

**SOIL PROPERTIES AND ROOT
DEVELOPMENT IN FOREST
TREES: A REVIEW**

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ABSTRACT

The literature is reviewed with the aim of consolidating silviculturally important information about interactions between root system development and soil properties; a complementary objective is to facilitate the reader's entry into the literature. The thesis is that root systems of forest trees develop in response to complex genetic, physiological and environmental (edaphic and atmospheric) interactions, subject to limitations imposed by aboveground growth and limiting levels of any of many individual factors. Fifteen "soil factors", the "soil-root interface", and six "plant factors" are examined in turn, though the importance of the web of interrelationships is stressed throughout.

RÉSUMÉ

Synthèse documentaire visant à rassembler les informations importantes dans le domaine de la sylviculture au sujet des interactions entre le développement du système racinaire et les propriétés du sol; un objectif complémentaire consistait à faciliter un accès plus large et plus approfondi à la littérature pertinente. Il est avancé que les systèmes racinaires des arbres forestiers se développent en réponse aux interactions complexes génétiques, physiologiques et environnementales (édaphiques et atmosphériques), sous réserve des limites imposées par la croissance au-dessus du sol et les niveaux limitants de l'un quelconque des nombreux facteurs individuels. 15 "facteurs du sol", "l'interface sol-racine" et six "facteurs de la plante" sont examinés tour à tour, bien que l'importance de la chaîne des interdépendances soit mise en évidence.

PREFACE

The secrets of the underworld of roots are yielded reluctantly, even to moles. Complex interactions between roots and the soil environment, and the responses of roots to soil properties, are normally hidden from the inquiring eye; root morphology and soil properties are highly variable.

Nevertheless, many investigators have been drawn to explore these relationships, and much information has been published, including: Day (1955), Lyr and Hoffmann (1967), Köstler et al. (1968), Harley (1969), Sutton (1969, 1980), Whittington (1969), HacsKaylo (1971), Marks and Kozłowski (1973), Carson (1974), Hoffmann (1974), Karizumi (1974), Fayle (1975), Sanders et al. (1975), Torrey and Clarkson (1975), Armson (1977), Russell (1977), Harley and Russell (1979), Hillel (1980a,b), Arkin and Taylor (1981), Brouwer et al. (1981), Ruark et al. (1982, 1983), Atkinson et al. (1983), Böhm et al. (1983), Foster et al. (1983), Jackson and Stead (1983), Taylor et al. (1983), Binkley (1986), and Gregory et al. (1987). A monograph on the terminology of roots and root systems has been published by Sutton and Tinus (1983).

As well, a rich lode of relevant information is concentrated in the proceedings of the seven North American Forest Soils Conferences (Anon. 1958, Youngberg 1965, Youngberg and Davey 1970, Bernier and Winget 1975, Youngberg 1978, Stone 1984, Gessel et al. 1990).

Finally, Volume 10(1) (1980) (*Planting Stock Quality*) of the *New Zealand Journal of Forestry Science* and Volume 17(8) (1987) (*Roots in Forest Soils: Biology and Symbioses*) of the *Canadian Journal of Forest Research* also contain many useful papers from working meetings of the International Union of Forest Research Organizations (IUFRO).

The objectives of this review are to consolidate silviculturally important information about root/soil interactions and facilitate the reader's entry into the literature.

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INTRODUCTION

The study of roots and root systems in the field is fraught with difficulties. Foremost among these are the variability of soil (Perrier and Wilding 1986, Daniels and Nelson 1987), on every scale from micro to global (Trangmar et al. 1985), and the variability of root systems (Sutton 1980). Taylor and Klepper (1978) listed 24 soil factors that affect rooting "to illustrate the almost overwhelming complexity of the soil-root system". Research resources are rarely sufficient to permit roots to be extracted and measured in sufficient quantities to produce statistically valid data (Sutton 1978, Miller 1987). If morphological quantification is difficult, rigorous physiological quantification is currently impossible.

Concealment of roots by soil and the lack of parallelism between below- and aboveground growth and development (cf. Troughton and Whittington 1969) are other obvious problems.

Furthermore, interactions between a particular root and the soil with which it is in contact may be influenced by soil-root relationships elsewhere in the root system. Indeed, not only whole root systems, but groups of root systems interconnected through root grafts and collectively supporting stands of trees, may have to be considered (cf. Stone 1974), as must the dynamic responses of roots and root systems to inherent whole-plant growth patterns (Reynolds 1975) and changes in site conditions.

Unfortunately, no technique currently available for quantifying the effects of soil on root behavior — measurement of root mass, root surface area, root number, root length, root number and root length combined, water extraction, the use of tracers, and descriptions of root morphology and root pattern — is wholly adequate (Pearson 1974). Models that seek to account for root distribution in space and time assume that roots are uniformly distributed in each homogeneous soil volume, "a questionable assumption, when so many field data show us that predominance of markedly nonuniform root patterns" (Hamblin 1985).

Soil-root relationships in forests are more complex than those in agriculture, in which most soil-root research has been conducted. Typically, forest soils differ from agricultural soils in having: greater surface relief; less depth; much stronger fertility gradients in the upper soil layers; lower overall fertility; no A_p horizon; greater variability in drainage; and narrower fluctuations of soil temperature, with lower summer maxima and higher winter minima, the result of shading by a perennial canopy and the presence of an insulating blanket of surficial organic matter. Likewise, most forestry crops

differ markedly from agricultural crops. Many of the latter, at least in temperate regions, are harvested after one growing season during which the root systems develop with great rapidity from seminal stage to maturity, their genetic potential interacting with the vagaries of weather during that one season, and with inter- and intraspecific competition highly controlled. In contrast, perennial vegetation competing with forest trees continues to develop dynamically, both above and below ground, for years; the root systems of trees continue to develop for decades, centuries, or even millennia. Furthermore, the lateral extent of tree roots is generally much wider than that of agricultural crops; single roots of *Acer rubrum* L., for example, have been traced 25 m or more from the stem through three or four distinctly different soils (Lyford and Wilson 1964). In both agricultural crops and forest trees, some elements of root systems are ephemeral, dying under stress or after a natural aging process (cf. Fogel 1983), but much of the root system of a tree is truly perennial (cf. Rogers and Head 1969). Thus, Tamm (1950) has emphasized: "In many cases... results of agricultural researches cannot without question be carried over *directly* into the field of forestry, since important differences exist in principle between agriculture and forestry, depending partly on natural causes and partly on man's activities."

Nonetheless, results from agricultural investigations illuminate many forest soil-root relationships. As the intensity of forest management on selected areas increases, the distinction between agricultural and forestry practices will diminish. In some aspects of the hybrid poplar program in eastern Ontario (Raitanen 1978), the two have merged. In such a domesticated forest, site potential is regarded not as a fixed entity but as a variable that may be increased by soil modifications or by combining treatments with genotypes or species responsive to them (Stone 1975).

In forestry, soil-root relations have been studied primarily by deduction from qualitative observations and limited measurements on naturally growing root systems. Experimentation to determine forest tree species' responses to different soil factors has been scarce but will probably increase for species and genotypes used in the domesticated forest. With sufficient input, the various soil properties (and some plant properties) can be modified to improve root growth and plant vigor, whether for a short-term need to establish regeneration or for the continued well-being of a stand. Surface horizons can be treated more easily than those that are deeper, which, however, may also require modification.

Therefore, we also need to determine the relative contributions to tree growth of the various parts of the root system. What, for instance, are the roles and relative efficiencies of roots in deep, cool, moist and nutrient-poor layers subject to slight seasonal temperature fluctuation through the growing season, compared with those of roots in warmer, nutrient-rich surface layers subject to much greater seasonal variation, particularly of moisture and temperature, and with greater root competition?

Genetic control of root growth is seen most clearly in the primary root development of young seedlings, but interactions with the soil environment soon become obvious; the initial root habit in all 100 tree species studied by Toumey (1929) responded to different environmental conditions. The plasticity of root systems varies greatly among species and increases with time (Sutton 1980).

With few exceptions, root system form (Sutton and Tinus 1983) is determined largely by secondary elements (Sutton 1969, 1980) that are highly plastic in response to interacting factors, of which Barlow (1983) recognized three categories: the external environment (physical features of the soil, physical obstacles, temperature, moisture, light, nutrients, pH and gases); internal physiological correlations (relationships with age, position of the root on the plant, the floral or vegetative status of the shoot, and genetic constitution); and internal physiological determinants of growth (permeability, turgor, and cell-wall extensibility). Indeed, not only the disposition but also the kind of root and even the presence or absence of roots depend on this web of interactions.

The general thesis proposed here is that root systems of forest trees develop in response to immensely complex genetic, physiological, and environmental (edaphic and atmospheric) interactions, subject to limitations imposed by (a) aboveground growth, and (b) a limiting level of any of many individual factors. Though individual factors can usefully be examined, the web of interrelationships must never be overlooked.

SOIL FACTORS

Physical soil properties, such as texture, structure and depth, affect root growth in two ways. They present mechanical obstacles to elongation and branching, and they regulate available moisture and aeration (Bilan 1968) and temperature. Texture and structure are critical factors in determining soil bulk density, one of the most useful soil properties to examine in relation to roots.

Soil Bulk Density

Soil bulk density is the mass of dry soil per unit of bulk volume before drying; bulk volume, the volume of soil occupied in the field, is determined before drying the soil to constant mass at 105°C (Ford-Robertson 1971). The relationship between particle density (i.e., mass of solids divided by their volume) (Buckman and Brady 1969) and apparent density is an indication of total pore space (Williams 1971).

Intimately related to structure, texture, porosity, aeration, and water-infiltration capacity, soil bulk density generally increases with depth as organic matter content, root and faunal activity, and porosity decrease. This increase with depth is greater in forest soils than in grassland soils (Lutz and Chandler 1946). In many forest soils, the bulk density of the A₀ horizon is about 0.2, and that of the uppermost mineral-soil horizon is commonly less than 1.0 (Lutz and Chandler 1946). The presence of rocks and sand in a soil favors high bulk densities, whereas the content of fine fractions favors relatively low values. Fragipans and compact tills often exhibit bulk densities of about 2.0 (cf. Mueller and Cline 1959). Bulk density can be affected by changes in soil moisture (Gill 1959).

Within similar soils, the higher the bulk density, the lower the porosity, the poorer the aeration, the slower the water-infiltration rate, and the greater the mechanical impedance to root penetration. Rates of ion diffusion are also affected by bulk density (Barber 1974). "The solid particles of soil create a tortuous path along which an ion must diffuse to reach the root; hence, this reduces the rate of diffusion... The rate of diffusion usually increases when bulk density is increased up to a maximum value; beyond this, the diffusion rate decreases rapidly with further increases in bulk density. Warncke and Barber (1971) found in a study with soft silt loams that the tortuosity (as measured by ³⁶Cl diffusion) was least at a bulk density of 1.3 g/cm³ (Barber 1974).

All these factors are potent influences on tree root development. In a given soil, the ease with which roots penetrate is inversely related to bulk density, unless other factors become more important (Russell and Goss 1974). Halverson and Zisa (1982), for instance, found that the rooting depth of seedling pitch pine (*Pinus rigida* Mill.), Austrian pine (*P. nigra* Arnold) and Norway spruce (*Picea abies* [L.] Karst.) was highly negatively correlated with bulk density; the mean root-penetration depth (over all species) after 90 days was 14.50, 8.85, 4.77 and 1.73 cm, respectively, in two soils

(one a silt loam, the other a sandy loam) compacted to densities of 1.2, 1.4, 1.6 and 1.8 g/cm³.

The bulk density that limits root penetration, designated the *critical bulk density* (Jones 1983), varies with species (Minore et al. 1969, Bowen 1981), soil moisture content (Gerard et al. 1982), and soil texture (Taylor et al. 1966, Jones 1983, Vepraskas 1988). Busscher et al. (1987), noting the difficulty of measuring the critical rooting bulk density (CRBD) directly, defined CRBD as the bulk density at 2 MPa soil strength (the ability of the soil to resist an applied force) and -100 kPa soil-water potential. The range in critical bulk densities reported in the literature is rather wide, 1.1 for a silty clay (Trowse and Humbert 1961), 1.3 for a horizon in some New York State tills (below a non-restricting horizon with a bulk density of 1.6 to 1.7) (Mueller and Cline 1959), and >2.0 for a clay loam (Zimmerman and Kardos 1961). If a mean specific gravity of 2.65 for the solid particles is assumed, the porosity would be about 40% just above, and about 25% within, the restricting till. In soils with root-restricting acid fragipans, however, the depth to the restricting horizon decreased with increasing wetness. In the lowermost non-restricting horizon, these acid fragipan soils with good or imperfect drainage had bulk densities of between 1.4 and 1.5, representing a porosity of about 45%, whereas porosity was about 30% in the restricting pan itself.

The data, tabulated by Jones (1983) from studies of rooting behavior at near-optimum soil water potentials (-5 to -33 kPa), include silt and clay percentages and the bulk densities at which rooting of several crop species were 100 and 20% of maximum. The bulk densities at which root growth was maximum ranged from 1.17 to 1.56 (mean = 1.397); bulk densities at which root growth was 20% of maximum ranged from 1.43 to 1.87 (mean = 1.637). The data showed that "in 10 studies representing 20 soils with a wide range in percentage clay and silt + clay, the two critical bulk densities for root growth [100 and 20% of maximum] decrease as soil clay or silt + clay percentage increases" (Jones 1983).

The moisture content of soil of a given bulk density generally affects penetrability (Taylor and Gardner 1963), though Mueller and Cline (1959) found that very firm, dense, calcareous basal till in west-central New York State formed root-restricting horizons at depths of 50 to 65 cm that were apparently unrelated to drainage within the range from well- through poorly drained moisture regimes.

The level at which bulk density has no effects on root growth may be lower than often supposed. In loblolly

pine (*Pinus taeda* L.) seedlings, root mass and depth of root penetration were significantly negatively correlated with bulk densities above 0.8 g/cm³ (Foil and Ralston 1967). This level probably varies among species.

