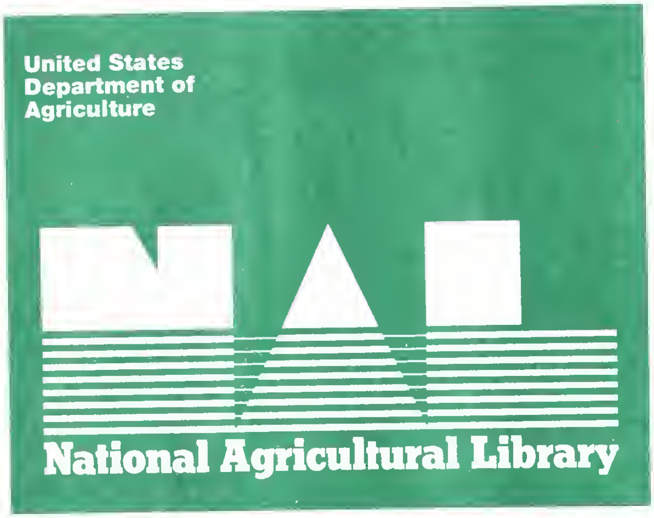
ROOT CHARACTERISTICS of SOME IMPORTANT TREES of EASTERN FORESTS: a summary of the literature

EASTERN REGION—USDA FOREST SERVICE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EASTERN REGION
FOREST SERVICE
U. S. DEPARTMENT OF AGRICULTURE

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TABLE OF CONTENTS

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(EASTERN REGION - USDA FOREST SERVICE)

INTRODUCTION

Although a fair amount of research has been done on the root systems of forest trees in North America, much of it has not been utilized by practicing foresters as a consideration when making silvicultural prescriptions. This summary of the literature is intended to help bridge this knowledge gap by making this information available in a format usable by all persons interested in forest management.

The summary is organized on an individual species basis, with each species generally conforming to the same outline for purposes of easier reference (see p. 9). No attempt has been made to include all trees within the area encompassed, although most of the commercial species are covered. Some of the species summaries are quite brief, while others are lengthy; this is merely reflective of the volume of material on that species in the literature. Occasionally, groups of species within a common genus were combined (e.g., Populus) for the purposes of organization and to help avoid repetition.

As stated above, the emphasis of this project was on consolidating information from a variety of sources into a single publication. Readers interested in greater detail than is provided on a given topic (such as mycorrhizae of sugar maple, for example) may usually obtain more information by obtaining the reference for that subject listed in either the "Publications Cited..." section (p. 10) or the companion USDA publication, Rooting Habits of Selected Commercial Tree Species of the Eastern United States: A Bibliography, by Smith and Every, Bibliographies and Literature of Agriculture No. 10, Nov. 1980. Reference numbers used in the species summaries to cite publications correspond to publication numbers used in the Bibliography. Only those publications obtained subsequent to printing of the Bibliography are listed in "Publications Cited..."; these are referenced in the text by author's name and date (e.g., Little, 1974), and not by number.

The Insect and Disease sections of most summaries is purposely short, since much of this information (except for very recent material) is readily available in two excellent U.S.D.A. publications: Hepting, G.H. 1971, Diseases of Forest and Shade Trees of The United States USDA-FS Handbook No. 386; and Baker, W.L. 1972, Eastern Forest Insects-USDA-FS Misc. Pub. No. 1175. Readers interested in the insects and diseases associated with the root systems of trees are advised to obtain these two publications for more complete coverage of these subjects than this summary provides.

In order to keep the project down to a manageable size, an effort has been made to restrict the scope of the subject to the root system alone, without getting too involved in such areas as site preferences of individual species, methods of artificial regeneration, etc. These topics are covered in such publications as Silvics of Forest Trees of The United States (Agric. Hndbk. 271) and the more recent Manager's Handbook Series issued by the North Central Forest Experiment Station. The reader should keep in mind, however, that, from an ecological standpoint, the root development of trees should be viewed as part of the tree's development as a whole.

THE ROOT SYSTEMS OF TREES: GROWTH, MORPHOLOGY, AND FUNCTION

The roots of trees have a number of different functions to fulfill, including anchorage to the soil, absorption of water and nutrients, storage of water and other substances, and modification of soil growth conditions for succeeding plant generations. Most early investigations of forest tree root systems attempted to divide species into morphological categories such as "tap-rooted" (Pinus, Quercus), "heart-rooted" (Fagus, Robinia), and "shallow-rooted" (Betula, Picea). With increasing evidence that site factors played a major role in determining root morphology, later investigators turned more to such problems as how root formation of tree species proceeds in specific soils, and the reciprocal effects between root and shoot systems. It is now well known that optimal conditions for vigorous root growth are as important for high productivity as are good conditions for shoot growth.

In many cases the structure and adaptibility of the root system are of critical importance in determining the site tolerance of a tree species. Whether or not a species is able to colonize a particular site is often decided in the seedling stage, with root development usually playing a key role. Rapid penetration to deeper soil layers which provide a constant moisture supply, and a sufficient ability to compete with roots of other plants, are decisive factors in seedling establishment.

A large number of investigations of tree root systems have been directed toward only the gross (large-root) system. While this knowledge is important, it should be remembered that the quantity and activity of fine roots are of greatest importance in terms of water and mineral salt supply to the tree. Analyses of the roots of young trees have shown that the major part of the root system usually consists of fine roots. Indeed, roots under 1 mm in diameter often represent 95% or more of the total root length.

In the case of trees beyond the seedling stage, it is common practice to distinguish between a horizontal (surface) and a vertical (deep) root system. The former is nearly always present, while the latter may be lacking in certain species under certain circumstances. Horizontal or lateral roots are those that spread more or less parallel to the soil surface, generally not exceeding a depth of about 2 feet (60 cm). Roots which originate along a lateral and orient upward toward the soil surface are known as "risers" (Figure 1). Vertical or deep roots descend at an angle of more than 45°. If there is only one large vertical root, or if among several one predominates, this is called a taproot. Vertical roots which originate along a lateral and orient downward are known

Figure 1

- ROOT MORPHOLOGY -

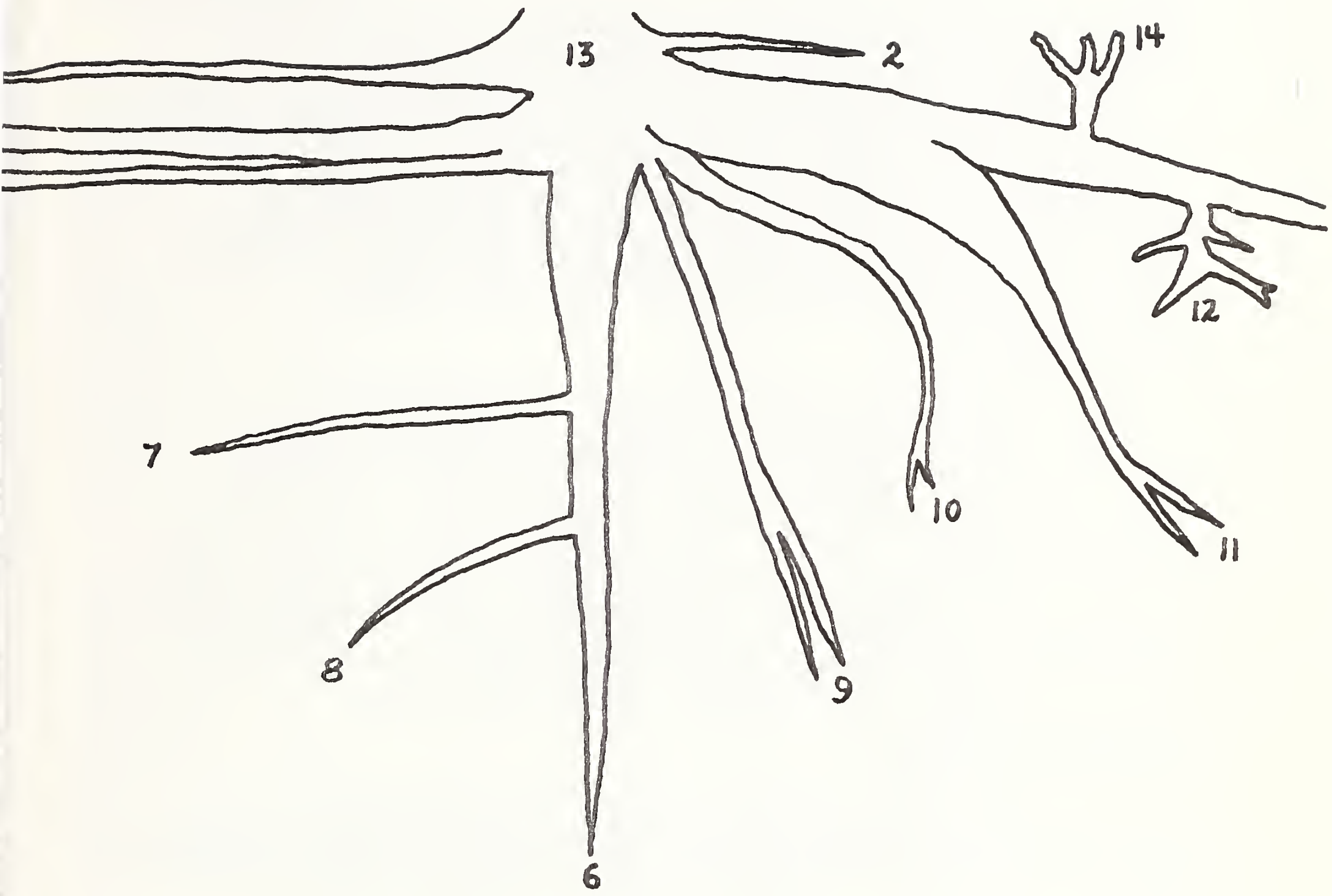

Figure 1. Composite root form of a coniferous tree showing the following roots: (1) Lateral, (2) Bur, (3) Supralateral, (4) Interlateral, (5) Infralateral, (6) Tap, (7) Tap-Lateral, (8) Tap-Oblique, (9) Proximal, (10) Heart, (11) Oblique, (12) Sinker, (13) Root-Stock, (14) Riser.

(adapted from Wagg, 1967)

as "sinkers". If a distinct taproot is lacking but the root system consists predominantly of vertical and slanted roots, we speak of a "heart-root" system. Many, but not all, taprooted species are those which have large seeds rich in reserve foods (Pinus is a notable exception) to serve as storage organs for the developing seedling.

It should be remembered that most studies of root systems, though certainly of value, give us but a static picture of a dynamic entity. The fine root portion, in particular, may lose and later regain a substantial portion of its biomass within the span of a single growing season. Much of this fluctuation can be explained by a non-homogeneous wetting of the soil due to old root channels, soil layers of differing permeability, soil fissures, etc. New sources of water and minerals must be constantly sought by active root growth, which is an important factor in ecological competition. Deficiency of water and nitrogen has been shown in some species to promote long root growth (elongation) while restricting side-root formation, thus favoring faster penetration of the soil.

LIGHT INFLUENCE

Root growth is virtually always more clearly affected by a reduction in light intensity than is shoot growth. While shoot weight may decrease slightly or even increase with a reduction in light (depending on shade tolerance of the species), root weight is almost always reduced considerably. Shaded plants are therefore apt to be more susceptible to drought than others in full light. It is also know that in seedlings of certain genera, such as Quercus, the reaction of root growth as a consequence of shading takes place more slowly than in other genera such as Acer. This is believed to be related to the higher food reserves in the former genus.

TEMPERATURE INFLUENCE

Root growth during the winter months, in species which do not have an endogenous dormant period, appears to be largely dependent upon soil temperature. Temperature is probably also a more dominant factor in spring and fall than in summer, since other factors as soil moisture and shoot activity exert a strong influence during the warmer months. In the case of older forest trees with deeply penetrating root systems, the temperature gradient with increasing soil depth may be of special significance. Within the range of approximately 5°C to 35°C lies the optimum soil temperature for tree root development in moderate latitudes, depending on species, stage of development, CO_2 and O_2 content of the soil air, and undoubtedly other factors.

The effect of soil temperature on root growth appears to be controlled by various physiological processes acting together. These include, at low soil temperature: impeding of water and nutrient absorption, slow conveyance of substances, impeded CO_2 diffusion from the roots, low production of growth substances, etc.; at high soil temperatures: consumption of nutrients after initial acceleration of growth, excessive root respiration, loss of synchronization of the metabolic processes, etc. In addition, soil temperature also affects root development indirectly by influencing the movement of water and the conversion of nutrients in the soil. And finally, it has been shown that a high air temperature can partially offset the effect of a low soil temperature and vice versa.

MOISTURE INFLUENCE

Detailed information regarding the importance of soil moisture to root growth is difficult to obtain, largely due to differences in methodology among the various studies of this subject. There are other complications as well, such as the fact that a sufficient water uptake by part of the root system can provide the necessary water for the whole system. It is known, however, that root growth is very slight or nonexistent when the soil water content reaches the permanent wilting point. Following a severe drought, water and mineral salt uptake may remain diminished even for a long time after conditions return to normal, since a large portion of the fine root system may have died. This, in turn, retards root regeneration by inhibition of photosynthesis and may bring long-lasting growth depressions in older stands. Similarly, root growth of most forest trees is impeded when the field capacity is exceeded for long periods of time, since this in most cases affects soil aeration.

Rapid changes of the ground-water level can lead to serious root damage because it takes some time before an older root system can adapt to the new conditions, which usually include decreased O_2 and increased CO_2. In many species, low soil moisture (within the range of moisture tolerance) impedes shoot growth more than it does root growth. In drier soils, in fact, the root system usually comprises a higher portion of the total plant weight. Extreme water deficiency, however, may lead to a cessation of root growth before any visible shoot injury becomes evident. In soils with water tables within the reach of tree roots, a zone of pronounced root branching can often be found in the area of frequent water saturation.

MINERAL NUTRITION

The fact that the addition of nutrients increases root development on most soils can be substantiated by the dense concentrations of fine roots that naturally occur in nutrient-rich zones of the soil. In most cases, however, growth of the above-ground parts is encouraged by fertilization even more than the roots, effectively shifting the shoot:root ratio in favor of the shoot. When the nutrient supply is low, a larger proportion of the total quantity of assimilates is in most cases consumed by root growth.

Nitrogen, phosphorous, and potassium (potash) have all been shown to produce strong growth responses in tree roots under a wide range of conditions. As compared to the latter two, N appears to encourage shoot growth to a greater degree. However, fertilization of forests generally stimulates superficial rooting because vertical translocation (especially of phosphorous) is rather slow, and because the recycling of nutrients by soil organisms favors the enrichment of nutritive elements in the upper soil horizons. One risk associated with fertilization is that it may increase susceptibility to root rot fungi.

ROOT-SHOOT RELATIONS

As mentioned briefly earlier (see Light Influence), competition for light mainly inhibits the root development of the plants affected, thus ultimately leading to a reduction of growth and an increase in sensitivity to other adverse factors. Hormonal mechanisms which determine correlative food distribution are undoubtedly of great importance in this relationship. The root: shoot ratio is also quite often affected by changes in soil moisture, soil and air temperature, nutrient supply, and stage of development of the plant. Pruning, crown cutting, and defoliation act like shading and inhibit root system development. The root: shoot ratio in some species may even change quite significantly during the course of a growing season because of the somewhat independent development of roots and shoots. As a general approximation, however, it is estimated by some researchers that in older trees about 20% of the total weight is composed of roots; the percentage for younger trees is usually quite a bit higher. Management of stands for good crown formation may be the best possible protection against windthrow, since the root systems of these trees are usually deeper and denser than those of their smaller-crowned competitors.

MYCORRHIZAE

A significant portion of the work of the last decade concerning root systems of North American trees has involved mycorrhizal relationships. Mycorrhizae-forming fungi are divided into two general classes depending on method of spore dissemination and whether or not their hyphae penetrate the cortex cells of the root. Ectomycorrhizae have aboveground fruiting bodies (wind- or water-disseminated spores), produce a fungal mantle, and do not penetrate the root cells; endomycorrhizae have no aboveground fruiting bodies (spores disseminated by root contact, ground water, or human activity), do not produce a fungal mantle, and their hyphae penetrate the root cells. Both types serve to increase root surface area, absorb and store nutrients, and convert complex organic substances and minerals into usable nutrients. The fungus mantle of ectomycorrhizae is also believed to deter feeder root pathogens, possibly through the production of antibiotics.

Mycorrhizae are believed to have great potential for increasing the growth of trees, as well as making it possible to revegetate areas previously considered unsuitable for plant growth of any kind. One mycorrhizal fungus in particular, Pisolithus tinctorius, has been shown to increase the growth of pine seedlings up to fivefold when introduced into fumigated nursery soils, and to increase survival of trees planted on strip-mine spoil banks by as much as 90 percent. Commercial production of the vegetative inoculum of Pisolithus has begun, with the intention of making it available for nursery use as soon as possible. And after that, expansion of the technique for manipulating natural systems is envisioned.

CONCLUSIONS

Many past failures of cultural techniques as well as growth stagnation of trees and whole stands have their cause in poor root growth or in damages to the root system. The early recognition of these problems and the ability to take corrective action are becoming increasingly important areas of silvicultural practice. As a small but significant example, tree species grown in mixtures that have proven to be highly productive are often complimentary to one another in the utilization of the site by the root system. New mixtures could theoretically be developed from the knowledge of the physiology and root system behavior of the various species involved. It is apparent that a better knowledge of all aspects of tree root systems could be extremely helpful in meeting the ever-increasing demands placed on forest managers.

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ORGANIZATION OF THE INDIVIDUAL SPECIES SUMMARIES*

ROOT SYSTEM DEVELOPMENT AND MORPHOLOGY

- Development of Form
- Distribution in Soil Profile
- Comparisons with other Species
- Grafting
- Adventitious Rooting

SEASONAL GROWTH PATTERN

- Temperature
- Moisture Stress

ROOT-SHOOT RELATIONS

- Coordination of Top Development with Root System Development
- Effects of Fire
- Root Biomass and Nutrient Content

EXUDATION

UPTAKE

RESPONSE TO COMPETITION

EFFECTS OF EXCESSIVE AND DEFICIENT MOISTURE

RESPONSE TO SOIL CHARACTER

- Texture
- Soil Temperature
- Root, Soil Fertility Relationships

MYCORRHIZAE

DESTRUCTIVE AGENTS

- Non-infectious

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*NOTE: This outline represents the most detailed subject breakdown used for any individual species summary. Many of the summaries are less detailed, since information was not always available on some specific topics (such as "Effects of Fire"). All of the summaries, however, conform to this general subject breakdown.

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Selected Root Terminology

The following glossary of terms has been included in an effort to better define some of the vocabulary used in the individual summaries.

Adventitious Root	A Root which develops out of sequence from either primary or secondary roots. "Adventitious" has been used by various authors to describe roots growing from stems and branches as well as from other roots.
Allelopathy	The influence of plants upon each other arising from the products of their metabolism.
Apical Dominance	The physiological process involving linking the inhibition of growth in one part of a plant (as the adventitious buds on the roots) to a hormone produced in another part (as the stem).
Apical Meristem	The elongating region (tip) of the root which gives rise to all primary tissues.
Auxins	Hormonal compounds believed to influence cell size and differentiation in both roots and shoots. Indoleacetic acid is the most prevalent naturally occurring tree growth hormone (auxin) identified to date.
Backflash	The translocation of poison, through natural root-grafting, from a chemically treated tree or plant to an untreated one, causing the latter's injury or death.
Bur	A young (1-or 2-year old) usually secondary root growing from a burl on the rootstock. Bur roots occur in groups and a burl forms from continual die-back and regrowth of roots.
Cortex	The primary ground tissue of a stem or root between the epidermis and the vascular system.
Damping Off	The rotting of seedlings, before or soon after emergence, by soil fungi attacking at soil level.
Diarch	Term used to describe the primary root xylem. Diarch xylem appears oval in cross section between two resin canals.

Fibrous Roots	Fine, brittle (when dry) roots which have root tips and are generally most plentiful in the A_0 and A_1 horizons. Sometimes called feeder roots or hair roots, they are the portion of the roots system through which the majority of water and nutrients enter.
Growth Ring	Annual rings which are laid down by the roots of most trees as they grow. These may vary greatly in size and in portion of the root at which they are most visible.
Heart Root	Root originating from a lateral root near the rootstock.
Hyphae	One of the filamentous elements of microscopic size that form the mycelium of a fungus.
Hypocotyl	That part of the axis of a developed embryo immediately below the cotyledons in seedlings.
Infralateral	A lateral root in the lowest whorl of lateral roots from the rootstock.
Interlateral	A term applied to all horizontal roots between the infralateral and supralateral roots.
Layering	The rooting of an undetached branch lying on or partially buried in the soil, which is capable of independent growth after seperation from the mother plant.
Lenticel	A body of cells formed in the periderm of a stem or root, appearing on the surface of the plant as a lens-shaped spot and serving as a pore.
Metacutinize	To become covered with a waxy protective substance.
Metacutis	A protective layer of suberized cells which isolates the meristem from the root cap in front and from the primary cortex laterally.
Mycelium	The vegetative (non-fruiting) portion of a fungus.
Periderm	The cork-producing tissue of stems and roots together with the cork layers and other tissues derived from it.

Primary Root	Root originating below the hypocotyl.
Proximal Root	Root originating within the rootstock itself.
Radicle	The primary root of a newly germinated seed.
Ramet	An individual member of a clone, descended from the ortet.
Rhizosphere	The area immediately surrounding a root or portion of a root; the microenvironment of roots.
Riser	Any second-order root originating on the upper side of a lateral root and branching out in the surface horizons into tertiary and fibrous roots.
Root Cap	The outermost surface of the apical meristem.
Root Collar	The lower continuation of the tree trunk underground, from which lateral roots and major vertical roots originate.
Root Fan	A structure of non-woody roots, consisting in idealized form of a first order non-woody root, 30 or more second order roots, and 5000 or more mycorrhizae. Root-fans are relatively short-lived, and become less frequent on older thicker roots. A group of root fans may become so intertwined as to form a "root mat", usually at or near the soil surface.
Root Graft	A union of tissue between two roots. May be interspecific (between two different species of tree) or intraspecific (between two members of the same species). Self-grafting refers to grafts between two roots of the same tree.
Root Pressure	The osmotic pressure difference between the external solution and root xylem fluid.
Root Sucker	The ability of some tree species to produce new stems from dormant or adventitous buds present along the roots (usually lateral roots).
Scion	Any unrooted portion of a plant used for grafting or budding on to a rootstock.
Secondary Root	Root originating from a branch or stem of a tree.

Second-Order Root	Any root branching off from a first-order root (taproot or lateral), regardless of the location or direction.
Sinker	Any second-order root originating on the underside of a lateral, usually going straight downward for several feet into the subsoil.
Stele	The central cylinder of vascular tissue, etc. in the stem or root.
Stilt Root	An adventitious root that develops from the butt of a tree above ground level so that the tree appears as if supported on stilts.
Stool	A living stump capable of producing sprouts.
Suberization	The impregnation of cell walls with suberin, causing the formation of cork or cork-like tissue.
Sucker	A shoot arising from below ground level, either from a rhizome, or from a root, when a root sucker.
Supralateral	A lateral root in the highest whorl of lateral roots from the rootstock.
Triarch	Term used to describe the primary root xylem. Triarch xylem is triangular between three resin canals.
Vascular Cambium	A sheath of embryonic cells extending from the beginning of secondary growth in the shoot tip to a corresponding position in the root.
Woody Root	Distinguishable from a non-woody root by the annual production of secondary xylem.

Sources:

Sinnott, E. W. 1960. Plant morphogensis. McGraw-Hill, Inc., N.Y.

Ford-Robertson, F. C., Editor. 1971. Terminology of Forest Science, Technology, Practice & Products. SAF, Washington, D.C.

MORPHOLOGY

Development of Form

If germination occurs on organic material of some type, balsam fir seedlings initially develop strong and only slightly branched lateral roots. Frequently they send down a heavy central root which appears to be a tap root, but which splits at the bottom of the humus into a number of laterals which remain in the organic layer. One rather small and comparitively insignificant root may continue into the mineral soil (860).

On drier upland sites balsam fir seedlings may produce prominent tap roots and vertical sinker roots. Greatest vertical penetration is attained on coarse textured sandy soils, where depths of up to 3 ft. (.9 m) or more have been reported for 3-year-old seedlings. Survival beyond the seedling stage on such dry sites is often poor, however (1052).

Distribution in Soil Profile and Comparisons with Other Species

On most sites where it occurs, mature balsam fir is fairly shallow rooted. One author found that balsam roots penetrated only as far as the B_1 horizon on a sandy loam soil (559). On a coarse textured sandy soil, balsam fir was considerably deeper-rooted than black spruce of the same age but slightly shallower-rooted than white spruce (1052).

The roots of balsam fir are generally thicker and less branched than those of either white or black spruce. Fir thus does not normally form the "mat" of fine roots that spruce often does. The absorbing tips of fir rootlets are greater in both diameter and length than those of spruce, however (860, 559).

The average depth of rooting for small balsam fir (15-40 in tall (.4-1.0 m) on a medium sand soil in one study was 6 ft. (1.8 m) (67). In general, the root system of balsam fir is considered to be less variable in habit than white spruce (67).

Grafting

Intraspecific root grafting in balsam fir has been reported by more than one author (658, 446), but was found to be specifically missing by another who used radioactive isotopes to test for grafts among several different species (596).

Adventitious Rooting

Layering occasionally occurs in balsam fir although it is not considered an important means of regeneration. The adventitious roots originate from dormant buds along the buried branch and, unlike in spruce, are distributed somewhat irregularly (71).

Branches so layered may be found growing as independent trees, the connecting branch having been decayed (253).

SEASONAL GROWTH PATTERN AND ROOT-SHOOT RELATION

As in many other species, root growth in balsam fir is periodic, with two major spurts of growth separated by a period of low activity. In New Brunswick, these two growth periods correspond roughly to the months of May and July. The June lull in root growth corresponded to the time of maximum shoot growth (740).

Carbohydrate reserves accumulated in the previous year after shoot elongation has ceased, in contrast to those accumulated in the current year before budbreak, apparently are important to current shoot growth in balsam fir (among other conifers). This is thought to be because larger amounts of reserves are accumulated in late summer and fall than in early spring. Accordingly, nursery practices interfering significantly with the accumulation of reserve carbohydrates would be expected to inhibit current growth only when performed in the previous year (Little, 1974).

Root weight for balsam fir seedlings grown at four different light intensities was greatest at 100%, only slightly less at 45%, and significantly less at 25% and 13%. Even at 13%, however, average root weight was 17.2% of the average weight at 100%. This was much higher than for any of the other 3 species tested, (black spruce, white spruce, and white-cedar), and serves to reflect the ability of balsam fir to survive under very low light conditions (746).

EXDUDATION AND UPTAKE

A study of various coniferous seedlings grown at different seed bed densities showed that balsam fir had the highest proportion of total biomass in roots, approximately 40%. Balsam fir also had a higher proportion of the 6 nutrients tested for in the roots than most other species, with Ca and Mg being especially concentrated by the roots of fir. Increasing density of seedlings increased the proportion of total biomass in roots only slightly (978). This latter finding was also confirmed for balsam fir in natural stands, where a 7-fold increase in stem density resulted in only a 1.6% increase in the proportion of total biomass in roots (86).

EFFECTS OF EXCESSIVE AND DEFICIENT MOISTURE

Little has been written concerning the effects of excessive moisture on balsam fir. One author, however, reported that the tap roots of balsam fir seedlings typically die after a period of contact with standing water, whereupon horizontal lateral roots appear above the water (349). Another study found that balsam fir exhibited the best survival of 5 coniferous species (including black spruce) inundated for periods of up to 48 days. The author noted, however, that more than 2 months of continuous inundation have been shown to result in heavy mortality of balsam fir (12).

MYCORRHIZAE

Fungi known to form mycorrhizal associations with balsam fir include Cenococcum graniforme, Suillus granulatus (1181), and Boletus granulatus (Hepting, 1971), and Suillus punctipes (Homola and Mistretta, 1977).

DESTRUCTIVE AGENTS

Non-infectious

Because of their shallow root system and thin bark, balsam firs of all ages and sizes are killed by even light ground fires (Fowells, 1965).

Balsam fir is subject to windfall, especially on shallow, wet soils. Trees larger than 8 in. (20.3 cm) D.B.H. and over 50 years old are most susceptible (Fowells, 1965). In some areas, stem breakage is much more common than actual uprooting of the trees (788). On bouldery or rocky soils, root injury due to repeated rubbing of roots against rock surfaces during windy periods may contribute to windthrow and/or entry of decay fungi (1126).

Balsam fir has been classified by 2 different authors as "moderately tolerant" and "sensitive" to salt in its root zone (871, 923).

Insects

Insect damage to the roots of balsam fir is caused primarily by 2 species of weevils, and by white grubs of the genus Phyllophaga. Warren's collar weevil, Hylobius warreni Wood and pales weevil, Hylobius pales (Herbst.) attack the roots of fir as well as several other conifers. In Quebec, injuries from Hylobius were found mainly on the root systems of trees of dominant, codominant, and intermediate crown classes. Injuries of undetermined nature, probably caused by defoliation and suppression, were predominantly associated with intermediate and suppressed trees. (1096). Refer to other summaries in this series or to Baker, 1972 or Wilson, 1977 for descriptions of the damage caused by these insects.

Extensive root mortality of balsam fir follows defoliation by the spruce budworm, apparently as a result of root starvation (Hepting, 1971). Rootlet recovery from budworm damage may lag behind foliage recovery for 3 years or more (1121). Damage caused by the balsam wooly aphid and the above-mentioned weevils also appears to indirectly affect the roots of balsam fir by predisposing trees to infection by the root-rot fungus Armillaria mellea (579).

Nematodes

Nematodes associated with the roots or root-zone of balsam fir include Criconemoides lobatum, Rotylenchus robustus, *Tylenchorhynchus maximus*, *Xiphinema americanum*, and unnamed species of *Paratylenchus*, *Pratylenchus*, and *Rotylenchus* (792; Ruehle, 1967).

Fungi

The root and butt rot caused by *Armillaria mellea* is probably the most important disease of balsam fir in the United States. The disease is characterized by root collar resinosis, black rhizomorphs, and mycelial fans under the root collar (Hepting, 1971). Up to 79% of the trees in some fir plantations in Newfoundland were found to be infected with *Armillaria*, with a tree mortality of 35% or more. The severity of the disease in Canadian plantations varies considerably among planting locations and among different planting methods, with bare root stock on cutover, moderately well-drained sites being the combination resulting in highest susceptibility (1085) (1087).

Many of the other important root-rot fungi of balsam fir are discussed by Hepting (1971) and will only be briefly mentioned here. *Corticium galactinum* and *C. fuscostratum* have been reported from several locations in Canada, with the former species the most important (1269). Other species of fungi associated with the roots of balsam fir included *Stereum sanguinolentum*, *S. purpureum*, *S. chailletii*, *Coniophora puteana*, *Poria asiatica*, *P. subacida*, *Odontia bicolor*, *Omphalia campanella*, *Polyporus schweinitzii*, *P. tomentosus*, *P. balsameus*, *P. abietinus*, *Merulius himantioides*, *Flammula alnicola*, *Fomes annosus*, *Trichoderma* spp., *Amylostereum chailletii*, *Graphium* spp., (Hepting, 1971; 696; 1111; 1096; 1122).

A study of balsam fir growing on a site having 2 different soil moisture contents showed that different species of root-rot fungi were very different in their moisture preferences. *Odontia bicolor* and *Graphium* spp. were not greatly influenced by moisture conditions whereas *Trichoderma* spp., and *Amylostereum chailletii* were much more prevalent on dry and wet sites, respectively. In addition, some fungi were only able to infect previously injured roots, a few to the point of attacking only roots previously wounded by a specific agent. Most fungi also showed a distinct preference for either root or trunk wounds with only a few, such as *Graphium* spp., having the ability to infect both with equal vigor (696).

The slow progress of root-rot fungi that frequently infect young balsam fir may be due to chloroform-soluble extractive compounds found in the root centerwood (1116).

MORPHOLOGY

Development of Form

The first lateral roots emerge from the red maple radicle about 2 weeks after germination. Soon after the first laterals appear, the taproot, now at a depth of 2 to 5 cm (.8 - 2.0 in), begins to turn and grow horizontally. By the end of the first year the taproot is generally about 10 to 20 cm (3.9 - 7.8 in) long and the major laterals are 5 to 10 cm (2.0 - 3.9 in) long. In some instances even the first order laterals on the taproot are mycorrhizal (762).

The lateral roots of 2- and 3-year-old seedlings are only about 1mm (.04 in) in diameter. There is no clear indication that these original laterals become the woody laterals of the mature root system. New roots often emerge from the taproot of older seedlings, so it is conceivable that the large root tips of woody roots develop only from adventitious primordia (762).

The root system of 10 to 15 year old red maples is already quite similar in form to that of mature trees. Woody roots are up to 1 cm (.4 in) in diameter and are morphologically similar to the rope-like roots of older trees. Several woody laterals are usually distributed more or less evenly around the stem. In some trees the root system is one sided because there are no laterals extending from the stem on the side opposite the horizontal taproot. Root fans (clusters of non-woody roots) are evenly distributed along most of the length of these young horizontal woody roots. The longest roots on these trees are about 5 meters and the root systems cover an area of approximately 50 square meters (762).

Distribution in Soil Profile

Root systems of mature red maple trees exist mostly in a relatively thin horizontal layer in the upper 25 cm (9.7 in) of soil. Infrequent vertical branches growing downward from horizontal woody roots probably make up less than 5% of the whole root system on most soils. Downward growing taproots are generally lacking (762).

The horizontal root system can be divided into 3 major portions. Several large, rapidly tapering roots extend out for about one meter from the base of the tree. These roots commonly taper from 10 to 15 cm (3.9 - 5.8 in) at the base of the tree to less than 3 cm at a distance of 1 to 2 m (3.3 - 6.7 ft). Beyond the zone of rapid taper are sparsely branched, rope-like woody roots. These may extend for 15 meters or more and are characterized by a scarcity of branches, a marked tendency to grow straight, and a small change in diameter over long distances. Root fans with their characteristic beadlike growths, grow from the smaller, distal portions of the woody roots to form the outermost portion of the root system. Root fans are relatively short-lived, become less frequent on the older, thicker roots, and are virtually absent from roots over 2 cm (.8 in) in diameter (762).

Adventitious roots may arise from various locations within a few meters or so from the stem. These roots are smaller, have fewer growth rings, and are lighter in color than the older rope-like roots, and have healthy root fans along their entire length. On wet sites, where water levels are commonly high, adventitious roots are found high on the root collar. On well-drained soils adventitious roots seem to develop when the larger roots have been injured or diseased, or possibly when their growth rate slow down (762).

Comparisons with Other Species

One author reports that in mixed stands of red maple and red pine, woody maple roots were within the upper 8 cm (3.1 in) of mineral soil, whereas the pine roots were found at depths of 8 to 30 cm (3.1 -11.7 in). Roots of black cherry and trembling aspen, when they occurred, were intermingled with or even occurred nearer the surface than woody red maple roots. In mixed hardwood stands dominated by red oak, practically all the non-woody tree roots in the forest floor were red maple; red oak rootlets did not seem to be competing for this portion of the soil (762).

Grafting

Natural root grafts between red maple trees is reportedly common (658, 659).

Adventitious Rooting

Adventitious roots most often arise from the stem or the zone of rapid tapering of lateral roots, but may occasionally arise from further out on the laterals. As previously mentioned, their development is usually related to injury or suppression of the parent root through such factors as nematodes, small rodents, frost heaving, fungal infection, or unfavorable moisture conditions (762).

SEASONAL GROWTH PATTERN

The diameter of lateral roots in red maple reportedly increases during the spring and early summer and then remains relatively constant during the rest of the summer. A decrease in diameter back to the winter condition then occurs in the fall. This autumnal decrease in diameter is thought to be associated with the period of root growth that occurs after the leaves have fallen (1313).

Studies of the initiation of cambial activity in the spring show that activity starts later in the root than in the stem, and moves from the stem out to the end of the root. Cessation of activity in the autumn occurs in the same sequence. As in sugar maple and several other species, root elongation and root cambial activity in red maple may occur at a reduced rate throughout the winter (1308).

ROOT-SHOOT RELATIONS

In one study, red maple was able to delay death after girdling longer than yellow birch or white birch, but not as long as sugar maple or beech (934).

Root-shoot weight relationships in red maple vary considerably between (but not within) different populations, suggesting some degree of genetic control. (856).

Due to its vigorous sprouting ability, young red maple shoots are often able to utilize the root systems of mature trees to achieve rapid growth. Root: shoot ratio (by area) of such sprouts may be as high as 24:1, as compared to about 4:1 or 5:1 for seed-origin trees (1135).

EXUDATION

It has been shown that red maple is able to exudate certain foliar-applied herbicides (including 2,4,5,-T) through the root system in considerable quantities (963).

Excised roots of red maple were found to surpass all other species tested (a total of 6) in total volume of exudate yielded per unit of root surface, but entire detopped root systems of red maple yielded very little exudate (890).

Radioisotopes of P and Ca introduced into stumps of seven red maples were found in leaves of 19 other species which were up to 24 ft. (7.2 m) from the donor maples. The mode of transfer was believed to be either by exudation from the donor and absorption by the acceptor species or through mutually shared mycorrhizal fungi (1326).

RESPONSE TO COMPETITION

It has been suggested that the paucity of ground vegetation in communities in which red maple is a dominant tree species may be partially due to the intense competition offered by the shallow-rooted maples (164).

See Comparisons with Other Species for further discussion of competition.

EFFECTS OF EXCESSIVE AND DEFICIENT MOISTURE

Red maple is reportedly intermediate in tolerance to water saturated soil conditions. Shoot growth of seedlings was only slightly affected by 60 days of inundation in one study, while adventitious root formation was abundant. Red maple was rated as more water-tolerant than american elm, sweetgum, willow oak and shumard oak, but less tolerant than green ash, water tupelo, and pumpkin ash (566). Red maple seedlings also reportedly recover from stunting induced by saturated soil at a very rapid rate (778).

The general absence of red maple in moist river bottom habitats is believed to be due to seedbed condition limitations or moisture-limiting growth conditions after the young seedling stage (778).

RESPONSE TO SOIL CHARACTER

The root system of red maple is considered to be quite flexible with soil character and moisture conditions. When the seeds germinate in swamps the taproot remains short and long laterals spread out beneath the surface. On the other hand, when the seeds germinate on upland, a somewhat more deeply penetrating taproot is developed and much shorter laterals (1178).

The lateral roots of red maple have been shown to return to their original direction of growth after having been deflected by a barrier, such as a large rock. This tendency results in efficient exploitation of the more fertile surface soil by the root system (1309).

Day-to-day variation in growth rate of red maple root tips was found to be highly sensitive to temperature. Roots of greenhouse seedlings in unheated trays showed day-to-day variations in temperature and growth rate that closely paralleled the variation in daily mean outside air temperature. Roots in trays with controlled temperatures grew at essentially constant rates, independent of outside air temperature. Although roots grew faster as the temperature was increased (up to 25°c), they also tended to be subject to more decay at higher temperatures. The optimum temperature for root growth in the trays seemed to be about 12 - 15°C (763).

Root morphology of red maple is greatly affected by soil sterilization. The non-woody root fan structures differed most between sterilized and non-sterilized in one study. The two possible explanations offered by the author were that: 1) soil organisms are influential in the morphological development of red maple roots, or that 2) variations in soil microenvironment (especially moisture) are important (828).

Soil type does not greatly affect root fan morphology. Seed source was found to be more important than soil type in influencing third order root characteristics and beaded rootlet characteristics of all orders (826).

