of the different root types and the significance of the morphological variability under various environmental conditions remain obscure (Wilcox, 1964). Nevertheless, for many of the commercially important conifers, discussion of root systems is simplified by separately considering long lateral and short lateral roots.

(b) Long laterals

Typically, long lateral roots are relatively long, sparsely branched, and relatively fast growing during one or more prolonged growth periods. The imagination has been spurred to coin more than 20 names for this type of root (cf. Wilcox, 1962b; Sutton, 1969), but the term "long lateral" has advantages in being simple, apt, and functionally non-committal.

Long laterals may arise either in normal sequence or adventitiously. In red pine (*Pinus resinosa* Ait.) grown in root observation boxes, the larger lateral root primordia seemed destined to become long roots; these emerged earlier than many of the smaller, slower-growing short-root primordia, and not in strict acropetal sequence (Wilcox, 1968). Long laterals commonly arise from the root collar region of planted spruces (Sutton, 1967a, b).

Individual roots exhibit cyclic activity. At any given time, some roots of a root system will be extending and some will not. Wilcox (1954) found that in noble fir (*Abies procera* Rehd.), even during periods when root activity was greatest, the main root apices that were elongating formed only a rather small proportion of the total number; and while the root system of a tree grown in the greenhouse grew for about 10 months of the year, some individual roots grew not at all during that time whereas others had several growth periods.

Each pause in growth of a root was marked by the formation of a dark brown suberised root tip, and each cycle of growth elongation for any individual root followed a typical sigmoid curve. The mechanisms controlling this root activity are complex and little understood, but the evidence provided by Wilcox (1968) from his studies with red pine strongly suggests that one of the controlling mechanisms involves soil-plant water relations.

This colour change in the tip of a long lateral root that has ceased to elongate reflects a process, termed "metacutization" by Wilcox (1954) after Müller (1906), in which the turgescent root tip changes to deep brown from the colour it displays during active growth, generally white, but in some species, including western red cedar (*Thuja plicata* D. Don.) brilliant red (Laing, 1932). This reflects simultaneous massive suberisation of cell walls and cell contents unlike the suberisation in thin lamellae that forms during the development of the secondary endodermis (Wilcox, 1954). In most conifers, within 8 to 20 days following cessation of root growth, browning of the tip occurs. This happens more quickly in spring than in summer (Engler, 1903). The dark brown "cap", formed by metacutization at the apex of roots of noble fir within a few days after elongation ceased, developed from the tip and moved basipetally. There is little or no reduction in diameter associated with this metacutization.

Browning also occurs in non-terminal portions of roots some days after formation. This is associated with the acropetal development of the secondary endodermis, as described, and involves collapse of the cortex and loss of diameter.

Wilcox (1954) also found that, in addition to the suberisation occurring in metacutization, the differentiation of vascular tissue in non-elongating roots of noble fir approached the apical initials much more closely than in elongating roots.

Growth rates of individual long lateral roots vary so much according to circumstances that, for the present purpose, no more is needed than a general indication of growth rates in nature. In 24-year-old stands of jack pine (*Pinus banksiana* Lamb.) growing in a cool temperate climate, Kaufman (1945) found that the growth rate of individual roots ranged from 12.7 cm to 1.8 cm in the 21 days of most active root growth, and from 55.0 cm to 6.5 cm for the whole of the growing season: in the following year, the maximum growth observed in a single root was 15.5 cm in 23 days, 48.3 cm over the whole season; and the last active root elongated 4.7 cm in 23 days, 9.9 cm over the season. The average annual rate of elongation of lateral roots of 7-year-old jack pine was 38 cm, while that of individual roots ranged from 61.8 cm to 21.1 cm.