However, except in limiting cases, bulk density *per se* does not constrain root growth: any constraint derives from the combined interaction of bulk density, pore characteristics and mechanical impedance (Taylor 1974, Gerard et al. 1982).

Various kinds of plowing and/or subsoiling that decrease bulk density and/or soil strength have been used to ameliorate soil conditions for rooting. In New Zealand, naturally dense clays, some compact gravels, soils with hard pans, and soils that have been compacted by forestry operations have increasingly been prepared for planting by the kind of site preparation termed "ripping" (Chavasse and Brunnsden 1977, Chavasse 1978). In this method, conventional rock rippers or rock rippers modified by the addition of two forward-winged tines are used to increase the depth of soil exploitable by the roots of radiata pine (*Pinus radiata* D. Don). The root systems of radiata pine 3 years after planting on non-ripped clay soils on New Zealand's South Island averaged an oven-dry mass of 42 g, with nine lateral roots and 10.4-cm deep tap roots; on ripped but otherwise similar soils, the comparable values were 133 g, 19 lateral roots, and 32.0-cm tap roots (Hetherington and Balneaves 1973). In several coniferous species on upland heaths in northern England and Scotland, the effect on rooting patterns of deep plowing and subsoiling to disrupt compact layers has been described by Yeatman (1955). The initiation of a trial in the Vanderhoof Forest District in British Columbia to determine the effect of tilling (with a three-tined winged subsoiler pulled by a D7 Caterpillar) on the density of a layer of compact clay at a depth of 20 to 40 cm was reported by Osber (1989), although no results are currently available.

Soil cultivation that increases the volume of soil exploitable by roots through its combined effect on bulk density and mechanical impedance often benefits the tree, but may compromise its stability (cf. Chavasse 1978, Brunnsden 1981). This illustrates the precept that unless a silvicultural prescription to ameliorate a soil condition takes all significant interrelationships into account, an attempted cure may be more damaging than the condition it is intended to ameliorate.

Soil Compaction

The distinction between a compact soil and one that has been compacted should be maintained. Root system

morphology can differ dramatically in the bulk soil and in zones of compaction. This has been well exemplified by de Roo (1961, 1969) for tobacco (*Nicotiana tabacum* L.) and by Lowry et al. (1970) for cotton (*Gossypium hirsutum* L.). Tree roots, no less than roots of agricultural crops, are constrained by such layers (cf. Yeatman 1955, Mueller and Cline 1959). Two soils may have identical bulk densities and yet exhibit important differences in rooting if the bulk density of one soil is the product of natural processes whereas that of the other has been obtained by compaction. Compaction modifies pore size and distribution; large macropores are the first to be reduced in volume (Warkentin 1971, McKyes 1985). Shear strength, penetration resistance, and the content and movement of water in soils are also altered thereby.

Soil compaction is the increase in a soil's dry density (McKyes 1985) caused by an artificially imposed force, such as trampling or the use of heavy equipment (cf. Lenhard 1986, Shetron et al. 1988). Tractor weight per unit area of contact, number of passes, and amount of wheelslip contribute to compaction (Davies et al. 1973, McKyes 1985). Compaction resulting from the growth of roots (cf. Barley 1954) is not considered further here, but is discussed later in this report under "Plant Factors". In forest situations, the direct effects of soil compaction may be difficult to distinguish from associated effects of soil disturbance (*in situ* mixing) and soil displacement (lateral movement), such as nutritional impoverishment (Castillo et al. 1982, Froehlich and McNabb 1984, Carr 1988). Puddling, which breaks down soil aggregates, may or may not be independent of soil compaction.

As noted by Rosenberg (1964), researchers have depended largely on data from penetrometer or bulk-density determinations for quantifying mechanical impedance; observation of root behavior has given only qualitative information. The values obtained with a penetrometer are determined not only by the bulk density and moisture content of the soil but also by pore pattern (Warnaars and Eavis 1972), organic matter, and the type of management (Sands et al. 1979, Gerard et al. 1982). Penetrometer resistance in fine sands examined by Warnaars and Eavis (1972) decreased with increasing moisture content, whereas determinations in coarse sands were relatively unaffected by moisture content; the force needed to effect successive 1-mm penetrations of the coarse sands varied greatly. Results in the finer sands were less variable.

Penetrometer values also vary with the shape and dimensions of the penetrometer probe used as well as

with the rate of penetration (Bradford 1986, Vepreskas 1988). The forces acting on the point of blunt and sharp metal penetrometer probes were analyzed by Farrell and Greacen (1966) and Greacen et al. (1968); the assumption was made that the total resistance to the point of a penetrometer is made up of a pressure component, required to expand the penetration cavity at the point of contact, plus the resulting soil-metal frictional component incurred in expanding the cavity.

Gravelly or stony soils give spuriously high penetrometer values, whereas vertically or areally heterogeneous soils have high coefficients of variation that "may simply reflect differences in water content between adjacent layers or peds; [n]ormal averaging procedures of penetrometer values obtained from such soils mask small-scale variations in soil strength and water status which markedly influence root growth distribution" (Hamblin 1985).

In any event, penetrometer data do not directly translate into root growth data; complex interrelationships link probe values, soil penetrability and roots. The main factors and interactions involved were usefully depicted by Greacen and Sands (1980) (Fig. 1). Some roots are able to penetrate soil that offers a resistance to penetrometer probes as high as 300 MPa (Barley et al. 1965), whereas the pressure that can be exerted by roots is probably no more than 50 to 120 MPa (Pfeffer 1893, Barley and Greacen 1967, Greacen et al. 1968), hence "the properties of the roots allow penetration by some mechanism other than that of an ordinary metal penetrometer" (Greacen et al. 1968). Similarly, Voorhees et al. (1975) concluded from their experimentation that friction between the root cap and soil may be negligible. An obvious mechanism for minimizing soil-root friction is the secretion of gelatinous non-cellular mucigel by the outer cells of the root cap (Russell 1977).

Although compacted soil can regenerate (i.e., return to its pre-compaction state) naturally or artificially (cf. Goss 1987, Monnier and Goss 1987), the effects of compaction may persist for decades (Froehlich and McNabb 1984). Compaction of subsoil to depths of 90 cm was still evident 4 years after it had been caused by heavy axle loads of equipment (Voorhees et al. 1986). Even after a soil undergoing compaction has developed sufficient load-carrying capacity to resist further changes in bulk density or total porosity, pore-size distribution can change and further adversely affect plant water relations, aeration and depth of freezing (Munns 1947, Lenhard 1986).

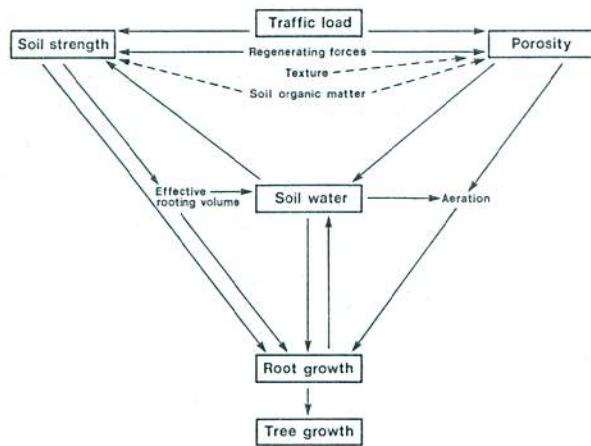


Figure 1. Interacting effects of soil compaction on root growth (after Greacen and Sands 1980).

In some soils, moisture content is an important factor controlling the degree to which compaction will occur under a particular load (Raghavan et al. [1977], cited by McKeyes [1985]); "optimum" soil moisture content for compaction in the test soil was about 15% moisture content by weight; all of the traffic levels produced four to five times as much increase in soil density (i.e., compaction) at a soil moisture content of 15% than in dry soil with less than 5% moisture.

Rooting typically responds to compacted soil by root flattening; reduced length, mass and penetration of roots; and markedly different root distribution compared with that of roots in non-compacted soil (Russell and Goss 1974, Heilman 1981, Feldman 1984, Asady and Smucker 1989). The balance between fungi and tree roots may be significantly disturbed by compaction (Egli 1983). Top growth may (cf. Cochran and Brock 1985) or, at least in the short term, may not (cf. Heilman 1981) be reduced when root growth is constrained by compact soil.

Levels of bulk density limiting to root growth vary widely among soils. On nine different variously compacted soils, Veihmeyer and Hendrickson (1948) observed the extent to which the soils were penetrated by sunflower (*Helianthus annuus* L.) roots: no roots were found at bulk densities of 1.9 or more; in some soils, penetration only occurred at bulk densities of <1.7; clay soils were not penetrated when their bulk densities were 1.6 or more; and the lowest bulk density not penetrated by roots was a clay loam of 1.46 bulk density.

Cultivation to break up dense pans developed by tillage in coarse-textured soils in the southeastern United

States (Cassel 1981) has produced variable relative yield increases in tobacco (*Nicotiana tabacum* L.) across different soils (Vepraskas et al. 1987); the greatest relative increases occurred during dry years on sandy soils with low water-retention capacity, and relatively large responses were obtained on sites characterized as having both bulk densities of 1.63 g/cm³ or more in the lower A_p or E-B horizon and 73% or more sand in the A_p horizon.

Rosenberg (1964) reviewed plant response to "induced pans", a term he applied to "those soils where the restrictive layer is the result of a recently applied compacting force, such as implement traffic or trampling, upon a soil that had, under virgin conditions, physical properties favorable to the penetration of roots and water (Raney et al. 1955). Plant response to compaction", noted Rosenberg, "will vary with soil type, plant species, and climate. It is clear that the plant in compacted soil may respond to alterations in mechanical impedance, aeration, moisture availability, and heat flux of the soil. Plant response can be attributed to any of these phenomena within critical density ranges for a given soil under a given set of climatic conditions. Further, it is clear that plant response to compaction, if expressed over a wide enough range, is parabolic... a parabolic relationship implies that interacting factors are affecting plant growth...".

Thus, the response of a plant to soil compaction may be effected by a combination of changes in any of several major factors (including mechanical impedance, aeration, moisture availability, and heat flux in the soil) within critical density ranges for a given soil under a given set of climatic conditions (Rosenberg 1964). Depending on the soil type, climatic conditions, plant species, and possibly on the stage of development of the plant when its roots encounter compact soil conditions, one or more of these factors may become critical for plant growth at any given time (Rosenberg 1964).

Soil Texture

Effects of soil texture on root growth (cf. Taylor et al. 1966, Sutton 1968, Gerard et al. 1972, Haag et al. 1989) are exerted largely through modification of other soil properties, especially soil structure, soil strength and soil fertility. An early study that pointed to the importance of mechanical impedance was one by Anderson and Cheyney (1934), who had set out to investigate the effect of soil texture on root development. However, Jones (1983) reported significant relationships among soil bulk density, soil texture, and root growth of several

crop species; he showed that soil texture can be used to estimate the bulk densities at which root growth will be severely constrained at near-optimal soil water contents.

Soil Structure

Soil structure refers to the aggregation of primary soil particles into compound particles or clusters of primary particles that are separated from adjoining aggregates by planes of weakness (Anon. 1951). Hamblin (1985) defined soil structure in terms of the pore system: "There is no question that sufficient field data now exist to convince us of the profound influence that the soil-pore system has on water and root growth...". Nevertheless, the specific structural properties of soils that affect crop growth have never been satisfactorily defined "and it is improbable that any single laboratory test, or group of tests, can be devised to do so" (Williams 1971).

Two main approaches have been taken in efforts to characterize pores and pore systems. The size of intra-aggregate pores can be inferred indirectly from the moisture-retention properties exhibited by a soil (Childs and Collis-George 1950, Bullock and Thomasson 1979). Direct methods include the use of polyester casts (Spurr 1969, Rogaar 1974) with ultrathin sectioning of resin-impregnated soil (Bui et al. 1989), non-stereological image analysis (Murphy et al. 1977), and stereological methods (Weibel 1979, 1980), including computer-assisted tomography (Yanuka and Elrick 1985, Moran et al. 1989, Warner et al. 1989, McBratney and Moran 1990).

Reid and Goss (1981) investigated the influence of roots of five agricultural species on the stability of aggregates in two soils; differences among species became obvious within 6 weeks. These workers concluded that an "important implication" of their results was that conventional studies of air-dried aggregates alone "could have led to some quite misleading conclusions concerning the effects of roots on aggregate stability"; in temperate regions, the rhizospheres in most agricultural and forest soils seldom become air-dry.

Soil Pores

That portion of a soil volume occupied by air and water is the pore space (Buckman and Brady 1969). Voids, ranging from 0.003- μm separations between clay plates to cracks or channels tens of centimetres across (Hamblin 1985) permeate the soil fabric. Porosity, i.e., the volume percentage of the total bulk not occupied by solid particles (Hamblin 1985), is often used to quantify soil pores, but pore space is more logically described as

the void ratio, i.e., the volume of voids to the volume of solids (Hamblin 1985).

The total volume of all voids, pores, or porosity in a given volume of soil may be calculated from the formula given by Buckman and Brady (1969):

$$\text{pore space (\%)} = 100 - 100 \frac{\text{bulk density}}{\text{particle density}}$$

The amount and character of the pore space is determined largely by the arrangement of the solid particles. Total pore space varies with tillage and compaction and with swelling and shrinkage of clay and organic fractions. For expanding clay soils, the volumetric change of the solid particles can be substantial, but the pore space in most soils is virtually constant; water entering the soil profile must displace the air that had filled the pore spaces of the dry soil (Huck 1984). The pore space in freshly tilled topsoil may be about 125% and, in some organic soils, as high as 140%; subsoils generally have about 45 to 80% pore space, whereas the pore space may be less than 25% in cemented or indurated layers (Hamblin 1985).