The beaded rootlets common to red maple are believed to be controlled primarily by heredity. Environmental soil factors, however, apparently enhance the expression of the heriditary beadedness (828).

Red maple is reportedly able to occasionally establish itself on a substratum of rotten wood (such as logs or stumps), although growth of such trees is usually poor (727).

Red maple seedling rooting habit and root weight were found to be very similar on a clay and a clay loam soil in one study. All trees had developed practically no main radicle but had a good development of secondary roots. Overall growth, however, was significantly better on the clay soil (336).

One author reports that less frequent branching and greater extension of woody roots in red maple are usually associated with poor tree vigor and poor soils, whereas more frequent branching occurs in fertilized areas or areas of high organic matter content (762). This may be partially related to the high rock or boulder content of some poor soils, since branching is promoted by root injury (1310).

One study of the effects of fertilization on red maple seedling growth found that on infertile silty clam loam soils, growth of both root and shoot was improved by a "low" level of fertilization - that is, roughly 25 ppm N, 25 to 75 ppm P, and 75 to 100 ppm K. Available nutrients exceeding these quantities accelerated top growth, but tended to depress root growth, a combination which could be detrimental to trees under drought conditions. (Pham, et al. 1978).

MYCORRHIZAE

Endotrophic mycorrhization in red maple is intense in all but very young seedlings. Most endotrophic mycorrhizae occur lateral to second or higher order non-woody roots. Single mycorrhizae are shaped like small 1mm (.04 in.) long beads, but about half of the mycorrhizal roots consist of a series of end-to-end "necklace" beads. Lateral root primordia develop within the beads rather than at the constrictions. In general, mycorrhizae are terminal; but occasionally as in other species a root tip resumes active elongation and continues to grow as an uninfected root. This frequently occurs just behind areas that are injured or diseased (762). Some mycorrhizae may occur on non-beaded roots; bead formation is normal for red maple and not dependent on mycorrhizal infection (278).

The growth of red maple was increased when the plants, grown in either sand or anthracite waste, were infected with the mycorrhizal fungi Glomus macrocarpus or Gigaspora gigantea (278).

DESTRUCTIVE AGENTS

Non-Infectious

Red maple is reportedly very sensitive to soil salts in the root zone (871).

The environmental pollutants sodium fluoride and lead chloride at concentrations as low as 2×10^{-4} M were found to adversely affect red maple seedlings in the form of leaf yellowing and an accelerated casting of leaves (582).

Injuries to red maple roots by small rodents, nematodes, frost heaving, fungal infection, and other agencies are common, so that the formation of replacement roots appears to be a quantitatively important type of branching (762).

Insects

Very few insects are reported to specifically damage the roots of red maple. Larvae of the leaf miner fly Phytobia setosa (Loew) may tunnel into the roots, but the majority of damage is usually restricted to the above-ground portions of trees (Baker, 1972).

Nematodes

Nematodes associated with the roots of red maple include *Criconema fimbriatum*, *C. inaequale*, *Criconemoides beljaevae*, *C. curvatum*, *C. macrodorum*, *Gracilacus aciculus*, *G. audriellus*, *G. elegans*, *Helicotylenchus sp.*, *H. platyurus*, *Hoplolaimus galeatus*, *Longidorus elongatus*, *Paratylenchus projectus*, *Pratylenchus crenatus*, *P. penetrans*, *Trichodorus aequalis*, *Tylenchorhynchus claytoni*, *Xiphinema americanum*, *Xiphinemella esseri* (Ruehle, 1967), *Dolichodorus* sp., *Helicotylenchus dihystera* (cobb) Sher, *H. digonicus*, *H. erythrinae* (Zimmerman) Golden, *Hemicriconemoides* sp., *H. chitwoodi* Esser, *Hemicycliophora* sp., *Meloidogyne* sp., *Rotylenchus pumilus* (Perry) Sher, *Scutellonema* sp. (Ruehle, 1968).

Fungi

Red maple is seldom killed or seriously damaged by root disease. *Armillaria mellea* can enter through root or butt wounds and destroy root and trunk wood, but it kills only trees already weakened from other causes. Other fungi known to cause root and butt rot of red maple, aside from the main trunk rotters, are *Polyporus spraguei*, *P. sulphureus*, and *Ustulina vulgaris* (Hepting, 1971).

Acer saccharum Marsh. - Sugar Maple

MORPHOLOGY

Much of the material in this section was summarized from the very thorough coverage of sugar maple rooting habit by Fayle, 1965 (143). Readers interested in greater detail are directed to this publication.

Development of Form

Upon emergence from the seed, the primary root of sugar maple proceeds obliquely downward, being easily deflected by slight variations in soil structure and texture. Nursery grown stock, however,typically exhibits a fairly straight primary root with relatively fine laterals. (372)

The primary root continues to increase in diameter, but increment in length is small after the first few years. By the time the tree has attained one or two inches (2-5cm) in diameter, the original primary root is almost indistinguishable from the surrounding side roots.

Side roots emerge in four planes from the primary root at an angle of divergence of about 65°. Thus the first lateral roots grow obliquely downward at approximately 25° from the horizontal. Probably few of these original roots develop into the lateral root system; many of the laterals in mature trees are believed to be of adventitious origin.

Roots on the upper side of the oblique laterals grow upwards and branch profusely into the humus layers, often forming a dense mat near the surface. Those on the lower side attain greater diameter and proceed more or less vertically downward, proliferating in the deeper soil layers.

The morphology of the early root system is gradually obscured by the criss-crossing of roots in the central area into one mass of wood tissue, and by mortality and re-invasion of areas by new roots, many of adventitious origin. Yearly elongation of individual roots may vary from a few inches to two or three feet (.6-1.0 m), depending on soil texture and other environmental influences. One hundred or more side roots may be produced per foot of root during the current year's growth, but few of these eventually survive.

Distribution in Soil Profile

The root system of mature sugar maple is characterized by a concentrated central rooting mass, with the main concentration of roots throughout the profile lying within the crown width. The root length of medium-sized sugar maple in a fully stocked stand with 1-2 feet (.3-.7m) of available rooting depth probably does not exceed 50 feet (15.5m). The radial extent from the stem is even shorter, because the roots take a meandering course. (372)

The downward extension and form of vertical roots, including the taproot if one exists, is largely determined by soil texture (and/or structure) and the level of the water table. A rather poor lateral system is found when these conditions or the presence of bedrock prevent the development of the central root mass. Trees growing on favorable sites may be quite deep-rooted and include a considerable amount of earth within the central root mass, making them quite windfirm (372). Trees on relatively fine-textured soils are also characterized by a dense mat of fine roots (less that 1/4 inch (.6cm) in diameter) within a few inches of the soil surface, and possibly extending to depths greater than 20 inches (50.8cm) (1056, Godman, 1957).

Comparisons with Other Species

In comparison to yellow birch, the rooting habit of sugar maple is less adaptable to a range of soil depth and moisture conditions. The roots of newly germinated yellow birch, however, are too weak to pierce the mat of litter which maple seedlings are able to penetrate. On good sites, yellow birch has a much more open, wide-spreading root system than sugar maple, with a network of prominent laterals which tend to maintain their identity throughout the life of the tree. The feeding roots of yellow birch tend to be finer and more fibrous than in sugar maple (860)(372); they also reportedly branch more in the lower (B_3) soil horizons (559).

The root system of sugar maple seedlings is only slightly reduced by shading the top, whereas that of yellow birch is greatly diminished. (743)

Yellow birch can be found that originated on rocks or boulders covered only by a very minimal layer of moss or humus. This is unusual with sugar maple, probably because there is insufficient early lateral spread of the roots to make contact with mineral soil. Also, sugar maple roots will not penetrate rotted wood to the extent that yellow birch will. (372)

The actual distribution of the root mass in relation to crown mass is less variable in sugar maple than in yellow birch. In addition, yellow birch lateral roots typically extend well beyond the crown perimeter, whereas those of sugar maple extend only a few feet beyond, if at all. (1186)

On deeper, drier soils sugar maple is reportedly firmer rooted than the other species which normally grow with it. (M.T.U., 1968)

The roots of sugar maple are reportedly less branched and interlaced than those of beech. (860)

The absorbing ends of sugar maple feeder roots are conspicuously different from those of its associates. In maple they are characterized by long white filaments up to 6cm (2.4 in) in length, each with a sheath which can be easily removed. (860)

Grafting

Intraspecific root grafting in sugar maple is reportedly common (446, 659, 690, 658). Fusion of adjacent or crossing roots may occur as a result of growth pressure at the points of contact (658). Limitations to available rooting depth, such as rocks or impervious soil layers, may also promote grafting (372).

Adventitious Rooting

Layering of sugar maple is reportedly quite common, especially in dense, closed-canopy hardwood stands. Layered stems may be easily mistaken for root suckers since seedlings may have several years' growth, and therefore buds, buried beneath the litter surface. Most stems arising through layering will exhibit poor growth, since conditions conducive to layering are not conducive to good growth. Good stems can develop, however, if the layer has an opportunity to grow rapidly and establish its own root system. (371)

The production of adventitious roots from both stems and old roots is believed to play a significant role in the development of the sugar maple root system. Adventitious roots may originate from dormant primordia persisting after the loss of fine side roots, a comparable situation to epicormic branching in stems. Adventitious roots commonly originate near the base of a small lateral. (372)

Stem cuttings of sugar maple are difficult to root, although response varies with the season at which cuttings are collected. Best results are obtained from cuttings collected immediately after their leaves have matured. This period coincides with a sharp rise in the concentration of root starch (Donnelly, 1977). Cuttings from younger trees also produce roots more readily than those from mature trees (416).

Sugar maple reproduces by means of root suckers to some extent, although stump sprouts are generally more common (Godman, 1957).

SEASONAL GROWTH PATTERN

Seasonal growth of sugar maple roots is of course influenced by various environmental factors. Slow root growth in winter, the upsurge in spring root growth, and slowing of root growth in summer all appear to be primarily correlated with soil temperature. Further root growth stoppage in the summer and fall is correlated with lack of soil moisture. Some internal form of growth regulation also must occur, however, since there is no upsurge in fall growth during the period in which soil moisture and temperature conditions approximate those of spring.

Soil texture and depth may influence seasonal periodicity in root growth through their influence upon soil moisture. Roots in thin exposed soils may exhibit a growth slowdown much earlier in the summer than roots in better, more moist soils. (?)

In the upper inch or two of soil, most yearly root growth consists of the formation of many new root tips, with comparatively little length growth. (?)

There is apparently no correlation between shoot growth, cambial activity, leaf activity, and root growth except that the maximum growth of each occurs during the spring of the year. There is however, a strong correlation between root growth rate and number of hours of chilling. For sugar maple, increased periods of chilling (at 5°C) up to 350 hours resulted in increased rate of root growth after chilling was ended. Chilling for longer than 3500 hours, however, resulted in decreased root growth. Silver maple and white ash, in contrast, were both able to endure longer chilling periods without reducing root growth. New root growth was observed in sugar maple at all sampling times from November to May regardless of degree of chilling or state of bud dormancy. (1256)

Several other authors have confimed that the roots of sugar maple do not exhibit a true winter dormancy, but continue to grow at a reduced rate throughout the late fall and winter months if the soil is not frozen (334, 1161, 333). Root growth resumes with soil thaw, reaches a peak from 2-4 weeks later, and continues at this level until the time of bud-break. Shoot growth then increases rapidly as root growth declines. Later in the summer, root growth again increases after shoot elongation has declined. (334)

ROOT-SHOOT RELATIONS

Starch is present in high concentrations in the root wood of sugar maple. Relatively low concentrations are found in stem wood and bark, and little or none is found in root bark. Cells which store starches appear to be specialized specifically for that purpose, and are also capable of reforming starch after its loss. (911)

The roots of trees which have been partially or completely defoliated due to insects, or other causes, or stressed by drought usually have very low starch content (1243, 912, 909, 1238). Root starch level can thus be used as a reflection of the level of stress on the trees. Low root starch levels may occur largely as a result of mobilization of food reserves, rather than simple starvation. Trees which have been defoliated show lower root starch reserves three weeks later than do trees which have been both defoliated and girdled. This indicates that a large portion of the reserves are used in an attempt to refoliate the crown (910).

Sugar maple can reportedly remain alive longer after stem girdling than red maple, yellow birch, or white birch, but not as long as beech. (934)

There is some evidence that in sugar maple seedlings root elongation is dependent, at least in part, on the current rate of photosynthesis of the shoot. Reducing light intensities to levels that limit photosynthesis markedly reduced root elongation rates in one study. In addition, after a period of reduced photosynthesis a changeover to reserve substances utilized for root growth apparently occurred. (1255)

Root weight of sugar maple seedlings grown in 13% of full light was not reduced as much as was shoot weight. Root weight was reported to be 87% that of the full-light seedlings, whereas shoot weight was only 52%. This is fairly typical of the very tolerant hardwoods. (747)

EXUDATION

The roots of sugar maple are known to exudate various compounds, including at least 5 carbohydrates, 12 amino acids, and 4 organic acids. Seedling roots exude more carbohydrates and fewer of the acids than do roots of mature trees. (1101)

The allelopathic relationship between sugar maple and yellow birch seedlings has been examined by Tubbs (1973). When the two species were grown together in a nutrient solution, birch root growth was repressed in proportion to the concentration of inhibitor detected. Exudation of the inhibitor was related to periods of rapid maple root growth, but some individual trees produced more of the inhibitor than others. This may have been due to genetic variation. The inhibitor never caused death or necrotic tissue in birch seedlings. (1184)

Root exudates from sugar maple were also shown to significantly reduce the growth of several conifers, especially tamarack and white spruce. (1185)

In terms of number and quantity of root exudates, sugar maple reportedly produces fewer and lower quanitites thatn either yellow birch or beech. (1103)

Defoliation of sugar maple results in the production of increased quanities of root exudates. This may be important in maintaining resistance to root pathogens during periods of stress. (1102)

UPTAKE

There is some evidence that uptake of certain nutrients in sugar maple is inhibited by the presence of others. One author reports that P uptake in sugar maple seedlings was strongly inhibited by Cu and stimulated by Mn, whereas a reciprocal inhibition of uptake between Mn and Cu was observed. It was suggested that such inhibition may partially explain the slow growth of sugar maple on some sites, where it cannot compete effectively with beech as a result. (467)

RESPONSE TO COMPETITION

Stout (1956) reported that root elongation or emergence in sugar maple is frequently related to the death of neighboring trees.

Another author reports that the effects of root competition from herbaceous vegetation are not as great in sugar maple as they are in shallower-rooted species such as black locust, but are greater than in taprooted species such as red oak. (13)

EFFECTS OF EXCESSIVE AND DEFICIENT MOISTURE

In a study of drought resistance of the roots of three tree species, sugar maple roots lost water by bark transpiration more rapidly than did roots of white ash or red oak. There were no significant differences in desication resistance (percent of cells surviving at various levels of relative humidity) among the three species. (908)

Sugar maple is quite intolerant to inundation during the growing season (174, 372, Zehngraff, n.d.). A study of 65 deciduous trees and shrubs in Tennessee rated sugar maple as the second most intolerant species (after post oak) to flooding one foot (.3m) deep for one growing season. Most sugar maples apparently succumbed after less than a month under these conditions (481). Trees are much more tolerant during the dormant season (174).

Satterlund (1960), investigating swamp forests in Michigan, found that live roots of sugar maple were restricted to a depth above even the high water level. If they penetrated deeper in dry years, they were apparently killed back during wet years. The absence of large maples in the swamp sites was attributed to the inability of the species to adjust to the restricted root zone. It was an aggressive invader of the sites and developed well for the first few years, but could not compete successfully later because of an inadequate root system.

RESPONSE TO SOIL CHARACTER

Sugar maple has proved to be a problem species to establish by planting on abandoned farm lands in Eastern Canada. Studies indicate that competition from surrounding vegetation is largely responsible, but site preparation and weed control measures effective with other hardwoods have been unsuccessful. Measures that have been suggested to improve survival include fall planting, application of growth inhibitors to buds before planting, or manipulation of temperatures during cold storage of fall-lifted nursery stock. (334)

The success achieved with spring plantings of sugar maple is largely dependent on the length of time provided for establishment of a vigorous root system between outplanting and the initiation of rapid shoot growth. Seedlings transplanted too late in the spring may be subject to severe damage of the already-active root system at a time when root reserves are needed for a burst of shoot growth. As a result, a marked imbalance in the root:shoot ratio may occur, thus decreasing the seedling's chances of competing effectively with weed vegetation. (334)

Texture and Structure

Minor changes in soil texture or structure appear to influence the branching and survival of roots; this may be a result of changes in moisture, aeration, and other related features. This is most evident on fine-textured soils, where roots are most numerous in the better-aerated surface layers. On leaving the upper layers, roots frequently bifurcate and the number of side branches is less. (372)

Very shallow soil over bedrock or dense fragipan layers may result in great pressure upon roots as they are compressed against the hard surface. On such locales root injuries may result from constant friction caused by tree sway. (372)

Gravel layers may also exert pressure upon expanding roots to the extent that their shape is distorted. Small groups of adventitious roots along a large vertical root are common in such situations. Fine roots of this nature are probably relatively short-lived, being killed during unfavorable conditions and originating anew in favorable periods. (372)

In loose sand layers, root penetration is uninterrupted and long vertical roots may extend five or more feet in depth. The many side branches of these roots gives them a feathery appearance. (372)

The external appearance of new roots varies with position in the soil profile, and is probably related to differences in temperature, aeration, moisture, and nutrient status. Roots in the humus layer are relatively strong, fine, and brown in color. Beaded mycorrhizal rootlets are abundant. Those deeper (.5-1.0ft; .15-.3 m) in the profile are longer, less branched, more succulent, and whitish. Roots from even deeper (2ft.+; .6m+) are stubby and have a thick cortex. (372)

MYCORRHIZAE

The roots of sugar maple reportedly form both endotrophic and ectotrophic mycorrhizae. Very few species of fungi have actually been named in these associations, however; only Cortinarius rubribes Kauff. has been named as an ectotrophic associate. (1181)

There is some disagreement in the literature as to whether the "beaded" rootlets typical of most maples are a result of endomycorrhizal infection or environmental factors such as fluctuating moisture conditions. The latter is now considered more likely since both beaded and non-beaded rootlets may be mycorrhizal, and rootlets growing in the deeper soil levels where moisture conditions do not fluctuate rapidly are non-beaded. (637)

A study of mycorrhizal growth in sugar maple has shown that activity is closely tied to soil moisture content. When the upper soil layer becomes too dry to support mycorrhizal growth, the tips metacutinize and become dormant. When excess moisture is present at the lower soil level, the mycorrhizae closest to the surface are the more active. Although excess moisture may not kill mycorrhizae directly, it can have the same physiological effect on the tree as does drought through disruption of absorption and translocation functions. (637)

A study of maple decline by Spitko & Tattar (1977) reported a correlation between the amount and vigor of mycorrhizal infection in the roots and the degree of decline shown by the crown. Healthy trees had young infections showing extensive arbuscle development, whereas trees in a state of decline showed little arbuscle development. Arbuscles that were present in the roots of these declining trees had undergone digestion of the fine branches so that only the collars were in evidence.

DESTRUCTIVE AGENTS

Non-infectious

Sugar maple was rated by one author as very susceptible to grade injury resulting from either filling or removal of soil from around the root system. (839)

Sugar maple has been rated intermediate in its tolerance to soil applications of salt (871, 131). In one study, application of 3,000 lb/acre sodium chloride resulted in moderate leaf scorching and slight defoliation of most trees (131).

There is some evidence that sugar maple is particularly susceptible to root strangulation or girdling. This may occur as a result of transplanting, erosion, water table changes, root injury, or other causes. Dieback of a portion of the crown is a major symptom. Root girdling may also increase the tree's susceptibility to disease or insect attack. (1209, 1210)

Insects

Larvae of the leaf miner fly, *Phytobia setosa* (Loew), feed in the cambium of living sugar maple, making long, gradually widening mines. These mines usually originate at the forks of upper branches and extend all the way down into the roots, causing wood defects known as pith-ray flecks. (Baker, 1972)

Nematodes

Nematodes associated with sugar maple include *Bakernema bakeri*, *Criconema fimbriatum*, *C. octanulare*, *Criconemoides beljaevae*, *C. informe*, *C. macrodorum*, *C. sphagni*, *Gracilacus audriellus*, *Hemicycliophora sp.*, *H. similis*, *H. typica*, *H. uniformis*, *Meloidogyne ovalis*, *Paratylenchus tenuicaudatus*, *Trichodorus aequalis*, *T. californicus*, *Tylenchorhynchus sp.*, *Xiphinema americanum* (Ruehle, 1967), *Helicotylenchus* sp., *Hemicriconemoides* sp. (Ruehle, 1968).

No causal relationships have yet been established between nematodes and specifc disorders of sugar maple. (Riffle and Kuntz, 1966)

Fungi

Only a few fungi specifically attack the roots of sugar maple, and these are discussed Hepting, 1971. *Armillaria melea* is the most important of these; other species include *Polyporus lucidus*, *Pholiota adiposa*, *Poria subacida*, and *Ustulina vulgaris*. None are believed capable of killing healthy sugar maple, although all may contribute to mortality through windthrow, or in combination with insects, enviromental disturbances, etc.

Betula alleghaniensis Britton - Yellow Birch

MORPHOLOGY

Development of Form

Upon germination, yellow birch produces an extremely short, slow growing tap root which seldom attains a greater penetration than 2-4 in. (5 -10 cm) the first season. After a few days, strong lateral roots begin to develop which occupy the first 4 in. (10 cm) of surface soil for a period of some months after germination (1178).

Distribution in Soil Profile

The root system of mature yellow birch has been characterized as open in nature, with a main network of fairly prominent laterals which tend to maintain their identity throughout the life of the tree. Taproot development is limited or absent, but vertical sinker roots may penetrate to depths of 5 ft. (1.5 m) or more on looser soils. Most lateral roots of yellow birch are within 2 or 3 inches of the soil-litter interface, and their prolific branching often results in the formation of a dense root mat. Most roots occupy an essentially circular or oval area around the tree with an expanding radius of about 3 ft (.9 m) for each inch in diameter at breast height. Individual laterals of some trees, however, may extend for considerable distances (35 ft. (10.5 m) for a 6 in. (15.2 cm) d.b.h. tree in one example) where soil conditions are highly favorable (486, 372).

Sinker roots extending down from the large main laterals usually occur within about 6 ft (1.8 m) of the tree stems. Most large laterals produce one or two sinkers, each penetrating downward a few feet (or until impeded) before terminating in a cluster of small branching laterals. A number of sinkers also originate from the area directly beneath the stem, often in place of a single taproot. Most of these sinkers in one study penetrated to a depth of 18 to 30 in. (.5-.75 m) in a sandy loam soil (486).

The feeding roots of yellow birch are very fine and fibrous (859). Small secondary roots are often found branching prolifically in surface depressions where leaf mold accumulates and around old root channels and stumps. These roots show little change in taper and have little secondary growth (486). Approximately 80% of the rootlets in one hardwood stand containing a high proportion of yellow birch were found within the top 5 cm of soil (957).

Comparisons with Other Species

The detailed comparison of sugar maple and yellow birch root systems by Fayle, 1965 will be briefly summarized here. The roots of newly germinated yellow birch are too weak to pierce the relatively thick mat of leaf litter that sugar maple seedlings are able to penetrate. Older roots of yellow birch are generally coarser than in sugar maple and their more varied growth direction is almost sinuous, with depth of individual lateral roots varying as much as 3 ft (.9 m) over their length. Yellow birch in sandy loam soil has about 16 side roots per inch of current year growth as compared to about 8 for sugar maple (372)

Overall, the root system of yellow birch is considered by Fayle (1965) to be adaptable to a wider range of soil-depth conditions than that of sugar maple. On a sandy loam and coarser textured soils, yellow birch will root to at least the same depth as sugar maple as early as the sapling stage and later.

Yellow birch does not normally develop the intensively criss-crossed central root mass that sugar maple does, although windfirmness is still achieved through the presence of large supporting lateral roots. The more acute branching angle of yellow birch, approximately 55° as compared to 65° of maple, also contributes to the morphological differences between the two species' root systems (372).

One author reported that, on a deep sandy loam soil, yellow birch trees consistently had more roots and branched more extensively in the B_3 horizon than either sugar maple, beech, balsam fir, or white spruce (559). Another (762) found that in mixed hardwood stands, woody horizontal roots of black cherry, yellow birch, and trembling aspen were intermingled with or even occurred nearer the surface than woody red maple roots; horizontal roots of white pine and red oak were considerably deeper.

Grafting

Intraspecific root grafting is very common in yellow birch, apparently on both well-drained and moist sites (372, 658, 710). Incidence of self-grafting of roots in individual trees is, according to one author, somewhat higher in yellow birch than in sugar maple (372).

Adventitious Rooting

As in sugar maple, adventitious roots can develop from the stem of yellow birch, particularly younger trees. Stem cuttings of yellow birch have been rooted with some success (322).

SEASONAL GROWTH PATTERN

One author reported that adventitious "replacement roots" originating from sections of yellow birch lateral roots placed in an inert medium were inactive from October 29 to May 5. Production of biomass in the form of adventitious roots was slightly greater during the first growing season as compared to the second. During the first growing season root N, K, Ca, and Mg concentrations were initially low; they increased during the growing season and declined at the end. Fe and Al, on the other hand, increased toward the end of the season, while P, Mn, and Zn decreased throughout the season. The data seem to suggest that root conditions favorable to the translocation of Fe and Al into replacement roots late in the season are not favorable for movement of P, Mn, and Zn. Increased mobilization of Ca and K was thought to be associated with root injury, though the exact process was unclear (1022).

ROOT-SHOOT RELATIONS

One author found that the average lengths of the main roots of yellow birch was greater than average crown length, especially among trees greater than 2 in. (5.1 cm) d.b.h. The horizontal distribution of birch roots in relation to crowns was irregular as opposed to sugar maple, which was much more regular. Longest roots of birch frequently were well outside crown perimeters, whereas those of sugar maple rarely did. Roots of both species were distributed away from the direction of lean of the tree (1186).

Yellow birch was found by one author to be the second most rapid species to succumb to stem girdling of five hardwood species tested. Only white birch died more quickly while red maple, sugar maple, and beech lived longer than yellow birch (934).

In controlled light experiments, one author found that the root system of yellow birch was greatly diminished by shade, weighing only about 30% of its full-light weight when grown under 13% of full-light. Silver maple and white birch showed a similar response, while sugar maple was affected very little by low light in comparison. Differences in the growth of yellow birch and sugar maple beneath a dense forest canopy were thought to be related to these differences in root development (1124).

EXUDATION AND UPTAKE

A study of the root exudates of three northern hardwood species showed that the quantity of exudates produced by yellow birch over a year's time was slightly greater than for beech and over five times greater than for sugar maple. Of the total for yellow birch, 70% was cations, 17% anions, 7% organic acids, 5% carbohydrates, and 1% amino acids. This pattern differed from the other species primarily in the anion category (SO_4 , Cl^-, PO_4 , NO_3-), which, at 17%, was significantly higher for birch than for beech or maple (1103).

In one study, leachate from actively growing sugar maple root tips indicated the presence of substances inhibitory to yellow birch growth. When maple and birch seedlings were grown together in an aerated nutrient solution, birch root growth was repressed in proportion to the concentration of inhibitor detected. The inhibitor did not result in the death of any birch seedlings, however, and its production was quite sporadic. This suggested to the author that in nature the inhibitor probably augments the competition which sugar maple could display without an inhibitor (1184).

EFFECTS OF EXCESSIVE AND DEFICIENT MOISTURE

One author, investigating swamp forests in Michigan, found that yellow birch roots penetrated well below high water levels and a few into gley, whereas live roots of sugar maple were restricted to a much shallower depth (Satterlund, 1960).

RESPONSE TO SOIL CHARACTER

The rooting pattern of yellow birch is frequently modified by germination on rotted wood. Aerial or "stilt" roots often occur when germination is on stumps; in high stumps these aerial roots often become completely fused. Lateral roots may be more or less linearly oriented if germination occurs on a fallen log (372).

The shape of the root system may also be modified by strongly competing adjacent trees and/or the presence of large surface or underground obstructions. During the early seedling stage, mechanical damage to root tips or the presence of small obstructions may ultimately influence the general shape of the root system of the tree (486).

Studies have shown that yellow birch seedlings grown in humus develop much more extensive root systems than seedlings grown in mineral soil (1183, 954). Fertilizer treatments of the mineral soil media did not significantly improve root development in one study (1183). In a subsequent study, however, it was shown that good root development could be achieved on mineral soils where deficiencies of P, in particular, are alleviated by P fertilization and liming (575).

It has been shown that, under a closed stand, the presence of organic material is more important than the prevailing temperature in determining whether a specific volume of soil is occupied by yellow birch rootlets. One Canadian study found that in pure hardwood stands containing a high proportion of yellow birch, over 75% of the rootlets were found in the humus layer. In hardwoods containing less birch or in stands containing a high proportion of conifers, over 90% of the birch rootlets were in the humus. This tendency was cited as a probable reason for the mortality of residual yellow birch in partially-cut stands, where the ground surface has been exposed to some degree to the sun and wind (957).

One author found that yellow birch roots will not grow in a Ca-deficient medium even though the upper root system has developed in a nutrient-sufficient layer. Rhizospheric Ca is thought to be necessary in order to moderate the detrimental influences of other soil elements, particularly heavy metal ions. This finding was cited as evidence that Ca deficiency is partially responsible for inhibiting root growth of yellow birch in many New England forest subsoils, although deficiencies of N, P, K, and Mg are common on such soils and undoubtedly contribute to the problem (577, 576).

As with many other plant species, yellow birch root growth is inhibited by Al in lower substrates. Al toxicity is apparently most severe on soils which also exhibit a Mg- or S-deficiency in addition to high levels of trivalent Al (577).

MYCORRHIZAE

Yellow birch feeder roots normally show good ectomycorrhizal development, although only Cenococcum graniforme has been mentioned in the literature as an associate (1181). Seventy-six percent of all seedling yellow birch feeder roots were mycorrhizal in one nursery study (33).

Yellow birch ectomycorrhizae seem to be able to grow under fertility rates which inhibit development of ectomycorrhizae in red pine (33).

Mycorrhizal roots of yellow birch were shown to exert a stimulatory effect on numbers of certain soil bacteria and soil actinomycete fungi. Other types of soil bacteria appeared to be repressed in the region surrounding mycorrhizal roots. This effect of mycorrhizae was thought to be important in influencing nutrient uptake (622).

DESTRUCTIVE AGENTS

Non-infectious

On shallow soils, yellow birch is considered susceptible to windthrow (Hepting, 1971).

Yellow birch is also affected by the decline known as "birch dieback", described under paper birch. Thousands of square miles of birch stands, mostly yellow birch, were affected by birch dieback in the Canadian maritime provinces and Northeastern U.S. in the 1930's and 40's (Hepting, 1971).

Various factors, both biotic and abiotic, have been cited as possible causes of birch dieback. A virus disease has been considered as the possible triggering mechanism to the dieback, with insects, climatic factors, and environmental influences then taking over and causing the main damage. Other researchers have attributed the decline to a series of very cold winters with little snow cover, resulting in severe rootlet damage to the shallow-rooted birches. More deeply-rooted species are apparently able to absorb moisture from below the zone of frozen soil, and are thus not damaged as severely (237, 955, 958, Hepting (1971)).

As with paper birch, yellow birch also suffers from the syndrome of post-logging decadence in areas which have been partially cut over. The rate and seriousness of this decline are in proportion to the intensity of the cut, with symptoms closely resembling those of birch dieback. Refer to the summary for paper birch for a discussion of how post-logging decadence may be related to root damage (Hepting, 1971).

Insects

Other than the two insects mentioned under paper birch (both of which occasionally infest yellow birch as well), no insects are known to specifically attack the roots of yellow birch.

Nematodes

Although several species of nematodes have been associated with the genus *Betula*, few or none have been associated directly with *B. alleghaniensis*. It is probable that many of the nematodes associated with other *Betula* species in Ruehle (1967 and 1968) are also (at least occasionally) associated with yellow birch.

Fungi

Root rot and so-called "collar crack" caused by the fungus *Armillaria mellea* is probably the most serious root disease of yellow birch. *A. mellea* typically causes a soft, white root rot in yellow birch, with black zone lines in the rotted wood and black rhizomorphs on the roots. "Collar crack" sometimes results when *A. mellea* infection occurs throughout the roots and butt, and is commonly followed by invasion of one or more trunk rot fungi (Hepting, 1971).

Additional fungi known to rot the roots and butt of yellow birch include *Polyporus spraguei*, *Poria subacida*, *Corticium galactinum*, *Flammula alnicola* (1269, 310, Hepting (1971)).

Betula papyrifera (Marsh.) - Paper Birch

MORPHOLOGY

Development of Form

Initial establishment of paper birch seedlings generally requires a mineral seedbed. This is due, in part, to the inability of the emerging radicle to push through a litter layer before the food reserves within the seed are exhausted. (1313)

The seedling primary root is initially very small, with a primary xylem diameter (PXD) of .04-.06mm near the stem. Early first and second order lateral roots are of similar size. As they elongate, the diameter of the primary root and laterals increases with distance from the stem. The maximum PXD observed in seedling roots in one study was .34mm. (562)

These initial roots continue to enlarge and eventually will become the main horizontal roots. Other main roots originate as adventitious roots on the stem (just below ground surface) of seedlings and older trees. Continued morphogenesis of the root system is largely dependent upon the frequency of events which result in root bending or root tip injury (561)(562). Root injury may result in a grouping of branches at a particular point, whereas a single long-root branch usually results when a root bends around a barrier. If the frequency of injury or bending is low, main roots continue straight and branch only sparsely, radiating from the base of the tree like spoles of a wheel (562). Lateral long-root branches may also be formed upon entry into or emergence of the root from dormancy, and during slow elongation growth of the parent root. The eventual form of paper birch root systems may thus differ significantly among different trees, even among those on the same site.

There is also some evedence that particular morphogenetic events result in the formation of roots of particular diameters. Lateral roots whose PXD (at the junction with the parent root) is less than 25% of the parent root PXD normally will not become permanent portions of the root system (562). A permanent long root often arises from a series of replacement root tips produced after an injury (1313).

Distribution in Soil Profile

Paper birch as a species generally is very shallow rooted. The root system is also typically wide-spreading, making the trees windfirm (Hepting, 1971). Rooting habit, however, may vary somewhat with soil depth and may differ considerably from tree to tree and from stand to stand (151). A tap root is usually lacking, but sinkers may appear in contact with rock fragments. Characteristically the roots are almost bare of small roots except near their tips (946).

The horizontal long roots of paper birch often reach a length of 20m or more. The tip diameter of these long roots is usually 1-2mm, much greater than other root tips in the mature root system or any tips in a seedling root system (1313). Long roots branch irregularly, with up to 2m between branches.

Comparisons with Other Species

The root system of paper birch is similar in depth to black spruce and tamarack; much shallower that balsam poplar, jack pine, and white pine; and similar to, but less variable than white spruce (946).

Grafting

Natural root grafts in paper birch are uncommon, but have occasionally been reported. (446, 659, 658, 693)

SEASONAL GROWTH PATTERN

Seasonal variation alone may account for more than a 200% change in the PXD of paper birch roots. (562)

PXD apparently increases during the spring and early summer and then remains relatively constant during the rest of the summer. The final decrease in PXD back to the winter condition occurs in the fall. This autumnal decrease in PXD may be associated with the period of root growth that occurs after the leaves have fallen (1313).

ROOT-SHOOT RELATIONS

Light intensity has a significant effect upon root growth in paper birch. One study found that root weight of 3-year old birch grown in 13% light was only 26% as great as root weight for trees grown in 100% light (747). At 45% light, root weight was 86% that of the full-light trees.

Dry weight of roots is influenced somewhat by stand density. One study found that total root dry weight in a stand of paper birch remained fairly constant at stem densities of 700-3000 per acre, but decreased sharply at 5000 stems per acre (86).

In a study involving the girdling of several hardwood species, paper birch was found to be the first to die. Yellow birch, red maple, and beech all lived longer after girdling; the author speculated that this was due to differences in root storage systems and "water efficiency" among the species (934).

EXUDATION

Allelopathic effects of paper birch upon other species have not been reported in the literature, although one European author found that aqueous extracts of birch and aspen litter reduced the germinative energy of larch seeds (Sargunova, 1969). It is also known that growth of paper birch may be severely inhibited by toxic substances produced by black walnut trees (*Juglans nigra*) (410).

EFFECTS OF EXCESSIVE AND DEFICIENT MOISTURE

Paper birch is very sensistive to flooding. One study found that submergence of roots for 48 days resulted in very high mortality (12). Aspen, american elm, rock elm, black ash, red maple, basswood, red oak, bur oak, and balsam poplar are all reportedly more flood-tolerant than paper birch.

Depth to the water table is an important determinant of root distribution and root growth rate in paper birch (562).

RESPONSE TO SOIL CHARACTER

There is some evidence that root morphology, including amount of branching, is strongly influenced by soil-site characteristics. One author reported that paper birch growing on a stony soil had straighter roots with fewer branches than trees growing on a finer textured soil. The author also emphasized, however, that other site factors may have contributed to the differences (562).

Paper birch root dry weight and volume was shown to vary with soil temperature, although good growth occurred over a fairly wide temperature range (19°-31°C). Highest root dry weight and volume occurred at 23°C, whereas highest shoot dry weight and volume occurred at 31°C. Root penetration varied very little from 23°-31°C. Below 19°C, sharp decreases in both root and shoot growth were reported (516, 1267).

One author reported that soaking of paper birch roots in indolebutyric acid before planting produced no beneficial response with respect to root or shoot growth (796).

Survival and growth of planted paper birch on old field sites in Maine was much improved when the sod cover was removed before planting. The grass roots reportedly adversely affect seedling birch roots by both absorbing moisture more rapidly than the birch and also by acting as a barrier to seedling root extension (Bjorkbom, 1968).

MYCORRHIZAE

Fungi reported to form mycorrhizal associations with paper birch include: *Cenoccum graniforme*, *Leccinum scabrum*, *Boletus scaber* var. fusca, *Cortinarius* spp. (729)(Hepting, 1971), *Boletus subglabripes*, *B. edulis*, *Leccinum atrostipitatum*, *L. insigne* (Homola & Mistretta, 1977).

DESTRUCTIVE AGENTS

Paper birch is reportedly quite sensitive to herbicides at levels required for effective weed control. This has been partially attributed to its shallow rooting habit and lack of taproot development (1267).

The roots of paper birch are reportedly particularly sensitive to immersion in salt water (Wyman, 1939).

The well-known decadence of birch on lands which have been partially cutover has been partially attributed to increased soil temperature. Experiments have shown that high soil temperatures indirectly affect the root systems by upsetting the population balance of root-inhabiting fungi and by disturbing mycorrhizal development (237). The fine feeder roots may also be killed directly by increases in soil temperature of only 2^{o}-4^{o}C for one growing season (237). Shallow larger roots may be killed by sunscald if the surrounding duff is partially removed, as may occur during logging operations (1107). Other experiments have shown, however, that high soil temperatures alone do not normally impair growth if soil moisture is maintained at or above field capacity (237).

Much research has also been directed toward the relationship between rootlet mortality and so-called "birch dieback" in undisturbed stands. Several researchers have noted a rather sharp increase in the percentage of dead feeder roots on affected trees, even before crown symptoms become apparent (957)(1275). It has been suggested that the deteriorated condition of root systems of affected trees may be an important factor in the normal restocking of the water supply in trees after it has been depleted by normal transpiration (957).

The root mortality associated with birch dieback has been attributed in some cases to a warmer and drier soil resulting from one or more years of higher than normal temperatures and less than normal precipitation (957). The first trees to die are normally those on dry, shallow-soiled areas (937).