Because root elongation rates are so important in relation to regeneration silviculture, the following data referring to young trees may be of particular interest. Laing (1932) found that the average lateral extension of the root system of Norway spruce (*Picea abies* (L.) Karst.) during their second year in a Scottish nursery increased from 7.7 cm in mid June to 25 cm in September: for Sitka spruce (*P. sitchensis*), the comparable increase was from an initial 5 cm to a final 10 cm. Individual long lateral roots of 2-year-old Norway spruce may reach a length of 1 m (Büsgen and Münch, 1929). Laing (1932) found roots up to 1.5 m long on 2 + 3 Norway spruce in the nursery. In white spruce in their second growing season, after outplanting as 3 + 0 stock, laterals up to 71 cm long have been found (Sutton, 1965). On a more fertile site in New York State, adventitious long laterals 19 cm, 22 cm, and 28 cm long developed in 42 days on one white spruce outplanted as 3 + 0 stock (Sutton, 1967b).

(c) Short roots

Variously called Kurzwurzeln, Angwurzeln (Sutton, 1969), absorbing roots, feeding roots, nutrition roots, etc. (Wilcox, 1962b), short roots are found throughout *Abies, Larix, Picea, Pinus, Pseudotsuga, Thuja,* and other genera in the Pinaceae, as well as in the Betulaceae and Fagaceae and a few other angiosperms (Wilcox, 1962b). The Cupressaceae, including *Libocedrus,* is one of numerous groups of woody plants that do not develop short roots (Wilcox, 1962b).

Short roots arise from root primordia similar to those giving rise to long lateral roots. However, in *Pseudotsuga* they tend to arise closer together and often in pairs on opposite sides of the parent root (Bogar and Smith, 1965), and are probably smaller than those giving rise to long lateral roots. They are characterised from the outset by a slow rate of cell division in the apical meristem. The short roots of most species have rounded tips (Sutton, 1969). In *Pseudotsuga,* at least, growth may cease at any time prior to emergence from the cortex up to a root length of about 5 mm (Bogar and Smith, 1965). According to these workers, the root cap cells become filled with resins and tannins, and outer layers are irregularly sloughed, sometimes leaving very few layers of cells over the apex. Differentiation proceeds to mature xylem elements close to the apex in a small diarch stele. No resin canals appear, and no secondary tissues are produced. The cells of the cortex do not hypertrophy.

The life of a short root may be a few days (Kinman, 1932), a few weeks (Childers and White, 1942), or more: Orlov (1960) found that, of the Norway spruce short roots that he observed directly *in situ* in the forest floor, 10% lived for a year or less, most lived between 3 and 4 years, 20% for more than 4 years, and a few more than 5 years. Most short roots of red pine died during their first or second growing season (Wilcox, 1964). Short roots as well as long laterals may show recurrent cycles of elongation and non-elongation.

Short roots are commonly but not necessarily mycorrhizal (Melin, 1923; Laing, 1932; McArdle, 1932; Bogar and Smith, 1965).

(d) Adventitious roots

Adventitious rooting (*sensu* Stone and Stone, 1943) is an important contributor to the development of many tree root systems. This is especially true for planted stock, though not equally for all species.

Adventitious roots may arise from root tissue, especially after injury, accidental or intentional (cf. Wilcox, 1955); or they may arise from main stem, branch, or other tissue (Sutton, 1967b). In both gymnosperms and dicotyledons, adventitious roots arise either from preformed root primordia or from induced primordia (Girouard, 1967) in tissue that would not have differeniated root primordia during normal development (Haissig, 1974a, b, c).

The adventitious root primordia are initiated by divisions of parenchyma cells, callus or otherwise, in a manner similar to the initiation of normal lateral roots in the pericycle of young roots (Esau, 1960). Primordium development precedes and then accompanies morphological differentiation which can be considered to begin as soon as a characteristic domed cellular aggregate can be distinguished (Haissig, 1974a). Before it emerges from the parent tissue, the adventitious root has differentiated a promeristem, a root cap, and the beginning of a vascular cylinder and cortex (Esau, 1960).

Adventitious rooting may be regarded as a mechanism of repair of root systems unbalanced by injury or stress. Silviculturally, common situations in which root system regeneration is important include: root damage by natural agency, e.g., insects, frost heave, drought, flood; root damage incidentally incurred by planting stock during any part of the entire sequence of operations culminating in outplanting; root damage deliberately inflicted on planting stock, usually for the purpose of facilitating handling; adjustment of an outplant's root system to soil conditions more inhospitable than those in which the plant was raised; rooting of cuttings; etc. Such repair to a root system, or the development of a more appropriate root system, is important not only for nutritional and water relations but also for the development of stability.