After rain, water will continue draining internally within a soil until the hydraulic potential is equal at all points (Hillel 1980a). Water flow depends on a hydraulic gradient determined by the difference in pressure potential between two points, and the flux depends on the product of the gradient and the water content, whereas the rate of flow depends on the pore geometry (Hamblin 1985).

The selection of pore-size classifications, together with the descriptions, dimensions, and terminology presented by Hamblin (1985), includes pores ranging from cryptovoids of 0.1- μm equivalent cylindrical diameter (ECD) and <-3000 kPa capillary potential (CP) to coarse pores >5000 μm ECD and >-0.06 kPa CP. Designations generally reflect size or supposed function: micropore, very fine pore, fine pore, medium pore, ultramicropore, microvoid, mesopore, macrovoid, bonding pore, residual pore, storage pore, transmission pore, fissure, pressure-gradient pore, gravitational pore and channel-flow pore. Hamblin's (1985) table of pore dimensions of biological origin or significance is well worth reproducing (Table 1).

Pores act as ports of entry into soil for water and oxygen and as ports of exit for carbon dioxide; the size, shape and arrangement of the pores are the most important factors controlling the movement of moisture, oxygen and heat within the soil. An important fact to note is that the pore-size distribution in a soil can vary independently of total porosity (Lenhard 1986).

Table 1. Pore dimensions of biological origin or significance (reproduced from Hamblin [1985]).

Average pore diameter (μm)	Biological significance	Reference
2,000 – 50,000	Ant nests and channels	Green and Askew (1965)
1,500 – 8,000		Barnes and Ellis(1979)
500 – 3,500	Wormholes	Barley (1959)
2,000 – 11,000		Ehlers (1975)
6,000		Bouma et al. (1982)
300 – 10,000	Tap roots of dicotyledons	
500 – 10,000	Nodal roots of cereals	Nye and Tinker (1977),
100 – 1,000	Seminal roots of cereals	Russell (1977)
50 – 100	Lateral roots of cereals	
20 – 50	1st- and 2nd-order laterals	
5 – 10	Root hairs	
1,000	Root-root hair cylinder in clover	Caradus (1979)
30	"Field capacity" (-10 kPa)	
0.5 – 2	Fungal hyphae	Griffin (1972)
0.2 – 2	Bacteria	
0.1	Permanent wilting point (-1500 kPa)	

Soil porosity depends largely on the arrangement of the solid particles, especially the aggregates. However, although structure is particularly important, the effect of texture is considerable. Porosity in sandy surface soils ranges between 35 and 50%; in silty and clay soils the range is from 40 to 60%, and is very occasionally higher (Buckman and Brady 1969).

Clay and organic matter are especially involved in the formation of aggregates and in maintaining porosity through the action of swelling and shrinking under the influence of changing water content. By no means immutable, the pore characteristics of soils change with wetting, drying, heaving and compaction (e.g., by traffic), as well as through the action of plant roots and soil fauna.

Pores largely determine the paths available for root penetration. The size of the openings is more important than the amount of porosity in plant and moisture relationships (Stephenson and Schuster 1939). The higher-order roots of many herbaceous species have been shown by Wiersum (1957) not to penetrate rigid openings less than 0.2 mm in diameter.

Pore size strongly influences moisture relations. Pores larger than about 0.05 mm in diameter are not filled with water at field capacity; residual water is held at a tension of about 0.01 MPa, sufficient to halve the rate of root elongation (Russell and Goss 1974).

Pores can constrain root growth mechanically in two main ways. First, elongation of a root into a rigid pore cannot occur if the cross-sectional area of the root exceeds the diameter of the pore (Greenland 1979). Secondly, once a root has passed through a pore, the diameter of the root can increase until mechanical impedance becomes limiting (Russell and Goss 1974). On either side of a constriction, a root may continue to thicken in the absence of such impedance. Except in sandy soils, the pore space of most soils is mostly made up of pores less than 0.001 mm in diameter (Greenland 1979). In loams and clays, in which few pores are larger than 0.05 mm in diameter, coniferous roots generally do not penetrate aggregates; penetration is restricted to fissures between aggregates. Conformance of roots to structure is well illustrated by Figure 11 in Sutton (1969), which shows white spruce roots in a silt loam (Fig. 2).

Wiersum (1957) calculated that sand with single-grain structure will have pores <0.2 mm in diameter when the soil particles are smaller than about 0.8 mm, i.e., in about the middle of the coarse-sand range of particle sizes. The significance of the 0.2-mm pore size is that root penetration is generally precluded by pores smaller than this (Wiersum 1957).

The factors that control the segregation of ice in soils subject to seasonal freezing are influenced by the pore

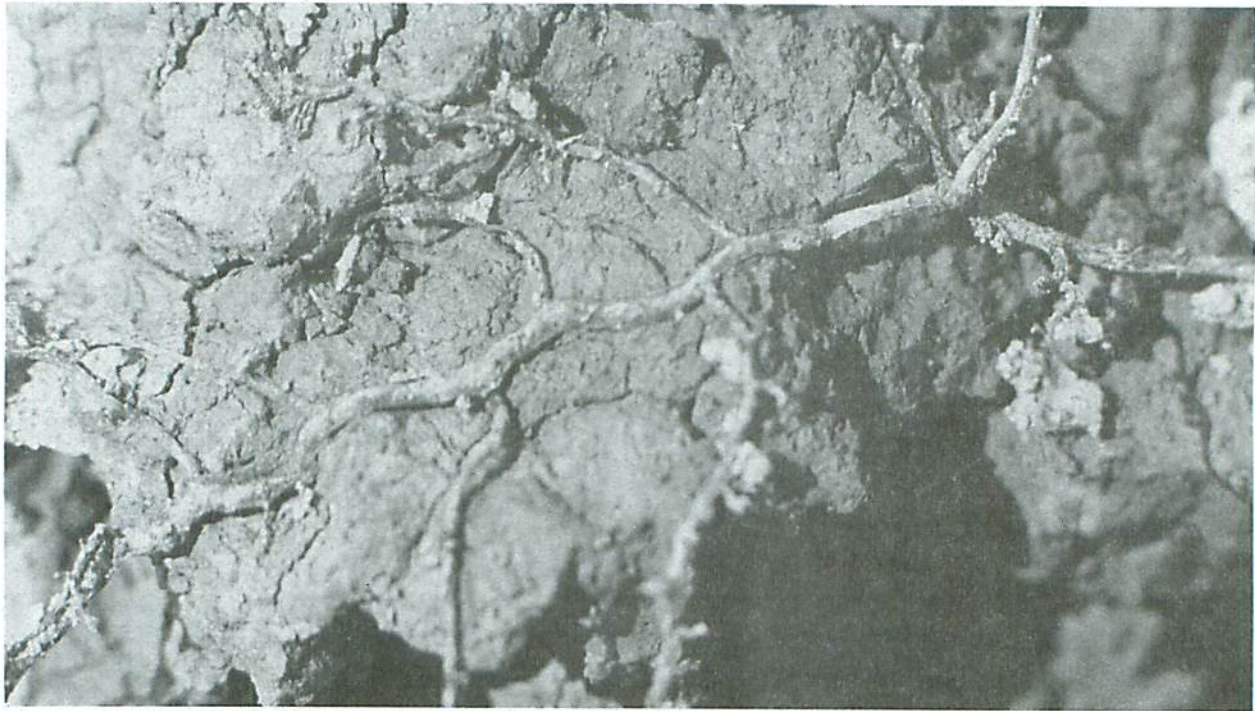


Figure 2. White spruce roots in a silt loam.

characteristics. To the extent that soil moisture solidifies as polycrystalline ice, the mechanical strength of the soil increases greatly and the capacity of the soil to transmit water declines (Miller 1980). Other important side effects of the freezing process, slight in gravels and coarse sands but increasing with decreasing particle size, include freezing-induced redistribution of water and frost heaving (Miller 1980). High levels of organic matter and/or clay promote frost heaving, provided that there are enough large pores for ice nucleation and small pores for capillary transport of water (Bouyoucos and McCool 1928, Taber 1930, Beskow 1935). Soils that are totally inorganic and that contain >3% by weight of particles finer than 0.02 mm have been classed as frost susceptible (Layton 1985). Plants undergo frost heaving when the frozen surface of a wet soil encasing their stems is thrust upwards by ice pressure (Schramm 1958); if the plants are rooted in unfrozen subsurface layers, their roots are pulled up or, if too firmly rooted, broken (Schramm 1958) or abraded (Haasis 1923). Annual natural pruning of roots of frost-heaved white spruce may occur for several years (Sutton 1968) or even decades (Sutton 1991) after outplanting.

Sturdy and apparently well established white spruce (*Picea glauca* [Moench] Voss) were heaved and left prostrate 4 years after outplanting on a sandy clay loam in eastern Ontario (Sutton 1968). Excavations revealed

that, especially on the loam soils, one side (in plan view) of many root systems of 4- and 5-year-old white spruce was well developed, with few tertiary and higher-order roots on the other side in striking contrast with a more juvenile form; this phenomenon always seemed to be associated with frost heaving, and the evidence suggested that it resulted from the relief of lateral and vertical forces developed during heaving through root shearing or stripping on the least-well-anchored side of the root system. Once begun, the phenomenon would be self-perpetuating until anchorage of the root system as a whole became sufficient to resist further frost heaving. In some old-field plantations of white spruce on clay soils in northeastern Ontario, recurrent frost heaving has left 20-year-old trees procumbent, attached to the soil by only two or three roots that are lying loose on the surface of the ground for, in some cases, more than 50 cm of their proximal length (Sutton 1991).

The definition of pore boundaries may be poor, as when clay particles are dispersed within the soil solution (Greenland 1979). In fact, the pores in a soil are not to be thought of as forming a rigid framework; they may vary in number, size, and/or arrangement in response to changes in temperature, moisture, flora or fauna. For some purposes, however, the static structure of soil pores may be usefully studied, for example, with the help of polyester casts (Rogaar 1974).

Soil fauna, notably earthworms (Darwin 1881, Lee 1985), are valuable in that the channels they create are continuous and allow roots to penetrate compact zones of soil that would otherwise be closed to them. Existing channels, which may have been formed during a rare combination of circumstances that provided briefly favorable conditions for root growth or faunal activity, may be important even when they are not initially large enough to accommodate a root; at least in some species, a root is able to widen an existing channel more easily than to make a new channel of its own (Greacen et al. 1969). This leads naturally to a consideration of soil strength.

Soil Strength

Soil strength has been defined as the ability of a given soil in a particular condition to resist or endure an applied force (Taylor 1974). Such resistance, termed *mechanical impedance* or *physical impedance* (Wiersum 1957), can distort normal root growth patterns (Jones 1983, Taylor 1983). Mechanical impedance is a difficult subject to study because of the similarity of the effects produced by dense soil, excess moisture and poor aeration, as well as by the interaction among these factors. Nevertheless, bulk density, soil water content and pore-size distribution are obviously important determinants of soil strength (Letey 1985). Models developed by Gerard et al. (1982) for soil strength and root growth varied with soil type, soil depth and/or clay content; root growth in two soils and at all depths was significantly influenced by soil strength, volumetric water content, the presence of voids and clay content. The critical soil strength (the measured probe pressure at which root elongation ceased) in Gerard et al.'s study was a function of clay content (%) and ranged from 600 to 700 MPa in coarse-textured soil to 250 MPa in clay soil.

Root growth decreases as mechanical impedance increases, in concert with decreasing soil aeration (Eavis 1972, Warnars and Eavis 1972, McCoy 1987). On the basis of an aeration-deficiency index designed to separate the effects of impedance from those of aeration, Eavis (1972) found that root growth of pea (*Pisum sativum* L.) was influenced by aeration in sandy loams with less than 30, 22 and 11% gas-filled pore space at low, medium and high bulk densities, respectively; effects attributable to restricted water availability were found only at soil strengths > 35 MPa, and in the absence of mechanical impedance, no effect due to moisture stress was seen until matric potential exceeded 18 MPa. According to Letey (1985), mechanical impedance,

particularly in poorly structured soils with high bulk density, may become limiting to root growth at a soil water content higher than that which would be limiting on the basis of available-water determinations. Even in sands, important variations in both mechanical impedance and aeration occur as a result of variations in grain-size distribution and moisture content (Warnars and Eavis 1972).

As mechanical impedance approaches root-limiting values, its influence on root morphology becomes increasingly apparent. This response varies with pore pattern. Roots of three test species were nearly straight and evenly tapered in fine sands, whereas those in coarse sands were "markedly crooked and varied in thickness and in cross sectional shape" (Warnars and Eavis 1972). The following is worth repeating:

"In the coarse sands the pores permitted the entry of the root tip into crevices in which it was wedged between a few individual sand grains. Because of the size and shape of the grains the stress distribution over the root tip was not balanced as in finer soils, and the cine films showed that growth took place preferentially at any place on the growing region where the stress encountered was low. The root bulged into the pores and took on the shape of the pore space when the tip was restricted. The swelling continued until there was sufficient reaction to allow penetration, or until the root had curved into a position from which further elongation could take place. The extent to which the root bulged to take on the shape of the pore space was very marked in pea and corn, there often being tuberous and winged-shaped pieces of tissue along the root. Impedance was greater and root elongation was less in [coarser] sand 2 than [sic] [finer] sand 1 since although the grains were smaller they were not small enough to prevent entry of root tips into individual pores. In the case of the thinner grass root the crooked appearance was especially marked in sand 2 but was also observed in sand 1 although many of the pores must have been larger than the roots. The [grass] roots were not able to steer a course completely avoiding mechanical impedance and in sand 2 there were signs that the grass root tip sometimes entered blocked pores" (Warnars and Eavis 1972).

Root growth ceases after soil strength reaches some critical value, which is influenced by texture and plant

species (Gerard et al. 1982); this value was taken by Busscher et al. (1987) to be 2-MPa resistance to a flat-tipped penetrometer 5 mm in diameter. Several studies were cited by Russell and Goss (1974) to support the conclusion that root elongation is reduced considerably when subjected to pressures of 5 MPa or less.