There is also a certain amount of evidence which suggests that one or more biotic factors may be the primary cause of birch dieback. Of the organisms considered as possible causative agents, nematodes, fungi, and viruses may be associated with the root system.

Fungi

Numerous fungi have been isolated from the roots of trees affected by birch dieback, but tests have failed to find any that were virulent enough to successfully invade healthy trees (956)(237). Fungi thus probably play a secondary role in the death of trees that are already declining rapidly.

Paper birch is susceptible to root rot by the fungus *Armillaria mellea*, though again, it is not normally the primary cause of mortality. The fungus reportedly usually enters at or near the root crown. Attack seems to depend upon dead bark (from previous injury) being located at or below the surface of the soil (1107). *A. melea* may be associated in some way with loss of paper birch due to windthrow, birch dieback, or decay resulting from logging wounds (Hepting, 1971).

Other fungi associated with root rot of paper birch, though apparently uncommon, include *Corticium galactinum*, *Phytophtora cinnamomi*, and Texas root rot (no genus indicated) (Hepting, 1971).

Insects

Although paper birch is suceptible to attack by a variety of insects, few if any attack primarily the root system.

The Birch Bark Beetle, *Dryocoetes betulae* Hopk., breeds in the trunks, roots of injured or dying trees, or in windfalls of paper birch and other tree species (Baker, 1972).

Larvae of the Alder Borer, *Saperda obliqua* Say, feed beneath the bark of alder and birch in the Northern and Central States, usually entering near the base of the stem (1347).

Nematodes

Nematodes associated with white birch include *Criconemoides* spp., *Tylenchus* spp., *Xiphinema* spp. (795), *Gracilus audriellus*, *G. sarissus*, *Hemicycliophora minora*, *H. similis*, *Paratylenchus* sp. (Ruehle, 1967).

Carya spp. - Hickories

MORPHOLOGY

Root growth and development in the genus *Carya* has been studied most intensely in the pecan, *C. illinoensis*. Although most of the material in this section pertains specifically to pecan, it can also be considered applicable to the other "bottomland" hickories, *C. cordiformis*, *C. myristicaeformis*, and *C. laciniosa*. The more "upland" species, *C. tomentosa*, *C. ovata*, and *C. glabra*, also probably have a similar initial root habit to pecan, although the mature root system may be somewhat different when these species are found on dry, upland soils. *C. aquatica*, the water hickory is a unique case among the hickories due to its preference for very wet sites, and will be considered separately (1321; 1178; 134; Fowells, 1965).

Development of Form

Most of the early root growth in pecan is directed into the taproot, which typically reaches a depth of from 1 to 3 ft. (.3-.9 m) during the first year. Small laterals originate throughout the length of the taproot, although a high percentage of these die back during the fall. During the second year the taproot may reach a depth of 4 ft. (1.2 m), with the laterals making considerable horizontal growth. Mycorrhizal roots usually become abundant during the second year. By the fifth year or so the root system has attained its maximum depth, and the horizontal spread of the roots is about double that of the branches. The height of the tree now exceeds the depth of roots for the first time. By age 10 the height of the top is about four times the depth of the taproot, while the spread of the branches is still only about half that of the root system (1321).

The initial root habit of water hickory is quite different from that of pecan. Lateral root development begins soon after germination and is emphasized to a much greater degree than in the other hickories. Numerous strong laterals arise from the base of the shoot at or near the soil surface. The taproot typically remains rather short, with height of the top exceeding rooting depth at an early age. This initial rooting habit of water hickory has been described as inflexible, since it has been shown to occur even among seedlings planted on well-drained soils (1178).

Early rooting habit of pignut hickory is similar to that described for pecan, although the lateral roots may be shorter and somewhat less strongly developed (1178).

Excavated root systems of 4-8 year old shagbark hickories showed that taproot diameter in the first foot of soil normally exceeded stem diameter at the base. At a depth of 3.5 ft. (1.05 m), however, taproot diameter was less than one-third its original diameter. Lateral roots in the uppermost horizon were sparse and small; the bulk of these arose between 6 and 17 in. (15.2-43.2 cm) depth. Many of the shallower laterals were furnished with fine absorbing rootlets that extended to within 0.5 in. (1.3 cm) of the soil surface. The deepest one-third of the root system was relatively poorly branched (128).

Distrib. in Soil Profile

The most distinctive characteristics of the mature root system of Carya are 3: The almost horizontal spread of lateral roots (emerging at nearly right angles to the taproot), the lack of development of any distinctly major lateral roots, and the deep, penetrating taproot (544, 134, 1135). The size of the taproot varies somewhat with the species and the situation, having its greatest development in the drought-enduring species and in the drier situations (134). A 20-year old hickory (unidentified species) in one study had a 1/2 in. (1.2 cm) diameter taproot at a dept of 6 ft. (1.8 m)(413); a pignut hickory in another study had a taproot which extended only to a depth of 3 ft. (.9 m), where it encountered a compact horizon (1135).

The roots of pecan are considered by one author (1321) to fall into 3 major classes: 1)Taproots, which grow straight down and determine the depth of penetration of the roots under the particular conditions; 2)Lateral roots, which grow straight from the taproot in a horizontal direction at a depth of from 1 to 2 ft. (.3-.6 m), and determine the lateral spread of the system, and 3)Fibrous roots, which grow in all directions from the laterals and are subject to constant dying and replacement due to varying growing conditions. Mycorrhizal roots, which grow in dense masses throughout the system, are considered a type of fibrous root. Root hairs are not present on roots of pecans.

The young nonmycorrhizal roots of pecan are bluntly pointed and increase in thickness toward the tip. The tips of mycorrhizal roots are usually rounded. The reader interested in anatomy of pecan roots is directed to (1321) for an excellent coverage of this subject.

A study of the root extension of forest trees in North Carolina indicated that smaller, younger hickories (all species combined) have more extensive root systems than older trees. The root systems of trees beyond a certain age, perhaps 120-140 years, were no longer increasing and actually appeared to be decreasing in extent (184). The area of greatest root density in pecan is usually a few feet beyond the spread of the branches (1320).

Comparisons with Other Species

A comparison of rooting extent in five seedling hardwood species showed that after 3 years, shellbark hickory was third behind bur oak and black walnut in maximum depth of rooting on a variety of sites (544).

Both mockernut and pignut hickory were found by one researcher to have an intensive network of roots in the zone nearest the trunk, although not as intensive as that of white oak (182).

Grafting

Intraspecific root grafting is common in pignut hickory, and probably also in other species of Carya. Interspecific root grafting has been reported between hickories and water oak, post oak, and elm (446).

Adventitious Rooting and Root Suckering

Hickory sprouts may arise from the stump, the root collar, and the roots following fire or cutting. The proportion of root suckers increases with the size and age of the tree; older stumps also tend to produce root suckers farther from the stump. The maximum distance is about 8 ft. (2.4 m) and the average about 2 ft. (.6 m). Suckers normally do not produce a taproot but merely appropriate the parent root. Root suckers may arise either from surface lateral roots or from laterals 6 inches (15.2 cm) or more below the surface. Coppice hickory is not as common as coppice chestnut or oak, partially because sprouting capacity in hickory diminishes rapidly with age. Also, due to their slow growth in comparison with other species, hickory sprouts are often outcompeted in even-aged stands (134) (373).

Bitternut hickory is reported to sprout more vigorously than other hickories. Sprouts of water hickory are reported to grow 3 or 4 times as fast as seedlings during the first year or two. Horticultural varieties of pecan are often propogated by budding and stem grafting (Fowells, 1965).

SEASONAL GROWTH PATTERN

The spring growth of roots in pecan begins a little in advance of the spring growth in shoots. Roots are more sensitive to adverse conditions either of the soil or weather but are also more responsive to the return of favorable conditions. As the season advances growth is less vigorous but branching is more profuse. There are normally from 4 to 8 cycles of root growth during the year, depending largely upon environmental conditions (1321).

The roots of shellbark hickory in Illinois were found by one author to commence rapid growth in April, diminish considerably in July and August, and increase slowly again in September before finally ceasing in late November (780).

Feeding roots are usually the only roots on a bearing pecan tree that are killed by freezing in winter. Only the roots actually frozen are killed, while those at lower levels in the soil continue to grow throughout the winter (in Georgia) provided moisture is available (1320).

EFFECTS OF EXCESSIVE AND DEFICIENT MOISTURE

Various of the hickories have been rated by different authors as follows for flood tolerance: Intolerant to moderately tolerant: Mockernut, shagbark; Moderately tolerant: Pignut; Tolerant: Water hickory (481, 104, 482, 174).

The dying of pecan roots is usually either directly or indirectly associated with the water supply in the soil. The absorbing tips of waterlogged trees are the first to die, followed by death of the older parts of the young roots, and later by the older roots. A permanent rise in the water table in a pecan orchard will kill the lower portions of all roots which penetrate the wet area; while a temporary rise in the water table during the winter seldom alters the root system, nor the vigor of the tree the following year. Roots growing into a water-logged area appear to gain momentum while passing through the adjacent region of optimum moisture, so that when they contact the saturated zone they grow into it for several centimeters before they become sensitive to it (1320).

RESPONSE TO SOIL CHARACTER

A study of root growth in seedling shagbark hickory found that the roots of trees grown in loess soil for one season under full sunlight extended to approximately 4 ft. (1.2 m), whereas those in the shade extended to 1.8 ft. (.5 m). In clay soil both sun and shade forms were about 2.4 ft (.7 m) deep (128).

Pecan roots tend to grow most profusely in those soil strata in which moisture and texture are most favorable for growth. In pecan orchards, deep cultivation tends to force the roots to lower levels, while shallow cultivation, a high water table, or mulch with litter or cover crops allows the roots to grow near the surface. Periods of drought or soil freezing may also hinder fibrous pecan roots from growing in the surface soil horizon (1321).

The presence of hard pan layers and/or high water tables have been shown to restrict rooting depth of pecan to less than 3 ft. (.9 m) in some cases. On the other hand, where the soil is loose, coarse, and nutrient-poor with a low water table, the taproot may penetrate more than 9 ft. (2.7 m). (1320)

The course of lateral pecan roots is seldom straight due to variations in soil texture and structure, together with rocks, holes, clods, insect injuries and the like. Laterals more than 2 ft. (.6 m) below the surface seldom attain a great length, generally due to either water-logging, lack of nutrients, or hardpan.

Retaining the lateral roots on transplanted hickories is of much less importance than retaining the taproot, since the latter serves as a storage area for water and reserve food. The origin of new feeding roots on transplanted trees is from the callus that develops around the wounds on the injured roots. Callus develops more perfectly when the lateral roots are cut rather than broken off, and also if the cut ends are not allowed to dry out (1320).

Nearly all of the bearing pecan trees in the Southeastern United States are nursery-grown trees that were transplanted when from 3 to 6 years old. An examination of the root systems of several of these transplanted trees, compared to natural seed-origin trees, revealed no major differences in one study; the author felt that check in growth subsequent to transplanting was completely overcome within 2 or 3 years (1321).

Treatment of seedling pecan roots with indole-3-butyric acid was shown in one study to stimulate increased root growth. The hard to transplant older trees (8-10 years old) were shown to especially benefit from the technique (1000).

MYCORRHIZAE

The mycorrhizal associations reported for the hickories are as follows: On *Carya* spp. - *Boletus edulis* and *Cenococcum graniforme*; on *C. illinoensis* - *Russula aeruginea*, *R. foetens*, *Xerocomus Chrysenteron*, and *Pisolithus tinctorius*; on *C. laciniosa* - *Laccaria ochropurpurea* (1181, 809, Hepting 1971).

The reader interested in a detailed discussion of the mycorrhizas of pecan is referred to (1322).

DESTRUCTIVE AGENTS

Insects

Several of the hickories are occasionally attacked by the asiatic oak weevil, *Crytepistomus castaneus* (Roelofs), although oaks and asiatic chestnut are the preferred hosts. Larvae of this weevil feed upon roots as deep as 6 inches (15.2 cm) or more in the soil, while the adults feed upon the leaves. The asiatic oak weevil was introduced to North America in the 1930's, and is now known to occur from New Jersey to Georgia and Missouri (Baker, 1972).

Several species of white grubs, including *Phyllophaga crenulata* (Froel.) and *P tristis* (Fab.), cause damage to the roots of hickory in nurseries, particularly in the Lake States (Baker, 1972).

Nematodes

Nematodes associated with the roots or root-zone of hickories include: *Carya cordiformis* - *Belonolaimus euthychilus*; *Carya ovata* - *Criconemoides beljaevae*, *C. macrodorum*, *Gracilus audriellus*, *Helicotylenchus platyurus*, *Hemicycliophora gigas*, *Trichodorus aequalis*; *Carya glabra* - *Hemicriconemoides minutus*; *Carya illinoensis* - *Meloidogyne incognita* (Ruehle, 1967; 515). Several other species were identified by one author from soil samples within a pecan grove, but these could not be positively associated with pecan roots since various weeds and grasses were also present (515). With the possible exception of *M. incognita* on pecan, none of the nematodes mentioned above has been cited as a significant pathogen of hickories.

Fungi

Root disease of hickories has been associated with several species of fungi, including *Armillaria mellea*, *Clitocybe tabescens*, *Phymatotrichum omnivorum*, *Helicobasidium purpureum*, and *Pythium* *irregulare*. All of these are discussed to some extent by Hepting, 1971.

Celtis occidentalis L. - Hackberry
& C. laevigata Willd. - Sugarberry

MORPHOLOGY

Development of Form

Hackberry (Celtis occidentalis) is a deep rooting species, utimately reaching depths of between 10 and 20 ft. (3 and 6 m) on most sites (509,465). On clay prairie soil in North Dakota, however, the roots reached only to a depth of 4.5 ft. (1.4 m) (1332). Strong taproot development occurs only occasionally (509). On the clay soil mentioned above, lateral extension was 41.5 ft. (12.6m) (1332).

The ultimate branches are very fine with rather short growing tips. The bark of the roots is yellowish when scraped (781). The ratio of the weight of small absorbing roots to the weight of the large conducting roots is about 4.7:17. In comparison, this same ratio for green ash is about 7 times greater than hackberry, and boxelder 3 times greater. But the ratio for hackberry is larger than those for walnut, butternut, black locust and balsam poplar, and about the same as for honeylocust (465).

In the clay soil mentioned above, the greatest numbers of roots, about 44%, are found in the second foot of soil. The first foot contains about 32% and the third foot 15% (1332).

The root hairs of hackberry are rather short and thin, with an average diameter of 8 microns and length of 170 microns in one study. Those of honeylocust, catalpa, and green ash were longer, ranging from 180 to 370 microns. Honeylocust and catalpa were broader than hackberry as well (321).

The root anatomy of the genus Celtis, along with a few other genera, is unique in that stereome is found as a primary structure in the phloem of the roots. The stereome, (which is sclerenchyma and collenchyma collectively) when present in roots, is usually a secondary structure as it is in Carya roots. In any case, its development in roots is not common (547).

Functional intraspecific and self root grafts have been observed on species of Celtis in Oklahoma (753).

Development of adventitious roots on hackberry seedlings in saturated soil is sparse. None were observed on sugarberry (Celtis laevigata) (566). Vegetative reproduction of sugarberry is accomplished by stem cuttings, grafting and budding. The same is true for hackberry, with the possible addition of layering.

EFFECTS OF EXCESSIVE AND DEFICIENT MOISTURE

Trees of hackberry and sugarberry often survive the first season of permanent flooding, but usually succumb during or after the second season (1333,481,174). Hackberry trees have occasionally been reported to live 3 years under flooded conditions, however, making fair growth in the second season (455).

Hackberry begins to show ill effects from inundation after 110 days (104). If the duration of flooding is less than 25% of the growing season, *Celtis* spp. can maintain good health indefinitely (482). Mature hackberry and sugarberry are classified as moderately or somewhat toleratant to flooding (481,482,104).

Current year seedlings are much more sensitive to saturated soil conditions. The root systems of hackberry and sugarberry seedlings situated in saturated soil are severely injured within 60 days, and are often unable to recover (565,566). Intolerance to flooding is attributed to injury to the root system, lack of strong adventitious root development, and also the inability of stem and leaves to resist dessication due to a poorly or non-functioning root system (566).

Soil saturation depresses dry matter production of hackberry by about 50%. Uptake of nitrogen, phosphorus, potassium, calcium and magnesium is reduced as well, unlike other species such as tupelo, pumpkin ash, willow, or cottonwood (752).

MYCORRHIZAE

Ectotrophic mycorrhizae are present on *Celtis* spp (781,321).

DESTRUCTIVE AGENTS

Seedlings of sugarberry are damped-off or rotted by the fungus *Helicobasidium purpureum* (Tul.) Pat. (*Rhizoctonia crocorum*). The infected roots turn a purplish or violet color. *Armillaria mellea* Vahl. grows unaggressively on hackberry roots until the death or injury or a root, whereupon the fungus enters and causes extensive root rot. *Celtis* spp. are resistant to Texas (*Phymatortrichum*) root rot. (386).

Fagus grandifolia Ehrh. - American Beech

MORPHOLOGY

Development of Form

Little has been written concerning the initial root habit of American beech, although it is thought to be similar to European beech. Seedlings of the latter species develop a very marked tap root that constitutes the main root system for the early years. Soil conditions largely determine the length of time that the taproot remains functionally important; under favorable conditions it may be retained for 25 years or more. As the tree ages, a mass of side roots develop near the root knot and penetrate obliquely into the soil. In this way the tap root is modified into the so-called "heart-root" type of system (490, 484).

Distribution in Soil Profile

The root system of mature beech is quite flexible in form depending upon soil characteristics. On deep soils it is characterized by diagonally-directed deep roots which may penetrate to depths of 5 ft. (1.5 m) or more (1135). On shallow soils the system is quite superficial and wide-spreading, with the larger lateral roots even occasionally arching above the soil surface (164). On gravelly soils the fine roots form well marked pockets or veins, corresponding with streaks of organic matter (859). On virtually all soils a dense mat of fine fibrous roots fills the upper several inches of soil (164, 484).

Comparisons with other Species

One author reported that, on a sandy loam soil, beech was generally shallower-rooted than either sugar maple or yellow birch, having no roots as deep as the B_3 horizon (559).

The shallow network of fine branches typical of beech has been compared to that of red and white spruce. In stands where both beech and spruce are growing in close proximity to one another there may be intense interspecific root competition between the two (859).

Grafting

Intraspecific root grafting is common in American beech (446, 484).

Adventitious Rooting and Root Suckering

Root sprouting or suckering is common in American beech. Injury to the tree or its roots stimulates suckering, although suckers are often present where no injury is evident. The quality of sucker-origin stems is generally considered somewhat inferior to that of seed-origin trees (Fowells, 1965).

Beech limbs will root in a single year when layered (Fowells, 1965).

SEASONAL GROWTH PATTERN

One author reported that American beech appears to prolong its root growth into the autumn longer than spruce. An investigation of a mixed stand of beech and red spruce in Maine in October revealed many growing root tips in beech but very few in spruce (859).

ROOT-SHOOT RELATIONS

In a study involving the girdling of several hardwood species, beech was found to be the last to die. White birch, yellow birch, red maple, and sugar maple all succumbed before beech (934).

As is the case with shoot growth, root growth of beech is most rapid at light intensities somewhat less than 100%. One study found that root weight of 4-year-old beech grown in full light was actually lower than that for beech grown in 13% light. The 45% intensity proved to be optimum for both root and shoot development (747).

EXUDATION AND UPTAKE

A study of the root exudates of three Northern hardwood species showed that the exudates of beech were less in quantity than yellow birch but much greater than sugar maple and contained a higher proportion of organic acids than either yellow birch or sugar maple. In total, unsuberized tips of new woody beech roots were estimated to release approximately 26.4 KG/Ha/Yr., of which 70% were amino acids. The author felt that root exudates definitely play a role in intrasystem nutrient cycling (1103).

RESPONSE TO COMPETITION

There is some evidence that soil changes accompanying beech invasion of sugar maple stands may interfere with nutrient uptake by the maple. A Quebec study showed that uptake and subsequent recycling of Cu, in particular, by beech may interfere with the uptake of P and Mn by sugar maple on some sites (467).

EFFECTS OF EXCESSIVE AND DEFICIENT MOISTURE

American beech is considered very intolerant of flooding. One group of authors classified beech as approximately the sixth most flood-intolerant of 41 species, exceeded only by yellow-poplar, yellow buckeye, white oak, sugar maple, and post oak in susceptibility to damage from prolonged inundation. They speculated that the survival of beech in many bottomland areas is possible because flood waters occur mainly in the dormant or early spring growth period, at which time inundation evidently does not affect the trees adversely (481).

Another study of 38 tree and shrub species in Kentucky ranked beech as fifth most flood-intolerant, after black cherry, flowering dogwood, hornbeam, and sassafras. Mortality of beech was quite heavy among trees flooded for more than about 15% of the growing season (482).

RESPONSE TO SOIL CHARACTER

The soil depth required by beech is extremely variable. Deep soils promote the best growth, but soil mantles as shallow as 6 in. (15.2 cm) can support beech if moisture conditions are favorable (484).

MYCORRHIZAE

Mycorrhizal associates of american beech include *Cenococcum graniforme*, *Cortinarius cinnabarinus*, *Lactarius subdulcis* (1181), *Boletus sensibilis*, *B. badius*, *B. ornatipes*, *B. affinis*, *B. chrysenteron*, *B. subtomentosus*, *B. subvelutipes*, *Gyroporus castaneus*, *G. cyanescens* (Homola and Mistretta, 1977).

The ectotrophic mycorrhizae of beech have been described by one author as short, stubby, and close together, with no root hairs (Hepting, 1971).

One author found that mycorrhizae formed on beech in Indiana by *C. graniforme* ranged from 51 to 86 percent of the total in seedlings and from 32 to 73 percent in large trees. *Cenococcum* were most abundant in samples from 7.5 cm depth or greater while non-*Cenococcum* types (not identified to genus) were most frequent at 0 to 7.5 cm depth (545).

DESTRUCTIVE AGENTS

Non-infectious

American beech has been classified as moderately tolerant to soil salts in the root zone (871).

Though the root sytem of beech is not as deep as some other species, it is not easily uprooted by wind, except on very shallow soils (484, Fowells, 1965).

Because of its thin bark and large surface roots, beech is highly vulnerable to fire injury (Fowells, 1965).

The shallowness of the root systems of beech in wet and poorly aerated soil has resulted in high mortality in some local areas during periods of prolonged drought (164).

The shallow surface roots of beech are quite susceptible to injury from grazing animals or heavy equipment (757). Beech was also noted by one author as being sensitive to changes in grade (soil removal or filling) around its roots (839).

Insects

Larvae of the introduced asiatic oak weevil, *Crytepistomus castaneus* (Roelofs) attack the roots of beech in some areas, although oaks and asiatic chestnut are the preferred hosts. The leaf-feeding adults of this weevil are generally considered more damaging than the larvae (Baker, 1972).

The larvae of another introduced weevil, *Polydrusus impressifrons* Gyll., also may damage the roots of beech in New York, Connecticut, and possibly adjoining states. Eggs are deposited beneath loose bark along the trunk; the young larvae drop to the soil upon hatching. Adults of this weevil can be serious defoliators in local areas (Baker, 1972).

Various white grubs of the genus *Phyllophaga* may be serious root-damagers of beech, especially in nurseries. Refer to Baker, 1972 for more detail concerning the damage caused by these insects.

Nematodes

Nematodes associated with the roots or root-zone of American beech include: *Criconemoides macrodorum*, *Gracilis audriellus*, *Helicotylenchus erythrinae*, *Hemicycliophora* sp., *Longidorus elongatus*, *Xiphinema chambersi* (Ruehle, 1967), *Criconema* sp., *Dolichodorus*, *Hemicycliophora* sp., *Hoplolaimus* sp., *Trichodorus* sp., *Xiphinema americanum* Cobb (Ruehle, 1968). None have been associated with root injury (Hepting, 1971).

Fungi

Beech suffers little damage from root diseases. *Armillaria mellea* can cause a wound-decay of butts and roots, but it very seldom kills trees unless they are already weakened. *Endothia gyrosa*, a fungus with fruiting bodies superficially resembling those of the chestnut-blight fungus, often fruits on the bark of exposed roots. It is doubtful, however, that it is ever more than a very weak parasite (Hepting, 1971).

Miscellaneous

Two species of broomrapes, a family of angiosperms that lack chlorophyll, have bract-like leaves, and are parasitic on the roots of many plants, may be associated with beech. These are the squaw-root, *Conophilis americana*, and beech drops, *Epifagus virginiana*. The impact of the broomrapes on their American tree hosts is not known, but is considered slight (Hepting, 1971).

Fraxinus nigra Marsh. - Black Ash,
Fraxinus pennsylvanica Marsh. - Green Ash,
and
Fraxinus americana L. - White Ash

MORPHOLOGY

Development of Form

The root system of one-year old green ash growing in well-drained soil was shown to be strongly vertical in nature, penetrating to an average depth of 23 inches (.6m). Lateral roots were not in evidence. (394)

Distribution in Soil Profile

In one study, eight 20-year old green ash trees in a chernozem soil reached an average maximum rooting depth of three feet (.9m). Fifteen and one-half percent of all roots were found below a depth of one meter. The "intensity" of the root systems was the highest of any of the 26 species examined, meaning that a high percentage of the systems were composed of small, absorbing roots. (465)

Green ash was classified as intermediate (5-10 feet; 1.5-3.0m) in rooting depth by one author, and was described as "usually strongly taprooted." (509)

The root system of a mature green ash growing on a deep prairie soil was characterized by the more or less vertical growth of the main roots and the almost complete absence of a superficial portion so pronounced in such species as honeylocust and boxelder. The taproot had a diameter of 13mm at the top, gave off seven branches in the upper six inches (15cm) of soil, and tapered rapidly to a diameter of one and one-half millimeters at the maximum depth of 61 inches (1.55m). Roots rarely grew in a horizontal direction and the greatest lateral spread was reached at 18 inches (45.7cm) deep, where it was only two feet (.61m). The main laterals grew outward and downward for only 5-10 inches (13-25cm) and then penetrated deeply, attaining depths up to 56 inches (1.42m). Nearly all were clothed by small horizontal rootlets at the rate of eight per inch, these usually being less than six inches (15.2cm) long. (238)

The root hairs of green ash are finer and longer than those of many other trees, averaging 5 microns in diameter and 370 microns in length on both secondary and tertiary roots. (321)

White ash generally possesses a taproot which branches into a few heavy roots that continue on a conspicuous downward trend. The taproot is occasionally absent, but some prominent branches always maintain their downward trend with the same type of vertical habit. From these characteristic vertical roots single lateral branches are developed at intervals; lateral branches do not come out in a mass as they do in conifers. Lateral branches proceed outward horizontally or very gradually downward while tapering only slightly. Long, vertical branches originate at intervals along the laterals, giving the appearance of hanging in long strings. (417)

One author reports that a 71-year old white ash growing on a shallow soil (bedrock at two feet; (.6m)) had the following root system characteristics. Root depth at the stump was 18 inches (.45m); mean depth of laterals was three inches (7.6cm); and the total root system covered an area of 574 ft^2. This particular tree should not be considered as typical of white ash on better sites, as its DBH of 5.8 inches (14.2cm) at age 71 further indicates. It would seem to show, however, that the root system of white ash is capable of adapting to adverse site conditions, though growth may be slowed considerably. (1135)

Grafting

Intraspecific grafting is common in white ash, but apparently uncommon in black ash. (446)(710)

Adventitious Rooting

Very little information is available on adventitious rvoting in Fraxinus, except that saturated soil conditions promote adventitious root formation in green ash (315). Rooting of green ash can be induced from stem cuttings, especially if cuttings are taken just above the root collar rather than higher on the stem (795). There is no reliable method for rooting cuttings of white ash (Fowells, 1965).

SEASONAL GROWTH PATTERN

One author reported that the largest roots of white ash began xylem increments about a week later than did the bole at one foot above the ground. Root growth was still active in mid-September, though the cambium was dormant in aerial portions of the tree. (741)

Root regeneration and time to first budbreak of two-year old white ash seedlings were found to be strongly correlated with the number of hours of chilling. Increased number of new white roots initiated during a 30-day growth period in the greenhouse were observed with increased periods of storage at 5°C up to the maximum period of 3,500 hours. Also, it was shown that root regeneration in white ash, unlike some other species such as silver maple, can take place at a time when the buds are strongly dormant, i.e., December and January. (1254)(1256)

ROOT-SHOOT RELATIONS

Average root collar diameter of white ash seedlings, as well as foliage and stem weight, was greatest at 45% of full light intensity in one study. Root collar diameter at 100% intensity was approximately the same as at 25%, some 15-20% less than at 45% intensity. (747)

EXUDATION

One author reported that green ash seedlings were antagonized by a substance exuded from the roots of Quercus robur when the two species were grown in close proximity. (1323)

RESPONSE TO COMPETITION

Both green and white ash appear to be particularly sensitive to competition with herbaceous and other shallow-rooted vegetation. This is thought to be related to the strong vertically-oriented root habit of ash, making the trees unable to compete with shallow-rooted vegetation where precipitation (rather than ground water) is the major source of moisture. (509)

EFFECTS OF EXCESSIVE AND DEFICIENT MOISTURE

Green ash is considered quite tolerant of flooded conditions, being nearly equivalent to such trees as water tupelo and black willow in this regard (566). This is believed to be at least partially due to the ability of the species to transport oxygen from the aerial portions to the roots (556). Secondary roots were found to deteriorate rapidly under flooding but were replaced by new, more succulent and less branched roots which originated from the primary roots (3). After 60 days of saturated conditions in one study, many adventitious roots were found to be developed at or near the soil surface (556). Another study found that total dry weight, as well as ash, P, K, Ca, and Mg content of the tops, were higher for green ash grown under saturated as opposed to unsaturated soil conditions. Only nitrogen content was lower for the saturated seedlings (568). Another author reported that green ash was able to survive three-four years of continuous inundation resulting from an impoundment (455). Although it may survive long periods of inundation, green ash is apparently more sensitive to depth of the standing water than are other bottomland species (1016). Trees covered to depths greater than 36 inches (.9m) did not live through a 17-month period in one study (306).

White ash is comparatively tolerant of temporary flooding, but not to the degree of green ash. Seedling white ash grown in nutrient solutions of varying oxygen content failed to develop new roots on some trees at 3-4% oxygen. The leaves flushed on these trees, but subsequent expansion was limited (482). Another study found that 39% of mature white ash did not survive three years of continuous inundation, and 71% did not survive five years (1333).

Green ash is able to tolerate dry soil conditions fairly well, as evidenced by its success as a shelterbelt tree in the Great Plains. One author reported that green ash and pin oak had good root systems at levels of soil moisture which significantly reduced root growth in sycamore (67). The mean soil-moisture percentage at permanent wilting for green ash was reported to be about 5.3% on sandy loam soils and 7.7% on loam soils (703).

Root segments of white ash were shown in one study to be more dessication-resistant than sugar maple, but less dessication-resistant than red oak. (908)

RESPONSE TO SOIL CHARACTER

Distribution of white ash roots in one study was found to be rather strongly influenced by soil type. On a loamy sand soil, the highest percentage of both large and fine roots was in the A horizon. On a fine sandy loam soil, the majority of fine roots were in the B_1 horizon, while the larger roots are nearly equally divided between the A and B_1 horizons. A comparatively small percentage of roots were found below the B_1 horizon in either soil, with fine roots being more abundant than large roots. (417)

Although most natural stands of green ash are confined to bottomland soils, the species also grows well when planted on moist upland soils. The root system of trees grown on such upland sites is normally quite extensive (1332). The normal taproot character of the tree may be altered due to certain site conditions. For example, the taproot of a 46-year old tree growing on a prairie soil in South Dakota was diverted toward the horizontal by a claypan layer at a depth of one foot (.3m), presumably due, at least partially, to the higher moisture supply above than within the claypan (509).

Although it is fairly tolerant of saline soil conditions (871), green ash was not able, in one study, to survive a soil salt level of 8,000 ppm (857). The inability of green ash roots to penetrate highly saline soil layers in some prairie soils (below which higher moisture is often found) has been suggested as a possible cause of slow growth or even death. (841)

An Iowa study showed that green ash was fairly tolerant of soil alkalinity, although a pH of 8.1 produced severe chlorosis (Hansen and McComb, 1958). Any disturbance of the A horizon (such as previous cultivation or erosion) has also been shown to adversely affect the growth of planted green ash (McComb, 1949)(236).

Cuttings from green ash seedlings may be used rather than seedlings for outplanting on certain sites. One study found that cuttings from 1-0 seedlings planted on clay and silt loam soils in Mississippi sprouted and grew well during the first growing season.

Cuttings from 1- and 2-year old sprouts and older material did not perform satisfactorily. Cuttings should be 10 to 15 inches long made from 1-0 seedlings and planted horizontally in slits one to two inches deep or planted vertically with two to three inches of cutting left above ground. Seedlings rather than cuttings should be used on sites where there is danger of standing water for long periods. (?)

Treatment of white ash seedling roots with indolebutyric acid prior to planting produced no significant growth response. (796)

MYCORRIHIZAE

Very little is known concerning mycorrhizal associations in the genus *Fraxinus*. *Gyrodon merulioides* has been reported to form mycorrhizae with white ash (?). Seedlings of both green and white ash artificially inoculated with the endomycorrhizal fungi *Glomus mosseae* and *G. fasciculatus* showed a marked growth improvement over non-mycorrhizal controls in one study (810).

DESTRUCTIVE AGENTS

Non-infectious

A decline of white and green ash known as ash dieback was reported from New England to the Lake States beginning in the 1940's. It is believed to be induced by periods of low rainfall, with fungi acting mainly as secondary invaders that accelerate the death of the tree through stem and branch cankering (Hepting, 1971).

Because of the extensive nature of their root systems, both green and white ash are normally quite resistant to windthrow.

Seedling white ash is relatively sensitive to damage from post-planting herbicide treatment for weed control. (1267)

Nematodes

Nematodes associated with the roots of white ash include *Aphelenchoides* sp., *Criconema* sp., *Criconemoides* sp., *C. beljaevae*, *C. macrodorum*, *Ditylenchus* sp., *Gracilacus audriellus*, *Helicotylenchus* sp., *H. platyurus*, *Hemicycliophora* sp., *H. gigas*, *Hoplolaimus* sp., *Longidorus* sp., *L. elongatus*, *Meloidogyne* sp., *M. ovalis*, *Paratylenchus* sp., *Pratylenchus* sp., *P. crenatus*, *Rotylenchus* sp., *Trichodorus* sp., *T. aequalis*, *Tylenchorhynchus* sp., *Xiphinema* sp., *X. americanum*, *X. chambersi*. *Meloidogyne* sp. is also associated with black ash, and *Criconemoides curvatum* and *Xiphinema americanum* have been associated with green ash (Ruehle. 1967)(797). Only *Meloidogyne ovalis* has been associated wtih injury to ash roots, that being white ash (Hepting, 1971).

Fungi

Root rot damage to green ash is negligible on light soils, but may be a serious factor to consider when planting green ash on heavy soils (Fowells, 1965). One author classified green ash in their "intermediate susceptibility" category, as possibly usable for shelterbelts on sandy-sites of the root rot belt (Wright & Well, 1948). Green ash is only moderately susceptible to attack by the root rot fungi *Corticum galactinum* (1181).

In the Great Plains States a bacterium known as hairy root (*Agrobacterium rhizogenes*) has been reported frequently from young white ash. This disease involves the protrusion of a great number of small roots either from the base of stems or from the roots (Hepting, 1971).

Juglans nigra L. - Black Walnut

MORPHOLOGY

Development of Form

Early growth of the seedling walnut root system is quite rapid. Vertical taproot extension during the first growing season is considerable, especially on drier soils. One researcher reported a taproot penetration of over 4 feet (1.2m) for 1-year old walnut seedlings on a prarie silt loam soil (142). Another reported 25-27 inches (.62 - .68m) for 1 - year old walnut on a more moist soil (1111). The second year of growth is characterized by the development of many lateral roots, while taproot extension continues. The first study mentioned above found that vertical and horizontal extension of the root system between the first and second years was 2 feet (.6m) and 1.5 feet (.45m) respectively. Development on more moist soils is somewhat slower, with greater emphasis upon lateral root growth as opposed to taproot growth (142). On very moist soils the uppermost lateral roots may be as long or longer than the taproot two weeks after germination (1111).

Distribution in Soil Profile

The root system of mature black walnut has been described as combining the deep taproot of more xeric trees with the strong laterals characteristic of more mesic ones. One or the other may be emphasized depending mainly upon soil moisture conditions.

Black walnut taproots show a strong tendency to follow the course of old root channels, especially on heavy soils. The presence of such channels may allow the establishment of walnut seedlings on soils which would otherwise be moisture-limiting due to the presence of impenetrable layers (254).

Comparisons with Other Species

The root system of 3-year-old walnut grown on 3 different soils was more extensive than bur oak, basswood, red oak, and shellbark hickory. Actual taproot penetration was second only to bur oak (142).

Adventitious Rooting and Sprouting

Black walnut is capable of reproducing vegetatively by sprouting from the root collar or higher on young stumps. Sprouts originating from the root collar area are most likely to be free from defect (Fowells, 1965).

ROOT-SHOOT RELATIONS

One study found that shading of black walnut seedlings for one season of growth caused a retardation of 3-6 inches in growth of the main vertical roots (209).

EXUDATION

An antagonism between black walnut and many other plants has been reported which excludes some species from the root zone of walnuts. Some tree species are apparently immune, but others such as white birch, red pine, white pine, apple and scotch pine are reportedly sensitive to the toxin (386, 374, 477, 129, 1242). This influence has been attributed to 5-HYDROXYL-1, 4-NAPTHOQUINONE, popularly known as juglone. That the adverse affects are due to a toxic product and do not result from a lack of water is substantiated by the fact that the vascular system is discolored for several inches above the point of contact with the walnut root. This symptom is very similar to that produced by vascular disease fungi (115). There is even some evidence that walnut seedlings may be affected where mature walnuts are present nearby, although this has not been proven (Fowells, 1965). Actual contact with the roots is apparently necessary before the associated plants are harmed (Fowells, 1965).

Root exudates from black walnut are believed to improve the growth of some herbaceous plants such as Kentucky bluegrass. This may be largely due to the higher soil pH within the root spread of walnut as compared to surrounding areas (374).

UPTAKE

Nutrient uptake and root morphology are influenced to some degree by soil fertility and bulk density. One study found that reduced bulk density of a nursery soil combined with the highest level of fertilization resulted in maximum foliar nutrient levels. Taproot penetration was reduced at the highest level of fertilization (551).

RESPONSE TO COMPETITION

There is some evidence that the depth of walnut lateral roots varies in response to root competition with its associates. One study found that lateral roots of walnut occupied a much shallower position in pure walnut stands than in mixed walnut-ash stands. This was explained by theorizing that the ash, having a strongly developed surface root system, pushes the walnut roots into deeper soil layers. Root competition with Norway maple, on the other hand, was not as intense (1119).

EFFECTS OF EXCESSIVE AND DEFICIENT MOISTURE

Black walnut is considered to be moderately tolerant of flooding. Mature trees are generally killed by 90 days of continuous inundation during the growing season, although some individuals may survive for 150 days or more (767). As compared to some of its associates, black walnut is more flood-tolerant than black cherry, shortleaf pine, basswood and shagbark hickory (972).

The initial root form of black walnut, with its rapidly growing juvenile tap root and wide spreading laterals, is characteristic of species that naturally occur on deep, fine textured soils in regions that experience well-distributed summer rains. These soils, due to their physical characteristics and due to the distribution of the precipitation, maintain a fairly uniform available water content to considerable depth. Walnut growing on such soils are thus able to draw their moisture and nutrients largely from the more fertile soil while still being able to rely on the deeper soil layers for survival during times of drought (1111).