These matters bring us to the crux of our deliberations at this workshop. A highly important component of the quality of planting stock is the ability to make new root growth quickly after outplanting. This has been considered essential for survival of outplanted ponderosa pine (*Pinus ponderosa* Dougl.), Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Stone, 1955), and the Southern pines (Gilmore, 1964; Wakeley, 1965); it may be generally true for any stock outplanted in any situation that subjects it to more than mild stress. Successful planting depends on re-establishing early functional contact between the root system of the outplant and the soil (Smith, 1962; Sutton, 1978). The greater the stress, the greater the need for speed. This was emphasised by Huberman (1940) and Wakeley (1954) who attributed the lower field survival of Southern pine planting stock that had been shaded in the nursery, as compared with otherwise similar stock that had not been shaded, to the greater tardiness of the shaded stock in producing new root growth.

Root "regeneration" has in fact become a central concern for the silviculturist and forest physiologist. It should perhaps be noted that this use of the term "regeneration" does not accord strictly with usage in the science of morphogenesis. True regeneration of a root takes place when a new growing point forms directly at the wound surface from the underlying tissue of the plerome after no more than the extreme tip, say 0.5 mm to 0.75 mm, of a root has been removed: if a little more of the tip is cut off, regeneration is only partial and takes place chiefly by the formation of new growing centres in the outer portion of the root: if still more is removed, true regeneration does not take place, but adventitious roots develop from the callus that is formed (Sinnott, 1960). Early work on root regeneration in conifers is covered by Stingl (1905) and Nemec (1905). However, the terms "root regeneration" and "root regenerating potential" (RRP) are well established in the forestry literature and their use here will not cause confusion.

The degree to which a tree for outplanting possesses this crucial ability to augment its root system, either adventitiously or by resumption of growth of existing roots, cannot be determined visually. Two batches of planting stock may be morphologically indistinguishable and yet differ so much that if they were outplanted side by side one batch would give total success and the other total failure. The concept of physiological grades was first articulated clearly by Wakeley (1948). Stone (1955, etc.) and his co-workers have since established many important relationships for forestation species used in the western United States (cf. Stone and Schubert, 1959a, b; Stone *et al.,* 1962; Hellmers, 1962; Stone *et al.,* 1963; Paul and Todd, 1965; Krugman *et al.,* 1965; Krugman and Stone, 1966; Stone and Jenkinson, 1970): for a given species, factors that have been shown to be important in determining the physiological condition, notably the RRP, of planting stock include provenance, lifting date, nursery climate, nursery cultural practices, and cold storage. Zaerr (1967) found that with ponderosa pine seedlings, disbudding did not affect root elongation, and that indole-3-acetic acid (IAA) applied in lanolin (0.01%) to disbudded seedling tops caused a slight increase in growth of newly initiated roots but had no effect on the elongation of pre-existing root tips.

Adventitious roots formed in layering provide clues to differences in rooting behaviour among species. Of the conifers, members of the genera *Picea* and *Abies* seem to be particularly able to root adventitiously from live branches in contact with moist forest floor (cf. Kunze, 1851; Cooper, 1911, 1931; Fuller, 1913; Stanek, 1961, 1967, 1968). Layering also occurs in *Tsuga, Chamaecyparis, Thuja, Juniperus,* and *Taxus* (Cooper, 1931; Lutz, 1930, 1939; Bannan, 1942). Instances of layering in *Pinus* have been reported, e.g., in mountain pine (identified as *Pinus pumilo*) (Büsgen and Münch, 1929), eastern white pine (*P. strobus* L.) (Lutz, 1939), and lodgepole pine (*P. contorta* Dougl. var. *latifolia* Engelm.) (MacArthur, 1964), but the incidence of the phenomenon in *Pinus* is distinctly uncommon (cf. Bannan, 1942). An important consideration in this connection is the intolerance of most pines to shade and the consequent death of lower branches before sufficient organic debris has accumulated to create conditions favouring rooting (Lutz, 1939). Also, the dryness and infertility of many pine sites militate against layering.