The response of lateral roots to mechanical stress has been studied less than that of root axes, but the development of both appears to be affected equally when the diameter of the pores in the medium is less than that of the lateral roots (Russell and Goss 1974). However, if only the root axes experience mechanical stress, as when pore diameters are intermediate between the diameters of the root axes and those of the lateral roots, there is considerable proliferation of lateral roots (Russell and Goss 1974). In this manner, a root system seems to compensate for rooting difficulties related to soil strength.

A compacted soil differs from a soil with high aggregate strength in that the former offers fewer zones of weakness for permitting root penetration (McCoy 1987).

If a root is to enter a zone of soil, entry must be effected either through a pore as large as or larger than the diameter of the root tip, or the root tip must be able to force its way between individual soil particles or aggregates. Differences in this ability exist among species. For example, root development of both jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* [Mill.] B.S.P.) was virtually unrestricted in a growing medium of fine-textured silica particles. With coarse-textured particles, however, jack pine root development was severely restricted, whereas there was little effect on black spruce rooting. Bulk densities of the two media were similar (Armson and Shea 1970).

In a rigid system, roots are able to penetrate only pores with diameters larger than that of the young root (Wiersum 1957). However, pores smaller than the root diameter will not prevent root growth provided the root can displace soil particles and enlarge the pore sufficiently to permit penetration (Miller and Mazurak 1958). Even modest pressures, far short of limiting, significantly reduced the elongation rates of barley (*Hordeum vulgare* L.) roots over a range of pore diameters between 16 and 157 μm (Russell and Goss 1974). Both the rigidity of the system and the size of the pores control root growth (Aubertin and Kardos 1965).

In Taylor's (1974) view, a particular root increases in length during primary growth when cells of the meristematic region divide, elongate, and push the root tip forward through the surrounding material. The driving force in the elongating cells is turgor pressure, which

must be sufficient to overcome the combined constraints offered by cell walls and the external material. Soil conditions will affect the magnitude of all three factors: cellular turgor pressure, resistance of the cell walls to strain, and resistance of the external medium to deformation. However, Russell (1977) doubted that the effects of mechanical impedance are explainable entirely on the basis of interference with the processes that govern elongation of vacuolating cells. Russell and Goss (1974) had found that, when a barley root was subjected to increasing mechanical impedance, the rate of elongation decreased most rapidly at low values of impedance. Russell (1977) also argued that the final volume of root cells is not reduced by mechanical stress, although there is considerable evidence to the contrary that cell elongation is more affected by mechanical impedance than is cell division (Eavis and Payne 1969, Goss 1977, Wilson et al. 1977, Goss and Russell 1980); cell division continues unabated (Wilson et al. 1977) except at extreme levels of impedance, when cell division is also affected (Eavis and Payne 1969).

Limited penetration of single-grain-structured sand by roots may be thought to be evidence of genetically controlled shallow rooting; however, penetration in such soils is often limited by mechanical impedance (Sutton 1969, Fayle 1975), which, rather than genetic control, may be the main cause of shallow rooting among trees of some species on some deep sands (cf. Bannan 1940). Other species and/or other sands are not associated with shallow rooting; the taproot of a mature longleaf pine (*Pinus palustris* Mill.) on deep sands in western Florida, for instance, was found to descend 4.32 m (Heyward 1933). Taylor (1974) considered that soil strength influences root growth more than does soil structure in sandy soils.

Soil strength may vary greatly with soil moisture conditions. It can also be ameliorated, albeit often temporarily, by cultivation, windthrow, etc. Roots may be able to enter or pass through zones of compact soil during times, perhaps few and brief, when one or more favorable factors effect a reduction in mechanical impedance. Such roots are commonly deformed (Sutton 1969). Once a zone has been penetrated, the prospects for recurrent penetration are enhanced.

A model for root elongation rate, developed by McCoy and Boersma (1986), includes a term that accounts for mechanical resistance. The model gives an equation for root elongation rate (R_{el}) as a function of the thermodynamic coefficients associated with tissue water relations, the tissue synthesis of biomass, the

Thus, soil hydraulic conductivity is an exponential function of soil water content (Gardner and Ehlig 1962). The more connecting points and the thicker the water films, the more easily water can move through the soil matrix (Huck 1984). The hydraulic conductivity of a saturated soil varies with the pore characteristics of the soil; the influence of texture *per se* is weaker than might be supposed. For example, values of hydraulic conductivity determined in the Netherlands varied from 0.1 m/day for fine sands to 30 m/day for coarse sands, from 0.01 to > 30 m/day for clays, and from 0.01 to > 10 m/day for peats (Hooghoudt 1952, van Beers 1983). Hydraulic conductivity can decrease by one or two orders of magnitude when compaction occurs (McKyes 1985). The reduction is generally logarithmic. Compaction also reduces the amount of available water that can be stored and the proportion of air in the soil; the health of most plant roots is compromised when soil air forms less than about 10% of the total soil volume. McKyes (1985) also noted that "drainage of a soil will also be slowed, which

where ψ_a and ψ_b are the respective soil water potentials at a and b , and R is the resistance to flow. Clearly, soil properties determine all three components of the right-hand side of the equation. Similar equations can be used to express the pathway of water through a plant, from soil to atmosphere, as a series of resistances. The significance of the resistance to water flow within the plant has often been neglected, however, and the location of the resistance to water flow within the plant vascular system and especially in the root system is not well established (Reicosky and Ritchie 1976).

$$F = \frac{\psi_a - \psi_b}{R}$$

ing force divided by the resistance (Kramer 1983), i.e.: behavior of water movement in soil and plants can be explained reasonably well through this concept of water potential, ψ . The components of ψ are considered to include matric potential (capillary and surface forces), osmotic potential, and pressure potential (hydrostatic pressure). The rate of movement, or flux (F), of water between two points (a and b) is determined by the driving force divided by the resistance (Kramer 1983), i.e.: behavior of water movement in soil and plants can be explained reasonably well through this concept of water potential, ψ . The components of ψ are considered to include matric potential (capillary and surface forces), osmotic potential, and pressure potential (hydrostatic pressure). The rate of movement, or flux (F), of water between two points (a and b) is determined by the driving force divided by the resistance (Kramer 1983), i.e.:

Of the many factors that influence root growth and root function, soil water is of particular importance since it acts on growth and function both directly and indirectly through its influence on other factors such as nutrition, aeration, mechanical impedance and soil temperature (Eavis and Payne 1969). As Kramer (1963) cautioned, however, a given level of soil water stress cannot be assumed to equate with a similar level of plant water stress. The interrelated effects of soil moisture, soil drainage, soil aeration, soil fertility, soil temperature and soil mechanical impedance, individually and collectively, are the prime determinants of root system architecture. The profound effect exerted by the distribution of water in the soil results in part from the fact that oxygen diffuses 10,000 times more rapidly through the gas phase than through the liquid phase (Greenwood 1969). Hydraulic conductivity is defined as the flux per unit of hydraulic gradient, the latter being the potential dif-

Soil Moisture

One of the difficulties in evaluating the effects of mechanical impedance on roots is to separate these effects from those of excess moisture and poor aeration (Wiersum 1957). More fundamentally, McCoy and Boersma's (1986) model shows that the interrelationships among the mechanical properties of the soil, the biophysical water relations of the root tissues, and biosynthetic considerations need to be considered jointly, although determinations of the water potential, mechanical properties of the cell wall, and tissue density in elongating root tips is a difficult task (McCoy 1987).

where N is the relative symplastic water content ($\text{cm}^3 \text{cm}^{-3}$), P is a tissue density term (g cm^{-3}), ψ is the total water potential at the root tip (J cm^{-3}), T_o is the overburden potential of the root tip as a result of a mechanical resistance (J cm^{-3}), ΔG is the Gibbs energy change for biosynthesis (J g^{-1}), α_p is the rate of strain biosynthesis (g cm^{-3}), and α is the tissue plasticity (J cm^{-3}). The constant 1.183×10^8 is a conversion factor to convert energy units of J g^{-1} to growth rate units of mm h^{-1} . McCoy (1987) used this equation to study the rate of root elongation in relation to penetration resistance and soil aeration.

$$R_{el} = 1.183 \times 10^8 \sqrt{\frac{d}{a} \left[\frac{N(\psi_o + T_o)}{\Delta G \alpha_p} + 1 \right]}$$

mechanical properties of the cell wall, and the overburden potential created in the root tip by the soil penetration resistance (McCoy 1987):

leads more readily to high degrees of saturation in rainy periods" and thus to deficient aeration.

Hydraulic conductivity of the bulk soil does not determine the rate of infiltration into a mineral soil exposed by cultivation; infiltration is controlled by the crust or seal that commonly forms on the surface of such soil under the impact of raindrops and/or slaking (McIntyre 1958, Sharma et al. 1981, Callebaut et al. 1986). A two-fold difference between the two soils has been measured (Freebairn et al. 1989); greater disparities may be common. The structural differences between a crust and the underlying soil have important consequences in relation to water infiltration (Boiffin and Monnier 1986, Kutilek 1986) and seedling emergence (Hanegreefs and Nelson 1986, Raats 1986).

The hydraulic conductivity of soil in the immediate vicinity of a root may also differ markedly from that of bulk soil according to Huck (1984), who cited supporting evidence from the work of Reicosky et al. (1982) and Zur et al. (1982).

The potential energy of the soil water and the soil hydraulic conductivity are the two physical properties or characteristics most useful in quantitatively describing the soil water system (Gardner 1983). Plant root systems affect the hydraulic conductivity of the surface soil layers (Stanhill 1986). The important parameter linking soil water with plant growth is soil water potential, not soil water content (Letey 1985). For a given soil, the relationship between water content and water potential is superficially simple, although the non-uniform depletion of soil water by roots results in non-uniform water potential through the rooting zone. Under field conditions, roots absorb water from soils at different depths, with different water contents and different physical properties (Taylor and Klepper 1978).

With minor exceptions, all the water used by a tree must first pass from the soil into a root. Provided that other factors such as aeration and temperature are non-limiting, the water in contact with absorbing roots is normally readily available. As a root depletes water from the surrounding soil, the movement of water through the soil towards the root becomes too slow to be important in supplying the requirements of a rapidly transpiring plant (de Roo 1969). With increasing depletion, the soil water accruing to a plant from soil penetrated by further root growth becomes increasingly important. Similar considerations underline the desirability of maximizing soil-root contact during out-planting of bareroot stock (Newman 1974, Sutton 1978).

Low soil water contents not only reduce photosynthesis (Reid 1974) and root elongation rates but also may accelerate root shedding (Taylor 1983). Increasing dryness of soil also decreases soil hydraulic conductivity, reduces root diameter, reduces the water potential of the soil around roots, and probably increases root suberization (Cole and Alston 1974, Taylor 1983). Tinker (1976), in reviewing root shrinkage in relation to radial resistance to water flow, has discussed the possible effects of mucigel, root hairs, vapor gaps, asymmetrical arrangement of shrunken roots in soil pores, and micro-scale arrangement of soil particles. Cole and Alston (1974) have shown that root diameters may decrease by 50% as they dry from -20 to -100 MPa. For a root that has grown along a ped surface, soil shrinkage may decrease soil-root contact, but if the root has created a pore through a ped of clay soil, the pore itself may shrink as the soil dries and thus maintain root-soil contact (White 1975). Generally, however, root shrinkage probably causes a gap at the root-soil interface (Taylor and Klepper 1978). Root tissues also shrink diurnally (Huck et al. 1970).

Stones have been used to aid plantation establishment in dry climates, e.g., by placing three flattish stones on the surface of the ground around each planted tree (cf. Heidmann 1963). While some of the beneficial effect can be attributed to vegetation control, condensation of moisture on and under the cool stones at night must also be beneficial.

The major cause of differences in the distribution of roots of agricultural crops under field conditions at any one place is variation in water supply (Russell 1977). The effect of such variation is more clearly apparent with agricultural than with tree crops, yet trees and their root systems must necessarily respond too, albeit over a much wider range of time scales. A good example of a medium-term response is to be found in the account by Stone et al. (1954) of the malady that began to affect red pine (*Pinus resinosa* Ait.) seriously on some sites in New York State in the mid-1940s:

"All of the affected plantations observed occur on soils classified as imperfectly, poorly or very poorly drained. These several considerations, together with evidence of massive root destruction in the absence of primary pathogens, strongly suggest deficient soil aeration as the major factor involved in the death and stunting of red pine plantations. According to this view the

stands currently affected were favored by a long sequence of near-normal or below-normal May precipitation, a sequence that at Ithaca endured from 1920 to 1939 with but one exception in 1929. Even the appreciable May excess at some stations in 1940 may have had little lasting effect. In 1943, however, and repeatedly from 1945 to 1947, heavy May and May-June rainfall caused prolonged soil saturation and often led to killing or partial destruction of all but the shallowest roots."

Day (1959) also provided a good discussion of the interrelations of soil moisture, root and crown development, and tree health with site and climatic conditions. Halle et al. (1978) emphasized "the dynamic image... of the environment yielding not steady, but pulsating, energy flows to the plant and of the latter's response by a pulsating, not steady, production pattern".

Soil moisture exerts its effect on nutrition through its contribution to the factors that control mass flow, which occurs only when soils are moist enough to permit uptake of water by plants. Crops usually obtain most of their requirements of calcium, magnesium and sulfur through mass flow (Binkley 1986). Diffusion, which occurs much more rapidly in water-filled pores than through water films, supplies most of the phosphorus and potassium required by plants. Nitrogen travels in significant amounts via both pathways.