A study of seedling walnuts grown at different levels of soil moisture showed that seedlings grown in a moist soil profile maintained near field capacity had an abundance of fibrous roots compared to seedlings grown in a dry profile. Field planting of fibrous and non-fibrous rooted seedlings revealed a small but consistent growth advantage for fibrous rooted seedlings during the first growing season (551).

RESPONSE TO SOIL CHARACTER

A study of root initiation on one-year-old seedlings planted against glass revealed that 80 percent of the new roots occurred as adventitious initials on fibrous roots. Only 6 percent of the new roots originated from fibrous root terminals because of loss during nursery lifting. In addition, seedlings root-pruned in nursery beds produced mutiple taproots and grew slightly better than unpruned seedlings when field planted (551).

A different study, however, found that fibrous rooted seedlings (produced by root pruning and soil texture modification) did not survive better or grow faster than the normal single taprooted seedlings (248).

Fertilization and control of weed competition have been shown to significantly increase establishment and growth of black walnut in plantations (91).

Black walnut responds well to containerized planting. One study found that root development was equally good in 3 types of containers tested (jiffy-7 pellet, plastic mesh tube filled with peat, and bonded wood pulp block), but growth after outplanting was best with the plastic mesh tube filled with peat (91).

Texture and Structure

A study of the roots of several tree and shrub species growing on clay soils in North Dakota found that the root distribution of a 25-year old black walnut was as follows: 41.4% of all roots were in the upper 1 foot (.3m) of soil; 46.7% in the second foot; 9.7% in the third foot; and 2.1% in the fourth foot. Greatest depth of root penetration was 5 ft. 2 in. (1.6.m.). The ratio of longest root length: tree height was 2.1, the highest of any of the 30 woody species examined (258).

The root development of a 10-year old walnut growing on a much drier grey chernozem soil was similar to that of the 25-year old tree described above (538).

Seedling black walnuts grown on 3 different soils in Missouri (clay, alluvial, and loess) showed significant differences in root development after one season of growth. Taproot penetration was 5.3 ft (1.6m), 2.7 ft. (.8m) and 3.0 ft. (.9m) on the loess, clay, and alluvial soil respectively. Lateral root development was greatest in the clay soil, but differences between soils were not as great as with taproot penetration (209).

MYCORRHIZAE

Little information is available concerning the mycorrhizal associations of black walnut. One study reported that 100% of the walnut seedlings in a southern Michigan nursery had endomycorrhizae. Examination of the feeder roots revealed an average of 83.2 percent of the feeder roots had endomycorrhizae, and all were rot free (749).

DESTRUCTIVE AGENTS

Non Infectious

Black walnut has been rated as very sensitive to the presence of salt in the root zone (654, 587).

Black walnut is quite resistant to windthrow, but seedlings can benefit from wind protection in some cases. One study found that both weight and stem weight were considerably greater in protected as opposed to wind-exposed seedlings. For this reason, establishment of walnut plantations in forest openings is preferred to more exposed sites (91).

Insects

Several white grubs of the genus *Phyllophaga* feed on the roots of black walnut, including *P. luctuosa* (Horn), *P. forsteri* (Burn.), *P. implicata* Horn, and *P. prunina* (LeC.) (Baker, 1972).

A study of maple decline by Spitko & Tattar (1977) reported a correlation between the amount and vigor of mycorrhizal infection in the roots and the degree of decline shown by the crown. Healthy trees had young infections showing extensive arbuscle development, whereas trees in a state of decline showed little arbuscle development. Arbuscles that were present in the roots of these declining trees had undergone digestion of the fine branches so that only the collars were in evidence.

Larvae of the Japanese beetle *Popillia japonica* Newm. are reported to damage the roots of black walnut in some areas (Baker, 1972).

Larvae of the Japanese weevil, *Pseudocneorhinus bifasciatus* Roelofs also feed on the roots of walnut (Baker, 1972).

Nematodes

Nematodes associated with the roots of black walnut include *Paratylenchus bukowinensis* (900), *Pratylenchus vulnus*, *P. musicola* *Meloidogyne* spp. (Reuhle, 1967). Many of these are considered "vagrant parasites" because of their transient association with the host (Hepting, 1971).

Fungi

Root rot fungi of black walnut in addition to those described in Hepting, 1971 include *Phytopthora citricola*, *Cylindrocladium scoparium*, and *C. floridanum*. These primarily affect seedlings in nurseries, the former in Indiana and the latter two in the Southeastern U.S. (768, 978) (Ploetz & Green, 1978).

Larix laricina - Tamarack

MORPHOLOGY

Development of Form

Root growth of seedling tamarack is generally very slow for the first few years. After the young tree develops an annual terminal shoot growth of more than about 2 inches (5.1 cm), the crucial stage of survival has passed and rapid root growth begins. Lateral root growth of 4 feet (1.2m) per year is not uncommon on some sites. Tap root development may begin, but vertical penetration is never very deep, even on deep sands. The tap root may simply cease its development or may turn horizontally so as to resemble a lateral root. Short side roots develop along sections of lateral roots which are 2 or more years old (99, 67).

Distribution in Soil Profile

The root system of mature tamarack is shallow, with a fairly inflexible form that has been described as flattened and plate-like. Most trees have very few roots below a depth of one foot, even on well-drained soils. The lateral root system may be extensive, however, often spreading over an area whose radius is greater than the tree height. Numerous small branch roots arise from he laterals, and may be quite numerous within the upper 1-2 inches (2.5-5.1 cm) of soil (99, 297, 946, 67). On wet sites the majority of lateral roots are often concentrated between the layers of decomposed and undecomposed sphagnum, which is the region of maximum nutrient availability (1340).

Comparisons with Other Species

The root system of tamarack is shallower but greater in lateral extent than most of its associates, with the possible exception of black spruce. It is also less flexible in habit than most of the other northern conifers. Branching of the lateral roots is reportedly more profuse in tamarack than in many of its associates (67, 297, 946).

Grafting

Intraspecific root grafting in tamarack is common (446).

Adventitious Rooting

Layering, although, uncommon in tamarack, sometimes occurs where branches are covered by fast-growing sphagnum moss or by drifting sand. One author reports that adventitious roots almost always arise in close proximity to dead or injured branch shoots along a larger branch (71). Layering is most common on wet sites where rising, moss tends to bury portions of the longer branches.

Tamarack roots are also known to produce shoots, although the circumstances under which this may occur are not yet clear (730).

ROOT-SHOOT RELATIONS

Root growth in Tamarack is very responsive to light intensity. Root weight of tamarack grown in 13% of full light for 4 years was only .05% that of seedlings grown in full light (747). Average root weight of larch seedlings grown at full light was 1.5 to 3 times greater than seedlings of jack pine, white pine, or red pine grown under the same conditions (744).

EFFECTS OF EXCESSIVE & DEFICIENT MOISTURE

Although the root system of tamarack is nearly always shallow, appearance of individual roots varies considerably with soil moisture conditions. Root in swampy ground are stringy, with no branches for about 6 inches back from the tips. Roots in well-drained soil may form swollen "knees" where the root bends sharply toward the horizontal (1191).

Abnormally high water levels often kill established tamarack stands. Other stands have developed under such wet conditions that submergence of roots, while not killing the trees, reduces growth to a minimum. Most seedlings will die if completely submerged for 3 or 4 weeks (Roe, 1975).

One-year-old seedling tamarack can reportedly withstand drying of the surface inch of soil down to about 50 percent by weight in peat soils (Roe, 1957).

MYCORRHIZAE

Fungi known to form mycorrhizal associations with tamarack include *Cenococcum graniforme*, *Gomphidius maculatus*, *Hygrophorus pseudolucorum* (1181), *Boletus elegans* (94) *Fuscoboletinus aeruginascens*, *F. grisellus*, *F. paluster*, *F. spectabilis*, *Suillus cavipes*, *S. grevillei* (Homola & Mistretta, 1977).

DESTRUCTIVE AGENTS

Non-infectious

Tamarack growing in swamps or other wet sites is susceptible to withthrow because of its shallow rooting habit (Roe, 1957).

Tamarack on upland sites in fairly resistant to fire except in the seedling stage. In swamps, however, because of its shallow rooting habit, the tree is usually killed by fire unless the burn is very light (Roe, 1957).

Insects

The pales weevil, *Hylobius pales* (Herbst) may damage the roots of tamarack throughout most of the trees range. The larvae invade the roots of living trees and cause flagging of the branches. Breeding occurs in recently cut stumps. Warren's collar weevil, *Hylobius warreni* Wood, has been reported to attack the roots of tamarack in Canada and the northern Lake States. Larvae feed in the bark and cambium of the root collar and large roots, forming large pitch tubes or masses at the root collar which are not formed by other weevils (Wilson, 1977).

Nematodes

Nematodes associated with the roots of tamarack include *Hemicycliophora uniformis*, *Rotylenchus sp.*, *Tylenchorhynchus claytoni* (Ruehle, 1967), *Tylenchus emarginatus*, *Pratylenchus penetrans* (1144). None are believed responsible for significant damage.

Fungi

The root-and butt-rot fungi reported on tamarack include *Armillaria mellea*, *Corticium galactinum*, and *Polyporus schweintzii*. None are believed capable of killing healthy trees along (Hepting, 1971).

Liquidambar styraciflua L. - Sweetgum

MORPHOLOGY

Development of Form and Distribution in Soil Profile

Very little information is available in the literature on the form of the root system of sweetgum. Braun (164) stated that the root system of very young trees shows strong development of laterals and pronounced twisting or curling of the taproot. Large trees were found to occasionally have superficial roots. Turner (1937) reported that a deep taproot and numerous horizontal rootlets usually develop early, except in wet areas, where the root system is typically shallow and wide-spreading. On drier upland sites, sweetgum develops a particularly strong taproot and is very wind resistant.

Grafting

Intraspecific root grafting in sweetgum has been reported, and self-grafts are common (446). Fenton (384) estimated that approximately 20 percent of the dominant trees in dense young sweetgum stands may have root grafts. In some cases, these grafts may serve as the mode for transport of herbicides used in thinning, between treated and nearby non-treated trees (60, 247).

Adventitious Rooting

Sweetgum reproduces prolifically from root suckers. The suckers or sprouts originate primarily from adventitious suppressed root buds and may be released by cutting the parent tree, by minor disturbances within the stand, or in some cases by unknown causes in undisturbed stands (554). Sweetgum sprouts may develop their own secondary root system or may remain entirely dependent upon the parent root system for support, water, and nutrients. Sprouts on smaller parent roots often develop a much better developed secondary root system than do sprouts on larger parent roots, although they are usually outgrown by the larger parent root sprouts for the first few years (651, 178, 554).

Root suckering in sweetgum differs from that in aspen in that suckering in sweetgum is almost wholly dependent upon pre-existing suppressed buds. The rapid development of adventitious buds following external stimulation, as occurs in aspen, has not been observed in sweetgum (651).

Sweetgum can be propogated vegetatively by means of layering, grafting, and rooting stem cuttings (Williams and Hanks, 1976).

EXUDATION AND UPTAKE

An examination of the cation exchange capacity of the roots of four tree species revealed that sweetgum had a root C.E.C. higher than yellow poplar, but lower than sycamore and white pine. This suggests that sweetgum, because it is less adept at cation uptake than sycamore or pine, is adapted to more fertile sites than either of those two species, though not as fertile as required by yellow poplar (870).

Absorption of water by the suberized (woody) portion of the sweetgum root system was found to occur primarily through wounds and to some degree around branch roots. Unlike in the roots of yellow poplar, absorbtion through lenticels was minimal in sweetgum (6).

EFFECTS OF EXCESSIVE AND DEFICIENT MOISTURE

As with most of the other bottomland hardwoods, much work has been done concerning the relative flood tolerance of sweetgum. As might be expected due to their similar site preferences, sycamore and sweetgum have essentially the same relative flood tolerance - intermediate among their major associates. One study found that mature sweetgum could tolerate continuous inundation for up to about one-third (34%) of the growing season and still remain healthy, while inundation for 44% of the season or more resulted in the death of nearly all trees (482). Unlike sycamore, however, the secondary roots of sweetgum normally survive under flooding, rather than deteriorating and being replaced by new adventitious roots (553, 552). As in sycamore and unlike water tupelo, the roots of sweetgum are not able to transport significant amounts of oxygen from shoot to root under flooded conditions, and are unable to tolerate high concentrations of CO_2 (552) (557).

A comparison of 60-day height growth between saturated and well-aerated seedlings of various seedlings revealed that under saturated conditions, sweetgum grew less than half the height of the control seedlings. Only two other species, willow oak and elm, were affected more adversely in terms of height growth, while fourteen fared better than sweetgum (566).

MYCORRHIZAE

It is known that sweetgum benefits greatly from and may indeed even have an obligate requirement for, associations with certain endomycorrhizal fungi. Bryan and Kormanik (186) reported that soil inoculated with naturally occurring endomycorrhizal fungi, or with a pure culture of Glomus mosseae, produced seedlings which averaged eight times taller and 80 times greater in ovendry top weight than the nonmycorrhizal controls. Because of this high degree of dependence on endomycorrhizal fungi and the slow rate of recolonization of these fungi once eliminated, fumigation of nursery soils prior to planting sweetgum is now strongly advised against (187, 186).

The secondary roots of endotrophic sweet gum mycorrhizal are beaded in appearance, as compared to non-mycorrhizal roots which are short, stubby, and unbeaded (1222).

Gray and Gerdemann (1967) found fifteen times as much radioactivity in leaves of mycorrhizal, as compared with uninfected, sweetgum seedlings, when their potted root systems were watered with equal quantities of ^{32}P-labelled phosphate.

DESTRUCTIVE AGENTS

Non-infectious

Ornamental sweetgums are occasionally affected by self-girdling of roots, often as a result of improper or careless planting technique and/or soil obstructions. In the majority of cases the girdling roots are above or level with the ground surface and are readily detected, though frequently little benefit derives from their removal if the constricted bark area is at all extensive (1210).

Nematodes

Nematodes associated with the roots or root zone of sweetgum include *Criconema* sp., *Criconemoides* sp., *C. beljaevae*, *Helicotylenchus* sp., *H. erythrinae*, *Hemicycliophora* sp., *Hoplolaimus galeatus*, *Tylenchorhynchus* sp., *Meloidogyne* sp., *Pratylenchus* sp., *P. penetrans*, *Trichodorus* sp., (Ruehle, 1967). Nematodes of the latter three genera have been reported associated with root injury to sweetgum in Mississippi (Hepting, 1971).

Fungi

Root rot of sweetgum has been associated with the fungi *Cylindrocladium scoparium* (Georgia), *Corticium galactinum* (Arkansas), *Clitocybe tabescens* (Florida), *Phymatotrichum omnivorum* (Texas), and *Ganoderma curtisil* (1175, 258, Hepting 1971). Sweetgum is resistant to attack by the root rot fungi *Phytophthora cinnamomi*, *Sclerotium bataticola*, and *Fusarium* spp. (1007, 1356).

Liriodendron tulipifera L. - Yellow-Poplar

MORPHOLOGY

Development of Form and Distribution in Soil Profile

The initial root habit of yellow-poplar is, according, to one author, quite similar to black walnut. It is characterized by a rapidly growing, deeply penetrating juvenile taproot with wide-spreading laterals. Taproot penetration is usually not as deep or as rapid in seedling yellow-poplar as in black walnut, however; the latter species often reaching depths of over 2 ft. (.6 m) during the first season as compared to about 12-18 in. (.3-.45 m) for yellow-poplar. In both species, however, two weeks or less after germination, the uppermost strong lateral roots are nearly as long and in some cases longer than the taproot (1178).

Rate of seedling root growth may vary considerably among different yellow-poplar clones. One author found that average root production (in terms of dry weight) was approximately 3 times greater in ramets of one clone as compared to another after one growing season. Corresponding differences in height growth were also observed. Although root weight differed considerably between clones, the proportional distribution of roots through the profile did not vary between them. Approximately 45% of the total root weight of both clones was in the plowlayer (0-12 cm), 50% at a depth between 12 and 28 cm, and about 5% below 28 cm. The longest roots horizontally and vertically averaged about 70 and 55 cm, respectively, for the superior clone, and 60 and 40 cm for the other clone. At one year of age, the fast-growing clone was therefore exploring more soil volume than the slower growing one (1114).

EXUDATION AND UPTAKE

A study of the cation exchange capacity of root segments of several tree species showed that yellow-poplar roots had the lowest c.e.c. of any of the trees, approximately 8.0 me/100g. The author suggests that this reflects site requirements to some degree, since yellow-poplar was considered to be the most nutrient-demanding species tested, and thus not adapted to extracting nutrients from infertile soils (as pines are) (870).

Radiocesium "tagging" of yellow-poplar seedling root systems was used by one researcher to delineate root nutrient pathways to the soil and estimate transfer rates. At the termination of the study 32% of the initial ^{134}Cs budget was above-ground. The roots contained 38% and 30% had been transferred to the soil. Root processes were found to be major contributors (67%) of the radiocesium to the soils, and soils proved to be major sinks. Fifty percent of the ^{134}Cs

transferred to the soil by root processes was released by root mortality; the remainder was attributed to leaching of pine roots and exudation, which could not be separated (268).

A study of mineral concentrations in yellow-poplar roots showed that K> Ca> Mg> P, with content increasing 2 to 4 fold with each decreasing diameter size class of root. This was due to a higher content of metabolically active tissue per gram dry weight in the smaller roots, as determined by respiration measurements (267).

Yellow-poplar has been noted by some researchers for its ability to absorb water in considerable quantities through the suberized, or mature, portion of its root system. Many other tree species also have this ability, but the particular anatomical characteristics of yellow-poplar, especially the high number of lenticels and high degree of coverage by periderm of the inner bark, apparently enable it to absorb water at a faster rate than many other tree species (669, 365).

EFFECTS OF EXCESSIVE AND DEFICIENT MOISTURE

Yellow-poplar is among the most intolerant of trees to soil flooding (553, 481, 174, 482). Mortality of some seedlings may occur after only 3 days of flooding during the spring or early summer, while over 4 weeks of continuous standing water generally results in almost complete mortality. Sprouts from the root collar may occur on flooded trees, indicating that the root systems may remain alive longer than other portions of the tree, especially the lower stem tissues (768, 769). After death of the roots, however, generally no new roots will develop; this is in contrast to other species such as sycamore, sweetgum, and green ash which will develop new roots while inundated (552). The death of inundated roots may occur largely as a result of excessive exosmosis or leakage of organic compounds from root tips due to their exposure to an abnormal atmosphere (water) (1335). The inability of yellow-poplar to tolerate prolonged flooding during the growing season is propably the main reason yellow-poplar is lacking on flood plain sites throughout its range (769).

RESPONSE TO SOIL CHARACTER

The root system of yellow-poplar, like black walnut, is considered characteristic of species that naturally occur on deep, well-drained, fertile soils of Regions that experience well distributed summer rains (1178). There is also some evidence that soils associated with a particular successional stage may be better suited to yellow-poplar root (and shoot) growth than others. A Virginia study found that yellow-poplar root weights were up to 10 times higher on soil from old field sites than on soil from hardwood stands. Root weights from pine stands were intermediate. The differences were attributed to a lower C/N ratio (and thus more available N) on the old field soils in addition to a decreasing P availability with time on the acid soils of the region (567).

Plantings of yellow-poplar seedlings on a sandy soil with layers of clay demonstrated the influence of soil texture on root characteristics. In the sandy strata, yellow-poplar roots were round, fleshy, and relatively easy to separate from the soil. But when the roots grew into a clay lens, they became flattened and almost flaccid. They were also much more intimately associated with the finer soil particles (1114).

Yellow-poplar root development is often inhibited when the seedlings are planted on severely disturbed soils associated with past cultivation, erosion, or other factors. Inhibition on such soils in Tennessee is thought to be due largely to a vombination of Ca deficiency and Al toxicity (742).

Initial survival of planted yellow-poplar has been extremely variable, largely due to either poor site selection or the use of low-quality planting stock. The degree of root pruning to facilitate the planting operation may also have an important effect on survival; seedlings above a certain stem diameter should not be heavily root-pruned. Excessive root-cutting of seedlings with large stem diameters does not retard the growth of the aerial parts during the first two growing seasons, but if a drought occurs the roots are not sufficiently developed to supply the amount of water needed for survival. A moderate amount of root-pruning, however, has been shown to improve survival of outplanted yellow-poplar (734).

Carbohydrate reserves in the roots of one-year old yellow-poplar seedlings are apparently not related to subsequent survival of transplanted yellow-poplar seedlings (434).

A study involving the effects of six different root media on early growth of yellow-poplar seedlings showed that two were much superior to the other four, those two being vermiculite and peat plus vermiculite. The average shoot-root ratio was much higher for seedlings grown in pure vermiculite, although average shoot height was nearly equal for both of the aforementioned media. Vermiculite was cited by the author as the medium which allowed the best expression of differential growth pattern between roots and shoots (1257).

Soaking of seedling yellow-poplar roots in indolebutyric acid prior to planting produced no beneficial growth response (796).

MYCORRHIZAE

The contrast between mycorrhizal and non-mycorrhizal roots of yellow-poplar is quite distinct. The endotrophic mycorrhizae are short, thick, and durable, without root hairs. The non-mycorrhizal roots are long, slender, and delicate (1222). One author reported that intense infection occurred in all root samples of yellow-poplar, regardless of age or origin of sample (155).

It is known that the inoculation of endotrophic mycorrhizae can greatly increase the growth of yellow-poplar sedlings, especially when planted on relatively infertile soils (Hepting, 1971).

The only species of fungi thus far identified as yellow-poplar associates are Endogone fasciculata and E. mosseae (565; Hepting, 1971).

DESTRUCTIVE AGENTS

Non-infectious

Yellow-poplar is very sensitive to the application of soil salts in the root zone (871) (131).

Dieback of yellow-poplar has in a few cases been associated with self-girdling of a major root, possibly resulting from improper planting (1209).

Yellow-poplar was found to be much more susceptible to damage from applications of the herbicide simazine than was black walnut (1288).

Insects

The borer Euzophera ostricolorella attacks mainly yellow-poplar over 10 in (25.4 cm) in diameter. The larvae feed in the inner bark, excavating tunnels which extend both above and below the ground line. Winter is spent in the pupal stage in the tunnel (Baker, 1972).

White grubs (Phyllophaga spp.) may damage the roots of yellow-poplar, particularly in nurseries (606).

Nematodes

Nematodes associated with the roots of yellow-poplar include Pratylenchus penetrans, P. pratensis, Meloidogyne sp. (Ruehle, 1967), Aphelenchoides sp., Aphelenchus sp., Hoplolaimus tylenchiformis, Tylenchorhynchus claytoni (900), Aorolaimus sp., Criconema sp., Criconemoides sp., Helicotylenchus sp., H. dihystera, (Cobb) Sher, H. erythrinae (Zimmerman) Golden, Hemicriconemoides sp., Hemicycliophora sp., Paratylenchus sp., Trichodorus sp., Xiphinema sp., X. americanum (Cobb), Gracilacus sp. (Ruehle, 1968). None are know to cause significant damage.

Fungi

Yellow-poplar has no major root diseases. Armillaria mellea can kill badly weakened trees, and its rhizomorphs are common on the roots of old trees (Hepting, 1971). Root rot caused by Cylindrocladium scoparium and C. floridanum has caused losses of yellow-poplar seedlings in southern nurseries

(256) (633) (634). Symptoms of the disease include lateral root necrosis and dark-brown to black cortical lesions at the base of the stem and on the taproot. Fusarium solani may cause some mortality through root infection, although a wound of some sort is generally necessary for entrance of the fungus (74).

One author studied the microflora in soil profiles of a yellow-poplar stand and found the highest counts of bacteria in the A_0 and A_1 horizons and the highest fungal counts in the B_2 horizon. He was not able to relate microbial counts to rate of tree growth (Hepting, 1979). Yellow-poplar is quite resistant to attack by Fomes annosus (681, 684).

Picea glauca (Moench) Voss - White Spruce

MORPHOLOGY

Development of Form

Early root system development in seedling white spruce is characterized by a rapid production of fine roots, distributed quite uniformly through the upper four inches (10cm) of soil (46). Shoot-root ratios (by weight) of one year old trees remains at about three-to-one or four-to-one throughout the first growing season, but decreases to about two-to-one during the second season as root growth increases (874).

The pattern of root growth in white spruce varies considerably from site to site and from tree to tree. Even mature trees with very similar root systems may have exhibited wide variations in form at different stages of development (1225).

Secondary or adventitious roots arising from dormant buds on stems and branches develop on white spruce in many different soils and sites, but especially where a build-up of moss or alluvium occurs around the trunk of the tree. They may develop throughout the life of a tree, but occur most frequently between 3 and 20 years of age (1225).

Growth of a taproot may be somewhat restricted by the development of adventitious roots, or due to soil texture, structure, moisture, or frost. Should adventitious roots grow to a large size, the primary lateral roots and taproot will slow down in growth and may eventually die. In the absence of adventitious roots and under favorable soil conditions, an elongated taproot may develop (1225).

Taproot development may also be abnormal or contorted as a result of contact with decayed wood, raw humus, or poorly-drained seedbeds. The horizontal growth results from the higher moisture content of decayed logs, the improved nutrient and moisture content of the mineral-humus interface, impediments in humus and decayed wood, and anaerobic conditions of poorly-drained soil (1225).

Distribution in Soil Profile

Eventual distribution of the root system in mature white spruce is highly variable with the textural and structural characteristics of the soil, especially as they influence soil moisture. A so-called monolayered root form may develop whenever the lateral roots, for whatever reason, either overgrow or outlive the taproot. A form of monolayering, the restricted taproot form, has been mentioned briefly already. Vertical root penetration in this type of root system commonly does not exceed 3 or 4 feet. This form of rooting is most common in trees growing on wet soils underlying humus.

The elongated taproot-form, though it does not occur frequently, is most commonly exhibited on course-textured sandy soils. Vertical sinker roots in this type of system may reach a depth of six feet or more (1052). The taproot may originate from a large lateral root rather than from the trunk directly (1225). Some adventitious roots may develop on trees growing on these well-drained sites, but they normally do not grow to a large size (1225).

It is also apparently not uncommon for white spruce to exhibit fairly strong vertical sinker root development even in the absence of a definite taproot. The reason for this is unclear, though inherent factors may be involved (67).

Multilayered root forms may occur on sites which are subject to periodic rises in the water table, or periodic alluvial or lacustrine deposits (1225)(600). They are characterized by several distinct whorls of adventitious roots, each presumably produced through the stimulus given by burial or inundation of the pre-existent feeder roots (600).

The lateral root system of mature white spruce may be quite widespread. One author reported that laterals of many trees may exceed 30 feet (9.1m), and that one root was traced to 61 feet (18.6m) from its source where it was still approximately 1/4 inch (.6 cm) in diameter (67).

Comparison with Other Species

Although the root system of white spruce is extremely variable, some comparisons can be made with other species growing on the same site. One author reports the following for mature trees on sandy soils in Ontario: balsam fir root systems were generally of similar depth, but less variable; tamarack and black spruce were both consistently shallower than white spruce, and tamarack was also more widespread; jack pine was much deeper than white spruce, but not as widespread (67).

Another author reported that on deep permeable soils in British Columbia white spruce exhibited a greater lateral root spread than either alpine fir or lodgepole pine. The ratio of foliage weight to root weight was about three-to-one in lodgepole pine, and two-to-one in both subalpine fir and white spruce (343). In addition, lodgepole pine had about 2.5 times the average total root length of white spruce of the same age, whereas subalpine fir had 35% less. Pine and fir also had larger proportions of roots greater than .6mm in diameter than white spruce (343).

The distribution of fine roots (< 1mm) for three seedling conifers in a sandy-loam soil was reported by another author as follows: white spruce had a relatively uniform distribution of fine roots in the upper four inches (10cm) of soil, whereas jack pine fine roots showed a maximum at three inches (7.6cm), and black spruce showed a maximum at the surface, decreasing in abundance with depth (46).

Grafting

The amount of grafting in white spruce root systems apparently varies considerably with both the site and the root morphology of individual trees. One author reports that grafting is common on wet sites in British Columbia, where trees have simple buttressed root systems, but is rare on dry sites among trees having shallow, wide-radiating root systems. He speculates that the resultant fused mass of roots on wet sites functions to provide better tree stability (344).

Adventitious Rooting and Layering

The ability of white spruce to develop adventitious roots arising from dormant buds on the stems and branches (the latter referred to as "layering") has been reported by several researchers (1224, 1128, 621, 386, 71, 253). Even where the primary root system has not been inhibited by soil properties, trees growing in soils with humus layers will often develop adventitious roots above the root collar. This is presumably related to the better nutrient supply in the humus layer, or at the humus-soil interface, and indicates that adventitous roots, which utilize the more fertile layers of the soil, are responsible for maximum growth (1224).

Adventitious roots develop from stems and branches when these parts are covered by a material (such as moss, humus, or alluvial deposits) that provides moisture, aeration, darkness, and warmth (1224). Roots arising from branches are usually restricted to the area of the terminal bud scars (71).

Reproduction by layering may be of considerable importance in habitats where regeneration by seed is infrequent due to unfavorable site conditions, such as deep surface humus. Within much of the southward range of white spruce, however, opportunities for reproduction by layering are only sporadic since persistence of live lower branches in contact with soil is uncommon in typical forest situations (1128).

In more northern latitudes adventitious rooting of white spruce on alluvial soils ensures an active feeding root system above the level of soil frost. Otherwise, the older and lower systems of primary and secondary roots would be enveloped in frozen soil and the tree would die (1224). This multilayering of adventitious roots also contributes to windfirmness (1224).

SEASONAL GROWTH PATTERN

One author reports that visible signs of root and top growth appear almost concurrently in the spring. Root elongation was reported to peak at the end of May, drop sharply in early June, increase gradually during late June and July, and peak again near the end of August. This pattern of dates was repeated even during years in which growth initiation in the spring was delayed due to cold weather. The depressed rate of elongation in early June occurred during the period of rapid shoot elongation (874).

ROOT-SHOOT RELATIONS

Unlike root growth, root initiation in white spruce (and likely in other species) is probably more closely related to hormonal activity than to photosynthetic activity. This is supported by the fact that, in one study, 98% of white spruce seedlings placed in complete darkness for two months still initiated new roots (214).

Another researcher reported that a 25% reduction in foliage significantly increased white spruce root initiation, whereas a 75% reduction decreased initiation. This was partially attributed to hormonal changes caused by bud removal. (215)

Average root weight of white spruce seedlings grown in 13% light for 9 years was only 8.5% that of seedlings grown in full light; shoot weight was 14.9%. Average root-collar diameter of the full-light seedlings was approximately 2.2 times that of both the 13% and 25% light seedlings.

Effects of Fire

Being normally shallow-rooted, white spruce is quite severely affected by slow burning, hot surface fires. A severe fire may burn living roots as large as eight to nine inches in diameter, leaving only stubs attached to the stumps (759).

UPTAKE

An apparent inhibition of white spruce seedling growth by reindeer moss (Cladonia) was reported by Fisher (1979). This growth stunting is accomplished by poor P & N nutrition that may be related to impairment of root system development.

Nutrient uptake in white spruce seedlings is fairly rapid when compared to biomass prduction (864, 978). A comparison of 10 coniferous species showed that at high seedbed densities, white spruce ranked eighth in total biomass production, fourth in ash content, seventh in N content, fourth in P content, eighth in K content, second in Ca content, and sixth in Mg content. The percentage of total plant nutrients contained in the roots was highest for Mg (30%) and lowest for N (19%) (978).

RESPONSE TO COMPETITION

Intense competition with shrubs or other trees may be reflected in the rooting habit of white spruce. Increased incidence of grafting, complex forking, or contortion of roots may occur. Contortion and twisting can result indirectly through the elimination of seedlings from shaded, mineral soil, thus restricting regeneration to marginal areas such as near boulders or on decaying logs (344).

Another author reported that low herbaceous vegetation appeared to have no significant effect on the growth of white spruce seedlings as long as only the roots were in competition and the crowns of seedlings were above the vegetation. Crowding without overtopping by herbaceous vegetation reduced the height growth of spruce only slightly, but small diameter increments occurred for several years. Stem and foliage weight were affected more by competition than was root weight (343).

On the other hand, there is some evidence that height growth of white spruce is more easily depressed by root competition for moisture than that of other species. This was concluded from experiments showing that growth was reduced at levels of soil moisture which produced maximum growth in three other conifers (29).

White spruce is difficult to maintain where it is growing in mixture with hardwoods. This has been partially attributed to its inability to become established within the dense mat of roots create by perennials, bracken fern, shrubs, and understory trees. Effects of associated vegetation on the seedbed may be more important than root competition, however (Ackerman, 1957).

The fact that white spruce exhibits its best growth on sites which are somewhat less moist than the sites on which it is most commonly found indicates that root competition may be involved. It may be that the development of a shallow lateral root system on a wet site, where competition is minimal, results in better survival (though lower vigor) than the necessary downward root development on drier sites, which is often not rapid enough to compete with other vegetation for available moisture (1080).

EFFECTS OF EXCESSIVE AND DEFICIENT MOISTURE

White spruce was ranked by one author as intermediate among six conifers in tolerance to flooding. Balsam fir and black spruce were more tolerant than white spruce, while red pine and white pine were less tolerant. Most of white spruce's hardwood associates are reportedly more flood-tolerant than white spruce (12).

Periodic inundation of white spruce may result in the death of fine roots that penetrated into the soil when the upper layers were aerated. On these sites the trees may depend almost entirely on the network of surface roots (343).

Initial height growth of seedling white spruce is apparently more responsive to moisture supply from above (precipitation) than that of some other conifers, including red pine and black spruce (873).

White spruce was ranked by one researcher as less tolerant of poor soil aeration than either black spruce or jack pine (1359).

RESPONSE TO SOIL CHARACTER

As previously mentioned, rooting habit of white spruce is greatly affected by soil properties. One author (343) reports the following variations in root morphology on three different soils in British Columbia.

On clays, the depth of root penetration is reduced. The main root system consists of large laterals forming a flat plate at the level of the incorporated organic material. The taproot is usually weak and short.

In shallow sands underlain by coarse gravel, the taproot is frequently distorted, diverted into a horizontal position, or branched. Diversion of the taproot does not necessarily reduce the depth of rooting, since penetration by laterals or sinkers often serves to compensate.

On loamy and sandy soils, root form varies considerably with age of the trees. A taproot system is characterstic of spruce up to three years of age; older trees show more extensive development of lateral roots. On these soils the average depth and penetration of roots is most closely correlated with size of the stem and crown.

"Stilt" root systems may occur on trees that germinate on stumps or fallen trees which later decay away. Trees growing on boulder-laden sites with thin soils typically develop long thin roots which embrace the boulder(s) (344).

Root growth of white spruce is quite sensitive to soil temperature. One author reports that, at a range of soil temperature from 15^{o} - 31^{o}C, root growth, shoot growth, and mycorrhizal development were all most rapid at 19^{o}C, and slowest at 31^{o}C. Mycorrhizae were completely absent at 15^{o}C only. Average root penetration at 19^{o}C was more than double that at either 15^{o}C or 27^{o}C (516).

There is some evidence that self-strangulation of roots resulting from improper planting may provide entry points for root rot fungi in white spruce (901).

White spruce seedling roots are quite sensitive to high temperatures and low humidity during transplanting. Exposure of 2-0 stock for 5 minutes at 93.5°C resulted in slight injury to feeder roots, whereas exposure for five hours at 95.4°C resulted in death of the entire root system (1193). Non-dormant stock is more easily damaged than dormant stock (876).

Soil moisture has been shown to greatly influence the success of establishment of outplanted white spruce seedlings through its influence upon root regenerative capacity. One author reports that land to be planted with white spruce should be close to field capacity, with soil moisture tension not exceeding 0.5 Bar, for best results (299).

In a comparison of four planting methods, the inverted V method was found to result in maximum survival, while use of the planting bar resulted in the highest mortality of white spruce seedlings, Seedling survival varies more than average root growth of surviving trees for each of the four methods (1033).

One author reported that planting of white spruce approximately 10.0cm (3.9 inches) deeper than normal resulted in better growth than seedlings planted at normal depth. He speculated that this may have occurred due to: a) rapid root contact with more favorable moisture zones, and b) the development of adventitious roots that supplemented rather than superseded the initial root system (1150).

Root pruning of 3-0 white spruce stock after the flush of growth (June 25) was found by one author to increase survival and growth after outplanting, over that of unpruned stock. Depth of root pruning had no significant effect (875). Another study, however, showed that second year height increment of root-pruned seedlings was significantly reduced over the first year. This time-lag effect may be a result of delayed water stress due to the slow growth rates of white spruce roots (1151).

MYCORRHIZAE

Only *Cenococcum graniforme* has been reported as a mycorrhizal associate of white spruce (Hepting, 1971).

DESTRUCTIVE AGENTS

Non-infectious

Excessively slow growth of white spruce, often accompanied by yellowing of the needles, occurs on some sites for some years after planting, and has been referred to as "check." Some workers have suggested that check is the period during which the damaged root system is regenerated (Mullin, 1963). The condition has also been attributed to water and/or nutrient stress (1152) which, in fact, may occur as a result of root damage. A study involving root pruning of white spruce seedlings seemed to show, however, that the effects of root damage per se were small in relation to other disturbances associated with transplanting; damaged roots were found to regenerate vigorously (1151).

There is some evidence that white spruce may be sensitive to micronutrient deficiencies on some soils. One author reported that a soil treatment of 1.3 lb. Cu plus 2.8 lb. Zn per acre resulted in an average growth increase of almost 11% over non-treated seedlings, in addition to increases in foliar nutrient content of nine other nutrients (593).

White spruce has been rated by different authors as "sensitive" and "moderately tolerant" to soil salts in the root zone (923, 871).

Roots of white spruce seedlings were found by one author to be able to withstand a soil temperature of -23.3°C before more than 50% of the root system was killed. This was the lowest temperature that any of the 38 species of trees tested could endure (502).

Shallow rooting, associated with a concentration of nutrients near the surface of sandy soils, has resulted in deterioration and low volume production in plantations of white spruce in Quebec (Paine, 1960). Summer drought also has a role in this decline.

White spruce is susceptible to windthrow on sites which promote shallow rooting, although black spruce and balsam fir are normally considered more susceptible (1123). Frost heaving may be a problem in heavy mineral soils (Fowells, 1965).

White spruce is most susceptible to foliar herbicides during the early part of the growing season (Arend, 1955).

Insects

White spruce is relatively free from attack by root-damaging insects. Larvae of the beetle, Dryocoetes caryi Hopk., may be associated with the root system of weakened or suppressed white spruce, though they are usually confined to the trunk (Baker, 1972).

The Northern Pine Weevil, Pissodes approximatus Hopk., occasionally attacks white spruce, though its preferred hosts are red and scotch pines. Winter is spent mostly in the adult stage in the duff and top soil beneath infested trees. Attacks occur beneath the bark surface from the roots up to small branches. Attacks also may occur at the root collar (Baker, 1972).

One or more species of root collar weevil, Hylobius spp., may breed in the root collars of white spruce in some areas, though several of the pines are more often attacked. Damage is heaviest on moist sites, especially those with a sizeable accumulation of decaying wood (1245). The larvae feed downward in the inner bark of the base of the trunk and in the bases of large roots, widening their galleries as they develop. Infested trees bleed heavily at the ground line (Baker, 1972).

Root injuries caused by Hylobius may be an important source of entry for root-damaging fungi (1273, 1087). A year or more may pass between the time of root injury and the time of establishment of the decay (1271). In Canada, the populations of Hylobius were found to be greatest in the sparse reproduction on white spruce cutover land (1271).