Anatomical observations of natural layers in several species of conifer native to Ontario were made by Bannan (1942): in the prostrate *Taxus canadensis* Marsh, adventitious roots were generally grouped near the bases of lateral branches. In *Thuja* *occidentalis* L., *Juniperus horizontalis* Moench, *J. communis* var. *depressa* Pursh, and, "when the opportunity offers", *J. virginiana* L., adventitious roots develop frequently. In *Abies balsamea* (L.) Mill. layering seemed to occur whenever a branch became buried, and the adventitious roots were scattered without pattern along the lower side of the buried parts of the branches. Layering in *Picea mariana* (Mill.) B.S.P. was very common, in *P. glauca* (Moench) Voss very uncommon. In *Abies*, the roots were distributed along the branch and were not as a rule associated with the terminal buds. In *Picea*, the roots were usually located immediately above the terminal bud scars. Nearly all the roots on layered branches of *Larix laricina* (Du Roi) Koch arose in close proximity to dead dwarf (leaf-bearing) branches. In some "hormone-treated" cuttings of *Picea abies* (L.) Karst. examined by Bannan (1942), most of the roots arose at the cut end of the branches, "the origin differing from that observed in the uninjured [natural] layers ..."

Additional clues as to the origin, development, and manipulation of adventitious roots are furnished by anatomical investigations of roots induced by pruning. In noble fir, for instance, Wilcox (1955) showed that wound-healing callus formed on the pruned surface of roots and that adventitious roots arose both from the undisturbed tissue beneath the wound surface and from the callus tissue itself. In roots pruned during the first or second season of their growth, the adventitious roots arose opposite the protoxylem poles, despite the lack of vascular connection between the new root and the protoxylem. In these young roots, and in unpruned roots, adventitious roots originated in the pericycle where the pericycle cells were close to the functioning xylem and phloem. In roots pruned at some time after their second year's growth, adventitious roots ceased to have any definite relation to the protoxylem points, originating at any position around the circumference of the vascular cambium, again in close proximity to functioning xylem and phloem (Wilcox, 1955).

Vascular maturation was much faster in the adventitious root than in the normal lateral root (Wilcox, 1955).

Mycorrhizas

Mycorrhizas influence root system form and development by their effect on the fleshiness, rate and amount of elongation, amount and type of root branching, root hair formation, and suberisation (Sutton, 1969). The mycorrhizal relationship may be important not only in these effects on root anatomy and morphology, and in its influence on tree nutrition, but also in the health of roots and their susceptibility to disease (Garrett, 1960; Marx, 1967; Marx and Davey, 1967). Mycorrhizas, first defined and named by Frank (1885), are very widely distributed and involve numerous species of fungi. Hatch (1937), Björkman (1942), Kelley (1950), Melin (1953, 1963), Harley (1959), Trappe (1962), Meyer (1974), and Slankis (1974), are among those who have reviewed various aspects of mycorrhizas.

Many different types of mycorrhizas have been distinguished on the basis of appearance. In ectotrophic mycorrhizas (Frank, 1885), the common coniferous type, short roots are covered with a mantle of hyphae from which hyphal strands extend both into the soil and inter- and intra-cellularly within the primary cortex to form the Hartig net (Björkman, 1970). Endotrophic mycorrhizas (Frank, 1885) cannot always be identified from exterior signs, for no mantle is formed, and the root maintains its normal appearance, the fungus penetrating the root cells only to be dissolved or digested therein (Björkman, 1970). Ectendotrophic mycorrhizas (Melin, 1923) are an intermediate form in which both a typical Hartig net and intra-cellular hyphae are formed: the form occurs most commonly in forest tree nurseries and is believed to be caused by a specific, as yet unidentified, fungus (Gerdemann, 1974). Wilcox (1976) considered the category to be valid and possibly more akin to endotrophic mycorrhizas than to ectotrophic, although according to Mikola (1965) ectendotrophic mycorrhizas are usually replaced by typical ectotrophic mycorrhizas in seedlings that have been outplanted in forest soil. Pseudomycorrhizas (Melin, 1917) also occur in the short roots of some conifers including *Picea abies*: infected roots lose or do not develop root hairs although no mantle is formed, and the hyphae penetrate but do not form a network between the cells, the cortical cells retaining their initial shape (Björkman, 1970). "Peritrophic mycorrhizas" (Jahn, 1934) signify a loose association between roots and fungi, which live on the surface of the root or in the rhizosphere without penetrating the root itself (Björkman, 1970).