The view that the effect of waterlogging depends on the physiological and metabolic condition of the plant is supported by Greenwood's (1969) work with cabbage (*Brassica* sp. L.) and mustard (*Brassica* sp. L.); the metabolism of non-woody plant roots under anaerobic conditions is quite similar to that of tree roots (Hook and Scholtens 1978). Greenwood (1969) concluded that "it is short periods of anaerobic conditions rather than long periods of low mean oxygen concentrations that are likely to cause restricted plant growth". In Greenwood's view, anaerobic zones and consequent growth restrictions will occur only when the soil is almost completely waterlogged, and the most dangerous period is when heavy rainfall and high temperatures coincide. In agriculture, a single day's waterlogging at a critical time can reduce final yields by more than one third (Erickson and Van Doren 1960). As Stone et al. (1954) and Day (1959) have pointed out, the influence of soil factors on a long-lived plant must be appraised in terms of the extremes presented as well as the average conditions, particularly when the extremes may have lethal consequences.

In permanently hydromorphic soils, the oxygen requirements of roots are satisfied by various adaptations that enable roots to obtain the oxygen they need (Kickuth and Grommelt 1983). Aerenchyma (Sutton and Tinus 1983) is common in the roots of plants that tolerate flooding, for instance, and the negatively geotropic pneumorhizae of some swamp-inhabiting trees may grow upwards from horizontal main roots and reach 30 cm above the waterlogged soil surface (Sutton and Tinus 1983). Slash pine (*Pinus elliottii* Engelm.) roots grown in seasonally or permanently saturated soils have been found to have a continuous pathway that permits longitudinal movement of air; segments of a large lateral root of the hydrophytic pond cypress (*Taxodium ascendens* Brongniart.) had much greater air conductivity than had the slash pine sinker roots (Anon. 1985). This suggests that slash pine roots function aerobically in soils that are saturated and anaerobic, rather than passively tolerating anaerobic conditions.

Much of what has been discussed in this section on soil moisture might have been included as appropriately in the next section on soil oxygen. Likewise, discussion of soil mottling would not be out of place in either section. Its inclusion here will serve as a connecting link.

Soil color, and especially mottling (cf. Simonson 1951), can offer clues about the moisture and aeration conditions within a soil. Bright colors in the mineral horizons indicate good aeration and good drainage; muted coloration bespeaks impeded drainage (Clarke 1957). The color of the soil in the immediate vicinity of roots is useful diagnostically: when the channels of living roots are picked out in paler colors than are presented by the surrounding soil mass, this suggests that drainage is impeded, as the roots have reduced oxidized compounds in the rhizosphere (Clarke 1957). After death and decay of the root, the root channel may allow oxygen to penetrate and reoxidize the gray-green reduced compounds to bright rusty yellows and browns.

Soil Oxygen

The term "soil aeration" encompasses a "complex group of processes that is altogether too elusive and too incompletely understood to be definable unequivocally by any single measurement" (Hillel 1980b). The mathematical analysis of gaseous diffusion in soils is discussed by Kirkham and Powers (1972).

The intimate relationship between soil aeration and soil moisture has already been noted. Soil aeration is expressed either as the oxygen tension in the soil profile (i.e., the difference between the partial pressures of

oxygen in the soil and atmosphere) or the oxygen diffusion rate (ODR) through the soil (Saglio et al. 1984, McCoy 1987). Oxygen supply to the root is reduced if either oxygen tension or ODR declines. Most agronomic and horticultural field crops are sensitive to oxygen deficiency before soils become strongly reducing (Letey 1985). Root elongation begins to slow when declining oxygen concentrations fall below about half atmospheric concentrations (Jackson and Drew 1984). The physiological response of the root to insufficient oxygen is that fewer new cells are produced, though final cell size is not affected (Lopez-Saez et al. 1969); mechanical resistance has the opposite effect (i.e., smaller cells but no reduction in number).

Plant roots consume large quantities of oxygen. In most cases, oxygen enters the root from the soil, though transport of oxygen from aerial plant parts may occur to a greater extent than popularly supposed (Greenwood 1969). Respiration in plant roots is an essential reaction for water and ion uptake (Pearson 1966). In tree seedlings, lenticels in the stem can certainly be a major avenue of gas exchange, but their adequacy in mature trees and the problem of the length of internal gas diffusion pathways have not been properly evaluated in flooded root systems (Hook and Scholtens 1978). Greenwood (1969) was able to show that, at least with mustard (*Brassica* sp. L.), the metabolic activities of roots were unaffected by lowering oxygen concentrations at the root surface until the concentration was extremely low. He criticized a number of other experiments that seemed to show relatively high oxygen partial pressures impeding root elongation because no attempt had been made to minimize the path lengths of oxygen diffusion through the aqueous phase in those experiments: "Thus, as oxygen partial pressures can drop steeply in the water and around roots, the oxygen partial pressure at the root surfaces when elongation was restricted must have been much less than the values in the gas phase".

On the basis of his experimental data and from theoretical considerations, Greenwood (1969) argued persuasively that "as far as the effects of aeration on root growth are concerned, the sole interest is in the extent of oxygen-free zones in the soil." The extent of such zones is influenced enormously by the distribution of water in soil, which in turn is highly dependent on the soil pore system. With a given amount of gas-filled pore space, the smaller the pores, the more effective the aeration; with larger pores, the area of interface is smaller and the extent of anaerobic zones larger.

Oxygen stress affects more than one plant function. Variations in soil oxygen supply, while affecting current rates of elongation, did not affect the growth potential of pea (*Pisum sativum* L.) roots in terms of elongation: after short or long periods of oxygen shortage, roots were found to respond immediately to an increased oxygen supply with elongation rates that seemed to be neither restricted nor stimulated by the previous treatment (Geisler 1965). Geisler postulated that the internal oxygen status of the roots was sufficient to maintain full viability.

Permanently saturated soil is not exploitable by the roots of the great majority of tree species. Waterlogged soil is detrimental to roots not only because of oxygen deficiency but also because some products of incomplete aerobic metabolism of microorganisms are toxic to root tissues. The relative tolerance of flooding among tree species is apparently correlated with specific physiological adaptations — accelerated anaerobic respiration and the ability to oxidize the rhizosphere (Hook and Scholtens 1978).

Several studies have seemed to show a marked interaction between oxygen supply and mechanical impedance. Gill and Miller (1956), for example, after ingenious experimental work, reported that the greater the compressive stress on a root, the greater was the oxygen requirement needed at the epidermis to maintain a given growth rate. Greenwood (1969), however, suggested that the interaction between oxygen partial pressure and soil compaction may be more apparent than real, perhaps merely an indication of the extent to which compaction reduces the surface area of root exposed to the gas phase.

Soil Carbon Dioxide

The composition of air in the soil is much more variable than that of air in the external atmosphere; whereas the air in a well-aerated soil is similar in composition to the external air, any impediment to gas exchange across the soil surface will generate differences between the two atmospheres. The greatest difference will be in the concentration of carbon dioxide, the main product of respiration of roots and soil macro- and microorganisms (Hillel 1980b). Concentrations of carbon dioxide in well-aerated surface soils are commonly about 0.2 to 1.0% (Black 1968), but often reach levels that are "ten or even one-hundred times greater" than the normal concentration of 0.03% in the external atmosphere (Hillel 1980b).

Under most circumstances, carbon dioxide concentrations in the soil are unlikely to affect root growth significantly. Because of the high solubility of the gas in water, the increase in carbon dioxide concentration is only about 5% of the drop in oxygen concentration in water-saturated soil. In the gas phase, the increase in carbon dioxide concentration approximately equals the decrease in oxygen concentration, "but as changes in concentration in the gas phase in soil are small, high carbon dioxide concentrations... are unlikely" (Greenwood 1969).

The response of root growth to carbon dioxide varies with species. To roots of some species, carbon dioxide may be toxic. Root growth of garden peas (*Pisum sativum* L.), for example, was depressed in an experiment that supplied a gas mixture containing only 1% carbon dioxide (Stolwijk and Thimann 1957); Harris and van Bavel (1957) found that a gas mixture containing 5% carbon dioxide and 15% oxygen depressed root growth of tobacco (*Nicotiana tabacum* L.). Grable and Danielson (1965), however, suggested that the injuriousness of excessive carbon dioxide during germination has probably been overestimated; they aerated corn (*Zea mays* L.) and soybean (*Glycine max* L.) seedling root systems with controlled mixtures of carbon dioxide, oxygen and nitrogen, and found that elongation of soybean roots was greater when exposed to a gas mixture containing 5% carbon dioxide than to air containing 0.03% carbon dioxide. This is not to deny that severe inhibition of root growth generally occurs at carbon dioxide concentrations greater than 15 or 20%, but such levels are rare in the soil atmosphere, except after large amounts of organic matter have been incorporated into the soil (Pearson 1966).

Soil Temperature

Soil temperature depends on the radiation balance at the soil surface, soil heat flux and soil water flux (Geiger 1950, Voorhees et al. 1981). Reflectance at the soil surface determines how much of the incoming radiation is converted into heat, and is influenced by moisture and organic matter content, particle size, the abundance of iron oxides and soluble salts, mineral composition, and other considerations such as cation-exchange capacity (Baumgardner et al. 1985).

Soil temperatures affect the anatomical and morphological characteristics of root systems (Taylor 1983). All physical, chemical, and biological processes in soil and roots are affected, including rate of cell division, root color, root morphology (roots tend to be filamentous at

high temperatures), and rate of maturation (Cooper 1973, Nielsen 1974). Rooting density and, probably, specific root uptake rates are influenced thereby. Soil temperature may also influence the severity of attacks by soil-borne organisms and affect the morphogenesis of root systems in some species (Pritchett and Fisher 1987). Temperature-related differences in root growth of young cembra (*Pinus cembra* L.) and mountain pines (*Pinus montana arborea* = *P. mugo uncinata* ? = *Pinus mugo* Turra, *P. montana* [Mill.] var. *rostrata* Hoopes.) close to the alpine timberline were much greater than were shoot-growth differences (Turner and Streule 1983), notwithstanding any tendency towards homeostatic equilibria between roots and shoots (cf. Szaniawski 1981).

The viscosity of water and of protoplasm, and the solubility of oxygen and of carbon dioxide in water, are all influenced by temperature. At low temperatures, pH may tend to decrease as a result of increased solubility of oxygen and carbon dioxide, but this is unlikely to affect root growth greatly, as root activity is minimal at low temperatures.

Temperature differences within a soil give rise to transport of both heat and moisture, and the theory describing this transport is complex (de Vries 1963). The differences result from heterogeneity of soil factors, especially those that influence soil moisture relations (Nielsen 1974), and from differential incidence and differential absorption of solar radiation at the soil surface. At a given latitude and for a given vegetation cover, the factors most important in determining soil temperatures are aspect, soil-surface albedo, thermal capacity and thermal conductivity.

Although soil in the rooting zone may be heated from above or below, soil surface temperature exerts the greater effect. Exceptionally, soil surface temperatures in excess of 70°C have been measured (e.g., Bates 1926, Ramdas and Dravid 1936). The virtual absence of loblolly pine roots in the upper 5 cm of soil on unshaded, scalped plots in eastern Texas was attributed by Bilan (1968) to high soil temperatures; on shaded, scalped plots, many roots grew within 2.5 cm of the soil surface. In many boreal forest soils, low temperatures are a major constraint on rooting depth and root growth (Sutton 1969).

Daily fluctuations in the temperature of soil close to the surface can be great; the amplitude of such fluctuations decreases from summer to winter and with increasing depth. Temperature gradients, however, are usually less than 1°C cm⁻¹, even close to the surface (de Vries

1963), but excluding the surface layer itself. For a homogeneous soil, de Vries calculated that the diurnal temperature variation penetrates to a depth of about 0.5 m and that annual temperature variations do not penetrate below a depth of about 10 m. Cooper's (1973) survey of naturally occurring soil temperatures showed that "temperature is rarely, if ever, constant and normally varies with both time and depth"; however, at some depth, which may extend into the rooting zone (cf. Hall 1933), the soil temperature is constant throughout the year (Smith et al. 1964).

Forest cover moderates soil temperature extremes, but the influence of temperature on roots and root systems in forested soils is nevertheless profound. The minimum soil temperature for root growth ranges from slightly above 0°C to 7°C; the optimum temperature ranges from 10 to 25°C, and the maximum temperature ranges from 25 to 35°C (Lyr and Hoffmann 1967). This varies with both species and environmental conditions (Pritchett and Fisher 1987). Root growth in cool-climate species begins and ceases at lower temperatures than in warm-climate or tropical species (Pritchett and Fisher 1987). The annual initiation of cambial activity in roots does not start until the temperature of the surrounding soil has reached 10 to 13°C (Ladefoged 1952).

The effect of flooding on roots depends very much on the temperature at which it occurs; for a wide range of tree species, both coniferous and deciduous, the duration of flooding is critical only during the growing season (Gill 1970). The aggravation of injury at this time is probably due both to greater root oxygen demand and increased respiration rates with increasing temperature and to reduced availability of oxygen because of increased microbial respiration, as well as decreased solubility of oxygen with increasing temperature (Veretennikov 1964). Drainage of soils subject to flooding during much of the growing season is therefore necessary if the soil is to be exploited effectively by tree roots.

An inducement that can be provided to roots to develop in cold forest soils may be to remove the superficial layer of insulating organic matter (cf. McMinn 1974). Rapid root development, which is highly desirable in securing the establishment of outplants and seedlings, can be promoted by exposing enough mineral soil to increase soil temperatures. If site preparation does not remove the nutrient resources too far from the young tree, and if the exposed soil is not hostile to root growth, roots could be expected to reach surrounding areas of higher fertility quickly. In northern Finland, such treat-

ment was sufficient to secure successful establishment of planted Scots pine (*Pinus sylvestris* L.) and Norway spruce on coarse-grained soils but not on soils rich in fine particles, where aeration was not improved. On both soils, however, best growth occurred with plowing and rototilling that produced mounds (cf. Sutton 1991) or mixtures of humus and mineral soil, with temperature, porosity and aeration all improved in comparison with the undisturbed condition (Lähde 1978). Waldron (1966), however, demonstrated disadvantages to white spruce as a result of mixing; after 6 years, naturally regenerated white spruce had reached total heights of 29.0 cm on a mineral-soil seedbed, 24.9 cm on a burned seedbed, and only 17.8 cm on a seedbed of mixed mineral soil and forest-floor material.