There is some evidence that the effects of white grub (Phyllophaga spp.) activity may intensify or prolong the condition of "check" mentioned earlier, notably on soils of low fertility or in years of subnormal rainfall (1154).

Nematodes

The dagger nematode, Xiphinema americanum, has caused stunting and increased sensitivity to winterkill in greenhouse-raised seedlings of white spruce (Griffin & Epstein, 1964). Root lesion nematodes, Pratylenchus penetrans, caused low vigor in white spruce seedlings in a great plains nursery (Peterson, 1962). The nematode Tylenchus emarginatus is believed to increase the susceptibility of seedling white spruce to damping-off fungi (1143). Other nematodes associated with white spruce include Paratylenchus projectus (1147), Aphelenchoides sp., Aphelenchus sp., Criconemides cylindricum, and Paurodontus sp. (792).

Fungi

Root rots of white spruce are most predominant in trees growing on shallow soils. Losses on these sites can be kept to a minimum by the utilization of frequent thinnings and short rotations (1208).

Fungi believed to cause root rot in white spruce, in addition to those species mentioned in Hepting, 1971 (pp. 268-269), include the following:

Cylindrocladium scoparium attacks the roots at the root tip first, gradually proceeding toward the crown. Black spruce, red pine, and jack pine are all more susceptible than white spruce. Symptoms include chlorosis and a drooping of the current year's growth (39, 31).

Fomes annosus infection may occur in middle-aged and older stands of white spruce. The central portions of roots are most commonly affected, with few penetrations of the cambium. Symptoms include retarded top growth and clumped shoots on lateral branches (615).

White spruce has been classed as moderately susceptible to infection by the damping-off fungi Pythium spp. (1206).

Armillaria mellea may attack white spruce through penetration of wounds in the roots or root collar, or by contact with other diseased roots or rotting wood. In Newfoundland, it is most common on drier sites which have been cutover and planted with bare-root stock (1084, 1087).

Additional damping-off fungi shown to infect white spruce include: Fusarium oxysporum, Alternaria spp., Panagrolaimus spp., Pythium spp., and Rhizoctonia solani (1204).

Root rot caused by Fusarium spp. has been reported on white spruce seedlings in New York. Occurrence of the fungus has been related to the presence of buckwheat residue, which had been grown as a cover crop on affected areas within the nursery (347).

Cylindrocladium floridanum Sob. and Seymour, is responsible for root rot of white spruce in Minnesota, Wisconsin, and Ontario (881).

Polyporus tomentosus Fr. root rot of white spruce is discussed briefly by Hepting, 1971. Additional publications on this fungus since 1970 include: (917, 1280, 1281, 880).

Pinus banksiana - Jack Pine

MORPHOLOGY

Development of Form

Early root system development in jack pine is characterized by rapid extension of the taproot followed by development of lateral roots. Emphasis on growth of the taproot changes to the lateral system over a period of about four years. Root development in the first year of a jack pine seedling is devoted to rapid downward growth, especially on dry sites. Generally, on deep sandy soil having a low water table, a depth of 6 to 12 inches (15 to 30 cm.) is reached. On moister soils development is somewhat slower (1118, 1079). The same rapid downward growth is exhibited by nursery stock after transplant to the field (1124).

During the second season the lateral roots begin to elongate, growing to a length of 3 to 5 inches (8 to 13 cm.) (297). The maximum surface area of roots less than 1mm. in diameter is attained at a depth of 3 inches (8 cm.), while the maximum surface area of coarser roots is slightly above that depth (46).

By the third and fourth year, downward elongation slows while the lateral system develops more fully (297, 1124). The lateral roots lie close to the surface of the soil, the majority at a depth of 2 to 6 inches (5 to 15 cm.). The taproot begins to branch, and sinkers grow from the laterals (1079). At this time a highly significant weight gain occurs in both the top and the roots coincident with the passage of the taproot below the greatest root concentrations of the herbaceous ground cover (1079).

By the eighth year the major horizontal roots of jack pine have extended to approximately 85% of their final length (1065).

Distribution in Soil Profile

The mature root system, at least on sandy soils, is often fairly deep although the proportion of vertical roots is smaller than horizontal roots. The fine roots form a fibrous mat near the soil surface, but not as dense a mat as that observed on black spruce (Picea mariana (Mill.)B.S.P.) (228, 946). A taproot may or may not be present. When present, its form and prominence vary even within the same stand (1065). Vertical roots other than the tap root originate along the length of the lateral roots, differing in habit from that of the taproot. The taproot maintains its vertical orientation despite obstruction, while a root branch may turn horizontally upon reaching a barrier such as a layer of very dense clay (946). The laterals which arise from different levels on the taproot, when present, or its larger divisions do not slope downward, but parallel the ground surface (67, 228).

More than 98% of the laterals are found above the lower limit of the B horizon of a sandy soil regardless of tree spacing, root size, or differences in the depth of the B horizon. The ends of the laterals are slender and simple in their branching, while the vertical roots of the laterals are profusely branched (2, 228). The combined surface area of all roots less than 1 mm. diameter constitutes 80 to 90% of the total horizontal root surface area, although roots less than 1 cm. diameter constitute only 5 to 10% of the root system by weight (1065, 865).

The ultimate depth of rooting of jack pine reported most often is between 4 feet and 6 feet (2 m.). In Minnesota, the average depth varied from 5.8 feet (1.77 m.) in the least vigorous crown class to 7.8 feet (2.32 m.) in the most vigorous (767). Jack pine roots have been found to extend below 9 feet (3 m.) in sandy soil in Vermont and Minnesota (4, 767). On a semi-arid clay prairie soil in North Dakota the roots of a jack pine extended to a depth of only 3.4 feet (1.04 m.). The length of the longest lateral root of that tree, however, was 38.5 feet (11.73 m.), indicating that the root system covered much more ground surface area than is usual (1332). More typical of the principal lateral roots is a length less than 30 feet (9 m.) (1332, 865, 67).

Grafting

Intraspecific root grafting occurs in jack pine, but is not common (446, 693, 228). Six cases of interspecific grafting were found in a plantation in Russia between jack pine and Scots pine (Pinus sylvestris L.)(446). The grafts not only increased the transpiration rate, but also affected the anatomy and morphology of the above ground parts (Beskaravainyi, 1961). Grafting attempts using jack pine as stock found it to be semi-incompatible with the five pine species tested (11).

Layering

Natural layering of branches is not a feature of jack pine (71). Even when the branches were buried by soil, and black spruce on the same site had layered branches, no rooting occurred (408).

Seasonal Growth

In study where the soil temperature never reached 19°C (Cloquet, Minnesota) and where maximum soil temperature at 6 inches was about 15°C, root growth was influenced most by the combination of available moisture and evaporation rate during the growing season. Low available moisture (still above the wilting coefficient), concurrent with a high rate of evaporation was accompanied by a reduction in the rate of root growth. At moderate rates of evaporation the effect of limited soil moisture was less pronounced. In northern Minnesota two peaks in root growth occur: the first during the middle of July and the second between late August and early September (623).

In 25 to 28 year-old trees the average growth of individual roots for a season (Minnesota) was from 9 to 12 inches (23 to 30 cm.). Younger trees averaged more growth (623).

ROOT-SHOOT RELATIONS

Roots comprise 13 to 14% of the total dry matter of a jack pine stand. Approximately 8% of the stand nitrogen, 9% of the potassium, 12% of the phosphorus and calcium, and 16% of the magnesium is bound up in the roots (865).

The aerial portion of the tree provides some indication of the development of the root system. Trees with dense crowns will normally have deeper, sturdier root systems than trees with more sparsee crowns (422). The bole diameter is also indicative of the massiveness of the root system (67, 865).

EXUDATION AND UPTAKE

An apparent inhibition of jack pine germination and seedling growth by reindeer moss (Cladonia) was reported by Fisher (1979). This stunting of growth is accommpanied by poor P & N nutrition that may be related to impairment of root system development.

RESPONSE TO COMPETITION

Jack pine root development is affected by competition mainly in that the ability of the top to photosynthesize is affected by a reduction in incoming light. In 8-month old seedlings, 20 to 30% of the photoassimilated carbon is allocated to the roots (65). The top-to-root ratio by dry weight is not affected by shading (1971).

Competition from roots of other vegetation also affects rooting, however. High density of jack pine plantings inhibits the development of the root system. Although seedling density does not affect the average length of the roots, average root weight decreases with increased density. As density increased in 2-0 stock from 18 trees per square foot to 74 per square foot, the average green weight of the roots decreased from 1.90 grams to 0.80 grams. (Stoeckeler and Jones, 1957). On older trees, vertical roots descend from the lateral roots at a point midway between adjacent trees where the horizontal roots from each tree contact each other (4). The ratio of lateral roots to vertical roots is dependent upon spacing. In close spacing the proportion is affected mainly by competition from other pines; in wider spacings ground cover plants may become important enough to influence rooting (2).

Table 1. Ratio of lateral roots to vertical roots (by weight) with reference to spacing and ground cover on a deep, sandy soil.

Spacing (ft.)	Lateral Roots:	Vertical Roots	Herbaceous Cover
2x2	1.2:	1	none
4x4	2.3:	1	none
6x6	9.0:	1	light
8x8	6.7:	1	heavy

EFFECTS OF EXCESSIVE AND DEFICIENT MOISTURE

The depth and spread of the root system is undoubtedly influenced by moisture conditions, whether the conditions are caused by competition from other vegetation or edaphic factors. Seedlings grown on upland, droughty sites tend to develop deeper, narrower root systems than those grown on sites with plentiful moisture (1124, 1072). This adaptibility to moisture situation plus the rapid early root extension aids the establishment of jack pine on dry sites (1124).

Drought resistance is enhanced in nurseries by deliberately subjecting seedlings to moderate soil drought during the period of active growth. Seedlings watered once every three days, maintaining moisture content just above the wilting coefficient, survived periods of moisture deficiency better than seedlings which were watered daily (1072). The morphological result is greater horizontal and vertical root development in proportion to the top in seedlings given less water (1072,1124). Drought resistance is lowered by overfertilization with nitrogen which results in an increase in top growth unmatched by the smaller increase in absorbing surface of the roots (1302).

Jack pine does not seem to have any special tolerance to flooded or bog conditions. It is less tolerant of poor root aeration than black spruce, but more tolerant than white spruce (Picea glauca (Moench)Voss). White spruce is more sensitive than jack pine regarding absorption of nitrogen at low levels of oxygen. Root length, root tip diameter and root weight all are reduced when oxygen levels are low (less than 3.3ppm. mean oxygen--5% O_2, 95% N_2--at 25°C for 18 hours day regime, 15°C for 6 hours night regime)(1359). Maximum root development occurred at the 5.4 ppm. O_2 level for jack pine, while maximum development for black spruce and white spruce was at 4.5 ppm. and 7.5 ppm. levels (1359).

RESPONSE TO SOIL CHARACTER

The presence of a dry organic layer 3 or more inches (8 cm.) thick is detrimental to the establishment of seedlings because the radicles dessicate before they reach mineral soil (10). Fire reduces the depth of this layer. However, germination of seeds immediately following a fire may result in high mortality because the high concentrations of soluble salts can be toxic to root hairs and young roots (10).

The type of humus affects the rooting habit through its influence on respiration of the root tips. Water extracts of humus types originating under jack pine stimulated the uptake of oxygen and the release of carbon dioxide, inducing a normal course of metabolism in the root tissues. A hard maple-yellow birch humus type and a balsam fir type, both from highly productive stands, stimulated the jack pine root tip tissues in a manner similar to that of jack pine humus, but to a higher degree. Humus from stands of low productivity effect a low stimulation of carbon dioxide release followed by greatly reduced activity. The enzymatic system of the root tips is rapidly depleted, indicating a general inhibition rather than a stimulation of growth (669).

Soil Temperature

Another way in which the organic horizon affects root growth is through its influence upon soil temperatures. Root growth, after winter, resumes when the temperature of the upper 6 inches (15 cm.) of soil rises above 4.4°C, but is severly limited until the temperature is higher than 10°C. Favorable temperatures occur earliest in young stands on bare mineral soil and latest in stands with closed canopies and several inches of litter and mull (623).

Soil temperature also affects the amount of root development. In a comparison of five soil temperatures--15°C, 19°C, 23°C, 27°C, and 31°C--jack pine seedling roots had the greatest volume, dry weight, and depth of penetration in soils held at 27°C. A second peak in root volume and dry weight, but not depth, occurred at 19°C. One contributing factor to this bimodal distribution may be the high incidence of damping-off disease at 23°C. Also, at 19°C the mycorrhizae were at maximum development. At 31°C root growth was severly inhibited (516).

MYCORRHIZAE

In laboratory tests, jack pine was found to be a moderate host (25 to 49% of feeder roots mycorrhizal) for the fungus *Pisolithus tinctorius* (Pers.) Coker & Couch (812). The fungus, on acid stripmine spoil in Missouri, was always found near jack pine which had been planted with several other species after the mine was abandoned (701).

Jack pine is a poor host for *Thelephora terrestris* Ehr. The mycorrhizae that do form have excellent development of the Hartig-net, but no fungal mantle (812).

Other fungi reported to produce root rot in living jack pine are: *Armillaria mellea* Vahl ex. Fr., *Cylindrocladium floridanum* Sob. & Seymour (formerly included in *C. scoparium* Merge.) *Fomes annosus* (Fr.)Cke., and *Polyporus schweinitzii* Fr. (32, 879, Morrison & French, Ag. Handbook 386). Decay by *Flammula alnicola* (Fr.) Kummer has been reported in Canada (Denyer, 1960). *Armillaria mellea* is highly virulent; trees need not be weakened by other injurious agents prior to an attack (900, 920). Mortality is high in young stands attacked by *Fomes annosus*, but trees older than 40 years are fairly resistant (615). Jack pine is more resistant to decay by *Polyporus tomentosus* than are spruces (1281).

Paxillus atrotomentosus (Batsch.) Fr. causes a brown root rot on dead jack pine. The fungus does not attack living trees (288).

The *Coryne sarcoides* (Jacq.)Tul. complex, which causes a heart rot of jack pine, is postulated to enter the tree through the root system (84).

Jack pine seedlings are moderately susceptible to damping-off mortality. *Pythium ultimum* Trow, *P. aphanidermatum* Heese, *P. pulchrum* von Minden (Syn. *P. epigynum* Hoehnk), *Phytophthora cactorum* (Lebert & Cohn) Schroeter, *P. cinnamoni* Rands, *Rhizoctonia solani* Kuehn., *Botrytis cinerea* Pers. ex Fr., *Aphanomyces eutreiches* Drechsl., *Fusarium oxysporum* var. *redolens* (Wr.)Gorgon, *F. roseum* (Lk.) em. Snyd. & Hans., and *F. solani* (Mart.)App. & Wr. em Snyd. Hans. are among the many fungi which are potential pathogens of damping-off. The virulence of the fungus depends not only on the particular strain, but also on interactions with other soil organisms and on the effects of environmental factors.

Nematodes

Although nematodes do not appear to be the major cause of decline in plantations, they are a contributing factor, and the wounds they inflict increase susceptibility to damping-off in seedlings. Jack pine is an exellent host for *Tylenchus emarginatus* Cobb and the dagger nematode, *Xiphinema americanum* Cobb (1144, 1143, 675, 74). It is a good host or the pin nematode, *Paratylenchus projectus* Jenkins and *Trichodorus californicus* Allen (1144, 74, 675). *Tylenchus emarginatus* is a migratory ectoparasite on the epidermal cells of the entire length of the rootlet.

Each nematode is able to make large numbers of wounds on a seedling root (estimated more than 550 wounds in 24 hours). When nematodes are placed near the root they begin feeding within on hour and lay eggs within 24 hours (1143). *Xiphinema americanum*, also an ectoparasite, is found in largest numbers where the greatest number of rootlets is to be found--2.5 to 5.0 inches (6.4 to 12.7 cm.) beneath the soil surface (675, 74). In Plainfield sand from a jack pine plantation, maturation of *X. americanum* was fastest at 32°C. Under *Picea pungens* with a Miami loam soil, fastest maturation occurred at 20°C (459).

Other fungi associated with ectotrophic mycorrhizae on jack pine are: *Amanita pantherina* (D.C. ex Fr.)Schum., *A. rubescens* (Pers. ex Fr.)Gray, *Cenococcum graniforme* (Sow.) Ferd. & Winge, *Gomphidius vinicolor* Pk., *Lactarius quietus* Fr., *Suillus cothurnatus* Sing., *S. luteus* (L. ex Fr.), and *S. (Boletus) tomentosus* Kaufm. (Trappe, 1962).

DESTRUCTIVE AGENTS

Non-infectious

On high pH, calcareous soils, jack pine is chlorotic unless mycorrhizae are present. On trees with uninoculated roots, applications of varying amounts of iron and fertilizers are ineffective in preventing chlorosis; acidification of the soil produces an increase in growth, but symptoms of chlorosis eventually develop. Additions of fertilizers to inoculated trees reduce the ability of the mycorrhizae to prevent the chlorotic condition (280).

Insects

A pathogen which causes great damage to jack pine and initiates the so-called "plantation decline" is the pine root tip weevil, *Hylobius rhizophagus* Millers. The larvae of the weevil hatch from eggs laid near root tips and larger roots at varying depths to 3 inches (8 cm.) and then tunnel beneath the root bark, feeding on the cambium and xylem. Sometimes they leave the tunnel and more through the soil, wounding the root at intervals before reentering. Some roots are completely girdled and rootlets severed. The galleries left behind are filled with their frass, a good growth medium for fungi (626, 915). The acres of major infestation are usually in plantations on old field sites. Low nitrogen levels in the soil are favorable to the weevils. Nitrogen fertilization not only improves the vigor of the trees, but also decreases the rate of larval feeding and retards larval and pupal development. Phosphorus levels have no known effect on the weevils (443).

Two other weevils attack jack pine roots: *Hylobius radicis* (Buchanan) girdles the root collar, and the *Hypomolyx piceus* (DeGeer) complex (which favors moist to wet conditions) attacks the roots (1244).

Fungi

Once the roots are wounded by weevils, they are susceptible to colonization by a succession of fungi which could not enter uninjured roots. Numerous imperfect fungi, including *Leptographium* sp., *Trichoderma* sp., *Penicillium* spp., "Phoma.," and *Pullularia* sp. are followed by sporadic invasions of wood-destroying Basidiomycetes. The decay fungi isolated from weevil-damaged roots were *Polyporus tomentosus* Fr., *Poria subacida* (Pk.)Socc., and *Corticum galactinum*(Fr.,) Burt (674).

Plantations have larger nematodes populations than natural stands (675). Trees of healthy appearance in declining plantations have more nematodes than trees from healthy plantations: average 1232/kg. soil *X. americanum* versus 281/kg. soil.(74) In pathogenicity tests, 1000 nematodes per seedling must be added before growth is significantly reduced (675, 74). *Trichodorus californicus* reproduces on jack pine, but does not build up large populations (675, 74).

Pinus echinata *Mill.* - Shortleaf Pine

MORPHOLOGY

Development of Form

Development of the root systems of shortleaf and pitch pines on the pine barrens of New Jersey is essentially the same. During the first growing season the taproot grows 3 to 12 in. (8 to 30 cm) and a maturity may reach a depth of 9 ft. (2.9m) (789).

Age (yrs.)	Length of Taproot (ft (m))	Length of Longest Laterals (ft(m))
1	0.25 to 1.0 (0.8 to 0.30)	taproot predominates
4 to 5	1.25 to 2.0 (0.4 to 0.6)	approx. same as taproot
8 to 9	1.5 to 2.5 (0.4 to 0.8)	approx. same as taproot
8 to 12	3 to 4 (0.9 to 1.2)	6 to 8 (1.8 to 2.4)
12 to 30	8 to 9 (2.4 to 2.7)	25 to 35 (7.6 to 10.7)

The framework of the shortleaf root system is completed in about 30 years. Sinkers and primary laterals continue elongation until they also reach approximately the same lengths as the taproot and largest laterals, respectively. Meanwhile, ramification of the root system is continually in process as higher order roots increase the root density in the soil (789, 1048).

The amount of branching is determined early on in the development of the roots; all branches originate in the primary xylem of the parent root, and adventitious roots are not found except infrequently in wound tissure developed following clean severence of the root (789). The increase in fine roots is rapid until the second decade, whereupon the rate slows and approached a saturation point around 30 years of age (1048). Fine roots (less than 0.10 in. diameter) make up about 75% of the total number of roots of 50 year-old shortleaf pine (244). The weight of fine roots did not differ appreciably from that of an uneven-aged sweetgum-yellow-poplar forest type stand (244).

Beyond 30 years, growth is primarily in the thickening of first order laterals upon reaching their full length and maintenance of the root density. The thickening of the lateral roots is greater in the vertical plane, and the increment is greater on the topside of the roots than the underside, resulting in a buttress shape. The basal thickening is stimulated by compression forces rather than tensile strain. The innermost vertical roots also tend to thicken (789).

In one study, the horizon of a Whitestore sandy loam soil contained over 90% of the roots of shortleaf pine. About 80% of the roots in the A horizon of this soil were less than 0.10 in. diameter (0.25 cm). The A_1 horizon alone contained about 75% of the roots, even though it averaged only 1.7 in. (4.3 cm) thick, less than any of the other horizons. (244)

Comparisons With Other Species

The form of the root system of shortleaf pine appears to be intermediate with respect to pitch pine and loblolly pine. It has a stronger taproot system than pitch pine, but is more finely branched than loblolly pine (789, 254, 127). The ontogeny of the shortleaf pine root system is very similar to that of pitch pine (789).

The basic form of the root systems of pitch and shortleaf pines is the same: 15 to 30 primary lateral roots radiate from the central taproot, the ends of the roots defining a rough circle. These laterals give rise to the higher order roots, some of which are vertical and extend into the subsoil.

The mature forms differ between the 2 species in the amount of emphasis on taproot development. The taproot system is more massive in shortleaf pine than in pitch pine, and the supportive laterals are correspondingly fewer and less developed (789).

Loblolly pine roots are reported to be generally fewer, stouter, and more deeply distributed than shortleaf pine (254). Roots of loblolly pine have also been described as slenderer than roots of shortleaf pine (127). In young trees, at least, the shortleaf pine root systems are heavier than loblolly pine (127, 1354).

The shortleaf pine root system is somewhat shallower than the root system of loblolly pine. In the first foot of various soils in South Carolina, shortleaf pine attained its greatest mean root diameter at 4 to 5 in. (10 to 13 cm). For loblolly pine this point was found at the 8 to 10 in. (20 to 25 cm) depth. The proportion of shortleaf pine roots is greater for the first 2 in. (5 cm) of soil than the proportion of loblolly roots, although loblolly exceeds shortleaf through the first foot of soil (1153) (254).

Shortleaf pine root systems have more dead roots than loblolly pine systems. On older healthy trees, shortleaf had 18% dead roots and loblolly had only 6.3%. On healthy young trees, however, the percentages of dead roots hardly differ between the two pines. Root mortality in young trees of both species and in older healthy loblolly was greatest in the diameter class of roots less than 0.25 in (0.64 cm.) In older healthy shortleaf it was highest in roots less than 0.5 in (1.3 cm) diameter (254). Root tips are replaced following death of the terminal portion of the root only if death has not extended back to the region where secondary wood completely encircles the primary xylem (789).

Grafting

Natural root grafting in shortleaf pine is apparently not common. In a study of root systems, grafting was not often observed, but the author indicated that his method of choosing specimens for study may have selected against grafted trees (789). Another reported to have found one growing stump. Yet another reports grafting to be specifically missing.

Root Suckering

Early accounts of root suckers in shortleaf pine have not been confirmed. The shoots that have been observed apparently arise from a bud cluster in a crook of the seedling stem near the soil line. Growth of the stem obscures the junction of the radicle and hypocotyl. Rootlets may sprout in close proximity to the bud cluster giving the impression of shoots arising from root tissue (1132).

ROOT-SHOOT RELATIONS

The limited research that has been conducted on genetic variation is shortleaf pine roots has not shown conclusive evidence for geographic variation in the roots, except, perhaps, as influenced by variation in the tops of the seedlings (22, 23).

Seasonal root growth of shortleaf pine does not appear to differ appreciably from that of loblolly pine (960, 1187). The reduced growth under shade is also similar (894, 656).

The coordination of top growth with root growth over the years was studied in pitch pine and also applies to shortleaf pine. Between the ages of 8 and 12 years, linear equivalence of the stem and taproot is obtained. The stem, which is shorter than the taproot to that point, is thereafter always longer than the taproot. In the years between age 12 and 30, a ratio of about 1.5:1 is maintained between the length of the largest laterals and the height of the tree (789).

Uptake

Suberized roots, even those covered with thick layers of cork, can absorb water from soil that has been either moist or dry (666). The roots of dogwood, yellow-poplar, and sweetgum, however, are more permeable to water than are pine roots (6, 666). This may be explained at least in part by the nature of the openings in the roots. The bark of shortleaf pine roots is of overlapping brittle plates of periderm, several inches long by about 1/8 of an inch wide. The plates of bark on mycorrhizal roots seem less brittle. Lenticels are few if not entirely absent. Water enters under the edges of the plates, but the plates effectively seal against water seeping into the living portion of the bark unless the root has been wounded (6).

Shortleaf pine in one study has significantly lower root CEC than loblolly pine or white pine. Species with low root CEC theoretically demand more fertile soils because they are less adept at cation uptake. However, shortleaf and loblolly pines, which occupy sites of similar fertility, are governed more moisture requirements than by fertility requirements (870).

Shortleaf pine roots possess the same ability as loblolly and slash pines to reduce nitrate (1165).

Shortleaf pine is less tolerant of water saturated soil conditions than either loblolly or pitch pine, but is similar to Virginia pine. (789, 481) In an extensive comparison of tree species of the Tennessee Valley, shortleaf was classed as intolerant to inundation, meaning that it does not survive continuous flooding of 1 ft. (.3m) depth for one growing season (481).

Shortleaf pine can withstand 3 months of continuous flooding with moving water, but intermittant flooding or continual flooding with stagnant water for 10 months results in severe damage to the root system; shoot growth does not accurately reflect the extent of the root damage (580). Survival of trees was not affected by winter floods of 2 months duration, but after 3 years, seedlings whose roots had been under water for considerable portions of each winter were 1/2 to 3/4 the height of nonflooded seedlings. A high water table (without flooding) did not have an appreciable effect on height growth (1306).

RESPONSE TO SOIL CHARACTER

Observation of the differences between root habit of loblolly pine and shortleaf pine in response to soil character have been rather casual for the most part. In general, shortleaf pine roots respond to soil texture the same way loblolly pine roots do. The noncapillary porosity and bulk density of the soil have the greatest influence on root distribution (254, 1048).

Shortleaf root systems do, however, show some differences from loblolly pine when grown on similar soils. On Caddo silt loam having poor internal drainage, shortleaf developed a shallower root system than loblolly (451). Loblolly pine is better adapted to poor soil aeration than shortleaf pine, as evidenced by a 22% reduction in root weight from the control for loblolly pine as compared to 54% for shortleaf pine when grown under a soil air treatment of 10.1% CO_2, 1.5% O_2, and the balance N_2. Shortleaf seedlings growing in Iredell clay also had a greater relative reductive in root growth than the loblolly seedlings under a heavy watering regime. The difference was not as distinct in soils of coarser texture such as Mecklenburg clay, which has a higher sand content.

Soil Series (B horizon)	% sand	% silt	% clay
Iredell clay	25.5	31.5	43.0
Mecklenburg clay	42.0	20.3	37.7

Conversely, growth of shortleaf seedlings was not reduced as much as loblolly seedlings under excessive watering of coarser soils. This relationship was demonstrated in the heights, top weights, and total weights of the seedlings tested. The best root growth for both species occurred in an unidentified silt loam, with poorest growth in the Iredell clay (1354). The response of shortleaf root growth to soil texture is not as pronounced as it is in loblolly pine. (1354, 127)

Shortleaf pine roots have adequate ability to penetrate subsoils of both friable and plastic clays. In these kinds of subsoils the roots are larger with less branching than in sobsoils with higher silt content. Root growth appears to be hampered most in heavy soils when aeration is poor. Site index is positively correlated with cross-sectional root area (1188).

From examination of one shortleaf specimen of average height planted on the eroded copper Basin in Tennessee, it was noted that taproot development was less pronounced than as described on the New Jersery pine barrens (21). The soil of the pine barrens is a deep, well-drained sand (789). The predominant soil of the Copper Basin is a sandy loam with a light red friable clay loam subsoil having good internal drainage; the surface soil has been eroded away, and in many places the depth to rock is shallow (21).

Applications of sewage sludge to eroded forest sites on which loblolly and shortleaf seedlings have been planted decreased root to shoot weight ratios in a manner similar to that produced by applications of N and P from commercial fertilizers. Foliar levels of Zn increased while Al decreased with increasing sludge levels; other elements did not differ noticeably between treatments (110).

MYCORRHIZAE

Good ectomycorrhizal development on roots of shortleaf pine is essential to seedling survival in the field. Mycorrhizae were reported abundant on nursery-grown shortleaf seedlings at about 45 days after germination (144). At least 5 culturally different ectomycorrhizal fungi of shortleaf pine colonized fumigated soil within 9 months in the greenhouse, presumably by airborne basidiospores (819).

High soil oxygen is necessary for good mycorrhizal development shortleaf pine. High CO_2 with adequate oxygen further stimulates myorrhizae. In soils of different textural grades, best mycorrhizal development occurs in loam-silt soils, poorest in heavy clays, with sandy soils intermediate (1354).

Ectotrophic mycorrhizae on feeder roots of shortleaf and loblolly pine act as protective barriers to infection by root pathogens, notably Phytophtora cinnamomi Rands. Antibiotic production has been shown to be involved, as well as the formation of a physical barrier in the form of the fungus mantle and Hartig net. Production of volatile organic compounds by the ectomycorrhizal fungi may also be involved (806, 678, 802, 821, 804, 822, 805).

Along with several other pine species, shortleaf seedlings inoculated with Pisolithus tinctorius showed better growth and survival on all types of sites than seedlings with ectomycorrhizae formed by other fungi. In one study, however, stimualtion of growth by Pisolithus was less in shortleaf than in loblolly pine (807). Significant growth effects resulting from Pisolithus inoculation have been reported on severely eroded soils treated with sewage sludge. Best growth was obtained at the intermediate sludge level (138 tons/HA).

Penetration of ectomycorrhizae by nematodes may allow entry of other root pathogens, notably P. cinnamomi, and also may lessen or destroy the beneficial activity of ectomycorrhizae. The nematodes Hoplolaimus galeutus, Helicotylenchus dihystera, and Tylenchorhynchus claytoni are reported to have this ability on shortleaf pine, and others may also (1016).

Mycorrhizae on shortleaf seedlings increase the salt absorbing capacity of the roots, primarily by adding to the supply or exchangeable hydrogen ion. The increased salt uptake may then be reflected in a greater rate of growth (1006).

In addition to *P. tinctorius*, fungi reported to form mycorrhizae with shortleaf pine include: *Amanita muscaria*, *Cenococcum graniforme*, *Laccaria laccata*, *Lactarius deliciosus*, *Leucopaxillus albissimus*, *Rhizopogan parasitieus*, *Suillus granulatus*, *Xerocomus chrysenteron*, *Thelephora terrestris*, *Clitocybe laccata*, *Boletus communis*, and *Boletus luteus* (807, 812, 188, 189).

DESTRUCTIVE AGENTS

Non-infectious

Shortleaf pine tends to be less windfirm than loblolly pine on soils with a heavy subsoil and poor internal drainage. On such sites, shortleaf may fail to develop a taproot, and isolated seed trees left standing after a harvest are highly susceptible to windthrow (523).

Zinc deficiency has been reported in shortleaf pine in some localized areas. Roots of affected trees are short and swollen at the apex (521).

Insects

White grubs of the genus *Phyllophaga* can cause extensive damage to shortleaf pine in localized areas. Grub-damaged plants can be detected by a wilting or browing of the needles, or by exerting a gentle pull; injured plants can be easily pulled up. Grub damage in nurseries in the southeast U.S. is most severe from mid August to late September (606).

Root development may be drastically curtailed if significant damage to the shoot occurs during the growing season, as may happen during insect attack. Defoliation by the Nantucket pine tip moth (*Rhyacionia frustrana*) has been specifically cited as an example (270).

Nematodes

Nematodes reported to parasitize shortleaf pine include *Meloidodera floridensis*, *Hoplolaimus galeatus*, *Pratylenchus brachyurus*, *Criconemoides xenoplax*, *Hemicycliophora vidua*, *Helicotylenchus dihystera*, *Trichodorus christiei*, *Tylenchorhynchus claytoni*, and *Criconemoides* spp.(596, 1014, 1013, 1148, 1012).

Fungi

Littleleaf disease of shortleaf and loblolly pines is reportedly caused by the fungus Phytophthora cinnamoni Rands in combination with poor soil aeration, low fertility, and periodic moisture stress. Zoospores of P. cinnamomi infect and kill the feeder roots and impair the ability of the trees to absorb water and nutrients. Major root damage is believed to occur for a few weeks in spring and later during the fall when soil temperatures and moisture are favorable for the parasite. Trees younger than 20 years of age rarely exhibit symptoms of littleleaf disease. But symptom expression increases with tree age. Symptoms of the disease resemble those of nitrogen deficiency, and affected trees usually die within 6 years after the onset of crown symptoms. Shortleaf is more susceptible to P. cinnamomi than loblolly pine (899).

The root systems of trees affected with littleleaf show an excessive exfoliation of bark, producing brown patches, dieback of the fine roots, and large, pitchy, cankerlike lesions. This may result in a serious loss of phloem wherein much of the reserve food is stored (384, 1034).

A relationship has been reported between type of ground cover and amount of littleleaf disease in the Piedmont district shortleaf pine stands. Sites with honeysuckle, brambles, & vines tended to have fewer trees with littleleaf symptoms than those sites having more grasses. This may have been more directly related to soil nitrogen level, however (899).

There has been some progress made in the development of littleleaf-resistant strains of shortleaf pine. Restoration of depleted sites which foster the disease is also believed to be essential.

Pythium spp. of the P. irregulare - P. debaryanum complex are pathogenic to loblolly and shortleaf pine seedlings. Little is known about their effects on the health and vigor of mature forest trees.

Root rot caused by Fomes annosus is a cause of mortality in younger shortleaf pine. One study attributed a mortality of 2% to F. annosus in a 2-year old shortleaf plantation. Spread of the fungus is from infected stumps, and subsequently from seedling to seedlings. Shortleaf is apparently slightly less resistant to F. annosus attack than most other southern pines.

F. annosus fruiting conks are characteristically found at or below the ground line, and this can be easily overlooked. The advanced stage of infection is typified by narrow, whitish pockets that reduce the wood to a spongy mass. Characteristics are seen best in broken roots of wind-thrown trees.

F. annosus frequently becomes established in healthy stands during thinning operations. Once roots become infected, the fungus may survive below ground for 50 years or more. Prevention of the disease has thus far centered mainly on chemical stump treatment with either borax, urea, or sodium nitrite. Chemical stump treatments are not recommended, however, in stands where F. annosus is already present (940, 514, 681, 933, 112).

Black root rot affects shortleaf pine the nursery, though slash and loblolly pines are more often affected. The cause of this disease has not been clearly demonstrated, though circumstantial evidence indicates a nematode-fungus complex. Symptoms include small, red, rough areas on the tap and larger lateral roots to blackening and roughening of the entire surface of the tap root in one study. A soil fumigation with methyl bromide gave complete control of the disease; ethylene dibromide (EDB) was only partially effective; and dichlorpropene (D-D) mixture was ineffective.

With one exception, all the nurseries where black root rot was found were located on light sandy soils, and more than one was established on newly-cleared forest land. The disease is most severe during the summer when higher soil temperatures prevail (533).

Pinus resinosa Ait. - Red Pine

MORPHOLOGY

Development of Form

The rate and extent of development of the red pine root system varies greatly with site factors, especially moisture. A general time outline of its development can be made, however. In the first 2 seasons, field-grown seedling roots in one study penetrated to an average depth of 4 inches (10 cm), and 5.4 inches (14 cm) respectively. Nursery seedlings grow about twice as deep in the same amount of time (1124). The first 5 years of growth are devoted to rapid horizontal extension; most of the major vertical roots are initiated. In the next 5 years the vertical roots reach their maximum depth (378). Horizontal extension is complete in 15 to 20 years (1207, 378). Also, at 15 years of age average current annual volume increment reaches a peak rate in horizontal roots with an increment of about 37 $in^3 yr^{-1}$ ($0.6 dm^3 yr^{-1}$) until about the age of 20 years (378).

Taproot development in red pine is quite variable (295, 34, 185). The primary root of a seedling becomes a prominent taproot because it has a faster growth rate and longer intraseason growth cycles than the other roots ((919). The taproot, which appears to be an extension of the root crown, tapers strongly and terminates in stubby, finger-like rootlets at a depth between 1 and 4 ft. (0.3 and 1 m) in the soil (1207, 295). Where double taproots have been observed, one is usually large and tapering while the other is smaller and well branched (1207).

The periphery of the area covered by the lateral roots is in the shape of an irregular oval, the short axis being about 2/3 to 3/4 the length of the long axis with the stump offset from the intersection of the axes (376). Ten to 15 major laterals radiate from the root crown at depths between 4 inches and 18 inches (10 cm and 46 cm) to horizontal distances up to 40 ft. (12 m) (185, 381, 1207). The longest laterals generally attain a length of between 30 and 35 ft. (9 and 11 m) (714, 376, 1120).

Vertical and horizontal branching of the lateral roots is pronounced in a 4-ft (1.3m) radius form the stem base. Branching of the lateral roots to sinker roots occurs mostly within 1.5 ft. (0.5 m) and 4 ft. (13m) from the root crown (381, 1207). Immediately beyond the point of origin of the major sinker roots, the diameter of the lateral parent root drops abruptly (381). On a 50-year-old tree, the thickness of the main laterals 1 ft. distant from the root crown was about 1 inch (2.5 cm), having tapered down from 2 or 3 inches (5 or 8 cm). At 4 ft from the root crown, the roots were about 0.5 inch in diameter, and, beyond that, tapered gradually and branched into smaller laterals and risers (1207).

The risers are small in diameter, but have considerable length. They normally ascend to within 0.5 inch of the ground surface, where they turn and grow parallel to the surface (295).

Sinker roots originate beneath the root crown and along the lengths of the laterals. Two types of sinker roots may be found in the system: shallow and deep. Deep sinkers penetrate into the subsoil without much branching; an average of about seven per tree has been reported (381, 1207). Often they follow old root channels, branching profusely in the cavity, filling it (295, 381). Depth of penetration is extremely variable, but the deep vertical roots are reported to often reach depths greater than 8 ft. (2.5 m), and they have been observed to reach 15 ft. (4.5 m) (1200, 307, 714, 381, 185). About three shallow sinkers descend 3 or 4 ft (1 m) into the soil, branching so that they have a fan-shaped appearance, and terminating in grouped growing tips (381, 295, 1207). Upon injury, the root tips of sinkers often are not replaced as they commonly are on lateral roots. Instead, one or more side roots further back from the tip take over as the new main tip(s), leaving the original tip as an appendix root (377).

The number of primary xylen strands, or archy, is important in determining the development and subsequent form of the root system. The side roots normally develop adjacent to the xylem strands of the parent root. Red pine roots are predominately diarch, as are Scots pine roots (1291, 377). Other species of Pinus often have polyarch roots (1291). Red pine roots occasionally have short lengths that are triarch or tetrarch. These sections may be a result of injury to the root tip. A red pine that has triarch roots may have a different ability to explore a soil volume than a tree with diarch roots since the roots branch along three planes rather than two planes (377).