Peyronel *et al.* (1969) proposed the terms ectomycorrhiza, ectendomycorrhiza, and endomycorrhiza, to replace the terms ectotrophic, ectendotrophic, and endotrophic mycorrhiza.

The importance of mycorrhizas to tree growth can perhaps best be judged from the very great responses to inoculation that have been obtained in conifers grown in several parts of the world where conifers are not endemic and where the soils lack the mycorrhizal fungi usually associated with conifers (cf. Rawlings, 1951; Bowen, 1965; Hacskaylo and Vozzo, 1967). The response is largely explainable in terms of increased uptake of nutrients, especially phosphorus (cf. Hatch, 1937; Stone, 1950), but vitamins and plant growth regulators may also be involved (Shemakhanova, 1958; Slankis, 1972).

Theodorou and Bowen (1970) have shown that the response of radiata pine (*Pinus radiata* D.Don) to the development of a mycorrhizal condition depends very much on the fungal species involved. Also, tree species vary in their ability to form mycorrhizas, Laing (1932), for instance, noting that in the same peat, mycorrhizas develop on *Pinus montana* but not on *P. sylvestris* whether or not the trees are mycorrhizal when initially planted.

A regular acropetal formation of mycorrhizas has often been observed in some species of conifer. Until Robertson (1954) demonstrated otherwise, this was taken as evidence that mycorrhizas were formed by external infection. Robertson, however, showed that in Scots pine the long lateral roots are normally infected by a Hartig net that produces no morphological effect unless a mantle is formed over the root tip, and the mycorrhizas arise from internal infection from the Hartig net as it extends along the lateral root.

Mycorrhizas may persist for years, exhibiting restrained cyclic elongation (cf. Goss, 1960; Laing, 1932).

Root hairs

Although root hairs are very widely distributed in nature (Dittmer, 1949), and were described by Chamberlain (1934) as almost invariably present on the roots of conifers, there is good evidence that reports of the absence of root hairs have not always been explainable on the basis of their inconspicuous nature. Certainly, root hairs are small; Dittmer (1949), for instance, found that the root hairs of 37 species in 20 plant families ranged from 5.10^{-6} cm to 17.10^{-6} cm in diameter and from 80.10^{-6} cm to 1500.10^{-6} cm in length; they are fragile and easily lost during washing and preparation; they are ephemeral; and they are generally restricted to a small region of a root, sometimes not more than 1 mm long. And yet, many careful and competent observers have on occasion sought them in vain. For example, Sachs (1887) failed to find root hairs on Scots pine and Norway spruce. Also, Strasburger was reported by von Tubeuf (1896) to have found root hairs abundant only in *Taxus*; entirely wanting in species of *Thuja, Sequoia,* and *Araucaria*; exceptionally present in *Ephedra*; and sparingly present in *Pinus* spp. However, von Tubeuf (1896) found root hairs on 24 coniferous species; and although he could not find any on seven other species he thought it not certain that these did not, at other times or under other conditions, form root hairs. Engler (1903), though confirming that root hairs were absent from many samples of roots of Scots pine and Norway spruce, found root hairs on other samples of these species at all seasons but especially during the autumn and winter.

The main root hair zone is proximal to the zone of elongation, generally on tissue that has recently become brown, presumably reflecting development of secondary endodermis (Büsgen and Münch, 1929). Root hairs of conifers arise not as outgrowths of an epidermis as in angiosperms but from a rhizodermis situated at the surface in non-mycorrhizal short roots or in the second or third layer of cortical cells in long lateral roots (von Tubeuf, 1896; Noelle, 1910; Hatch and Doak, 1933; Bogar and Smith, 1965). The rhizodermis is bounded on the inner side by a many layered sheath of large roundish cells (Büsgen and Münch, 1929). Root hairs grow in their apices only (Ekdahl, 1957).