The texture of soil affects soil temperature in various ways, mainly through its effects on the amount and distribution of soil moisture and on thermal conductivity; stony forested soils in Sweden were 1 to 3°C warmer in summer than nonstony soils (Troedsson [1956], cited by Armson [1977]).

The chemical and mineralogical natures of a soil also affect the thermal properties of that soil. Mineral components differ rather widely in their thermal conductivity, as demonstrated by Chudnovskii (1962) with two sands, one calcareous, the other quartzitic, of the same grain size and the same porosity; in the dry state, the two sands showed similar thermal conductivities, but at 20% moisture contents, the conductivity of the quartz sand was 1.5 times that of the other. Chudnovskii argued that because the difference between the sands increased with increasing moisture content, the major factor is not the mineralogical composition *per se* but rather the strength with which moisture is held.

Soil Organic Matter

In soil, any organic carbon assembly, "large or small, dead or alive" is classed as soil organic matter (Jenny 1980). Books (e.g., Waksman 1936, Kononova 1961, Anon. 1966, Dickinson and Pugh 1974, Giesecking 1975) have been written on this subject. The topic is too broad to be treated exhaustively here.

Several terminologies have been developed in relation to organic materials in and on forest soils; here, it will suffice to use Jenny's (1980) simple subdivision of soil organic matter into *humus*, which has been incorporated into predominantly mineral-soil horizons, and *forest floor*, which rests as predominantly organic matter on underlying mineral soil.

Root growth and development, indeed, whole-plant growth and development from germination onwards, are strongly influenced by the fertility status of the soil. A noteworthy phenomenon is the concentration of fine roots in nutrient-rich zones of the soil (Lyt and Hoffmann 1967, St. John et al. 1983). Nobbe (1862) first demonstrated this response to localized nitrogenous enrichment of soil in nitrogen-deficient plants (Barley 1970). Another striking phenomenon is the strong positive response in tree growth that, in some circumstances, follows the application of soil from an area supporting good growth of trees to poorly growing trees of the same or similar species (Hatch 1936, Wakeley 1965). Amaranthus and Perry (1989) found that Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) seedlings on an old, unvegetated clearcut formed 62% more root tips in the initial 6 weeks after 150 mL of soil from an estab-

The number and arrangement of such components of root systems as root hairs and mycorrhizae also have strong nutritional implications, but the "importance of finely divided surface area provided by root hairs is not well understood, partly because of limited technology for quantifying fluxes and exchange surfaces" (Grunes et al. 1987). Root length and radius, through their relationship with surface area, also interact with soil fertility (Barber and Silbertush 1984). The mean rate of nutrient uptake per unit of root surface depends both on the uptake kinetics of the root and the nutrient-supply characteristics of the soil (Barber and Silbertush 1984).

of the root system."

paths are determined chiefly by the configuration of the root system."

of magnitude less than those known for dilute aqueous solutions, soil scientists were led to believe that soils offer a large resistance to the transfer of nutrients to the plant root. For example, in their review Movement of Nutrients to Plant Roots, S.R. Olsen and Kemper (1968) conclude that, although nutritional adequacy has historically been characterized most often by the amount of nutrient in the soil, the rate at which the nutrient can move... is an equally important factor. This may be so, but it needs to be emphasized that the resistance to nutrient transfer cannot be inferred from knowledge of soil properties alone; nor is it sufficient to know in addition how well the roots can absorb... [T]he resistance offered by the soil to the transfer of nutrients to the root depends upon the size and shape of the paths along which nutrients must travel. The

Root system form can be markedly influenced by nutrient supply (Meiden 1962, Röhrig 1966, Sutton 1969). In the introduction to his classic paper on *The configuration of the root system in relation to nutrient uptake*, Barley (1970) wrote:

"Because the values of the apparent diffusivity found for ions in soils were one or more orders

Soil Fertility

Water-holding capacities of forest floors range from about 1.0 to 5.0 cm (Remozov and Pogrebnyak 1969, Woodbridge 1970). The high hydraulic conductivity of the forest floor allows ready infiltration of water, but whereas its large pores tend to improve aeration on wet sites, they cause this layer to dry quickly on exposed sites, where "plant roots can frequently occupy the forest floor only temporarily" (Pritchett and Fisher 1987).

Humus consists of two fractions, one that breaks down relatively quickly (in weeks or months), liberating carbon dioxide and nutrient elements, and one that is remarkably stable, persisting for centuries (Atiwill and Leeper 1987). The stable fraction plays major roles in forming water-stable aggregates and holding cations by virtue of its negative charge. Organic materials are the most important stabilizing agents in many topsoils (Hamblin 1985).

The physical and, especially, the chemical properties of the forest floor vary widely, but the forest floor is an important nutrient reserve, particularly in temperate and boreal forests, where its nitrogen content equals or exceeds that in the living, aboveground biomass (McColl and Powers 1984). Indeed, the forest floor "is the home of most soil organisms, the reservoir of most nutrients involved in the cycling process and the very life of the soil itself" (Pritchett and Fisher 1987). The forest-floor layers and their associated microflora and fauna are "probably the most dynamic phase of the forest ecosystem and are of great importance to several aspects of forest land management" (Woodbridge 1970). The microflora and microfauna are essential to nutrient cycling, particularly of nitrogen, phosphorus, and sulfur (Pritchett and Fisher 1987). Forest litter layers "physically insulate soil surfaces from extremes in temperature and offer mechanical protection from rainfall impact and erosional forces" (Woodbridge 1970). Fine roots are commonly concentrated in close association with the interface between the forest floor and the underlying mineral soil (Sutton 1969); this component of forests plays a much greater part in carbon cycling than has been conventionally accepted (Persson 1983b).

lished Douglas-fir plantation had been added to the planting hole compared with seedlings planted similarly in other respects, but without soil transfer. Root growth and mycorrhizal formation were stimulated by the soil from the established plantation. Introduced ectomycorrhizal fungi, however, are unlikely to be able to maintain themselves under "foreign" conditions (cf. Danielson and Visser 1989).

Fertility comprises a highly complex set of soil conditions, with various levels of nutrient elements and various ratios among them. Each of the essential nutrients supplied by the soil has "a different chemistry, a different plant requirement, and a different pattern of circulation in plant and soil" (Stone 1983). Quantitative investigation, conducted mainly in the agricultural context, has been concerned primarily with relationships between yield and level of fertilizer application (Kamprath 1986, Westerman and Tucker 1987). Nitrogen, phosphorus and sulfur have been found to increase the shoot:root ratio in tomato (*Lycopersicon esculentum* Mill.) and barley (*Hordeum vulgare* L.) at high levels of supply, whereas potassium, calcium and magnesium had much less effect (Steineck 1983). In general, however, a fertile rooting medium favors a high shoot:root dry-mass ratio.

In terms of root spread, however, the situation is reversed, at least insofar as nitrogen supply is concerned. Long, slender roots are typically developed under conditions of nitrogen deficiency, whereas shorter and stubbier roots are developed at higher levels of nitrogen supply (Bosemark 1954); however, different forms of nitrogen may have different effects (Evers 1964). The ratio of root length to weight is highest for most species in soils of low fertility (Fitter 1985); this ratio reflects diameter if root density is uniform.

Similarly, Hartmann (1951) noted the relationship between site fertility and root branchiness; long and seldom-branched lateral roots indicate soils of low fertility, whereas compact complexes of fine roots indicate high fertility. Binkley (1986) hypothesized that low nutrient availability might require that the plant develop a larger root system than under conditions of higher nutrient availability. Nadelhoffer et al. (1985) found that both the mean annual N content and the biomass of fine roots (≤ 3.0 mm in diameter) were negatively correlated with N uptake. Citing work by Keyes and Grier (1981) and Santantonio and Hermann (1985), Binkley (1986) suggested that fine-root production may be lower in fertile than in less-fertile soils, though he acknowledged that Axelsson (1983) had found little variation in the

production of fine roots by Scots pine with respect to soil fertility. Perhaps none of the pine soils was highly fertile.

Certainly, the percentage of the annual carbon budget allocated to root growth in a 20-year-old stand of Scots pine decreased after fertilization was begun (Persson 1980, 1983a). Nitrogenous fertilization of Sitka spruce (*Picea sitchensis* [Bong.] Carr.) for 2 years altered the numbers, biomass and seasonal activity of fine roots and mycorrhizae: production and mortality decreased, and longevity increased (Alexander and Fairley 1983). Alexander and Fairley suggested that an important consequence of fertilization may be a reduction in turnover of the fine-root (including mycorrhizal) system, freeing resources, otherwise expended in producing new roots, for growth of other tissues.

Axelsson (1983) showed that fine roots in fertile soils may be very short-lived, but production of fine roots and mycorrhizae may be very high despite the low average fine-root biomass under fertile growing conditions. "Much work remains to be done before patterns between soil fertility and the biomass and production of roots can be established definitively" (Binkley 1986). The estimation of even net root production is difficult (cf. Lauenroth et al. 1986, Vogt et al. 1986).

Coutts and Philipson (1976), using divided root systems of Sitka spruce seedlings, found that both length and thickness of roots supplied with nutrients and water were substantially greater than in the other half of the root system, which received water only. Robinson and Rorison (1983) demonstrated a similar response in three grasses. These results relate to the response of root subsystems to localized zones of higher fertility; they are not to be interpreted as a comparison between root systems developed under different levels of soil fertility.

Notwithstanding the view, attributed to Mae West, that "Too much of a good thing is wonderful!", even a necessary growth factor can be harmful in excess. An excess of a nutrient ion may have an effect precisely similar to that of a toxic ion: "While the trace elements are necessary for the normal growth and development of plants, excess of them may be as injurious as their deficiency. Trace elements in excess are, in fact, poisons, and toxic symptoms... have been recorded... Such injurious effects are, of course, not limited to micronutrients and may be produced by a large number of elements, particularly the so-called heavy metals" (Stiles 1961).

The nutrient status *within* a root also influences nutrient influx into the root; influx appears to be negatively correlated with the tissue concentration of the

particular ion (Läuchli 1984). Nutrient uptake has been modeled mechanistically by Nye et al. (1975), Claassen and Barber (1976) and Cushman (1979), among others.

Mycorrhizae are difficult subjects to study *in situ* and are hard to separate from soil (Fogel 1983). They are undoubtedly important in tree nutrition (Harley 1969, Hacsckaylo 1971), and mycorrhizal development is undoubtedly influenced by fertility relationships (Björkman 1942, 1970; Reid et al. 1983). As Binkley (1986) pointed out, exploitation of soil volume per unit mass of tissue is maximized when these tissues are of the smallest possible diameter. The hyphae of mycorrhizal fungi are much finer than the fine roots of trees. Typically, the diameters of hyphae (1 to 3 μm) are less than half those of root hairs. Binkley noted that, with similar mass-to-volume ratios, mycorrhizae can produce about four to ten times more surface area per unit mass of tissue than would root hairs.

Phosphorus nutrition is known to be enhanced by mycorrhizae in some soils (cf. Hatch 1937, Stone 1950), but since hyphae also take up water, other nutrients may enter by means of mass flow and contribute towards observed growth responses. Barber (1984) has argued that the effect of the fungus is merely to increase the soil volume exploited rather than to access nutrients that roots are unable to take up (Binkley 1986). Nye (1979), however, hypothesized that the very much greater zone of phosphorus depletion around rapeseed (*Brassica napus* L.) roots than around onion (*Allium* L. sp.) roots is attributable to the release of organic chelating anions, which exchange with surface-bound phosphate, from rapeseed roots. The model developed by Nye (1979) for nutrient uptake by root systems growing in homogeneous soil gives reasonable predictions of nitrate and potassium uptake but not of phosphate uptake; part of the difficulty may be variation in root exudations that was not accounted for in the model.

Soil Reaction

The direct effect of hydrogen-ion concentration (pH) on root growth is rather small in the physiological pH range as long as sufficient calcium ions are present in the rooting medium (Moore 1974). In other circumstances, pH has large effects on roots, and natural soils can be too alkaline or too acidic to support tree root growth and development.

The concentrations of Ca^{2+} and Mg^{2+} in the soil solution are both usually > 0.001 M and are high enough to be changed little by root uptake; however, the solution concentration of sparingly soluble ions, such as phos-

phate and trace elements, may be sensitive to levels of pH and complexing ions (Nye 1984).

Extreme acidity in a soil increases aluminum solubility. In cotton (*Gossypium hirsutum* L.), characteristic symptoms of aluminum toxicity include discoloration, loss of turgidity, thickening and distortion of the main roots, and the development of short, stubby laterals (Reicosky 1983). At acidities greater than about pH 3, the root growth of many species ceases and membranes begin to break down (Jacobson et al. 1950, Russell 1977).

At high pH, the availability of some nutrients, including phosphates, iron, zinc, and manganese, is very low; as well, soil structure tends to become water-unstable, thus exacerbating problems of poor aeration and low permeability to water (Russell 1961). Plants growing on calcareous and saline soils may be subject to iron deficiency, but not all such soils induce iron chlorosis, and crops differ greatly in their susceptibility (Russell 1961). The same condition may arise in plants growing on other soils following drought (Kramer 1983). A high salt content around a root markedly reduces the absorbing power of that root (Russell 1961). The rates of most nutrient transformations in the soil are affected by pH (Binkley 1986). Some effects, such as phosphate solubilities, are direct; others, such as the regulation of microbial populations, are indirect. The interactions of pH with nutrient cycles are not all in one direction (Binkley 1986); the cycles themselves generate and consume large quantities of hydrogen ions.

The direct effects of pH on roots are difficult to separate from the many indirect effects. The form and solubility of many soil nutrients, for instance, depends on pH (Bear 1964); the solubility of phosphates is outstanding in this regard. Again, acidity is chief among the ecological influences that govern nitrification (Alexander 1961). In acidic environments, nitrification proceeds slowly even with adequate substrate, and the nitrifying organisms are rare or absent under very acidic conditions, with a variety of physico-chemical factors determining the exact limiting pH (Alexander 1961).