In red pine the primary xylem diameter (PXD) of a horizontal root generally increases with distance from the stem from an average of about 0.001 in (0.25 mm) at 8 in (20 cm) from the stem to about 0.024 in (0.60 mm) between 6.5 and 10 ft (2 and 3 m). Beyond 16 ft (5 m) the average PXD values declined slightly to 0.022 in. (0.55 mm) at 23 ft. (7 m) distance. The PXD decreases from a parent horizontal root to a sinker root, and then increases with distance in a manner similar to the increase in the horizontal root. At 8 in (20 cm) from their origin, the PXD of sinker roots averaged 0.012 in (0.30 mm) diameter; at 6.5 ft. (2 m) they averaged 0.018 in (0.47mm).

The long roots which are important in developing the framework of the red pine root system can be divided into three classes: pioneer, mother, and subordinate mother roots. The pioneer roots are the largest diameter roots and are characterized by rapid elongation and sparse branching. They are found in abundance on red pine. The greatest numbers are found during the peak root-growth periods in late spring and early autumn. Mother roots are smaller in diameter than pioneer roots and are profusely branched. They are never found more consistently throughout the season than pioneer roots. Subordinate mother roots are of the same dimensions as short roots, but differ in that they are more like mother roots in character and in that their root apices possess a pointed root cap while the root apex of a short root is rounded (1291).

Distribution in Soil Profile

The main concentrations of roots are in the A_0, A_1, and B_2 horizons. Few roots are found in the A_2 horizon. The C horizon is usually devoid of lateral roots (1207). The lateral roots of maximum radial extent are found in the B horizon (714). A dense mat of small diameter roots can be found at the forest floor/A_p interface. Only taproots and sinkers extend into the C horizon, with deep sinkers often penetrating far into the subsoil (1207). The weight distribution of the roots by soil horizon of a 39-year-old red pine on a deep, highly stratified outwash Hinckley loamy coarse sand in New York was as follows:

Horizon	% of total root weight (714)
A_p	33.7
B	48.1
C (1.86 m of the C)	18.2

Comparisons with other Species

In comparison with jack pine root systems, red pine root systems have a more developed vertical component. Sinkers are larger in diameter and penetrate deeper. Lateral roots are not concentrated as close to the surface as in jack pine.

In terms of weight, 4-year-old seedling root systems of red pine weighed less than those of jack pine. When grown in full sun, the oven dry weight of the red pine root system was about half that of jack pine (744).

Red pine also has a smaller root mass and a smaller total number of roots than white pine. The fibrous roots of white pine form a heavier, more compact mat than red pine. The laterals of white pine have greater radial spread and have a less sharp downard tend (417). The taproot is retained less often in white pine, but sinkers are more numerous and better developed (185).

In the first and second years of growth on droughty soil, the depth of penetration of the red pine seedling root system is similar to white pine, but somewhat less than that of jack pine (1124).

	Depth Penetration	(1124)
Species	First year	Second year
jack pine	5.35 in (13.59 cm)	9.5 in (24.1 cm)
red pine	4.00 in (10.20 cm)	5.4 in (13.7 cm)
white pine	3.50 in (8.90 cm)	4.7 in (11.9 cm)
white spruce	1.75 in (4.44 cm)	3.4 in (8.6 cm)

Grafting

Red pine roots grafts intraspecifically more frequently than other pine species of the northeastern United States (690). In a plantation having a 6x6 foot (1.8x1.8 m) spacing, individual trees grafted with at least three other trees on the average (1125). Grafting occurs most frequently between lateral roots growing in opposite directions. Grafts between roots growing at right angles to each other are least common (50).

The frequency of natural root grafting in red pine is greatly reduced in stands of mixed composition, presumably because of less frequent root contact with other red pines (50). No true interspecific grafting has been observed with red pine.

Periodic thinnnings appear to increase the frequency of grafting. A possible explanation is that the roots of the remaining trees increase substantially in diameter growth upon release which causes pressure on closely lying roots. The contact eventually induces grafting of the roots. A period of 2 years is the maximum time required for roots to from a continuous common xylem once a graft has started (50).

Reports of seasonal fluctuation in intensity of backflash damage are conflicting. One report says backflash is more apt to occur in midsummer of a dry year (252). Another says that backflash occurs more frequently in spring treatments just before budbreak and 6 to 8 weeks thereafter, dropping to minimal injury to stands treated in July. In this report 10% of the trees treated in July with sodium arsenite were the source for blackflash, while in April 87.5% of the treated trees were the source for backflash in other trees (1136).

Adventitious Rooting

Adventitious rooting of red pine has not been intensely studied. In one rooting study, 62% of 1-year-old cuttings from seedlings rooted. Three and 7% of 2- and 3-year-old seedlings rooted, respectively (416). In a nursery, 1-year-old red pine seedlings were observed to put out new roots after the death of the original system during a wet spring (452).

SEASONAL GROWTH PATTERN

The seasonal pattern of growth of the red pine root system appears to consist of an inherent surge of growth occurring within a period extending from spring the midsummer, a summer lull, and renewed growth within another period from late summer to early autumn (1290). External factors alter this basic pattern only in the precise timing of events and in the quantity of response (837, 836). Dormancy appears to be partially subject to environmental factors, since it occurs not only in the cold season to the entire root system, but also to individual roots during the warm season (1293).

Root growth of red pine commences in spring about a week before the separation of the bud scales in the terminal leader of the shoot.

This is somewhat delayed when compared to spruce and larch in which active root growth occurs 4 to 6 weeks before there are any visible signs of shoot growth. The roots do not all begin growing at once, but increase the number of growing tips in a fairly orderly fashion. Second- and third-order roots become active before the first-order laterals from which they arise. Since the growth period of high-order root branches is shorter than that for first-order roots, many of the third-order branches have ceased elongating by the time the first-order laterals begin to grow. One or 2 weeks after breaking dormancy, the elongation rate of the roots reaches a maximum (1293).

In June the greatest numbers of the root tips are growing. In the July-August lull, only apices of the larger roots remain active. The late summer-early autumn growth period may appear more vigorous than the spring period because of the additional activity from new roots initiated during the current season. The later growth period is characterized also by a stimulation of mycorrhizal formation (1293).

The onset of dormancy, under field conditions, begins in November; most of the roots are inactive by mid-December. Dormancy continues until late April or early May. If temperatures are maintained at a favorable level throughout the winter the roots will continue to grow, but will lack the vigor of growth exhibited during the normal growing season (836).

Temperature

Temperature affects both the timing and quantity of root growth. Both for shoot and root, the optimum air temperature for red pine is 20°C, although root growth is affected more readily by temperature changes than is shoot growth. Root dry weight per seedling is decreased more (as compared to seedlings grown at the optimum 20°C temperature) when grown at 25°C than at 15°C (657).

Temperature (°C)	Percent Reduction in Growth*	
	shoot	root
10	36.3	60.6
15	5.3	25.0
25	34.2	46.2
30	35.2	56.1

---

* compared to final dry weight of roots of seedlings grown in the 20°C regime (657).

The higher temperatures also reduce the time interval between growth initiation and peak acitivity. Bundled trees exposed to warm temperatures during transport or trees heeled-in into warm soil show poor survival as a result of the shortened period of root growth activity. Fall planting requires about a month of favorable soil temperatures and moisture (period required for root regeneration is not less than 3 weeks). Lacking this, the trees will remain dormant throughout the winter, thereby increasing chances for mortality and spring frost heaving (836).

ROOT-SHOOT RELATIONS

Reduction of sunlight has an effect similar to that induced by needle damage: root growth is stunted. Seedlings grown in full sunlight have greater root and shoot weights than seedlings grown under various light intensities less than full sunlight. The magnitude of response above 50% full sunlight is less than that through the lower range of intensities. So, 50% or more shade is much more critical to the root growth of red pine seedlings than shade less than 50% (853, 1071, 744).

From 11% through 20% full sunlight, the change in red pine dry root weight is similar to that of white pine, but at 43% full light, red pine weight increases are greater. Jack pine root weight increases more than red pine up to 50% light, and, when grown above 50% full light, jack pine root weight more than doubles that of red pine (1071).

ROOT-SHOOT RELATIONS

During the first 10 years, the rapid increase in height growth is associated with rapid vertical and horizontal extension of the roots (45, 381). At 5 years of age the stem height is about 1/3 the length of the longest horizontal root. By age 24 they are the same length (381).

Ratio of stem height to length of longest horizontal root	Age (yrs.) Dry site	Age (yrs.) Fresh site
1/3	5	5
1/2	10	9
3/4	16	15
1/1	24	20

The roots reach their maximum annual elongation 6 to 10 or more years before the stem, so that by the time annual height growth of the stem reaches a maximum rate, root extension is virtually complete (381).

Once the root system has reached its bounds it begins intensification of rooting within the defined soil volume. The rate of height growth, meanwhile, is high although variable. This period lasts about 15 years. When height growth begins to slow, intensification of the root system continues, but large numbers of dead roots can also be found (45).

A comparative study of the production of root and stem wood in terms of volume shows that, as the red pine tree develops, a decreasing portion of materials is alotted to root wood. At 10 years, root wood represents about 35% of the total root and stem volume. At 20 years, it decreases to 20%, and at 30 years to 15%. The current annual increment in root wood volume expressed as a percentage of stem plus root wood decreased from an initial 50% to 20% at 15 years and 10% at 25 to 30 years, which may be the minimum level of production to sustain an adequate root system (378).

Root Biomass & Nutrient Content

Of 2-year-old red pine seedling growing in near-optimal conditions, roots, on the average, comprise 22% of the total biomass, varying somewhat with bed density. White pine roots comprise 29% and Scots pine 13% (978). On plantations of older red pines growing in sand in New York and Michigan, the roots were found to make up about 15% of the total red pine biomass (714, 882). The nitrogen content of the roots of the Michigan trees (3-0 stock outplanted for 8 years) was found to be 8.6% of the nitrogen content of entire trees, while in the 2-year-old seedlings mentioned above it was 13% (882, 978). Nitrogen comprises about 0.44% of the root biomass. Needles, as may be expected, have a greater proportion of their biomass composed of nitrogen, while stem and branches have less. Potassium, which is 0.16% of the root biomass, follows nitrogen in comparison of the top and root (882). Of total tree potassium, the roots have about 11% (978, 882). The root content of the 2-year-old seedlings of calcium, magnesium, and phosphorus was 18%, 16%, and 18%, respectively (978).

EXUDATION

In a study which identified substances exudated from red pine roots, gamma-amino butyric acid was most abundant. The amino acids asparagine, glycine, serine and alanine were present in large amounts. Valine, leucine, glutamine, aspartic acid, glutamic acid and proline were found in progressively smaller quantities. The sugars glucose and fructose were abundant, with traces of arabinose. All of these substances, except serine, leucine and arabinose, when supplied singly or in combinations, stimulated the growth and germination of sporangia of the damping-off pathogen *Pythium ultimum* Trow (8).

UPTAKE

Various tree species of the same age (2 years), all grown under the same favorable conditions (through not necessarily at the same stage of development), show relative differences in nutrient content. White pine, Scots pine and Norway spruce all show a generally greater content of calcium, magnesium, nitrogen, phosphorus, and potassium than red pine (978). White spruce contains more boron, iron, magnesium, manganese, nitrogen, and zinc than red pine, but less calcium, phosphorus, and potassium (593, 978). Black spruce contains less magnesium, nitrogen, phosphorus, and potassium, but similar quantities of calcium. Generally, differences in nutrient content reflect the differences in biomass production between species (978).

The uptake of phosphorus by red pine roots is stimulated by applications of simazine; in one particular case, at levels of 5 and 10 ppmw. At higher levels uptake of phosphorus was inhibited. Simazine appears to stimulate the translocation of phosphorus from the roots to aerial portion at any concentration (313).

RESPONSE TO COMPETITION

In a 5x5 ft (1.5x1.5 m) spacing on a sandy old-field site in Ontario, the root system of one red pine invaded the prescribed area (projected to the soil) of 23 other trees, while the roots of 11 other trees entered its own 5x5 ft area. In an older stand in New York, the root system of a 39-year-old dominant red pine made up 28.6% of the weight of all the tree roots found within its rooting soil volume (714).

In a stand of 6.5x6 ft (2x2 m) spacing, overlap of root systems begins within 10 years, which is about 5 years before crown closure has started (378, 882).

Under conditions of non-limiting nutrient and moisture supply, seedbeds of red pine increased 2.5-fold in biomass with a 4-fold increase in bed density. Increase in root nitrogen content was about 2-fold, and root content of phosphorus, potassium, calcium and magnesium increased 3-to 3.5 fold with the 4-fold increase in density. Total nutrient uptake increased 2.1 to 2.7 fold. As a comparison, similar density increases resulted in somewhat smaller increases in nutrient uptake for white pine, Scots pine, and black and white spruces, for the most part (978).

The distribution and numbers of roots in the soil changes with stand density. In one study, a decrease in density from 2x2 ft (.6x.6 m) spacing to a 6x6 ft (1.8x1.8 m) spacing resulted in an increase in root density in the first 4 in (10 cm) of soil from 158 roots ft^{-2} to 348 roots ft^{-2} (1695 roots m^{-2} to 3741 roots m^{-2}). There was also a decrease in root density with wider spacing in the next foot of soil. With higher densities the root system tends to develop more deeply into the soil, responding in the same manner as on a droughty soil. Total numbers of roots per unit volume, especially for roots less than 1 in. diameter, decreased with increased density.

Red pine is susceptible to the toxins produced by black walnut. As with white pine, mortality is high and trees whose roots extend within the spread of walnut roots are typically stunted (1051, 175).

EFFECTS OF EXCESSIVE AND DEFICIENT MOISTURE

Drought resistance, with respect to roots, appears to be related to the ability of the root system to exploit the soil, including the ability to reach down far enough to contact moist soil. Under this assumption, young red pine is less drought resistant than jack pine. In one study of growth on upland and lowland sites, jack pine root extension, both parallel and perpendicular to planting furrows, was greater than that of red pine on either site. The difference in rooting depth was not as great as the difference in lateral spread, especially on the lowland site (1124).

Exceptions to the idea that greater root penetration yields better drought survival occur where particular site factors influence survival. For example, red pine growing on a soil with an average of 2 ft (60 cm) to bedrock survived drought better in areas where the bedrock was fractured than where the bedrock was intact, even when the soil was more shallow above the fractured bedrock. The trees over the fractured bedrock apparently can obtain moisture from the silt-coated fissures (389). Another example is that of red pine growing on a droughty, low site quality sand with no continuous subsoil moisture supply. Development of the vertical system was very weak; the tree depended entirely on periodic replenishment in the surface horizons. Lateral roots on this site were no longer than on other, better quality sites (1207).

Small groups of trees in drought-stressed red pine stands may succumb simultaneously. It is suggested that the stress allows greater moisture transfer through root grafts, resulting in a group of intergrafted trees to be brought to the critical stress point at the same time (389).

Red pine roots are very intolerant of poor aeration. They can tolerate several weeks of immersion in water from mid-April to mid-July, but a longer duration leads to serious damage (376). Almost all 2-year old red pine seedlings died when grown in nutrient solutions at oxygen levels of 4.5%, 10%, and 19%. Black spruce survived these particular conditions (49). Balsam fir, white spruce, and white pine, as well as black spruce, are all more tolerant of flooding than red pine (12).

Excellent growth of red pine may be achieved where the water table is at depths between 3 and 9 ft. (1 and 3 m). Naturally, the optimum depth to the water table for establishment of seedlings is shallower. Optimums on coarse soils are shallower than on finer soils; for example, maximum seedling height growth was attained at 29 to 31 in (75 to 80 cm) depth on a loamy sand as compared to 22 in (55 cm) on a sandy soil (873).

In general, the wetter the site, the shallower the penetration of the root system (excluding unusual site conditions such as the one previously mentioned) (10, 1129). On dry sandy sites where rooting usually would be deep with little branching, fine-textured soil layers promote branching and growth of fibrous roots on the short vertical roots (381). On poorly drained soils, sinkers are few and are usually stubby with little branching. The lateral system, likewise, is shallow, with a dense surface mat of fine roots. Where drainage is very poor, some of these roots may ascend 1 or 2 in (2.5 or 5 cm) above the ground line, protected by bark scales and low branches. Under these conditions the root system of red pine fares poorly, with very weak development of the main roots (1129).

RESPONSE TO SOIL CHARACTER

Texture

Lenses of fine silty sand within rooting depth (6 to 7 ft. (1.8 to 2.1 m)) and 4 or more inches (10 cm) thick are beneficial to the overall growth of red pine. These silty-sand layers are often encountered in the outwash soils of the northeastern United States and Ontario, Canada. Not only do they improve moisture conditions, but they also contribute small but significant amounts of exchangeable potassium (1268). Root elongation is impeded by compacted layers of bulk density greater than 1.40 (51, 377, 381). Gravelly layers may also impede root growth. Such layers are not detrimental to tree growth unless the effective rooting depth is restricted to less than 18 to 24 inches (46 to 61 cm), the deeper requirement for soils of loam or clay-loam textures (1207).

Upon contact with a zone of high bulk density, vertical root tips may cease further elongation, while a side root takes over, exploring a more favorable area. The original root does not necessarily die, but becomes a small-diameter appendix root (378). The hand or fan shape of shallow verticals has been attributed to growth of the roots along slippage faces between intersecting planes of soil of easier penetrability in zones of high bulk density (376).

Soil Temperature

Temperature has been suggested as another factor limiting the depth of rooting. At 5 to 10 ft. (150 to 300 cm) in soils of the Upper Hudson River Valley in New York, there is a marked reduction in the length of time during the year that the temperature is above 10°C. This depth also coincides with the limits of the red pine root zone (714).

At soil temperatures above 21°C root branching in red pine seedlings decreases, although diameter and length of long roots increases. At 16° to 21°C seedling root systems are well branched, while seedlings grown in soils of higher temperatures have only a few, relatively long, unbranched, first-order laterals (1298). The higher temperatures reduce the time interval between root growth initiation and peak activity in terms of numbers of elongating roots, but the overall root activity is still greater at 16°C than at higher temperatures (836). Temperature, however, has no effect on the fresh weight of roots of nonmycorrhizal seedlings (1298).

The optimum temperatures for water absorption by roots is somewhat higher than that for root growth activity. Also, habitat differences between species are reflected in the absorption of water at different soil temperatures. Considering 25°C as 100% water absorption efficiency, red pine absorbs 60% and 25% as much water at 10°C and 0.5°C, respectively. White pine can absorb more efficiently at cooler soil temperatures than red pine, but red pine is more efficient at cool temperatures than either slash pine or loblolly pine (665).

Root-Soil Fertility Relationships

Red pine roots affects the fertility of the soil they inhabit. Root sloughings, under experimental conditions were found to be responsible for the liberation of water soluble and exchangeable potassium from unweathered biotite. Dead root tissue plus the biotite released 30.9% of the total potassium content of the mineral, compared to 5.5% released by the mineral in absence of root tissue. The amount released in combination with root sloughings is large enough that even in a 5-foot-deep soil containing 0.1% biotite, with the fine roots and mycorrhizal mycelia occupying 1/50th of the soil volume and releasing potassium at 1/10th the rate observed in the experiment, a stand of red pine can obtain adequate potassium. Other alumino-silicate minerals may also be subject to weathering by root sloughings (715).

Roots of young stands of red pine also release nitrogen and phosphorus from organic compounds in the soil. This source of the nitrogen and phosphorus is rapidly exhausted, the effects fading with the completion of exploitation of new soil by the growing root system (389).

MYCORRHIZAE

Fungi associated with ectomycorrhizae on red pine include: Amanita muscaria (L. ex Fr.) Pers. & Hook, Boletinus pictus (Peck) Peck, Cenococcum graniforme (Sow.) Ferd, & Winge, Gomphidius superiorensis Kauffm. & A.H. Smith, Gomphidius vinicolor Peck, Pisolithus tinctorius (Pers.) Coker & Couch, Suillus cothurnatus Sing., Suillus granulatus (L. ex Fr.) O. Kuntze (Boletus granulatus), Suillus luteus (L. ex Fr.) S.F. Gray (Boletus luteus), Suillus subluteus (Peck) Snell (Boletus subluteus), Thelephora terrestris (Ehrh.) FR., Tylopilus felleus (Bull. ex Fr.) Karst (Boletus felleus) (323, 1001, 1296, 680, 887, 450, 831, 1149, 974, 812, 807, 809).

Two ectendomycorrhizal fungi on red pine have been described in detail. One, a black imperfect fungus, is tentatively identified as a species of Chloridium. The other is somewhat similar to species of Endogene, but the ectendomycorrhizae caused by it are very different from the forms of vesicular arbuscular mycorrhizae caused by endogonous species (1226).

The ectendomycorrhizae develop on short roots and on long roots up to 0.06 in (1.5 mm) in diameter (1294). In the first 3 months of development the infection is primarily intracellular with only scattered loci of intercellular hyphae (1296). Upon emergence and 0.08 to 0.12 in (2 to 3 mm) beyond, ectendomycorrhizae appear smooth and white. They turn amber-colored and remain that color for 2 to 3 months, whereupon they darken uniformly (1128). After 5 months the infection transfers to a sparse intercellular Hartig net which becomes highly developed (1296). The life span of a mycorrhiza is often less than three seasons (1128).

Ectomycorrhizae are found on both long and short roots of red pine with increasing frequency after the second year in the nursery, and, under natural conditions, become the predominant mycorrhizal type (323, 1294, 1128). However, at least until the fourth year the hyphae of ectendotrophic fungi continue to be the initial colonizers of the long roots (1128).

In the northcentral region of the United States, 80% infection of feeder roots in red pine is considered adequate mycorrhizal development. However, recent counts taken in nurseries in the Lake States revealed that ectomycorrhizal development in the nurseries was not adequate, none being more than 50% infected. A combination of nursery practices such as fertilization, fumigation, pesticide use, watering schedules, seeding dates, and cover crops are likely to be inhibiting to the development of ectomycorrhizae. No mention was made of ectendomycorrhizal development (34-37, 38).

On some extreme sites the quantity of infection alone is not enough for good tree development. The requirements and abilities of the particular fungus forming the symbiosis are very important . The mycorrhizae that are commonly formed is nursery seedbeds evidently are not as effective in aiding growth, especially on strip mine spoils, as are other ectotrophic fungi such as C. graniforme, S. luteus, and P. tinctorius (831, 807). P. tinctorius, which favors soil temperatures around 34°C, has been found associated with red pine growing on coal spoils in Indiana, Pennsylvania, Ohio, Virginia, West Virginia, Kentucky, Tennessee, and Alabama (807). In a laboratory with an average soil temperature of 21°C, it was found to make moderate ectomycorrhizal development on red pine (25% to 49% of feeder roots mycorrhizal) (812). C. graniforme, which grows best on droughty soils, tends to favor red pine as a host over white pine (450). Under laboratory conditions red pine is a moderate to excellent host for T. terrestris, varying with the strain of fungus used. The basidiospores of T. terrestris are able to quickly initiate colonies on fumigated nursery soil or other soils lacking mycorrhizal fungi (812). Red pine seedlings growing in sand and inoculated with T. felleus showed greater growth and absorption of potassium from orthoclase than control seedlings or those inoculated with S. granulatus or A. muscaria. Inoculations with mycorrhizae were not effective in stimulating growth in sand cultures with apatite as the source of potassium (1001).

Ectomycorrhizal seedlings, as well as ectendomycorrhizal seedlings, exhibit greater weights and stem heights, and better developed root systems than nonmycorrhizal controls. Although survival of red and white pine growing on bituminous strip mine spoil plots was not increased by inoculations with C. graniforme, S. luteus, soil, and macerated roots (the last two from established spoil plantations), the inoculated pine seedlings did show 2.6 to 35.3% more growth than the control (831).

On highly acid spoil (Brandy Camp, Pennsylvania) the addition of lime benefits the establishement of P. tinctorius as a symbiont of red pine, although the growth of the pine is not enhanced. P. tinctorius is best established on spoils of intermediate toxicity ~~(887)~~.

C. graniforme produces an antibiotic from the mycelium in pure cultures (680). A similar antibiotic occurs in nature in the mycorrhizae, roots and needles of red pine, as well as white pine and Norway spruce (680). However, no link between occurrence of the antibiotic in the fungus and in the tree has been established (680, 450). Under laboratory conditions, the symbiont S. granulatus on red pine prevented the stunting effect of Mycelium radicis atrovirens (Phialocephalas dimorphospora Kendrick), probably also through production of an antibiotic (974).

Despite contentions otherwise, neither Polyporus tomentosus Fr. nor P. tomentosus var. circinatus Fr. form mycorrhizae on red pine, even under conditions favorable for symbiosis between other fungi and red pine and white spruce (1277).

DESTRUCTIVE AGENTS

Non-infectious

The deterioration of immature stands of red pine may be brought about by various organisms affecting the roots, but one predisposing factor is present in most, if not all, cases of decline. Declining stands are almost invariably found on imperfectly or poorly drained soils. Only a few instances have been found on soils within the moderately drained class (587, 1129, 307). One case of decline was attributed to a highly compacted B horizon about 16 in (41 cm) below the surface of a badly eroded loam soil, which impeded root growth (1029). However, healthy stands of red pine can be found on well-drained silt loam soils (307).

Improper planting, either during transplanting within the nursery of outplanting in the field, can cause deformity of the root system. J-rooting, root clumping, and horizontal growth can occur when the planting hole is inadequately excavated, or the tree is planted too deeply, forcing the roots into a horizontal position. The result is that the trees may be unduly stressed during periods of drought. Needle droop is a symptom of this malady (107). In one study nearly 33% of the planted seedlings had deformed root systems; of these 66% showed no other evidence of injury (399).

Red pine appears to be more sensitive to some pesticides than some other pines, possibly because the toxic substance is distributed more evenly throughout the plant. Red pine is sensitive to the herbicide simazine, as is Scots pine, while white pine is not. The needles of red pine were found to have about three times the amount of simazine found in the needles of white pine, although the quantity of uptake was similar. Red pine is apparently more severely affected than white pine because the simazine blocks the Hill reaction during photosynthesis. Likewise, red pine shows more severe top symptoms of toxicity from arsenic than other northern pines. The arsenic is apparently transported more readily from the roots to top in red pine than in other species. The arsenic in this case had been applied 35 years earlier in the form of arsenic trioxide to control white grubs. Tipburned seedlings essentially lack fine roots except for a few mycorrhizal clusters on the upper laterals. In arsenic treated plots where red pine showed no visible symptoms, the root systems had only fair development, with a low density of fine roots (1127).

Red pine is sensitive to salt applied in the root zone (923). Red pine did not survive beyond the 40% level of "sea water" in automatically-irrigated sand cultures, while loblolly pine survived the 100% level. The root weight of the red pine was severely reduced at lower levels (213). Red and white pines show leaf symptoms from calcium chloride within about 3 weeks after application, whereas hardwoods show leaf symptoms by the sixth day (1141).

Insects

Two groups of insects do the most damage to the roots. In seedlings especially, the white grubs feed on the roots of red pine. The other group consists of the larvae of weevils that tunnel and feed on roots.

Of the genera of larvae called white grubs, *Phyllophaga* causes the most damage to seedlings. Other genera associated with roots of red pine include *Serica*, *Diplotaxis*, *Dichelonyx*, *Aphodius* and *Geotrupes*. *Aphodius* and *Geotrupes* are dung feeders, although some *Aphodius* may feed on living roots (448, 397). In one study, *Phyllophaga* accounted for 56% of all the grubs collected, *Serica* 31% and all other genera 13%. The amount of damage by other genera is insignificant in comparison to the amount of damage by *Phyllophaga* alone (398). Attacks by white grubs on red pine have been reported in Wisconsin, Minnesota, and Michigan (1010, 448, 397, 1066, 398).

The white grubs live beneath the soil surface feeding on the roots of young trees, especially red pine and white pine. Jack pine and Scots pine are not as heavily attacked. The roots are cleanly severed; several roots of the same plant are usually cut off at the same level. When the soil is dry the grubs move further down in the soil (1010).

Seedlings are most susceptible to attack in their first season. Few plants are killed by grubs after their third year, even though the grub population may be high enough to cause extensive damage (399). Mortality in the first year has been reported up to 15% (1066). In this same study, 53% of the trees were damaged, which is four or more times greater than the percentage of damaged trees on plots treated with the insecticide Aldrin (1066).

Aldrin is effective in controlling damage by white grubs without harming red pine (399). Other measures that can be taken are to plant only where grub populations are low, to postpone planting until the population declines, and to plant more resistant species such as jack pine in areas where the population is high (1010).

By taking a survey of the density of the grub population one can estimate the damage to be expected in a planting (397, 398).

The larvae of weevils cause damage to the roots of immature red pine, and are important agents in contributing to plantation decline. Species that most commonly attack the roots are *Hypomolyx piceus* DeG., *Hylobius radicis* Buchanan, and *Hylobius rhizophagus* Millers. *H. piceus* is indigenous to the northern forest zone of North America (1245). *H. radicis* is found from the New England states, south to Virginia, west to Minnesota, and in Canada from Newfoundland westward throughout the southern portions of the provinces to Manitoba (353). *H. rhizophagus*, however, has been found only in Wisconsin and the Upper Peninsula of Michigan (625, 626, 1314). *Hylobius warreni* Wood is common in Canada and has been known to infest trees in upper Michigan. Other species of weevils that feed on roots of red pine are *Hylobius pinicola* Couper in Newfoundland, *Pissodes affinis* Rand, and *Hylobius pales* Herbst (1084, 1246, 1314).

H. piceus, *H. radicis*, *H. warreni*, and *H. pinicola* feed on root collars and roots below the ground line, whereas *H. rhizophagus* does not feed on the root collar (1245, 353, 626, 1084, 1246). The larval galleries of *P. affinis* start near the root collar and extend in various directions including into the roots. *H. pales* usually feeds in recently cut stumps, but they will leave the stumps and invade the roots of living trees (1314). Weevil wounding is characterized generally by frass-filled galleries and exudation of resin, so that the duff removed from the base of an infested tree reveals clumps of pitch-infiltrated soil (353). Small trees may be completely girdled; the main roots of large trees may be girdled or severely debarked at or adjacent to the root crotches (1245).

Red pine is not the preferred host for *H. radicis* or *H. rhizophasus*. Jack pine is more heavily attacked by these species; the infected trees may die within two years. Red pine is attacked only when in mixture with jack pine or at the perimeter of a jack pine stand. Infected trees may live 5 or more years before succumbing to death (626, 353, 625). A great danger to red pine from weevil infestation is the wounding that gives entrance to other disease organisms.

Other insects occasionally result in damage to the roots of red pine. In the Sault Ste. Marie District in Canada, cicada nymphs (*Okanagana rimosa* (Say)) were observed feeding on roots of young red pine. The general site where adults were collected was a dry sand flat with scattered hardwoods growing among red pine plantings. Oviposition is on hardwood trees and shrubs, but not on conifers (643).

Nematodes

Nematodes may play a part in the initiation of stand decline of red pine, but their role appears to be minor (915). Many nematodes are associated with red pine, but only a few are parasitic on the roots, and of these none has been reported as pathogenic. The nematodes that have been reported as parasitic on the roots of red pine are *Helicotylenchus dihystera* (Cobb), *Trichodorus californicus* Allen, *Tylenchorhynchus claytoni* Steiner, *Tylenchus emarginatus* Cobb, and *Xiphinema americanum* Cobb (1147, 1143, 675, 1144).

Fungi

Post-emergence damping-off of red pine is caused by many species of *Fusarium*, *Pythium* and *Rhizoctonia*. Other damping-off agents of red pine are *Cylindrocladium scoparium* Morg.*, *Phomopsis juniperovora* Hahn, *Phytophtora* spp., *Pythiacystis citrophora* Sm. & Sm., *Sclerotium bataticola* Taub., *Sphaeropsis ellisii* Sacc. (*Diplodia pinea* (Desm.) Kickx.), and *Verticillium* sp. (952, 1170, 347, 387, 1169, 1007, 346, 1005, 1024, 271, 594, 266). Damping-off by *Pythium irregulare* Buism. is greatest at cool temperatures around 12°C with soil moisture content at saturation. *Rhizoctonia solani* Kuehn (*Corticum vagum* B. & C.), on the other hand, causes greatest damping-off at temperatures between 24°C and 30°C in drier soil,reaching a maximum around 68% moisture content (1005). Red pine is more susceptible to post-emergence damping-off by *Fusarium* spp. than either Scots or jack pine (1169). The seedlings vary in susceptibility to attack by the pathogens according to their age as well. In a Quebec nursery and in greenhouse tests, recently emerged red pine seedlings were first most susceptible to *Pythium debaryanum* Heese. By age of 20 days susceptibility of the seedlings to attack by *Rhizoctonia solani* reached a peak, and peak susceptibility to *Fusarium* spp. followed thereafter (1170). Susceptibility to attack by *Sclerotium bataticola* did not peak until 50 to 70 days after germination (1170).

Fungi that rot the roots of seedlings and/or immature trees include *Armillaria mellea* Vahl. ex Fr., *Corticum galactinum* (Fr.)Burt, *Cylindrocladium scoparium**, *Fomes annosus* (Fr.) Cke., *Fusarium* spp., *Phytophthora cinnamomi* Rands, *Polyporus tomentosus* Fr., *Poria subacida* (Pk.) Sacc., *Sclerotium bataticola*, *Sphaeropsis ellisii*, and possibly *Verticicladiella procera* Kendrick (940, 32, 1198, 572, 158, 582, 266, 846, 272, 920, 31, 1246, 560, 615, 1081, 932, 30, 879, 674, 594, 1007, 616, 1269, 917, 307, 587, 1277, 1068, 1169; 293, 880, 399, 1087, 1085, 387, 207, 1170, 233, 347, 271).

P. cinnomomi attacks nursery stock, rotting the root systems of older stock almost completely before symptoms appear above ground (272). It has not been found in natural stands (207). The infection produces a dry red-brown rot with deposition of resin in the wood (272, 233). Red pine is highly susceptible, and wet weather or poor drainage aggravates the situation (272). The disease caused by *Sphaeropsis ellisii* on red pine resembles that by *P. cinnamomi* in that it causes rot at the root collar to a point below the soil line. The invaded bark tissue turns deep red with black streaks continuing into the xylem and often into the stele (271). *Cylindrocladium* root rot develops first on small roots and moves toward the crown of the plant. Pine is somewhat more susceptible than spruce (32).

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* In the Lake States *C. scoparium* may be confused with *C. floridanum* Sob. & Seymour. (166)

V. procera has been isolated from root lesions of red pine growing in imperfectly drained soil in New York, and *P. tomentosus*, *P. subacida* and *C. galactinum* were isolated from weevil wounded roots of red pine on old-field sandy sites in Wisconsin. The pines on these plantation sites were in a state of decline (307, 674). *V. procera* apparently causes the lesions which can kill the root when they are numerous (307). *P. tomentosus* grows in the root xylem and inner bark causing a reddish-brown stain. The tree exudes resins in reponse to the infection. The inner bark of grafted roots provides a pathway for the spread of the infection to other trees. There is no evidence of passage of the disease through the xylem of the grafts, and the fungus appears to be blocked from the xylem of the grafts by a barrier of resin (880).

F. annosus attacks red pine in the same pattern as it does other susceptible pines, but red pine plantations are the least affected of the pine native to the eastern United States (1). The sapwood of red pine roots is moderately resistant to decay by *F. annosus* (932). Decay is confined to the wood present at the time the fungus kills the cambium of the root collar. The severity of the attack on the root collar depends on the size and number of infected roots. When *F. annosus* enters the root collar region, the healthy lateral roots wall-off the infection by laying down a barrier of resin-soaked wood along the rays inward. Wood which forms after the compartmentalization of the decay is protected from decay unless a new invasion is initiated (1068). The roots of a tree which has become infected in the course of the spread of the disease from an infection center usually have not been colonized on the side of the tree opposite the infection center until conks appear on the tree. This observation is important in determining the zone for soil fumigation in order to contain an infection center (572).

Red pine appears to be susceptible to disease by *A. mellea* without predisposition to infection, although incidence is higher in dense stands than open stands (with no regard to individual tree vigor) and in trees with previous damage by *Hylobius* weevils, even though the weevil wounds may not have directly contributed to the entrance of the fungus (233, 920, 1085, 1246). Plantations established with bare root stock also have greater incidence of *Armillaria* root rot than those established by other methods (1087).

Pinus strobus L. - Eastern White Pine

ROOT SYSTEM DEVELOPMENT AND MORPHOLOGY

Development of Form

The woody root system of eastern white pine is a deep, wide-spreading system of taproots, laterals and sinkers. A primary taproot may be present, but is often ephemeral; the lateral system is much more prominent. The laterals emerge from the root crown and grow outward at a downward angle. The lateral roots are found at depths from 3 to 38 inches (8 to 96 cm.) in the mineral soil (583, 762). Horizontal extension is roughly comparable to the height of the tree (185). The longest lateral observed in a 60 to 80 year-old stand was 60 feet (18 m.) (185). The horizontal extension of white pine roots is greater than that of both Pinus sylvestris and Larix decidua. The vertical roots consist of both sinkers and taproots either of which may attain a depth of 15 feet (5 m.) (185).

Non-woody roots are most dense around the root crown, and occur in clusters along the lengths of the lateral roots. (417, 185, 859). They may be found at depths of 30 to 56 inches (76 to 142 cm.) (818).

The root distribution in the soil profile is largely dependent upon moisture and nutrient conditions. The most commonly found distribution is that of decreasing numbers of roots with depth, following the decreasing availability of nitrogen and phosphorus in the profile. The greatest concentrations of roots are found in the O_2 horizon, followed by the A and then B horizons (760, 859). These horizons have, among other properties, greater contents of nitrogen, organic matter, fine-textured materials, and better moisture holding capacity and structural development (760). In soils which have layers or pockets of nutrient-rich and/or finer textured material in a coarse soil, the roots branch more profusely in those areas, giving the root system a stratified or otherwise irregular appearance (417). In comparison with red spruce, balsam fir, and northern white-cedar, a greater proportion of the roots of white pine are found in the mineral soil than in the humus (859).

The root systems of trees grown from cuttings rather than from seed differ primarily in the development of the lateral roots. The root crown is shorter and the laterals radiate in a horizontal plane; the resulting adventitious root system is shallower than a lateral system of seedling origin. (918) The trees in the following table were examined after eight years in a plantation (918).

Depth (inches)	Proportion of root system (% total rooting area) cutting origin	seedling origin
0-6	47	26
6-10	41	45
10-14	8	22
14-18	4	7

The depths attained by individual vertical roots of seedling origin and cutting origin are comparable. Nor is there a difference in the distribution of non-woody roots (918).

Roots of all sizes are numerous in comparison with other tree species (417). Compared to 2-0 seedlings of red pine, Scots pine, spruces, and balsam fir, 2-0 seedlings of white pine have greater root dry weight with corresponding greater contents of nitrogen, phosphorus, calcium and magnesium. At higher seedbed densities, both red pine and Scots pine have greater potassium content in the roots. Of the above-mentioned species, only Scots pine had greater total (root plus shoot) dry weight and nutrient content than white pine (978).

White pine and red pine root systems, whether seedlings or transplants, develop at approximately the same rate of magnitude. This rate is less than that of jack pine, but greater than that of white spruce (21, 179).

Grafting

Intraspecific and self root grafting in eastern white pine are common, varying with the frequency of root contact and only indirectly with edaphic factors or age. Between 30 and 70 percent of the trees in a stand may be involved in root grafts (150). One complex involving 6 trees had 35 separate intraspecific grafts in less than half of the entire root network (444). In another case, 31 roots transported dye to 13 receptor trees (150).