Nevertheless in Douglas fir at least, three or four "generations" of root hair may co-exist along a 30 cm length of root (Reynolds, 1975). In Douglas fir, the innermost layer of the root cap becomes suberised, though remaining rather thin walled, and it is just beneath this layer that root hairs usually originate (Bogar and Smith, 1965). The fact that these root hairs generally become suberised as the cortex degenerates and persist as long, "undoubtedly non-functional" (Reynolds, 1975), brown hairs on older roots, probably provides the basis of McMinn's (1963) observation that root hairs occur sporadically on Douglas fir roots remote from their growing points as well as in the usual position close to the root tip. Reynolds (1975) also commented on the versatility of Douglas fir with respect to root hair production: more than 80% of the root surface of his samples was bare, while elsewhere the density of root hairs and their lengths were quite variable.

The relationship between root hair development and mycorrhizas is not entirely clear. The view, held by Engler (1903) and others, that root hairs and mycorrhizas are incompatible seems to be true only in respect of mantle mycorrhizas, for the occurrence of root hairs on mycorrhizal long lateral roots is well established (cf. von Tubeuf, 1896). In Douglas fir, second- and third-order long lateral roots with a Hartig net but no mantle may closely resemble uninfected roots complete with root hairs, which were numerous on most such roots observed by Bogar and Smith (1965). Development of the outer layers of long mycorrhizal roots with a Hartig net but no mantle was similar to that of uninfected long lateral roots.

The absence of root hairs on all Douglas fir mycorrhizas with a mantle was explained by Bogar and Smith (1965) as follows: "All mycorrhizal short roots observed in this study had a well-developed mantle. Sometimes near the tip a distinct root cap layer is identifiable, but back of the apex cells are killed progressively from the outer layers inward by enveloping hyphae. Most mycorrhizae show 2-4 layers of isolated, collapsed cells embedded in the mantle, a layer of heavily tanninized cells, and then enlarged cells in the cortex. The layer of tanninized cells represents a stage in killing of cortical cells by the fungus. Hence the persistent root cap layer and rhizodermis found on long laterals have [here] been destroyed on such mycorrhizae."

Root hairs, for the quantities of structural carbohydrates involved, might be an economc method of increasing the radial diffusivity of water and solutes to the roots under certain conditions (Reynolds, 1975). At any rate, it seems clear that soil moisture conditions influence root hair formation (Büsgen and Münch, 1929; Wilson, 1936), and Leyton[1] has pointed out that root hairs are not normally formed by conifers growing in solution culture.

That plant growth regulators are probably involved in root hair formation was demonstrated by Slankis (1951). Working with Scots pine (*Pinus sylvestris* L.), Slankis showed that isolated roots treated with IAA at concentrations of up to 3×10^{-7} M produced root hairs in abundance but developed swellings devoid of root hairs at higher concentrations.

Finally it may be noted that root hairs play an important role in root nodulation, and therefore in the nutrition, growth, and development of the root system as well as of the plant as a whole, in both legumes (Dart, 1975) and some non-legumes, including *Alnus* (Becking, 1975).

ROOT SYSTEM DEVELOPMENT

As Romberger (1963) so aptly put it: "Apical meristems are small. Lateral meristems are thin. Together they constitute a physically insignificant fraction of the total mass of a tree or shrub. Yet the whole future of the plant depends upon the activity of its meristems. Growth and morphogenesis, and the control of these processes, are largely localized in the meristems proper and in their ancillary regions of occasional cell division, continuing cell enlargement, and cell differentiation."

Starting from a single root apical meristem, one root system may generate millions of root tips each with its own meristem. The root system of one 100-year-old Scots pine possessed 5 million root tips (Kalela, 1954). Lyford (1975), on the basis of some "exceedingly conservative" assumptions that he spelled out in full, suggested that for the root system of one mature red oak (*Quercus rubra* L.), 500 million live root tips is a reasonable first estimate.