Another facet of nutrient relations affected by pH is nitrogen fixation. As well as the legumes, plants of several genera are able to develop nitrogen-fixing root nodules at some stage of their life cycle. For example, naturally growing alder (*Alnus glutinosa* [L.] Gaertn.) typically possess nodules that may approach the size of tennis balls (Alexander 1961). The optimum acidity for nitrogen fixation is in the vicinity of pH 5.5 to 6.0, though growth of nodulated plants in nitrogen-free

solutions is good between pH 4.2 and 7.0, and Becking (1975) stated flatly that soil pH is not limiting for the occurrence of nodulated nonleguminous plants.

Mycorrhizal development, an important component of root system form, takes place only within a rather narrow range of soil conditions, including pH (Marx and Bryan 1975). Alkaline conditions in the rhizosphere inhibit the growth of some mycorrhizal fungi (Theodorou and Bowen 1969); at soil pH 8.0, radiata pine seedlings developed only one-third the number of mycorrhizae per seedling as they did at pH 5.2.

The carbon dioxide given off by soil organisms contributes acidity to the surrounding soil, but plant roots may increase or decrease the pH of the rhizosphere, depending on the ionic species of nutrients supplied (Marschner et al. 1986).

Soil Organisms

Most soils teem with organisms. Microorganisms and various symbioses have undoubtedly played major roles in the evolution of tree ecosystems, especially in nutrient-poor soils and in highly competitive ecosystems (Bowen 1985). This living portion of the soil, including various small invertebrate animals and microorganisms, makes up <1% of the soil volume, but is essential for soil fertility (Alexander 1961). The microbial population of soils is made up of five major groups: bacteria, actinomycetes, fungi, algae and protozoa. The soil fauna have important influences on soil structure and soil porosity (Jenny 1980), creating biopores that improve penetrability and aeration. A multitude of soil organisms is associated with the cycle of root formation, functioning, death and decay (Waid 1974).

The microbe-root associations of greatest consequence in forestry are the leguminous *Rhizobium* and the non-leguminous *Frankia* ("actinorhizal") nitrogen-fixing symbioses (Nutman 1965, Akkermans et al. 1984). Results from a study by Hendrickson and Burgess (1989) suggest that fixation by naturally occurring *Lupinus arcticus* Wats. and *Shepherdia canadensis* (L.) Nutt. may contribute more than half the annual input of nitrogen into a regenerating stand of lodgepole pine (*Pinus contorta* Dougl.) in southern British Columbia. *Lupinus arboreus* Sims is introduced artificially to assist in the establishment of pine on infertile sand dunes in New Zealand (Gadgil 1983).

Rhizosphere populations of microorganisms are much higher than those of non-rhizosphere soil. Bacteria predominate close to root surfaces, often exceeding one billion per gram of rhizosphere soil (Alexander 1961).

Nitrogenous exudates containing amino acids from living roots and decay products from dead and dying roots, microbes and other organic matter preferentially benefit bacteria (Alexander 1961). Rhizosphere characteristics seem to be rather similar among diverse groups of plants, including cultivated and intertilled crops, grasses and trees (Clark and Paul 1970), though species differences occur (Russell 1961).

Bacteria that readily colonize roots epiphytically are termed *rhizobacteria* to differentiate them from *rhizoplane* and *rhizosphere* bacteria, which may not be root colonizers and which may be transients (Schroth and Hancock 1982). Rhizobacteria may be beneficial, neutral or deleterious to the plants whose roots they colonize. Typically, rhizosphere populations are made up of non-pathogenic microorganisms (Alexander 1961, Curl and Truelove 1986). Fluorescent pseudomonads, for instance, can exclude pathogenic or deleterious microorganisms from the rhizosphere (Lifshitz et al. 1987). Thus, the rhizosphere commonly acts as a microbiological buffer against soil pathogens. Most of the beneficial *Pseudomonas* rhizobacteria fall into the heterogeneous group containing *P. fluorescens* and *P. putida*. *Pseudomonas* species have been found to be particularly aggressive in colonizing root systems when inoculated onto seeds and other plant parts (Schroth and Hancock 1982). In soil, the many bacterial species that have been shown to produce plant growth regulators, including gibberellins and indole-3-acetic acid (Kloepper et al. 1989), *in vitro* can presumably influence root (and plant) growth.

The size of fungal populations is not much influenced by the presence of roots in soils, but some fungal genera are selectively promoted (Alexander 1961). Competitive relationships among mycorrhizal fungi are influenced by ecological conditions (McAfee and Fortin 1986), including soil pH (Theodorou and Bowen 1969, McAfee and Fortin 1987). Even within a genus, tree species may vary greatly in their response to a given mycorrhizal treatment (cf. Richter and Bruhn 1989). Shifts in the species composition of fungal colonizers of roots have occurred after inoculation with plant growth-promoting rhizobacteria (Schroth and Hancock 1982).

As a rule, the other major groups of soil organisms are not significantly affected by proximity to roots (Alexander 1961), though sloughed off root tissue is no doubt utilized by earthworms. Some lumbricid species ingest roots (Lee 1985). Increases in root mass and depth of penetration of barley roots in plots inoculated with earthworms were attributed to roots following earthworm burrows (Lee 1985). Roots would probably make

similar use of periodic disturbance of soil by cicadas (Homoptera: Cicadidae: *Magicicada* spp.), whose nymphs live underground, construct cells near roots on which they feed, and eventually tunnel vertically to the soil surface (cf. White and Lloyd 1975, White and Strehl 1978, Luken and Kalisz 1989). Production of an auxin-like substance "seems probable" in *Lumbricus rubellus* but not in *Aporrectodea caliginosa* (Lee 1985). Secretion or excretion of B-group vitamins by earthworms also seems likely, but this may be an indirect result of microbial activity stimulated by the presence of earthworms (Lee 1985).

The carbon dioxide liberated by the organisms inhabiting the rhizosphere forms carbonic acid; this increases soil acidity and promotes the solubilization of some inorganic nutrients.

Soil microbiology "must be taken fully into account equally with soil physical and plant physiological aspects" when considering interactions between plant roots and soil (Russell and Goss 1974). The influence of microorganisms on root behavior has been largely ignored in laboratory experimentation.

Soil Depth

Soil depth is generally determined by convention, convenience or an arbitrary control section, rather than by rooting depth (Stone 1987). Roots, whether of trees (Sutton 1969) or field crops (Brown and Scott 1984), are usually concentrated in the upper layers of soil. When the decrease in rooting with depth is abrupt, as is commonly the case, it defines the boundary between favorable and unfavorable soil conditions for maintaining normal growth rates and extension of the terminal roots (Brown and Scott 1984). Some of the limitations to downward penetration of roots into soil are obvious: bedrock (though fissures in bedrock are often exploited by roots), pans of various kinds, and water tables. Other less-apparent but equally important factors include limiting levels of porosity, soil strength, soil aeration, soil temperature, soil reaction and perhaps soil fertility. At some distance below the soil surface, root growth and development are inhibited more or less completely by one or more constraints, which determine the depth of soil available for rooting (soil depth).

Not easily defined except in a few special cases, soil depth shapes the root system of most forest trees. Bedrock beneath glacial sediments can be detected by ground-penetrating radar (Collins et al. 1989); dense soil layers and shallow bedrock can be detected by seismic and resistivity methods (Sutton 1973).

Soil depth influences water relations; Shea and Armson (1972) related current height increment in jack pine to the restriction of rooting by subsoil layers and associated limits to moisture supply. The stability of trees and stands is also affected, and fissuring in shallow-to-bedrock soils and pockets of deep soil are important modifiers of rooting behavior. The absolute amounts of nutrients and the concentrations of nutrients become increasingly consequential as the volume of exploitable soil diminishes, but enrichment by nutrient-rich, moving (aerated) groundwater can compensate for local deficiencies.

Exceptionally, living tree roots may penetrate to 45 m (Campion 1926) or 53 m (Phillips 1963) below the ground surface, but the rooting zone of trees is generally much shallower, especially in the peat and shallow-to-bedrock soils typical of much of the Canadian Shield.

The statement made by Schuster (1936) after studying root development in orchard soils in Oregon may be cited as a general truth: "The depth of root penetration... is believed to be more often controlled by the characteristics of the soil than by the characteristics of the tree itself. In other words, the ideal soil is too often lacking... and only in the ideal soil do the individual characteristics of the plants express themselves fully."

Soil Movement (Including Heaving)

Soil that moves differentially with respect to roots can affect root system form and development. Though the presence of roots tends to stabilize soil (cf. Schiechl 1980, Coutts 1983) and minimize solifluction (Armson 1977), such movement is not uncommon; mechanisms include drying, wetting, freezing, erosion by wind and water, and downslope gravitational creep. Roots can become exposed, buried, compressed, desiccated, wounded or broken. Soil movement influences root system development, both root position and root branching (Jochimsen 1983).

In pioneer plants on raw soils, both the position of roots within the soil and the degree to which root systems ramify are influenced by soil movement (Jochimsen 1983). On shallow, stony soils in New Zealand, Watson and O'Loughlin (1985) found that manuka (*Leptospermum scoparium* J.R. et G. Forst.) and kanuka (*Kunzia ericoides* [A. Rich.] J. Thompson) root systems develop predominantly upslope, and this is probably true for all plants on such soils.

In short-term studies, Fayle (1968) found that cell production increased over a longer period, radial and tangential cell diameter and cell length decreased, and

cell walls were thicker in exposed parts of coniferous roots compared with unexposed parts; in hardwoods, vessels decreased in size, and in ring-porous species, a ring-porous zone tended to be formed.

Root systems also respond to burial. Soil placed on the surface of the ground around existing trees can cause problems related to gas exchange in the root zone; soil aeration is the critical factor (Harris 1983). Plant species vary in their ability to withstand the deposition of additional soil atop existing root systems (Schiechl 1980). The spruces seem generally well able to adapt their root systems to the new conditions imposed by such an event. Multi-layered root systems, developed by floodplain white spruce as a result of periodic accretion of sediment, were described by Wagg (1967).

The forces generated by soil shrinkage during drought and by frost heaving are quite enough to break roots. Frost heaving is a physical upward movement of soil and associated vegetation caused by ice formation and accumulation (Portz 1967, Perfect 1986, Perfect et al. 1987, Cary 1987, Pikul et al. 1989). Seedlings and small trees are highly vulnerable to heaving on certain soils under the influence of a temperature gradient that ranges from below freezing at the soil surface to above freezing at depth, and generally with soil water in the liquid state available at depth for transfer to the freezing zone (Anderson et al. 1967). Broken roots of white spruce have been commonly observed on either side of cracks in clay during drought in northeastern Ontario (Sutton 1991). I have invoked desiccation cracking and natural root pruning by frost heaving to explain the maintenance of the youthful character of white spruce root systems for several years after outplanting on clay and loam soils in eastern Ontario (Sutton 1968); on loam soils, excavation revealed predominantly one-sided root systems in vertical projection, one side of the root system with normal development, the other side sparse, youthful, and exhibiting little more than vestigial development. The evidence suggested that this form resulted from the relief of lateral and vertical forces developed during the heaving process by means of root shearing or stripping on the least well-anchored side of the root system. Once begun, the situation would be self-perpetuating until anchorage of the root system as a whole became able to resist further heaving. The essential mechanism whereby tree seedlings and outplants are heaved involves the firm encasement of the stem in the frozen surface of a moist soil and the upward thrust of the frozen surface caused by elongating ice columns (Schramm 1958); the roots in unfrozen subsurface layers

are either pulled upward or, if rooted firmly enough to resist this pull, may be broken (Schramm 1958) or bark-rubbed (Haasis 1923).

Similarly, a root that moves differentially with respect to the soil in which it grows can develop striking morphological modifications through abrasion (cf. Stone 1977).

THE SOIL-ROOT INTERFACE: INTERACTION BETWEEN SOIL AND PLANT FACTORS

Just as soil fertility influences the development of a root system, so the root system influences nutrient uptake by plant roots (Barber and Silberbush 1984). Although the soil-root interface, as the surface through which water and nutrients pass from soil to plant, has received attention (cf. Harley and Russell 1979), this interface remains "one of the most ignored frontiers of the agronomic sciences" (Smucker 1984). Certainly the important functions of anchorage (Bowling 1976) and support have received little attention from plant physiologists (Coutts 1983), though the nature of the plant-soil contact has long been the subject of lively debate (cf. Greenland 1979). The forces involved in root anchorage have been studied by a succession of workers in Britain (Fraser and Gardiner 1967; Coutts 1983, 1986; Anderson et al. 1989); surprisingly, Anderson et al. showed that the difference in stability between Sitka spruce on a brown earth and on a deep peat cannot be explained in terms of the force required to extract individual roots.

Root length and radius determine root surface area, on which the rate of increase in nutrient uptake, uptake per unit of root surface area, and total nutrient uptake depend (Barber and Silberbush 1984). The mean rate of nutrient uptake per unit of root surface depends both on the uptake kinetics of the root and on the nutrient-supply characteristics of the soil (Barber and Silberbush 1984).

The rhizosphere and rhizoplane (root surface) microbial populations are determined directly or indirectly by root exudates. These populations are made up of components of both the microflora (bacteria, actinomycetes, fungi and algae) and the micro- and mesofauna (protozoa, nematodes, mites and insects) (Curl and Truelove 1986).

PLANT FACTORS

Root Systems

Root system morphology is at once a consequence of soil properties and an expression of whole-plant physiology conditioned by the genetic constitution of the

organism. At any given time, the physiological and morphological consequences of the juxtaposition of a particular rhizoplane with a particular rhizosphere will be determined partly by soil properties and partly by the plant itself. For example, as noted by Barber and Silberbush (1984), the significance of a given amount of root surface area also depends on the nutrient requirement per unit of root.