White pine is a good root stock species. It has good compatibility and survival with itself, _Pinus peuce_, _P. koraiensis_, and _P. cembra_. _Pinus resinosa_, _P. banksiana_, and _Abies balsamea_ do not fare as well as _P. strobus_ as stock for the afore-mentioned scion species (11).

Adventitious Rooting

Adventitious roots occur naturally on white pine. They have been observed near the base of stems of young white pine and on a naturally layered branch of a 30 year-old tree (399, 416, 758, 452). The layering occurred on a basal branch that had been covered by a mixture of mineral and organic soil to a depth of 6 to 10 inches (15 to 25 cm.) (758).

Stems of seedlings that have been severed just below the ground by grubs can develop a new set of roots and survive, provided that the surface soil moisture is adequate (416). Cuttings from first year white pine seedlings will root readily in a rooting medium. However, the ability declines with age, and by the third year only about 12 percent will root (416).

ROOT-SHOOT RELATIONS

The roots and shoots of 2 year-old white pine seedlings growing on a favorable nursery soil and examined in autumn show fairly constant proportions of elements, despite wide variation in seedbed density. The proportion of dry weight in roots compared to the entire seedling is about 28%, ash content 38%, nitrogen 17%, phosphorus 20%, potassium 10%, calcium 28%, and magnesium 22% (978).

The magnitude of root development, however, varies greatly with the factors affecting the growth of the shoot. The effect of shading on root development of white pine is very pronounced. Since shading a seedling limits the amount of photosynthate produced, and growth of the shoot is emphasized, the growth of the roots is reduced accordingly. Seedlings a few weeks old, grown under different light intensities, show decreases in weight and length of the total root system with decreasing light intensity (197, 853, 744).

The development of the root system of a shaded seedling is very weak. Few, if any, laterals are produced. Seedlings of comparable age grown in full light have several lateral roots (197). The roots of a plant grown in full light receive more materials translocated from the shoot than a shaded seedling, even when the root systems are the same size and they are tested under the same light conditions (1073).

On fertile soils, uptake of nutrients is stimulated by increased radiation up to full sunlight. On very infertile soils the stimulation is not detectable above 30 to 50 percent of full sunlight (853). High light intensity is conducive to better root development and function, on the whole, of young white pine.

Shading also affects soil temperatures, and hence, root growth and development. With increasing soil temperature at least up to 32°C, (i.e. decreasing shade), length, stoutness and numbers of roots increase (935).

In a temperate zone environment, growth of roots of white pine is periodic. Question exists as to whether it is autonomously controlled. The rate of root growth during the summer shows a definite slacking period between the end of June and the middle of August, although not all roots decrease their rate of elongation at the same time, and some have more than one slack period. This period of slow growth is most pronounced in late July and early August. The peaks in growth rate occur in the first half of June and in September through early October.

In young trees, at least, the rate of root growth appears to increase over the rate of each previous peak growing period. This implies that younger trees in a plantation may be at a disadvantage because the exploitation of the soil is carried on faster by the older trees.

Throughout the growing season there are always some elongating root tips. However, again in late July and early August, the number of growing root tips is fewest. The peak numbers occur in early May and in September. So, the period in the middle of the summer season is characterized by the greatest number of dormant root tips and the slowest growth rate of the elongating tips (1119).

In winter, the roots will elongate if soil temperatures are favorable, above 5 to 6 degrees C. It appears that, environmental conditions permitting, roots elongate vigorously throughout the year.

Variation in seasonal starch content and patterns of translocation of recent photosynthate parallel the pattern of root and shoot growth. Experiments performed under various moisture regimes found translocation of materials to the roots to be curtailed in June and July (1202, 736). During early summer, the shoot continually utilizes recent photosynthate as a respiratory substrate. During this period, translocation is low, root growth rate is low and shoot growth rate is high. When the utilization of the recent photosynthate by the shoot has dropped, (early and late in the season), translocation and rate of root growth are high (736).

Starch content reaches a minimum throughout the tree in midsummer. A secondary minimum occurs in winter in the above-ground parts. The roots, which do not develop a deep winter hardiness as the aerial portion does, do not exhibit a secondary minimum in winter (907). Minimums of starch content appear to coincide with periods of quiescence; in midsummer in both roots and shoot, and a lesser minimum in winter in the shoot alone. Larger amounts of recent photosynthate appear to be translocated to the roots at times when it is not being utilized for shoot growth.

EXUDATION

White pine roots have been found to exude more than 35 compounds. Among these are the sugars glucose and arabinose; the amides glutamine and asparagine; and the organic acids oxalic acid, glycolic acid, malonic acid, malic acid, shikimic acid and cis-aconitic acid. Malonic acid is the major compound liberated. All of the compounds except arabinose have been reported to be exuded by the roots of other plants, or are compounds commonly found in other plants. Arabinose is rarely found in the free state in plant tissues, although it is reported to occur in conifer heartwood. Malonic acid may influence oxidative reactions occurring in the various inhabitants of the rhizosphere. Shikimic acid has been shown to be a key intermediate in the pathway by which many microorganisms synthesize the aromatic amino acids phenylalanine and tryosine (1093).

One of the factors affecting water uptake is soil temperature. At 10°C white pine absorbs 60% as much water as at 25°C. At 0.5°C the transpiration of white pine is only 38% of the transpiration at 25°C. The southern pines, loblolly and slash, transpire only 14% at 0.5°C, and even red pine transpires less than white pine, 25%. The different species responses are thought to be due to differences with respect to changes in viscosity and permeability of the protoplasm of the roots. The ability of white pine to absorb water at low soil temperatures is an advantage in winter when sun and wind may cause excessive transpiration while the ground is frozen or very cold (665).

A comparison of different species of 2 year-old conifer seedlings grown under the same conditions showed seedling white pine stands to absorb greater quantities of nutrients than red pine, black spruce, white spruce or balsam fir. One exception is the greater calcium uptake by white spruce. Scots pine was the only species to show greater overall nutrient uptake than white pine (978).

In testing tree species for tolerance to the herbicide simazine, white pine was found to be more tolerant than red pine. The simazine was found to be concentrated in the roots of white pine, while it was more uniformly distributed throughout the red pine plants. Simazine affects the photosynthetic process in the leaves, so it follows that white pine would be more tolerant to the herbicide than red pine.

RESPONSE TO COMPETITION

Root closure in a 6 x 6 foot spacing begins within five years on a sandy soil. On predominantly clay soils, the competition begins in about 10 years (1119).

In a mixed stand, horizontal woody roots of red and white pine were found primarily between depths of 3 and 12 inches (8 to 30cm.), while most of the horizontal woody roots of red maple were found above 3 inches (8 cm.) and red oak below 10 inches (25 cm.) (762). In a mixed stand containing red spruce and white pine, the white pine roots were noted to form large, non-woody root clusters of a temporary nature, while the spruce lacked these clusters but had a pervading system of root tips which eventually became woody (859).

White pine has been observed to have poor form and vigor when growing within the root area covered by certain other tree species, notably black locust and black walnut (925, 1287). Aspen, yellow-poplar and red maple were reported to produce no such substances antagonistic to white pine (925). A rough guide for planting white pine near black walnut is to plant no closer to the walnut trees than the anticipated height of the walnut trees (1287).

Aside from allelopathic effects, competition affects the root biomass production and nutrient uptake by the stand. With increasing density the white pine roots increase in biomass, with proportionate increases in nutrient content. Root growth of 2 year-old white spruce, black spruce, and Scots pine is impaired by high density more than white pine stands. Norway spruce response is similar to that of white pine. Red pine root growth is less affected by high density than white pine. On favorable nursery soil, the root biomass of 2 year-old white pine was 1890 kg./ha. at 300 seedlings/sp.m. and 3842 kg./ha. at 1200 seedlings/sp.m. The increases in content of ash, nitrogen, phosphorus, potassium, calcium, and magnesium in the roots were also only about 2-fold with a 4-fold increase in density, from 300 to 1200 seedlings per sp. m. Total nutrient content also increases about 2-fold.

Intraspecific responses of red pine, white spruce and Norway spruce to varying intensities of competition are similar to white pine, except that red pine shows a less marked change in phosphorus and calcium uptake with change in density; and in Norway spruce the uptake of nitrogen and potassium is more severely affected by density changes than is uptake in white pine. Overall, uptake by white pine is less severely affected by high density than either Scots pine or black spruce (978).

Although total stand biomass increases with density, biomass of individuals decreases. Two year-old white pine, grown from "normally-sized" seeds at two seedbed densities, one sown at half the density of the other, showed marked differences in length, sturdiness and development of the root systems. With decreasing density, taproot diameter increased 34%, taproot length increased 29%, total length of laterals increased 75%, and the number of laterals increased 21% (967).

EFFECTS OF EXCESSIVE AND DEFICIENT MOISTURE

As deficient moisture from competition affects morphology of white pine root systems, so does excessive moisture. A water-saturated soil causes the seedling taproots to grow horizontally. If the soil is poorly aerated, even at the surface, no laterals are produced; the seedling topples over and dies. If enough air can be obtained at the surface of a near-saturated soil, strong horizontal laterals appear, and the taproot ceases to grow (349, 452). Trees growing on such wet sites develop shallow, plate-like root systems characteristic of white pine growing in bogs (765, 185). Root diameter tends to be smaller on lowlands than on uplands (710).

In comparison with other species, white pine is less tolerant of poor aeration than Norway spruce and larch, similar in tolerance to Scots pine, and more tolerant than red pine (90, 185). Red pine, in addition to having fewer live roots in poorly aerated zones, also has less extension of the lateral roots (185).

RESPONSE TO SOIL CHARACTER

White pine, along with some other conifers, is important in secondary succession on old-field sites because of the ability of its roots to increase nitrogen and phosphorous availability in the soil. Some organic fraction of the soil nitrogen and phosphorus that is resistant to microbial activity under the previous regime of grasses and forbs is made available by the pine roots. Because the nitrogen is derived from an organic source, the mineralization does not occur on severely eroded soils, mine spoils, or other sites lacking degradable organic matter. The mineralization effect is temporary and appears to last as long as the root systems continue to exploit new areas of soil. By age 30 the stand ceases to exhibit the increase; a second generation may not grow as well as the first. However, herbaceous and hardwood understory does appear to profit from this nutrient bonus (390).

In studies of nitrogen and phosphorus nutrition of white pine, intermediate levels of both were found to yield the greatest root weight, dry or fresh. The greatest root-to-shoot ratios are achieved under somewhat lower levels of nitrogen (850, 737, 851). In one set of experiments the concentrations of phosphorus used were 0, 173, and 692 mg./l., and the concentrations of nitrogen used were 0, 2.5, 53, and 265 mg./l.; both were applied every second day. Greatest root weight was found at 173 mg./l. of phosphorus and 53 mg./l. of nitrogen; greatest root-to-shoot ratio at 173 mg./l/ phosphorus and 2.5 mg./l. nitrogen. Individual roots are more highly developed at low nitrogen levels. With increasing nitrogen concentration, the lateral roots decrease in number, branching, and length. Non-woody roots also decrease in number and development (850, 497, 736).

Different concentrations of nutrients affect not only the size and proportions of roots, but also the amount and distribution of carbon translocated from the shoot to the root. The percentage of carbon found in the sugar fraction decreases with increases in nitrogen, while more carbon is found in the amino acids and organic acids. Sucrose is the dominant form in which recently translocated carbon is found. An increase in nitrogen results in increased hydrolysis of the sucrose to hexoses, while the effect of phosphorus is an increase in the amount of sucrose (737). High phosphorus levels depress translocation of photosynthate from the shoot to the roots; the depression is somewhat relieved by increasing the levels of nitrogen (736).

MYCORRHIZAE

Mycorrhizae are most abundant on white pine at intermediate levels of nitrogen and phosphorus, the same levels at which the sucrose translocated from the shoots to the roots is metabolized into a variety of different substances (497, 737).

Photoperiod also affects the abundance of mycorrhizae. Fewer mycorrhizae were found on seedlings grown under a 20-hour day than on those grown under the natural photoperiod. The long photoperiod did not affect the relative abundance of mycorrhizae on Virginia or loblolly pines (477).

White pine forms mycorrhizal relationships with a wide variety of fungi. Individual trees may have up to 4 different species of fungi in mycorrhizal association, but usually they number 3 or less (154). Fungi known to form ectomycorrhizae with white pine are: *Amanita muscaria* (L. ex Fr.) Pers. ex Hook, *Amphinema byssoides*...., *Boletinus porosus* (Berk.) Peck, *Boletus bovinus* L. ex Fr., *B. brevipes* Peck, *B. castaneus* Bull., *B. granulatus* L. ex Fr., *B. luteus* L. ex Fr., *B. pictis* Pk., *B. rubellus* Krombh., *Cantharellus cibarius* Fr., *Cenococcum graniforme* (Sow.) Ferd. & Winge, *Clitocybe diatreta*.., *C. rivulosa* var. *angustifolia*..., *Gryrodon merulioides* (Schw., Sing.), *Gyroporus castaneus*....., *Hebeloma hiemale*....., *H. mesophaeum* Pers. ex Fr., *Laccaria laccata* (Scop. ex Fr.) B. & Br., *Lactarius chrysorrheus* Fr., *L. deliciosus* (L. ex Fr.) Gray, *Lycoperdon gemmatum* Batsch., *Pisolithus tinctorius* (Pers.) Cok. & Couch, *Russula lepida* Fr., *Scleroderma aurantium* Vaill. ex Pers., *S. vulgare* Fr., *Thelephora terrestris* Ehr., *Tricholoma personatum* (Fr.) Quel., *Tuber albidum*......, and *T. maculatum*... (816, 94, 323, 324, 812, 393, 369, 365).

The fungus *Pisolithus tinctorius* is well known for its ability to live and form mycorrhizae on adverse sites. It does form ectomycorrhizae with white pine, but development is slower than on Virginia or loblolly pines (816). In a test where the soil temperature averaged 21°C, mycorrhizal formation with *Pisolithus* was poor on white pine (812). Even so, in a North Carolina nursery, fresh shoot and root weight increased 100% over the weight of noninoculated controls; on a good site white pine demonstrated a 3-fold increase in survival and growth with inoculation. (The weights of loblolly and Virginia pines increased 140% and 107%, respectively) (816, 94).

DESTRUCTIVE AGENTS

Non-infectious

Several diseases of white pine have been attributed to site factors, with no direct biological pathogens involved. Some basal cankers, root rot, and even death are thought to be the result of poor aeration of the soil during periods (especially spring) when the tree is most metabolically active (1078, 452).

Soils of high pH, low porosity, or shallow depth to an impervious layer promote the disease (452, 1078, 896). In the case of seedling root rot, there is some recovery in June and July with the development of adventitious roots (452). Trees with basal cankers are eventually girdled and die in 2 to 5 years or more (1078). A needle blight is attributed to deficient root action resulting from drought injury in the previous year (66). White pine is very windfirm except where the rooting depth is limited, as on sites with fragipans or along edges of swamps and bogs (1123).

Another non-biological disease affecting white pine is salt toxicity along roadsides. On a scale of 1 to 5 (very tolerant to very sensitive) white pine rates about 4 in sensitivity to soil applied salts. Chloride uptake by white pine is greater than that for eastern hemlock and Norway spruce, but injury is somewhat less. Northern white cedar, white spruce, eastern redcedar, and balsam fir are all more tolerant than white pine (871, 923, 131).

Insects

The beetles *Hylobius radicis* Buchanan, *H. rhizophagus* Millers, and *Hypomolyx piceus* DeGeer all will attack white pine, although it is not the favored host species (1244, 626). *H. radicis* attacks trees of all ages, but shows a preference for those between 5 and 20 years of age. Trees growing in sandy, well-drained soils are more susceptible to attack. *Hypomolyx* prefers slightly larger trees, though normally not older than 40 years. Moist to wet sites have the highest populations of *Hypomolyx*. Sandy, well-drained soils with thick ground covers of moist moss are suitable habitat for these beetles (1244).

The larvae of *Phyllophaga* sp. and related genera are reported to girdle roots (1154).

Hylobius pales (Herbst) and *Pachylobius picivorus* (Germar) breed in white pine stumps and roots. In the southeastern United States, great damage can be done to new winter plantings on land harvested in the previous summer or fall. Up to 90% mortality has been reported (1108).

Nematodes

Of the many species of nematodes associated with white pine, at least 6 of them are parasitic. In Pennsylvania nurseries, species of *Pratylenchus*, *Tylenchus*, and *Xiphinema* were found to be parasitic (1347). In the southeastern United States, parasitism by *Meloidodera floridensis* Chitw. *et al*, *Hoplolaimus galeatus* Cobb, *Pratylenchus brachyurus* (Godf.) Fil. & Schuur, and *Hemicycliophora vidua* Raski was demonstrated (1014, 1013). *Dolichodorus silvestris*, observed in West Virginia, may be parasitic on white pine (428).

Fungi

Damping-off and seedling root rot in white pine is often caused by *Rhizoctonia solani* Kuehn, *Fusarium* spp., *Pythium debaryanum* Hesse, *P. ultimum* Trow., *Phytophthora cinnamomi* Rands, *Cylindrocladium floridanum* Sob. & Seymour, *Diplodia pinea* (Desm.) Kickx, (*Sphaeropsis ellisii* Sacc.), and *Rhabdospora mirabilissima* (Pk.) Dearn. *Rhizoctonia* is predominant on seedlings 6 months old or less, while *Fusarium* predominates on older seedlings up to 3 years old (264, 992). *Cylindrocladium* is very pathogenic on white pine seedlings (265).

On seedlings up to 4 years of age, the growth of the taproot can be terminated by infection. Young roots typically die back from the tips to the older tissues, and new roots proliferate just above the diseased areas (266). Roots of 3 to 4 year-old seedlings can be killed by *Rhizinia undulata* Fr. (*R. inflata*).

Important fungal pathogens of older white pine are *Armillaria mellea* Vahl ex Fr., *Corticum galactinum* (Fr.) Burt., *Fomes annosus* (Fr.) Cke. and *Polyporus schweinitzii* Fr.

White pine of all stages of vigor can be attacked by the root rot fungus *Armillaria mellea*, although trees of low vigor are more susceptible. In the white pine region of Ontario, *A. mellea* accounted for 20% of the mortality in a plantation of 6 year-old trees (560). Red pine had 51% mortality attributed to *A. mellea*, while white spruce had 14% mortality.

The percentage mortality due to *A. mellea* was similar on different site types. In a 32 year-old plantation in New York (6 x 6 foot spacing), 38% showed infection by *Armillaria*. Here, nutrient deficient soil led to low tree vigor, hence the trees were predisposed for an attack (1077). Artificial inoculation of 8 to 10 year-old plantation trees in Wisconsin resulted in 27% of the inoculated trees showing infection. Most of the infections occurred near the root collar. In northern Michigan, *Corallorhiza maculata* Raf. (spotted coralroot, Orchidaceae) and especially *Monotropa uniflora* L. (Indian pipe, Ericaceae) have been found in association with *A. mellea*, which in turn was parasitizing roots of white pine and other trees (207).

Another important wood-rotting fungus is *Fomes annosus*. The root sapwood of white pine and loblolly pine is less resistant to decay than that of eastern redcedar, red pine, Virginia pine or shortleaf pine; and, unlike other species, the root wood and stem wood of white pine are almost equally susceptible to decay. Root wood is slightly more susceptible. Susceptibility is positively correlated with the nitrogen and reserve carbohydrate contents in the roots (933).

Although white pine root wood is less resistant to decay by *F. annosus*, shortleaf, loblolly, and Virginia pines all had greater mortality from infection in greenhouse experiments. White pine mortality was 64%, while the mortality of the others ranged from 72% to 82%. Eastern redcedar had only 28% mortality (685).

Root grafts and contacts are pathways of infection from infected trees or stumps to healthy trees. Wounds or dead roots are not necessary for infection (161). The infection often progresses from the roots into the innermost rings of the stem sapwood, from which the heartwood may be colonized before the death of the tree (243). Trees may show no crown symptoms despite extensive root rot (161).

Fruiting bodies of *F. annosus* on white pine are often completely hidden below the duff. Stands of any age can be infected, but usually it occurs in young stands less than 40 years old (615, 161).

Ployporus schweinitzii causes a brown cubical rot of the heartwood and basal portions (90, 1140). Infections by *P. schweinitzii* seem to be associated with resinosis disease, but are not the cause of that disease. Seedling roots may contract the disease, and stands may be infected at only 10 years of age (90). A pocket rot is caused by *Ployporus tomentosus* on white pine roots.

Corticum galactinum can cause a white root rot. The infected trees found in Connecticut, New York, Delaware and Pennsylvania were dwarfed and chlorotic. Root and butt rot due to C. galactinum has also been found in Michigan and in Ontario (1269).

A species of Leptographium is held responsible for disease in 3 to 15 year-old plantations in Indiana, Kentucky, Maryland, Ohio, Pennsylvania and West Virginia. The fungus attacks the root cambium and eventually girdles the root collar (327). A fungus of the Leptographium type in the genus Verticicladiella appears to cause a somewhat similar disease on planted white pine in the northern Rocky Mountains. The disease can be transmitted through root grafts (717).

Pinus sylvestris L. - Scotch Pine

MORPHOLOGY

Development of Form

As it is for shoot characteristics, genetic variability in the root systems of scotch pine is quite high. One author studying seedlings from several locations throughout the range of scotch pine found significant differences in type of root system, rate of growth, root regeneration potential, and growth at different moisture-fertility combinations (179). Northern European provenances were distinctly tap-rooted, with lateral rooting confined to branching from upper portions of the tap root. Central European provenances had more moderate expression of the tap root character. Laterals were long, much branched, and occurred along most of the tap root. Sources from isolated, southern portions of the range were distinctly tap-rooted, with little branching of the laterals.

The same study found that differences in root growth rate during the first 80 days after germination were related to temperature and precipitation of areas of seed collection. In all cases initial root growth was confined to tap root elongation. Lateral growth was not pronounced until after tap root growth began to decline. Rate of root growth was most rapid for northern sources from areas having short growing seasons and was slowest for southern origins from moist climates. Root regeneration potential was generally higher for the more southerly origins, although the correlation was not as high as for root growth rate.

Distribution in Soil Profile

The mature root sytem of scotch pine in sandy soils has been described as strongly developed and deeply penetrating, with a considerable capacity to exploit adverse soil conditions (1334). One study found that the longest lateral roots of a mature pine on a sandy soil reached approximately 25m (83.2 ft.) from the trunk. Cases where the horizontal root system surrounds the trunk to a radius of 20m (66.6 ft.) (and thus theoretically covers an area of approximately 1/8 hectare) are not rare.

The extent of lateral roots reportedly reaches a maximum when the trees are in the early pole stage. With increasing age, roots often die off for several meters; in their place new roots are formed which cause the horizontal root system to become denser instead of longer. Tapering of these roots also tends to increase with age, as root diameter near the trunk increases (1334). The total root length per cubic meter of soil space may far exceed 10 km in old stands (1097).

The deep-root system of scotch pine in well-drained sandy soils is characterized mostly by a strong taproot. It is always present in younger trees; in older trees a bending or branching (often caused by mechanical obstructions or fungal infection) may alter the typical tap-root character. Vertical root penetrations as deep as 8m (26.6 ft.) have been reported by some authors, although 4-6m is a more common maximum depth (999).

The vertical root system also reaches its largest spread at a relatively young age of a tree. The vertical roots arising from the stump area are supplemented by sinkers arising in some cases from considerable distances out along the lateral roots. Generally the volume of the vertical root system is considerably larger than that of the horizontal root system, although this is dependent to a considerable degree upon age and on soil properties (999).

One author reported that mean root diameter in a scotch pine plantation increased steadily down the profile to a maximum value of 1mm (.04 in) at a depth of 138-153 cm(54-60 in); below this level there was a decrease in diameter. Root density, however, was by far greatest in the uppermost soil horizon (0-15 cm; 0-5.8 in). Root density also declined with distance from the trunk, due mainly to changes in the fine root fraction (995).

Another author reported that, on a sandy soil, the largest amount of scotch pine roots were found in the topsoil, followed by a gradual reduction through the A_2 and B horizons, and then a gradual increase lower in the B horizon. The large lateral roots had their maximum spread in the A_2 and B horizons. This distribution pattern was thought to be strongly related to soil moisture conditions.

Comparison with Other Species

The root system of scotch pine is reportedly considerably deeper and larger in total volume than the root system of white pine (*P. strobus*) of similar age and on similar soils. Austrian pine (*P. nigra*), on the other hand, is considerably deeper rooted than scotch pine, and nearly equal in lateral extent (999).

One author reported fairly large differences in root distribution between scotch pine and spruce (*Picea excelsa*). The spruce had a much higher percentage of roots in the uppermost soil layers than did scotch pine (999).

The root system of scotch pine, though slower growing than white pine (*Pinus strobus*) on the same site, was in one study unable to penetrate fragipan-like horizons which white pine was to penetrate .

Grafting

Intraspecific root grafts in scotch pine are reportedly common, as are grafts between roots of individual trees. A few cases of interspecific grafting have also been reported (446).

Adventitious Rooting

Adventitious (stem-origin) rooting under natural conditions has not been reported for scotch pine. Roots can be induced from cuttings, however (386,416).

SEASONAL GROWTH PATTERN

Root growth of scotch pine in one study increased with temperature and radiation in spring and reached peaks in April and May. Despite further rises of radiation and temperature into June and July, root activity declined after the May peak as soil water content declined. A second increase in the fall occurred in some years but not in others, with roots in the uppermost soil horizon showing the largest fluctuations from year to year. This was correlated with annual fluctuations in soil mositure.

One author reported that initiation of root growth in scotch pine, though barely discernable, began an average of 17 days before the time of bud break (999). When marked growth does begin it is very sudden and is simultaneous along the whole root (1289). This was confirmed by a German study which also found that root growth in scotch pine did not reach a peak until late July, some 2-3 weeks after shoot growth had essentially stopped (543).

The early (April-May) period of root growth is characterized by the production of fibrous roots, while the fall growth period is characterized by growth in length of the stout root leaders. Cessation of growth of the thicker roots progresses towards the base of the trunk, so that growth in the regions common to root and trunk ceases at about the same time as it does in the aerial parts (442).

One study found that survival of outplanted scotch pine varied cosiderably with time of transplanting, seed source, and intensity of root pruning. Root growth and root regeneration were slight while top growth was active. Survival was nearly 100 percent for trees transplanted after top growth had stopped (179).

Another study found that scotch pine seedlings grown in plastic pots for one growing season showed a high incidence of spiral rooting. No plants grown in peat pots developed spiral roots. Plants with spiral roots showed greater height growth than those without. Root strangulation was not the cause of any plant mortality as of the time the study ended, when the young trees were eight years old.

ROOT-SHOOT RELATIONS

Starch is never totally absent from the roots of scotch pine as it is from the trunk during the winter minimum. During the growing season there is a marked rise in starch towards the growing apices of the roots (1289).

EXUDATION

Scotch pine has been shown to be sensitive to root exudates produced by black walnut (Juglans nigra). One author recommends that scotch pine be planted no closer than about 50 feet to mature walnuts or walnut sprout clumps (1051).

There is some evidence that the roots of scotch pine are able to produce a substance which aids in the extraction of soil nitrogen (390).

RESPONSE TO COMPETITION

One author reports that the roots of some woody ground vegetation (bilberry, in this case) can compete with the fine roots of scotch pine to a considerable degree. European beech was found to be an even stronger competitor than bilberry .

Regeneration of scotch pine was found to occur most prolifically from 3 to 5 years following fire on a British Heather moor. Regeneration fell off rapidly after 5 years due to competition with the returning heather (Calluna spp), which prevented the developing pine tap roots from reaching mineral soil (317).

EFFECTS OF EXCESSIVE AND DEFICIENT MOISTURE

Root growth in scotch pine was found to be very much reduced at an O_2 content of the root space of less than 10%. At an O_2 content of 14%, root growth was not adversely affected. If no oxygen at all was provided, the seedlings died within two days. Above-normal O_2 content lead to a brief increase in root growth which after about one day reverted to the level present under normal soil aeration (999)(731).

One author reports the following order of tolerance to water-logging among the species of trees on a British upland heath (in order of decreasing tolerance): shore pine, lodgepole pine, scotch pine, Corsican pine, Japanese larch, and sitka spruce (1334).

A study of scotch pine growing on peat soils showed that a decrease in soil aeration due to waterlogging resulted in impairment of the trees' ability to absorb or assimilate nitrogen. The uptake of other nutrients was not affected (177).

A German author reports that a stand of scotch pine, which originally only produced superficial roots in a very wet soil, later grew very deep vertical roots when the soil had become drier as a result of the roots of the trees forming the stand (755).

RESPONSE TO SOIL CHARACTER

Soil character has a major effect upon the rooting habit of scotch pine. In very dry soils containing little humus, one author found a very varying, but generally shallow root distribution. Most laterals were very close to the soil surface, had few branches, and exhibited evidence of repeated dying-off of feeder roots (999).

In nutrient-deficient, compacted soils, trees showed less overall root development than in deeper fertile soils, but they attained a greater root depth. This was contrasted to root development on gley-type soils, which was characterized by little or no taproot development and pronounced development of surface roots (999).

On moor soils in Finland, roots of scotch pine were found to be concentrated mainly in the upper 10 cm of soil. A particular feature in moors is the high proportion of fine roots (999).

One author reports that soil horizons composed largely of glacial till were almost devoid of scotch pine roots .

Sinker roots, which take advantage of any weakness in the subsoil structure, are distributed along the length of laterals where vertical development is inhibited but are clustered beneath the butt on freely rooted soils. Ironpans, although not entirely excluding roots from the lower horizon, do check vertical penetration and possibly delay sinker initiation. The ultimate limit to penetration is a bulk density of about 1.5 g/cc (370)(377).

Four to five foot-tall scotch pine trees planted along highway rights-of-way in Michigan showed good survival. The pines made their best growth when planted at grade level (sandy sites) or 4 to 5 inches (10.2 - 12.7 cm) below grade (clay sites). They did not grow as well when the surface of the root ball was planted 4 or more inches (10.2 cm) above the grade of the planting site. Root-pruned plants showed significantly better growth on the clay sites than did non-root-pruned plants. Among the non-root-pruned plants, there were no significant differences between potted plants and those that were balled and burlapped (287).

MYCORRHIZAE

At least 118 fungi are known to form mycorrhizae with scotch pine, a number which reflects the intensity of study accorded scotch pine in Europe. Many of these are listed in (1181).

There is evidence that exudates of some fungi (both mycorrhizal and non-mycorrhizal) promote elongation and dichotomous root production in scotch pine. The basidoimycete group of fungi were found to be particularly effective in this regard (1189). Certain auxins, notably B-indole-acetic acid and oc-naphthaleneacetic acid, are believed to be the exudate components principally responsible for the effects on root growth (1090).

Uptake of certain nutrients by scotch pine roots, notably phosphorous, was shown to be increased for mycorrhizal roots as compared to the non-mycorrhizal control.

Seedling scotch pine planted in a prarie soil in southwestern Wisconsin were shown to grow much better if they had received prior mycorrhizal inoculation than if they had not (843).

Examination of scotch pine seedlings grown in pot cultures has shown that only in the autumn, after elongation of the rapidly growing long roots has nealy ceased, do the tips of the latter frequently acquire the mycorrhizal structure. This would appear to indicate that rapid elongation is the primary reason long roots ordinarily escape attack by mycorrhizal fungi (498).

DESTRUCTIVE AGENTS

Non-infectious

Scotch pine normally is not very susceptible to windthrow except on shallow soils (370; Hepting, 1971). On gravelly soils, however, the incresed incidence of root injury may lead to the introduction of rot into vertical roots especially, thus leading to increased risk of windthrow (117).

Scotch pine is considered quite resistant to root injury due to soil freezing, drought, or the addition of fill around the base (Hepting, 1971).

Insects

The roots of scotch pine may be damaged by Warren's Collar Weevil, Hylobius warreni Wood. Larvae feed in the bark and cambium of the root collar and large roots. Roots more than 2 inches (5.1 cm) in diameter are sometimes girdled; small trees may be girdled at the root collar (Baker, 1972; Wilson, 1977).

Scotch pine is particularly susceptible to damage by the pine root collar weevil, Hylobius radicis Buch.. Complete stands have been wiped out by the larvae of this pest in the Lake States. The root collar beneath the duff is commonly constructed and irregular larval galleries occur in the bark and cambium of the root collar and primarly roots. Larvae are in the root collar or in tunnels in soil nearby; pupae usually are in earthen cells in the pitch-infiltrated soil (Wilson, 1977).

Larvae of the root tip weevil Hylobius rhizophagus M.B. & W. and pales weevil Hylobius pales (Herbst.) also attack the roots of scotch pine and several other conifers. Descriptions of these species and the symptoms of their damage are found in Baker, 1972, Wilson, 1977, and (626).

In recent years a number of scotch pine plantations in the Lake States have been under simulataneous attack from *Hylobius rhizophagus* and *H. radicis*, resulting in more mortality than would be expected from either insect alone. Recommendations for curtailing this complex included favoring red pine in affected areas, avoiding stump culture of Christmas trees, and basal pruning of young trees (868).

Plantations of pine on sandy infertile sites are most susceptible to *Hylobius* damage. The most severely attacked trees are those exposed on the edges of plantations and in windbreaks, or scattered throughout old fields (1043).

The northern pine weevil *Pissodes approximatus* Hopk. attacks scotch pine from the roots up to branches as small as 1/2 inch (1.3 cm) in diameter. Winter is spent mostly in the adult stage in the duff and top soil beneath infestedtrees and beneath the bark. Damage is often severe in regions where there are large quantities of breeding material, such as fresh stumps in Christmas tree plantations and in stands under intensive management (Baker, 1972).

The Red Turpentine Beetle *Dendroctonus valens* LeC occasionally attacks scotch pine. Galleries bored by the female begin at the ground line or above, and may continue below ground along a large root. The larvae feed gregariously away from the gallery in the phloem. Damage can be reduced or prevented by not digging up or damaging roots, pushing deep earth fills over roots, or piling lumber or green logs near trees (Baker, 1972).

Nematodes

Many nematodes have been reported from the roots or root zones of scotch pine, both in North American and elsewhere in the world. There has been little association, however, between nematodes and damage to the trees (Hepting, 1971).

Species of nematodes associated with the roots of scotch pine include *Criconemoides irregulare, Ditylerchus* sp., *Helicotylenchus* sp., *Hoplolaimus galeatus, Longidorus maximus, Paratylenchus projectus, Pratylenchus crenatus, P. penetrans, P. pratensis, Trichodorus cedarus, Tylenchorhynchus* sp., *T. claytoni, Xiphinema americanum* (Ruehle, 1967), *Aphelenchus* sp., *Rotylenchus* sp., *Tylenchus* sp., *Aphelenchoides* spp. (1347).

Fungi

Scotch pine seedlings in nurseries have been attacked particularly by *Phytophthora cactorum*, *P. cinnamomi*, *Pythium debaryanum*, *Rhizoctonia solani*, and *Cylindrocladium scoparium*, all of which can cause damping-off and root rots (Hepting, 1971), (1024)(1205)(266)(1206).

In older trees, root and butt rots have been caused by Armillaria mellea, Fomes annosus, and Polyporus schweinitzii in the Northeast. Variable degree of resistance are shown by the different genetic strains of scotch pine, especially with regard to F. annosus (Hepting, 1971, (785)).

There is some evidence that penetration of scotch pine root bark by F. annosus mycelium may be correlated with nutrient content of the bark. Infection with F. annosus through the bark of healthy roots sterilized with propylene oxide could not be induced in one study, suggesting that soil microorganisms are not the primary factor in the prevention of F. annosus root rot (1233).

It has been shown that establishment of the fungus Peniophora gigantea into stumps in pine stands, either by artificial inoculation or by cutting scattered trees several months before a regular thinning may afford protection against stump invasion by F. annosus (162).

ROOT SYSTEM DEVELOPMENT & MORPHOLOGY

Development of Form

The primary root of loblolly pine emerges horizontally from the split seed coat 12 to 20 days after the seed contacts soil. The tip turns down in a day or two and enters the soil. Weather is critical during this period before anchorage is secure; if wind or beating rain dislodges the radicle it may dessicate and fail. The elongation of the primary root is rapid; rate of elongation increases until reaching a maximum by the fourth month of growth (578). The rate of elongation of the main root of seedlings growing in acrylic resin tubes in a greenhouse reached a maximum just before the appearance of buds for the secondary needles and lateral branches at 10 to 12 weeks after germination. From this time on, the rate of elongation gradually declined (122).

The elongation of the primary root of loblolly seedlings planted from seed in early March in Louisiana was rapid until late May to mid-July. By September the primary root ceased elongation, whereupon the diameter of the root crown and the amount of mycorrhizae increased (578). First order lateral roots of the seedlings in resin tubes appeared in the third week of growth and achieved a maximum elongation rate in 9 to 12 weeks. From about 7 to 17 weeks the number of elongating first order laterals was about 20 per seedling. Five to 8 new roots appeared per week for about 15 weeks. Most laterals ceased growth a few weeks after initiation, although a few continued growing for 24 weeks (122). In the Louisiana planting numerous growing points appeared on the lateral roots in October (578).

In the first decade the proportion of roots, especially fine roots, increases in the A horizon (244). Up to 20 years of age the increase is rapid (1048). After 20 years the concentration of fine roots near the surface becomes noticeable (245). The increase in fine root weight continues at a slower rate until about the age of 30 when the rate of increase reaches a near-constant value. At 60 years the surface soil is almost saturated with fine roots (1048). Although the total mass of fine roots increases, the proportion in relation to the larger root classes decreases in 70 years beginning after the first decade (245, 885).

The proportion of dead roots, by numbers of roots, of healthy loblolly pine increased from 3.7% to 6.3% in a 17- and a 37-year-old stand, respectively (254).

Thinned stands require only a few years before the soil is once again fully exploited by the larger roots. A thinning of a 9-year-old stand which had been planted at a 6 x 6 ft. (1.8 x 1.8 m) spacing left the trees at a spacing of approximately 21 x 21 ft. (6.4 x 6.4 m) or 100 trees per acre. Immediately after thinning the roots occupied about 10% of the total area available. After two growing seasons roots fully occupied 30% of the space, and after three seasons 60%. The surface 24 in. (61 cm) were considered nearly 100% utilized in five growing seasons after thinning (1350). Another study reports reoccupation of the root zone by fine roots in 3 or 4 seasons in a 30-year-old loblolly stand thinned to 55 ft.^{2} basal area per acre (5.1 m^2). Roots of trees on plots thinned to 130 ft.^{2} (12.1 m^2) were competing within the first season (87).

The root growth of the seedlings is so sensitive to environmental influences and subject to such genetic variation that quantitative descriptions of the early root growth are not very meaningful in themselves (660, 617, 245, 336). For example, on three different soil types the total length of lateral roots of one-year-old seedlings ranged from 3.70± 0.59 in. (9.4± 1.5 cm) to 19.49± 4.02 in. (49.5± 10.2 cm), and weight from 12.5± 2.0 mg to 63.1± 13.0 mg. (336). The averages of 24 Georgia seedlings growing on sandy loam were 1125 mg weight and 27.0 in. (68.6 cm) in length at the age of 23 weeks (722). Seedlings of various progenies, all grown under the same conditions so that observed differences would be primarily genetic, had a full range of total root system lengths and weights from 7.44 in. (18.90 cm) to 46.28 in. (117.56 cm) length and from 7.96 g (fresh weight) to 66.38 g weight. The heaviest root system was not the longest. The mean length for all progenies was 21.62 in. (54.91 cm), and commercial nursery seedling stock averaged 9.94 in. (25.25 cm).