The length of roots developed by a single plant is no less impressive. Kalela (1950) calculated that the root system of a single Norway spruce (*Picea abies* (L.) Karst.) increases in total length of roots by more than 40 m per annum between the tree's 50th and 110th years. In the root system of a single century-old Scots pine, there may be 50 000 m of roots (Kalela, 1954).

Incidentally, Richards and Wadleigh (1952) reported an astonishing 5.05 km per day of new roots developed by the root system of a single plant of winter rye (*Secale*

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[1] Leyton, L. 1968. Department of Forestry, Oxford University, personal communication.

cereale L.). Little wonder that the competition offered to trees by graminaceous species is typically intense.

The form and development of each root system are probably unique, being determined by the rate, direction, and duration of growth, absolutely and relatively, of its various constituent elements.

If we consider first the root system that begins as a primary root emerging from a tree seed on the forest floor, the factors controlling its development are an interacting complex of soil factors (especially bulk density, pore characteristics, strength, moisture, oxygen, temperature, fertility, toxicity, reaction, and depth) and plant factors (including genes, plant growth regulators, influence of the plant on the soil, and previous environmental history of the plant) (Sutton and Fayle, 1979).

Root system development is further complicated by transplanting. Most root systems are deformed rather severely when they are planted (Sutton, 1969). Loss of roots, damage to remaining tissue, deformation, and placement of the root system in soil usually much more inhospitable than the nursery soil from which it was lifted, all affect growth and development of a plant, including its root system.

MANIPULATING ROOT SYSTEM FORM

Attempts to produce planting stock of optimum quality must include consideration of both morphological or shaping factors and physological or conditioning factors, and their interactions.

Genetics

Species vary greatly in root system plasticity (Toumey, 1929), and the care and technique needed to produce stock of given quality will probably vary with species. For example, whereas spruces often adjust to a new situation by readily developing adventitious roots including strong laterals from the root collar and stem (cf. Wagg, 1967), pines generally seem to have difficulty in readjusting their root systems to changed soil conditions, and concern about the long-term stability of pine plantations continues to be expressed (cf. Wibeck, 1923; Schantz-Hansen, 1945; Rudolf, 1950; Hoffman, 1960; Little and Somes, 1964; Bergman and Häggström, 1973; Hay and Woods, 1974a, b; Burdett, 1978; Hultén and Jansson, 1978, etc.), notwithstanding Wakeley's (1954) considered opinion that, at least in the case of bar-planted (i.e., virtually dibbled) Southern pines, there is nothing to worry about.

In this regard, stock quality, i.e., fitness for a purpose (Sutton, 1979), must be assessed on the basis of its potential for achieving the objectives of management. If, for instance, a plantation grows satisfactorily with respect to these objectives, and, because of close spacing to promote the development of communal (Stone, 1974) or interlacing (Wendelken, 1955) rooting, is able to resist toppling and windthrow, then any amount of root system deformation is of no consequence.

As well, intraspecific variation (cf. Allen, 1967, 1969; Savic, 1969; Clarke, 1975; van Buijtenen *et al.,* 1976) may offer opportunities for improving stock quality (Fayle, 1978).

Age or size of planting stock

Restricting size of root system by using younger or smaller planting stock would generally reduce the chance of deformation prior to and during planting. This may be especially important in pines, as discussed in "Genetics" above, especially on sites subject to root depredation by white grubs and other larvae (Sutton and Stone, 1974; Fowler and Wilson, 1974).

Pruning, etc.

Mechanical excision of parts of root systems is commonly used to reduce size in order to facilitate lifting, handling, and planting, and to induce root proliferation (Rook, 1971; Will *et al.,* 1971; van Dorsser and Rook, 1972). A sophisticated form of "box" pruning of precision sown seedlings, whereby roots are cut off in five planes, has been described by Chavasse (1978).

The time at which excision is carried out may greatly influence the results obtained. Riedacker (1976) has demonstrated that, at least in some species, to modify the morphogenesis of a root system, excision immediately after germination is needed.