Three parameters of root morphology (root length, rate of root growth, and average root radius) are among the ten used by Claassen and Barber (1976) in their model of nutrient uptake; for potassium, the correlation (r^2) between predicted and observed uptake by corn (*Zea mays* L.) from four different soils was 0.87. For phosphorus uptake from six Indiana soils that varied greatly in organic-matter and clay content, Schenk and Barber (1979) found that the Claassen-Barber model gave an r^2 of 0.83 between observed and predicted uptake. The model did not take into account the effect of root hairs, which is of particular importance in relation to nutrients (e.g., phosphorus) that diffuse slowly. Root hairs are important for any nutrient that has an effective diffusion coefficient of $1.0 \times 10^{-9} \text{ cm}^2 \text{ s}^{-1}$ or less (Barber and Silberbush 1984).

Predicted potassium uptake in the Cushman (1979) model was more sensitive to changes in root surface area than to the same relative change in the other parameters (Barber and Silberbush 1984). Grasses with long, fine roots usually compete for potassium uptake more effectively than do the thicker, shorter roots of legumes (Barber and Silberbush 1984).

Nye (1984) has stated that the concentration profiles of important nutrient ions such as K^+ and NO_3^- near absorbing roots, and their rates of uptake, can be satisfactorily explained by a model in which the ion moves to the root by mass flow and diffusion. However, this claim is not unreservedly true in that the sorption isotherm for a nutrient depends on the concentrations of other ions in the system, and these may be changed in the rhizosphere soil by root uptake or excretion.

Genetic Influences

Although Barber and Silberbush (1984) were justified in stating the generality that variations in root-system morphology are greater among species than within species, the precisely controlled genetic program that governs development in plants is allowed full expression only in the absence of environmental constraints. Thus, trees owe their commonly distinctive stem and crown forms to their genes, but, below ground,

genetic expression is generally much weaker. Under field conditions, root systems commonly vary more in form than do aboveground parts of plants (Russell 1977). Precise growth patterns of trees are much disrupted by exogenous environmental factors since most woody plants are both large and long-lived, with proportionately extended opportunities for environmental disturbance (Halle et al. 1978).

The greatest expression of genetic control of root and root system development may be seen, therefore, under conditions of minimal stress, as with young seedlings in hydroponic culture. In natural soils, the inherent form of root systems is also most clearly apparent in young seedlings. For instance, some species tend to be shallow rooted, some more deeply rooted. But even in species that develop strong tap roots, root-system form is often modified very early by injury or an adverse soil factor. Transplanted jack pine very seldom develop a tap root to repair or replace the tap root damaged during the continuum from lifting through planting, although a taproot may be well expressed among natural jack pine on the same site. With increasing maturity or size, tree root systems become increasingly dominated by soil conditions, the more so as these depart from the ideal soil, freely penetrable by roots.

Even in an unstressful soil environment, genetic variation in root-system form would be expected both among and within provenances (Zobel 1975, Kleinschmit and Sauer 1976, Fayle 1978), as well as among species. Zobel (1983) identified seven levels of complexity (genetic, enzymatic, biochemical, physiological, anatomical, morphological and agronomic) at which genetic diversity occurs. At every level, the gene-environment interaction will influence root growth and root-system development.

Brown and Scott (1984) concluded that root distribution in the soil profile is a function of the interaction of the genetic characteristics of the plant with the microclimate in the plant canopy and the physical, chemical and microbiological properties of the soil profile.

Plant Growth Regulators

Regulation of plant growth by minute quantities of specific chemical substances affects or determines the rate, pattern and distribution of plant growth. The wide variety of substances known to be involved includes auxins, gibberellins, cytokinins, vitamins and physiologically active cations. The role of such growth factors in controlling cell division and cell elongation in roots is much less well understood than are their effects on shoot

growth (Zimmermann and Brown 1971). These growth factors appear to be affected by the environment of the root tips, because the quality and quantity of root wood can differ within a root system (in addition to those differences relating to position with respect to the stem). Thus, large-diameter vessels in angiosperm roots tend to occur in fertile, well-cultivated, periodically moistened soil. In contrast, small-diameter vessels tend to occur deep in the soil, where growth is physically restricted, where nutrition is poor, and where water supply is constant or excessive and probably associated with poor aeration (Fayle 1980).

Roots are major sites of synthesis of gibberellins and cytokinins and can therefore no longer be regarded solely as absorbing or anchoring organs (Skene 1975, Russell 1977). Auxin seems to be synthesized mainly in the shoots, although roots do not depend on auxin supply from shoots for primary growth (Lyr and Hoffmann 1967).

Tropisms (cf. Rufelt 1969, Audus 1975), though still incompletely understood, are undoubtedly controlled by plant growth regulators, and have obvious relevance to the development of root-system form. Pilet (1983), working with maize (*Zea mays* L.) roots, has found that the role originally ascribed to indole-3-acetic acid (IAA) by Went (1928) has been filled by abscisic acid (ABA), at least in root growth and gravitropism, but Pilet noted that data related to the effects of exogenous auxin on root gravitropism have tended to be contradictory. Some reports claim that ABA stimulates water movement, others claim that it inhibits water flow (Collins and Channa 1983).

The conditions that affect photosynthesis, the amount and efficiency of foliage, and the utilization of photosynthate within the stem and crown determine the supply of photosynthate (and auxin) to the roots to effect another sort of growth regulation. Anything, in fact, that affects the growth of stem or leaves also affects the growth of roots; roots and shoots are interdependent. The hormonal mechanisms that coordinate the growth of the entire plant depend on growth substances contributed by both roots and shoots, and the effects of unfavorable soil conditions are sometimes primarily a result of interference with these mechanisms rather than of decreased uptake of water and nutrients (Russell 1977).

The amount of radiation received by the crown of a tree has a great influence on root system development. The strongest and generally the deepest root systems are developed by trees exposed to full daylight (Shirley

1929, Logan 1966, Köstler et al. 1968); the effect, however, varies with the shade tolerance of the species (Lyr and Hoffmann 1967). In all probability, this shading effect results from combined direct and indirect causes. Photosynthate production is reduced by shading; it also seems certain that there will be changes in the amount of growth regulators synthesized and, therefore, in the gradients of growth regulators within the tree. The proportions of the various growth-regulating chemicals may also change. Björkman (1942) found that shading greatly reduced mycorrhizal incidence.

Neighboring Vegetation

The root systems of neighboring plants compete for soil resources, though the manner in which the root systems interact and compete "is neither obvious nor well studied" (Caldwell 1987). The lateral spread of individual root systems may be small in dense herbaceous stands (Neilson 1964, Barley 1970), but a high degree of overlapping is normal among the root systems in forest stands (Sutton 1969). Interactions among the plants occupying a given area depend on many factors, including the species and vigor of plants supported by the soil conditions. Allelopathic influences, such as those described by Jobidon and Thibault (1982), Rice (1984), and Putnam and Tang (1986), whereby exudates from the roots of one species of plant inhibit root growth of other plants, obviously depend on the species composition supported by any given soil.

Soil that receives root exudates or leachates from one plant may influence the growth of a nearby plant negatively or positively (Curl and Truelove 1986). The term *allelopathy*, originally applied to such effects, whether positive or negative (Molisch 1937), has come to refer solely to inhibitory effects (cf. Jobidon and Thibault 1982, Rice 1984, Putnam and Tang 1986). Not all plant species respond similarly to a given allelopathic exudate (Newman and Rovira 1975). Allelopathic compounds have been identified in a wide variety of chemical groups, including acids, alcohols, acetaldehyde, coumarins, alkaloids, sulfides and mustard-oil glycosides (Curl and Truelove 1986).

Even without allelopathy, the presence of other roots competing for water and nutrients can severely limit root growth, particularly during reproductive phases of growth (Brown and Scott 1984)

Physical and Chemical Effects

Since vegetation is one of the factors in soil formation (Jenny 1980), soil properties will inevitably be influenced by the vegetation supported by that soil. The

effect has been studied in relation to plantations of introduced conifers. Turner and Lambert (1988), for example, compared soils beneath introduced radiata pine with those beneath adjacent native eucalypt forest; they found that soil pH, total nitrogen, and exchangeable magnesium concentration at an infertile pine site were lower, and organic-matter and exchangeable-aluminum concentrations higher, than under adjacent natural forest. At a relatively fertile site in the same study, only the concentrations of soil nitrogen and organic matter, which were lower, differed significantly between the pine and native forest soils.

Plant roots greatly affect soil stability (cf. Watson and O'Loughlin 1985). The tensile strength of soil is 3 to 5 orders of magnitude weaker than that of roots under tension (Coutts 1983). Soil slip will occur many times more readily when roots are few or absent than when the soil is permeated with roots. Soil-profile development will proceed further in soil that is stable than otherwise. Ironically, the presence of tree roots can also curtail soil-profile development as a result of windthrow.

The "plowing" of forest soils that results from windthrow (Lutz 1940, Stephens 1956, Norton 1989) is important in the morphogenesis of forest soils and, therefore, in root and root-system morphogenesis. Mueller and Cline (1959), for instance, after studying soil factors, rooting, and windthrow in west-central New York State, concluded that "much" of the upper 60 cm of forest soil has been "disturbed" during the past 500 years. Lyford and MacLean (1966) found a distinctive microrelief of about 1200 mounds and 1500 pits per hectare resulting from the disturbance by windthrow on representative forested areas at the Acadia Forest Experiment Station in New Brunswick, Canada. The plowing produces a roughened surface topography (Lyford and MacLean 1966, Norton 1989) that reduces the soil's reflectance (Baumgardner et al. 1985) and modifies soil-temperature relationships (Radke 1982).

The physical presence of a root in soil subjects the surrounding soil to pressures that influence the shape and size of the soil's structural elements (Clarke 1957). During the course of a year, innumerable additional pulses of pressure may be imposed by a root on the soil surrounding it as that root responds to stresses induced by the action of wind on the stem and crown (Hintikka 1972). In some soils, roots may move through a vertical distance of several millimetres (Hintikka 1972), though movement is often transverse or oblique rather than longitudinal only (Stone 1977). By no means restricted to mountainous areas, root abrasion and associated soil

effects are greatest in very shallow soils in which soil-root cohesion is not strong, and in locations exposed to high winds (Stone 1977); I have seen such abrasion of roots particularly well developed in tamarack (*Larix laricina* [Du Roi] K. Koch) on moist till with a boulder pavement. Some degree of lamination may often be found associated with large, shallow root systems of wind-stressed trees (Clarke 1957).

The physical presence of a living tree root system in a soil usually, but not invariably (cf. Lanner 1961, Eis 1972), implies the presence of an aboveground stem and crown. The presence of a forest canopy exerts marked effects on the soil beneath, reducing the amount of radiation reaching the ground, reducing and redistributing the amount of precipitation reaching the ground, reducing windspeeds within the stand, and changing the form, if not the amount, of organic matter reaching the ground (Zon 1941, Geiger 1950). The distribution of nutrient elements returned to the soil from a forest canopy is much influenced by that canopy (cf. Foster and Gessel 1972, Foster 1974).

Roots affect the distribution of ions in soil because of the physical presence of the roots and because they deplete water, oxygen, and nutrients through uptake and thereby create gradients in these factors (Barber 1974).

Roots also exert strong biochemical effects on soil within the rhizosphere (Rovira 1962, Giddens and Todd 1984, Foster 1986, Halverson and Stacey 1986, Elliott and Fredrickson 1987): carbon dioxide content increases; changes occur in the ionic composition of the soil solution; the partial pressure of the oxygen is reduced; and a wide variety of organic compounds are exuded into the rhizosphere by growing roots (Dangerfield 1975, Reid and Mexal 1977). The amount exuded from a root appears to be proportional to the concentration of exudate at the root surface, since removal of the compounds increases exudation (Smucker 1984). Roots can change the rhizosphere pH by as much as 1 to 2 units (Nye 1981).

Root exudates are no doubt the prime determinant of the differences that distinguish the rhizosphere from the rest of the soil body. The rhizosphere of forests may be a particularly appropriate place to apply biotechnology (Gordon and Smith 1987).

Previous History

In forestation by outplanting, the initial growth of roots into the soil and their disposition are conditioned by the previous history of the planting stock and by the planting method. The questionable ability of some out-

planted stock, especially the pines (*Pinus* L. spp.), to develop root systems able to confer stability on the trees has caused widespread concern among foresters (see papers in Van Eerden and Kinghorn 1978) and landscape architects (Harris and Davis 1967, Lumis 1979). Soil conditions will have a further influence, as Yeatman (1955) pointed out with respect to the inability of pines to develop adventitious roots at a later date: "Thus any ground treatment, or lack of it, which tends to confine the root system to the surface, to prevent the free division of primary roots, to induce a shallow storied character in the root system, or to align the major roots in any one direction, must risk growing a forest more liable to windblow and/or possible early senescence."

In any discussion of soil/root interactions, long-term as well as short-term effects need to be considered. This is particularly important in relation to the problem of formulating prescriptions for site preparation that secure the short-term objective of establishing a crop without jeopardizing the long-term growth of the trees. The need for long-term study is illustrated by Väre's (1989) report of markedly reduced growth of both the root system as a whole and of mycorrhizal formation among Scots pine in Finland planted 15 years earlier on sites prepared by plowing, where early development had been generally good (Lähde and Pohjola 1975, Pohtila 1977). Tikkanen (1989) also described lethal deterioration among 8- to 15-year-old Scots pine on plowed sites in northern Finland after good initial development; he noted that the evidence pointed to a deficiency in phosphorus and, to some extent, nitrogen, seemingly attributable to the reduction in the thickness of the humus layer and changes in its chemistry, the increased proportion of the soil phosphorus in the form of poorly soluble inorganic compounds, a decline in soil microbial activity, deterioration of the pine root systems, and the leaching of nutrients or their binding to acidifying non-crop vegetation.

Root growth and root system development can also be influenced by the changes to soil, notably to structure but probably also to fertility, effected by the roots of vegetation formerly supported by the soil; main vertical roots of red pine took 5 or 20 years to penetrate to a depth of 1 m, depending on whether or not the roots followed old root channels (Faile 1974).

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