Containment

A root system may be shaped simply by confining it within a container. Kinghorn (1978) and Riedacker (1978) have proposed the development of containers that would promote natural root system form after outplanting. Meanwhile, deformation of root systems within containers continues to cause concern (cf. Bergman and Häggström, 1973; Alm, 1974; Endean and Carlson, 1975; Ball, 1976; Owston and Seidel, 1978).

Rooting volume significantly affects total dry weight production as well as root system morphology (Scarratt, 1973; Endean and Carlson, 1975).

Chemical shaping

The effect of copper in stunting root growth has long been known (cf. Forbes, 1917): it was used by Saul (1968) to limit root development out of containers. More recently, Burdett (1978) devised a technique that holds great promise, raising lodgepole pine (*Pinus contorta* Dougl.) seedlings in Styroblock cavities whose walls he had painted with exterior latex paint containing 0.1 kg/l of basic cupric carbonate. Contact with this cavity wall completely inhibited elongation of lateral roots, but when the plugs were outplanted these roots very quickly resumed growth, and the root systems that developed were quite similar to those of natural seedlings.

Mycorrhizal inoculation

Inasmuch as ectotrophic mycorrhizas tend to produce compactness in a root system (Laing, 1923) and will improve phosphorus nutrition in particular, there would seem to be advantages in inoculating root systems at an early age. However, since mycorrhizal fungi infecting root systems in fertile nursery soil may not survive in different edaphic conditions (cf. Benecke and Göbl, 1974), fungal tolerances would have to be ascertained.

Plant growth regulators

Wheat plants treated with CCC (2-chloroethyl-trimethylammonium chloride) produce roots that penetrate more deeply than do roots of untreated plants (Humphries, 1968). CCC, an inhibitor of gibberellin biosynthesis (Torrey, 1976), is not a panacea to secure deeper rooting — it has much less effect on barley, oats, and rye than it has on wheat — but it illustrates the possibilities that may follow the unravelling of the complexities of plant growth regulation. This will be difficult, for not only are ratios of regulators important (Hitchcock and Zimmerman, 1940), but also there are indications that growth regulation is effected by regulators acting in a well defined sequence, e.g., gibberellin-induced cell enlargement followed by kinetin-induced cell division followed by IAA-induced cell enlargement (Wain, 1968).

IBA (indolebutyric acid), one of the most effective rooting stimulators, has weak auxin activity, but it is destroyed relatively slowly by auxin-destroying enzyme systems, and it translocates poorly so that it remains near the site of application (Weaver, 1972). NAA (naphthaleneacetic acid), also used often to promote rooting, is more toxic than IBA.

Growth regulators affect the type of roots produced (Coutts and Bowen, 1973) as well as the number and length (Coffman, 1971). IBA produces a strong fibrous root system whereas the phenoxyacetic acids, for instance, often produce a bushy root system of thick, bent roots (Weaver, 1972).

Fertility manipulation

A wide range of effects with respect to root system form and development can be obtained by manipulating fertility, especially the nutrient characteristics, of the rooting medium. Nitrogen (cf. Bosemark, 1954) and phosphorus (cf. Bowen *et al.,* 1974), and nitrogen plus phosphorus (Philipson and Coutts, 1977), are particularly influential in this regard, but humic compounds also have an effect (cf. Lafond, 1951; Schnitzer and Poapst, 1967). Evidence from studies by Hackett (1972), Coutts and Philipson (1976), and Philipson and Coutts (1977) shows the morphological importance of nutrient levels *external* to developing roots. Internally translocated nutrients did not compensate for the lack of external nutrient sources. The permutations are legion.

CONCLUSION

The degree to which root system form may be manipulated, while not unlimited, is potentially very great. There are many avenues of approach, but in every case we shall need to understand the controlling mechanism and then develop appropriate cultural practices to achieve the desired result. The quality of planting stock, including root system quality, of course, will be determined by field performance in relation to the objectives of management. Documentation of field performance is therefore essential to the evaluation of attempted manipulations of root system form.

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