Comparison with Other Species

In comparison with hardwood seedlings, the root system of loblolly pine is sparse or superficial. Loblolly seedling regeneration cannot compete with oak under typical forest conditions. The oak seedling taproot is much more strongly developed. When grown in full sun on abandoned fields the root development of loblolly is stronger than under shaded conditions, but is still superficial in comparison with the taproot of the shaded oak (245). Dogwood seedlings had an average of 3,000 roots while loblolly seedlings numbered 1,000 (660). Black locust roots had 520 root hairs per cm^2 compared to 217 root hairs per cm^2 on loblolly roots (660).

In comparison with other Southern conifers, loblolly, again, has less root system proliferation. The taproots of 100-day-old loblolly pines on direct-seeded sites were approximately 50% of the total root length, while slash and longleaf taproots were only 30%. Longleaf pines had more extensive lateral root development than either loblolly or slash pines (617). Shortleaf pine seedling root systems are heavier and more fibrous than loblolly systems having comparable top weights (127, 1354). The loblolly roots are long and slender in comparison with shortleaf roots which are shorter and thicker. Variation in weight among roots growing in different soils, however, was greater in loblolly root systems than in shortleaf pine (127).

Distribution in Soil Profile

The taproot of older loblolly pines may extend down to a depth of 5 ft. (1.5 m) (885, 1360). The maximum lateral extension of three 6-year-old trees was 12.4 ft. (3.78 m), 18.3 ft. (5.58 m) and

24.2 ft. (7.38 m) (157). A sawlog tree in a stand thinned at 9 years from a 6 x 6 ft. (1.8 x 1.8 m) spacing to a 21 x 21 ft. (6.4 x 6.4 m) spacing had lateral roots 16 ft. (4.9 m) long 3 years after thinning (1350). In th same stand at 9 years the roots were concentrated in a radius of 3 ft. (1 m) from the root crown at a depth of 24 in. (61 cm). At shallower depths the roots extended radially up to 8 ft. (2.4 m) (1350). Vertical roots also achieve some lateral spread with depth, descending at angles of 10 to 15 degrees. The verticals of 2-year-old Texas seedlings extended to 4 ft. (1.2 m) depth on unmulched plots. They tended to be stouter, shorter and more tapered than the horizontal roots. Laterals of these seedlings grew slightly upward from their juncture at the taproot (118).

The majority of roots (in terms of both number and weight) tend to be concentrated in the upper portion of the soil. Over 90% of the roots were found in a 5 in. (12.7 cm) thick A horizon of a 35-year old stand (244). In this stand the density of the roots less than 0.1 in. (0.25 cm) diameter was 160 roots ft^{-2} (1722 roots m^{-2}) (244). Another stand, 20 years old, had 88 roots ft^{-2} (947 roots m^{-2}) of the size class of roots less than 0.1 in, and a 70-year-old stand had 77 roots ft^{-2} (829 roots m^{-2}) (245). In a 6-year-old plantation 83% of the total root biomass was in the upper 18 in. (46 cm) of soil (157).

Values for total root biomass were found to be about 32,000 lb. A^{-1} (36 mt ha^{-1}) for loblolly pines between 12 and 16 years of age (average DBH of the 16-year-old trees was 6.5 in. (16.6 cm)) (1258, 885). However, another study estimated the root biomass of trees within these ages to be 16,000 to 19,000 lb. A^{-1} (17.9 mt ha^{-1} to 21.3 mt ha^{-1}) (949). Quantities similar to the latter two were found for 5- and 6-year-old loblolly pines (885, 157).

The reports concerning which root size class contains most of the biomass are not in agreement. One claims the taproot alone comprises 66% of the total root biomass at age 16, and that roots less than 0.12 in. (0.3 cm) made up about 12% of the biomass (1258). Others attribute the major portion of the biomass to the fine roots (157, 885). Roots less than 0.2 in. (0.5 cm) diameter made up 53% of the total root biomass of 12-year-old trees. However, the author of the study felt that the estimate may be too large (885). It is probable that the dominance of the fine root fraction shifts to the main root system with increasing age (885).

In terms of numbers of roots, in a 35-year-old stand 85% of the roots were in the size class less than 0.1 in. (0.25 cm) diameter, 14% in the 0.11 in. to 0.30 in. (0.28 to 0.76 cm) size class and 2% in the class of larger roots (244).

Disregarding size class, about 96% of the surface area of the loblolly pine root system is suberized. The unsuberized portion usually consists of less than 1% growing tips and 3% mycorrhizae (669).

The percentage of dead roots on healthy, 37-year-old loblolly pine was about 6%. The proportion of dead roots on healthy shortleaf systems was almost three times greater (254).

However, the general habit of shortleaf is different from loblolly. On the average, shortleaf produces a greater number of roots which are generally of smaller diameter than loblolly of comparable age. The distribution of the roots is also different. Loblolly has a greater portion of roots at the 3 in. (8 cm) depth than shortleaf, which exceeds loblolly at shallower depths (254).

The proportions of elements in the roots were found to be similar in two studies. One was of a 16-year-old plantation on the Duke Forest in North Carolina and the other was a 6-year-old plantation in Louisiana.

Weight of element component to total root weight (%)

	N	P	K	Ca	Mg	
6 years	0.19	0.05	0.065	0.12	0.04	(157)
16 years	0.17	0.04	0.172	0.12	0.06	(1258)

Trees growing on fertilized plots in the Louisiana plantation had somewhat greater elemental contents (157).

The rootwood of loblolly pine has a higher caloric value than root bark, the opposite of the relationship between stemwood and stem bark. The difference between caloric value of loblolly rootwood and slash pine rootwood is not significant (885).

Genetic Variation

Genetic variation has been observed in the root characters of loblolly pine. Research has been conducted primarily in the area of drought resistance.

Differences have often been noted between geographical groups of Loblolly pine. Root systems from Maryland seed sources have exceptionally well-developed fibrous roots. This was noted independently in both Maryland and Texas nurseries (1228). Root weight between west Texas (dry) and east Texas (wet) sources differed at the 5% level under the age of 24 weeks. The west Texas source was not only heavier but also averaged more root tips. In the upper 6.3 in. (16 cm) of soil the eastern source had a comparable number of tips, but below 6.3 in. it had fewer. The eastern source had more root tips of roots originating on the upper 1.2 in. (3 cm) of the main root, but the western source exceeded the eastern below 1.2 in. Seedlings of the disjunct (western Texas) population source generally had faster growth rates. They were also able to utilize phosphorus at lower concentration levels than were eastern Texas sources (1344). Growth of the primary root of most upland sources was faster than for lowland sources (1344).

Survival after transplanting is correlated with the number of new roots regenerated and transpiration per day. Genetic differences have been found in the number of new roots. No such findings were indicated for the root to shoot ratio. Of various planting dates, the early June date brought out the greatest differences in survival between progenies, with survival ranging from 39% to 84% (102).

Despite these observed differences between populations, the differences between individuals are usually considerably larger than the average differences among seed sources. Distribution of the roots in the soil profile, numbers of roots, and the growth rate of roots appear to be most related to the root aspects of drought hardiness (686). However, the correlations between these traits and seed source are not significant, at least in the case of east Texas sources vs. west Texas sources. Nor were seedling dry weight or root lengths correlated with families that had been previously determined as drought-resistant or drought-susceptible. Certain root traits are correlated with drought resistance, but the variation within family groups is too great to ascribe particular characteristics to any one group.

As mentioned before, the large variation in loblolly pine is in response to both heredity and environment. The two cannot be entirely separated because of intergenotypic interactions between unrelated families of loblolly pine. The relative seedling root surface area, as well as other shoot characteristics of a family, differs statistically according to the influence of competition from another family, with the degree of response dependent upon the particular families involved. So, a "pure" stand grows differently from a "mixed" stand. Quantitative aspects of this phenomenon have not been studied (5).

One heritability study conducted on seedling loblolly pine found narrow sense heritability to be low for the characters observed. The characters with the highest estimates were the number of lateral roots longer than 4 in. (10 cm), root weight, and the ratio of shoot weight to root weight. The authors concluded that dominance variation is more important in the genetic variance of the traits studied than additive variation (1134).

Grafting

Root grafting is common in loblolly pine stands (845, 1054). Between 5% and 25% of the trees in pole and sawtimber stands are grafted to other trees (845, 1054). The frequency is inversely related to the distance between trees (1054).

Average distance between trees (ft)	Stumps with root grafts (%)
4.5 (1.4 m)	3
3.2 (1.0 m)	6
2.0 (0.6 m)	14

Grafting frequency is also influenced by site (1054). In one stand, 9 living stumps were found in an area of approximately 0.5 acre of thin rocky soil; only a few were found in the surrounding area (1054). Also, natural stands have a higher frequency of root grafting than plantations due to the irregular spatial distribution of the trees (1054).

In the relationship of a stump grafted to a living tree the translocation rate is inversely related to the proportion of root-grafted tissue, which usually decreases with increasing distance between the stump and the donor tree. The reason for this involves the proportion of stump xylem tissue to total xylem tissue that must be traversed in the movement of the materials. The new tracheids of the stump tissue are short and disoriented. Stump and donor that are close together have a slower translocation rate because a greater proportion of the total xylem tissue is from the twisted xylem of the living stump than is so in a union of trees farther apart (1054). Many root grafts appear non-functional in translocation except during periods of water stress. The rate is often greater than 5 ft. hr^{-1} (1.5 m hr^{-1}) Most grated stumps die within 20 years (1054).

Adventitious Rooting

Loblolly pine does not easily form adventitious roots. Buried stems do not grow rootlets above the root collar (1094). Forty-six percent of cuttings took root from a test of cuttings from 1-year-old seedlings (416). Rooting cuttings in January produced the best results. The response was least in May. (968) Loblolly at 2 to 3 years of age can be air-layered with about 80% success, but the rate drops sharply beyond that age (770). Shortleaf pine air-layers much more readily than loblolly pine, although loblolly pine exhibits considerable variation (1352, 770).

SEASONAL GROWTH PATTERN

Loblolly pine roots show no regular periods of peak growth, except that, in general, the activity is greatest in spring to early summer, and again in late summer to fall. Little growth occurs during the winter season (1187, 960, 669). In winter, growth is limited by low temperatures and in summer by low moisture. Under favorable conditions root growth may continue year-round (1187, 960, 119, 121, 124, 31). Below 12°C increased moisture had no accelerating effect on the rate of root growth (1187). Root elongation ceased entirely after two weeks under a regime of 10°C/2°C day/night temperatures. Increasing the night temperature to 4°C resulted in a rapid increase in root elongation (123). Warm day temperatures offset low night temperatures over a prolonged period (123, Fig. 3). During the summer, roots will enter dormancy during periods of moisture stress.

The moisture content of the needles can give an indication of the growth activity of the roots. One study found that when the moisture content of the needles fell below 150% root elongation ceased. The needle moisture content, expressed as a percentage of the oven dry weight, was about 200% at field capacity and 85% at the permanent wilting point (126).

New root tips of short roots appear within two weeks after transplanting, regardless of the time of planting (moisture not limiting). But the period of time elapsing between transplanting and commencement of elongation of lateral roots shortens from 10 weeks in a November planting to 4 weeks in a March planting. At least up to late spring, the amount of new root growth of later plantings (from the previous fall) did not overtake that of the earlier plantings, even though commencement of root growth of the early plantings was delayed (119).

Root growth of loblolly pine is clearly controlled by temperature and moisture, but other factors may also be influential. Girdling and defoliating experiments have shown that the stimulus initiating root growth after transplanting most likely comes from the needles; it is not a carbohydrate (433). Changes in light intensity induce changes in the rate of root growth. Roots of 3-month-old loblolly seedlings grown at 25°C with 12 hour illumination responded to various light intensities. At 295 foot candles average daily root growth increased from 0.073 in. (1.86 mm) per day on the third day to 0.120 in. (3.04 mm) on the fifth day. At 119 f.c. the rate of root growth decreased from 0.045 in. (1.14 mm) per day on the fourth day to 0.390 in (0.99 mm) on the sixth. A sudden large increase in light intensity from a low initial intensity may retard root growth for a few days before it starts to increase. A moisture deficit may be involved. An abrupt increase form 991 f.c. to 5330 f.c., however, resulted in a steady increase in daily growth from 0.251 in. (6.38 mm) on the second day to 0.324 in. (8.22 mm) on the twelfth day. Both length growth and formation of lateral roots increased. Growth cessation lagged 2 or 3 days after abrupt darkness from 5330 f.c. (10,000 f.c. is commonly considered full sunlight). Low light intensity is probably a contributing factor to the slow growth and short periods of cessation of root growth of loblolly pine observed during the winter (82). It also probably contributes to poor root development under heavy overstory (894).

Light Effects on Roots

The root system of loblolly pine seedlings, especially as it develops in shade, is not extensive enough to compete with most larger trees, as compared to young oaks which have deep, strongly developing root systems among other characteristics developed to cope with forest competition (245). Hence, loblolly is a poor competitor for soil moisture in heavy shade (894).

Other aspects of the root system are also affected by light conditions. Mycorrhizal development is greatly affected by light intensity, indicating that "surplus" carbohydrates promote mycorrhiza formation (1260). Mycorrhizal growth is greatest at full sunlight under natural daylengths. The effect of an extended photoperiod (extended at a rate of 45 f.c.) on loblolly and Virginia pines was not great; the effect on white pine was much greater (477). Shading of loblolly seedlings in the seedbed and cold storage of lifted seedlings lowered the carbohydrate reserves of the roots. A correlation existed between survival of shaded or stored seedlings and carbohydrate reserves (431). It did not exist in untreated plants; and there was no correlation between subsequent root growth and food reserves of the roots (431, 432).

ROOT-SHOOT RELATIONS

The ratio of root weight to top weight has been found to be 0.17 to 0.23 for trees 12 to 16 years old (1258, 949, 885). Root to top ratios for seedlings range anywhere from 0.14 to 1.2 (245, 336, 146). In one study, seedlings maintained a ratio of 0.14 for the first two-thirds of their first growing season and increased to 0.50 by the end of the season (146).

The relative proportion of root to shoot may be constant for a given tree weight, according to recent experiments and reinterpretation of data. It does not respond to alterations in nitrogen, soil moisture, or light intensity except indirectly with a change in plant weight. Only the most drastic treatments will alter the relationship (724). The ratio has even been reported to remain constant for seedlings grown under different light conditions even though the rate of increase in total dry weight was greater in sun-grown seedlings. This has been interpreted as an indication that the mechanism which governs distribution of photosynthate maintains the same apportionment under different light conditions.

Root biomass may be estimated with some accuracy from measurement of above-ground parts. A study conducted in North Carolina above the Haw River compared the estimated root biomass of 14-year-old trees (calculated from the diameter at breast height and diameter at stump height) with the root biomass as estimated from soil core sampling. They were in reasonable agreement (949). The equations that were used imply that as stem diameter increases so does root weight; this is probably true only up to a point, since root growth eventually stabilizes as the canopy does upon closure.

When stems are buried in transplanting, changes occur in the periderm layer, although adventitious roots do not form. The underground portion of the stem becomes covered with a smooth brownish layer of cork cells, similar to that covering roots. The phloem of the buried stem is approximately the same thickness as the upper stem but appears to contain a higher concentration of starch grains and no chlorophyll (1094).

The density of rootwood is less than that of stemwood. Tracheids of roots are longer, larger and thinner-walled than those of the stem. The difference between spring- and summer- wood tracheids is not apparent in root tracheids as it is in stems. These differences may partially account for the more rapid movement of materials through the roots than through the stem (861).

Root growth contrasts with top growth in terms of seasonal activity. Root growth proceeds for 12 months of the year. About 80% of the root growth occurs during the 5-month period when the shoot is growing (960). Rapid growth of both shoot and root coincide with rising temperatures and abundant moisture in the spring (960). Root growth is much more sensitive to environmental influences than the shoot. Under moisture stress the needle growth is relatively unaffected, while stressed roots will enter dormancy (624).

A tendency may exist toward alternation between root and top activity (578).

Nutrient accumulation in loblolly seedling tops is much more variable than in roots. Uptake of P, K, Ca, and Mg by the roots did not diminish throughout the study period in one study. In the tops, P and K followed the pattern of weight increase, and Mg accumulation followed foliage development and showed almost no increase after late August. Uptake of Ca by the tops was nearly linear from July to December. Uptake of Fe was similar in both roots and tops, neither showing much accumulation until late July and mid August, respectively. The accumulation pattern of Mn was similar, but the roots reached 50% uptake in September, whereas this point was not reached in the tops until a month or two later (284).

In a 16-year-old plantation on coarse sandy loam soil in the Duke Forest in North Carolina where the root biomass was 23% of the top biomass, the elemental biomasses of the roots, expressed as percentages of the top biomasses, were as follows: N 24.9, 0 54.7, K 37.0, Ca 27.8, Mg 47.4. Excluding leaves and dead branches (which avoids errors inherent with variable dead branch weight and seasonal changes in leaf weight), the percentages were: N 42.9, P 87.1, K 54.0, Ca 37.1, and Mg 62.0 (1258). Similar percentages were found for K, Ca, and Mg in another study (1258).

UPTAKE

Mineral Uptake

Seedling root concentrations of K, Ca, P, Mg, Si, Zn, B, Fe, Mn, Na, Al, and Cu did not differ significantly between loblolly, shortleaf and white pines in one study. Foliage and stem concentrations of loblolly pine did differ from shortleaf pine for the minerals Zn, Fe, Al, Na, and Mn. All concentrations of minerals except Fe were significantly different in the top among the three species tested (870).

The study discussed above was conducted in a greenhouse on seedlings growing in sand. Loblolly pine generally had greater mineral content than shortleaf pine, with some exceptions. Likewise, white pine had a higher mineral content than loblolly pine (870).

	K	Ca	P	Mg	Si	Zn	B	Fe	Mn	Cu
Higher content	LL	WP	WP	WP	SL	WP	LL	SL	WP	LL
	SL	LL	LL	LL	WP	LL	SL	WP	LL	WP
Lower content	WP	SL	SL	SL	LL	SL	WP	LL	SL	SL

(LL=loblolly pine, SL=shortleaf pine, WP=white pine)

Salts are absorbed through suberized roots as well as through the apices. Dormant roots show a very low uptake of P which probably reflects the low level of physiological activity during dormancy (234).

As uptake of nutrients is not limited to unsuberized roots, neither is it limited to the surface fine roots. The taproots of loblolly seedlings extending into the subsoil were shown to absorb a notable portion of the water and nutrients. Maximum growth was attained when both surface roots and taproots were supplied with a full complement of nutrients (764).

Of three nitrogen sources--nitrate, ammonium, and urea--nitrate was associated with the least total nitrogen content, soluble nitrogen content, and free amino acids in the foliage. The most extensive root development occurred in the presence of the nitrate source of nitrogen. Root nitrogen content itself was little influenced by nitrogen source. The urea source was associated with highest total N content and soluble N content of foliage, and ammonium with the largest amount of free amino acids (929).

Loblolly pine as well as other Southern pines can utilize nitrate as a source of N. Roots of slash, shortleaf and loblolly pines were found to possess the necessary enzyme to reduce the nitrate. The enzyme activity, however, is influenced by the substrate pH and N source. Under the conditions of forest soils typical of the lower Coastal Plain, the activity of the enzyme is low. Metabolism of ammonium may produce an end product that inhibits the nitrate reductase (1165).

Nitrogen source affected the calcium content of the foliage, the greatest occurring with the nitrate source (929). Conversely, the N content was affected by applications of Ca. Total N content of roots decreased with application of Ca to sand culture in which the loblolly seedlings were growing, although foliar N increased (929).

Water Uptake

Water and salts are absorbed by both suberized and unsuberized portions of the root system (234). Although permeability of the apical root segments is greater than in suberized roots (permeability=absorption rate per unit surface area), the total uptake by suberized roots accounts for the major portion. Mycorrhizal roots make up most of the difference (669, 234). Permeability of suberized roots increases with diameter, probably due to more breaks in the periderm and to the shorter distance from the root surface to the xylem. This distance is shorter in larger roots because the stele makes up a greater portion of the cross section (669).

Low soil temperature reduces the absorption of water by loblolly pine more than it does in red or white pines. Loblolly and slash pines absorbed only 40% as much water at 10°C as at 25°C, while red and white pines absorbed 60% (665).

The roots are responsible for the failure of a wilted loblolly plant to recover after reaching the wilting point. Detached leaves will regain turgidity after being stressed to a point where leaves of intact plants will not recover. It is likely that the increasing dehydration causes discontinuities in the water columns of the roots (172). However, root systems of 2-year-old seedlings that had been killed by heat have maintained turgidity in the foliage for two weeks. In this case the resistance to flow that eventually wilted the plants was found in the stems. Water continues to pass through dead root systems. Resistance is thought to build up from blockage by materials escaping from dead root cells (664).

EXUDATION

Detopped root systems of loblolly pine do not exhibit root pressure exudation. However, solution is readily exuded when pressure is applied. The salt concentration of the exuded solution eventually stabilizes at a level slightly less than the external solution. Individual root segments do exude at a slow rate relative to the rates of white spruce and hardwoods (891).

EFFECTS OF EXCESSIVE AND DEFICIENT MOISTURE

Drought-hardy loblolly pine seedlings generally have deeper root systems and wider ranging laterals than drought-susceptible seedlings (1227). Higher Ca content in the roots has been correlated with greater drought resistance (430). Survival for the first two years is most critical to the seedling. Beyond that age the root system is well enough developed to cope with all but the most severe drought.

The usual response of roots under moisture deficiency stress is to enter dormancy. Although the number of active roots diminishes substantially during periods of low rainfall, the lessening of daily average increment is less conspicuous (1187). After severe stress dormant roots may not resume growth even when watered daily. The roots may become active again if the stress was less severe. Three 7-day cycles of drying and wetting resulted in reduced root growth in one study. Only 6% of the total root growth occurred during the third cycle, while seedlings that were watered daily continued growth in the third cycle as in the first (624).

Two months of inundation during the dormant season does not affect the survival of loblolly or shortleaf pine seedlings and may even increase growth (1306, 199). Flooding for 14 or more weeks is detrimental to growth, especially if the period extends into the growing season (199). When dormant season flooding of the roots continued for three years, the height of flooded seedlings was only 50% to 75% that of unflooded checks (1306).

During the growing season, flooding initially causes an increase in water uptake and then a decline after 2 or 3 days, indicating injury to the roots. Seedlings drained after a month of inundation showed a continuing decline in uptake for a week or two more (906). Roots of seedlings that were flooded for 3 months and then drained and allowed to dry down below field capacity appeared normal, light brown in color, with growing tips appearing after 10 months. Continuous flooding for the 10 months resulted in serious injury to the root systems, with many roots dead and the others a blackish-brown color. Alternating cycles of flooding for two weeks out of every four left no apparent injury symptoms on seedling tops, but roots were blackish-brown with no growing root tips, and many roots were dead (580).

Fertilization of seedlings standing in water ponded over a gleyed clay loam with a plastic B horizon resulted in higher mortality than nonfertilized seedlings. When the water table was held at or below the soil surface, height growth was stimulated through the second growing season. Needle lengths and foliar N, P, and K increased with drainage and fertilization (1229).

Older trees can typically survive one season of flooding, but will succumb during the second season of continuous flooding

(481). Loblolly pine is more tolerant of flooding than either shortleaf, Virginia or pond pines (481). Seedlings of loblolly and shortleaf both had reduced root weights when subjected to oxygen-poor soil air, but the root weight of loblolly pine was reduced much less than that of shortleaf pine. High levels of carbon dioxide did not affect root weight (1354). Loblolly pines were healthy on sites that were flooded as long as 16.1% of the growing season in Tennessee (April 1 to October 1) (482).

RESPONSE TO SOIL CHARACTER

Microrelief

Loblolly pines growing on "pimple mound" sites of southwest Louisiana show definite differences in the root system with differences in microrelief. The mounds are less than 115 ft. (35 m) in diameter and less than 6.5 ft. (2 m) in height, and often less than 49 ft. (15 m) diameter and rise 1 to 2 ft. (0.3 to 0.6 m). The land between the mounds is flat to slightly concave. Flat sites are wetter than the mound sites. Dimensions of above-ground parts of the trees growing on both site types were similar.

The roots on mound sites appeared healthier than those on intermound sites. Mound site roots had tight reddish-brown bark that exfoliated in thin layers. There was more branching of fine roots from large laterals and fewer dead roots. Roots on flat sites were thick with dark grey or black bark. "Brown patch", which is excessive and premature formation of rough bark on roots, was common. The brown patch indicates starvation of outer phloem from either age, impeded synthesis, or impeded translocation of food, disease, or injury. The lenticels of flat site roots were hypertrophied.

The general form of the root system was also different. Roots on mound sites had a deeper distribution (855). The laterals descended at a steeper angle than on flat sites. The roots of trees on flat sites were more concentrated at the surface. A dense mat of roots formed about the base of the tree; many lateral roots paralleled the surface at a shallow depth. The only vertically oriented roots were found immediately beneath the trunk. Roots that originated on mound sites and entered the flat areas decreased sharply in diameter upon entrance, after which taper and branching were minimal. The intermound sites had greater numbers of roots within the profile at 0 to 8 in. (20 cm), although, overall, the average root surface area on mounds exceeded that on flat sites in both years of observation.

Mycorrhizae were very responsive to moisture changes. The average mycorrhizal surface area fluctuated during the period of observation more than it did for all roots 0.2 in. (5 mm) or less in diameter. Nodular forms of mycorrhizae were prevalent during times of excess soil moisture. In times of deficient moisture the clusters of mycorrhizae tended to turn black. The surface area of mycorrhizae of the wet, flat sites peaked during the driest periods, however. On mound sites the mycorrhizal surface area decreased during these spells (751).

Texture

Roots of loblolly pine grow to greater lengths in coarser-textured than in finer-textured soils, but somewhat slower and with less proliferation (617, 938, 1048, 124). The lower moisture holding capacity retards growth during dry periods when loam and clay soils may retain enough moisture for continued growth (617). Additions of organic matter or finer soil material to sandy soil can increase the proliferation of the roots (42). The taproot is likely to be most prominent on sandy soils (1360). On clay soils the roots grow along the cleavage planes between the peds. This phenomenon may be due to moisture collection in the joints between the peds as much as it may be due to high bulk density and low noncapillary porosity of the clay, acting as a barrier to root growth (617, 392). In any case, root systems growing in clay tend to have restricted growth. Most root development is in the lateral roots. Root systems developed in heavily compacted soils are also comprised largely of lateral roots (392). Incorporation of sand into a heavy clay soil or loosening of the soil increases the penetration of the roots and produces finer roots (392, 938, 124). Taproots in stiff clay soil are stout and short in comparison with those in sand (1360).

Heavily compacted soils bar seedling establishment. The emerging radicle cannot penetrate dense soil. Germination may be high, but puddled soil, compacted soil, or even undisturbed dense clay significantly reduces the number of successfully established loblolly seedlings (392).

Instances are reported where the effective rooting depth of loblolly pine is limited by a dense subsoil horizon (127, 244, 124). One study compared the properties of the soil horizon from which 75% of the root mass was found to the properties of the soil deeper in the profile where few roots were found. With the change in depth from shallow to deep, bulk density increased from 25.89 g in^{-3} (1.58g cm^{-3}) to 29.17 g in^{-3} (1.78 g cm^{-3}); soil oxygen decreased from 19% to 13%; total pore space decreased from 36% to 33%; the sand fraction increased from 55% to 78%; and the silt fraction decreased from 25% to 9%. The fine roots less than 0.01 in (0.25 cm) in diameter appear to affected most by the proportion of fines in the soil, while larger roots 0.4 in. (1.0 cm) or less in diameter were influenced most by bulk density. Roots larger than 0.4 in diameter were influenced most by field capacity (170).

Loosening compacted soil by means of a subsoiler in effect prunes the roots. The tree reponds by sending out two to five new roots from the vicinity of the cut end. Some of these roots grow in the same general direction as the parent root. Others turn and grow horizontally or vertically along the subsoiler slit.

On the eroded soils of the Copper Basin in Tennessee root development of pine was very shallow; adequate moisture at the surface and shallow depth to underlying rock were the reasons given. Examinations were made of one specimen each of loblolly pine, pitch pine, Virginia pine, and shortleaf pine. The loblolly pine had the weakest root development of all (21). However, on Caddo silt loam in southeastern Arkansas when prolonged rains had softened the upper soil layer, loblolly pine was more windfirm than shortleaf pine. This soil is a silt loam for the top 6 to 10 in. (15 to 25 cm) and a silty clay loam for the next 3 ft. (1m) or more. The internal drainage is poor (170).

Soil Temperature

Root growth of loblolly pine increases with increasing soil temperature above 5°C to a maximum at 25°C. At higher soil temperatures the root growth declines (82). Respiration increases with rising temperature. In fine roots with active mycorrhizae, a peak rate in oxygen consumption was reached at about 18°C. Nonmycorrhizal roots less than 0.2 in. (5 mm) diameter and roots with moribund mycorrhizae showed no decrease in respiration up to 20°C (75). Nonmycorrhizal short roots of seedlings growing at 40°C root temperature for 5 weeks tended to die off, even causing mortality of the seedlings (813). A sudden increase in temperature from 20°C to 35°C caused a marked increase in growth during the first hour and then a decline. Root growth ceased almost completely after 30 hours. Resumption of growth was delayed 6 days after the temperature was returned to 20°C. Part of the delay was due to the roots having entered dormancy at 35°C (82).

The effect of decreasing the root temperature was to cause an increase in the starch content of the root tips and a change in transpiration (82). As previously mentioned, transpiration was reduced by 60% in loblolly pine with a gradual cooling of the soil from 25°C to 10°C. The reduction is presumed to result from changes in viscosity and permeability of the root protoplasm (665). An abrupt decrease in temperature produced a lowering of the transpiration rate and then a gradual increase to a constant rate at the new temperature. A sudden increase in temperature reversed the procedure. A large increase in transpiration was followed by a gradual decrease toward a stable rate (82).

Root Growth, Soil Fertility Relationships

Calcium is essential for root development. In an experiment where the surface roots of loblolly pine seedlings were growing in fertile topsoil to maintain top growth, and the taproots were growing either in a nutrient solution or infertile loamy sand, the taproots elongated when Ca was the only cation present in deionized water. Without Ca, root growth was very poor. Maximum growth occurred when all nutrients were available to both surface and subsurface roots (764).

Amendments of calcium may be needed on some soils, especially plantations on coarse textured soils where high-analysis, low-Ca fertilizers are being used. Where the soil solution ratios of a_{Ca}/a_{Mg} and M_{Ca}/M_{Mg} are below 0.75, root length growth may be stunted. Because of the divalency of both Ca and Mg, changes in concentration due to changes in soil moisture content are proportional where there is an adequate supply of Ca and Mg in exchangeable form. The ratio $a_{Ca}/\sum a_{cation\ i}$ can also be used; the critical ratio is 0.10, below which loblolly pine taproot growth is inhibited. When using this ratio soil moisture content must be taken into account (764).

The relationship of N:P concentration is also important to the early growth of loblolly roots. However, in this case the top weight and root weight are affected proportionately. Additions of N reduce both top and root dry weights in P deficient soil. Weight was also reduced when N was added at rates of 160 ppm or more and P was added at a rate of 20 ppm (943).

Loblolly pine roots increase the N supply of deficient soils. Plantings of hoop pine (*Araucaria cunninghamii* Ait.) on a lateritic podzolic soil in Australia failed until they were underplanted with loblolly pine. The effect is noticeable as far as the loblolly pine root system extends, but the exact mechanism through which soil N is increased is not known (976).

MYCORRHIZAE

Ectomycorrhizae

Fungi associated with ectomycorrhizae on loblolly pine in synthetic culture: *Agaricus placomyces* Pk., *Amanita citrina* (Schaef.) S.F. Gray, *Amanita muscaria* (L. ex Fr.) Pers. ex Hook., *Amanita parcivolvata* (Pk.)Gilb., *Amanita rubescens* (Pers. ex Fr.) S.F. Gray, *Amanita virosa* (Fr.) Quel., *Boletellus betula* (Schw.)Gilb. (*Boletus betula*), *Boletus rubellus* Krombh (*B. bicolor*), *Boletus miniato-olivaceus* Frost, *Cantharellus cibarius* Fr., *Cenococcum graniforme* (Sow.) Ferd. & Winge, *Laccaria laccata* (Scop. ex Fr.) Berk. & Br. (*Clitocybe laccata*), *Leccinum chromapes* (Frost) Sing. (*Boletus chromapes*), *Pisolithus tinctorius* (Pers.) Coker & Couch, *Rhizopogon luteolus* Fr. & Nordh., *Russula lepida* Fr., *Suillus brevipes* (Pk.) Kuntze (*Boletus brevipes*), *Suillus cothurnatus* Sing., *Suillus granulatus* (L. ex Fr.) Kuntze (*Boletus granulatus*), *Suillus hirtellus* (Pk.) Kuntze, *Suillus luteus* (L. ex Fr.) S.F. Gray (*Boletus luteus*), *Thelephora terrestris* (Ehrh.) Fr., *Tylopilus eximus* (Pk.) Sing. (*Boletus eximus*), *Xerocomus chrysenteron* (Bull. ex St. Am.) Quel. (*Boletus communis*) (1327, 130, 188, 962, 188, 325, 323, 809, 812). In synthetic culture *Paxillus atrotomentosus* (Fr.)Fr. and *Russula emetica* (Schaef. ex Fr.) Pers. ex Fr. (*R. fragilis*) formed mycorrhiza-like structures on *P. taeda* but lacked the fungal sheath (1327).

Effects of Ectomycorrhizae

Carbon, applied as glucose and sucrose, has been shown to be translocated from the foliage of loblolly pine to the roots and to enter the external hyphae of mycorrhizae formed by *Thelephora terrestris* and *Pisolithus tinctorius*. Phosphorus was transported from apical foliage of loblolly pine to the roots, but none moved into the hyphae of the mycorrhizae formed by *Boletellus betula* (962). The mycorrhizae, however, do accumulate more P from the growing medium per unit surface area than nonmycorrhizal root tips, as well as providing greater absorbing surface area (673). Also, the mycorrhizal fungus *Suillus granulatus* on loblolly pine roots has been shown to be capable of providing carbohydrate to the plant in an atmosphere devoid of carbon dioxide (1342).

Another physiological aid to pine by mycorrhizae may be associated with the uptake of K. In the region of the root most effective in salt uptake, Na-activated ATPase was found in the nuclear portion of the cells. K-activated ATPase was found only in mycorrhizae, not in root cells, suggesting a relation between uptake of K and the dependence of pine on mycorrhizae for growth (772).

Utilizing these relationships and others, abundant ectomycorrhizae can improve the performance of loblolly pines over those deficient in mycorrhizae, at least in certain situations. On infertile soils the mycorrhizae can stimulate growth; survival and growth can be increased on adverse sites; and some mycorrhizae may aid in resistance to disease from root pathogens.

However, an increase in photoperiod either by extending daylength or interrupting the dark period does not greatly influence the abundance of ectomycorrhizae on loblolly or Virginia pine seedlings as compared to those growing in full sunlight. This is not true of eastern white pine, which has fewer mycorrhizae under an unnaturally long photoperiod (477).

Carbohydrate content of the roots is also affected by N and P levels (823, 977). A negative correlation exists between the high levels of N and P and the sucrose content of short roots. A negative correlation also exists between high levels of N and P and susceptibility of short roots of loblolly pine to infection by P. tinctorius (823).

Nitrogen appears to be primarily responsible for reduced numbers of mycorrhizal tips (833). Chlorosis and poor mycorrhizal development of loblolly pine at high pH can be relieved without changing the pH by applying an iron complex. Sodium nitrate inhibited formation of mycorrhizae, while application of sodium carbonate did not have this effect even though it raised the pH to 7.4 (977). The nitrate ion, rather than the alkalinity per se, inhibits the development of mycorrhizae. Mycorrhizal root tips were fewest in plantation plots fertilized with N alone, while P applications alone appeared not to affect the total number of mycorrhizal root tips. However, P fertilization did increase the relative populations of Cenococcum graniforme on loblolly pine. The relative population of another mycorrhizal type benefitted from fertilization with N+P+K, while yet another type was inhibited by all fertilization treatments. Top growth was not adversely affected by the abundance or species of the mycorrhizae in this study (833). Loblolly pine on highly-leached acid fine sandy loam from southeastern Georgia had its most extensive mycorrhizal development when the tissue concentration ratio for N and P of the seedling tops was 20:1. This was also true for slash pine on another fine sandy loam (943).

The effects of fertilization with N on ectomycorrhizal development are most apparent within 6 months after application. By the second year after fertilization the effects on the number of mycorrhizal root tips are no longer noticeable (833). Overall, the greatest mycorrhizal development is on relatively infertile soils or at medium levels of fertilization on very poor sites. Stimulation of growth by mycorrhizae is less noticeable on fertile soils, and, accordingly, the mycorrhizal development on very fertile or fertilized soils is suppressed (477, 110, 111).

Another site factor influencing mycorrhizal development is soil moisture. On adjacent mound and flat sites the periods of greatest mycorrhizal development were opposing. Mycorrhizal surface area decreased on mounds during drying periods, while on the flat sites the surface area of mycorrhizae peaked during the driest periods. The increase on flat sites during stretches of dry weather was probably in response to improved soil aeration; high soil oxygen is believed to be necessary for good mycorrhizal growth (751, 1354). High levels of carbon dioxide with adequate oxygen can further stimulate development of mycorrhizae (1354). The development of isolates of *P. tinctorius* and *Trichoderma viride* Pers. ex Fr. was inhibited by ozone, while sulfur dioxide stimulated growth at low concentrations but inhibited sporulation of *T. viride* at high concentrations (239).

Much study has been made recently comparing performance of loblolly seedlings and other pines having indigenous mycorrhizae, including the common nursery species *T. terrestris*, with those inoculated with *P. tinctorius* on routine reforestation sites as well as on adverse sites. Outplantings of loblolly pine seedlings with *P. tinctorius* ectomycorrhizae on good quality sites have shown greater plot volumes (plot volume = mean seedling volume x number of surviving trees) than seedlings with natural ectomycorrhizae or *T. terrestris*. On poor quality sites the difference is even more pronounced (810, 817). In both North Carolina and Florida, the plot volumes of seedlings with *P. tinctorius* ectomycorrhizae on the poor sites were nearly identical to the seedlings on good sites that had natural ectomycorrhizae (810).

P. tinctorius has the potential to aid in the establishment of loblolly pine and other trees on adverse sites. The fungus flourishes in temperatures too warm for other ectomycorrhizal fungi. At 27° to 39°C, *P. tinctorius* forms abundant ectomycorrhizae with loblolly and shortleaf pines, but few form within the range of 18° to 21°C (802). The mycorrhizae of *P. tinctorius* can withstand higher temperatures than can those of *T. terrestris* (818). At 14°C, seedlings with mycorrhizae formed by *T. terrestris* are slightly larger than those with mycorrhizae formed by *P. tinctorius*. At 19° to 29°C their growth is similar; at 34°C seedlings with *P. tinctorius* surpass seedlings that are mycorrhizal with *T. terrestris* or nonmycorrhizal (818). Survival of seedlings in high temperatures is related to the numbers of viable mycorrhizae surviving the heat. In a study of asceptically grown loblolly pine seedlings, approximately 80% of the mycorrhizae formed by *P. tinctorius* were viable at 40°C. Survival of the seedlings was 95%. The survival of seedlings mycorrhizal with *T. terrestris* was only 70% at 40°C, and only 30% of the mycorrhizae were viable (813).

Survival of loblolly and other pines inoculated with *P. tinctorius* was greater on coal spoils of Virginia and Ohio than seedlings inoculated with *T. terrestris* by 11% and 34% on the two sites, respectively (807). On acid coal spoils in Virginia and Kentucky, and on kaolin clay wastes of Georgia and the eroded Copperhill, Tennessee, the growth of loblolly pine seedlings inoculated with *P. tinctorius* was significantly greater after two years than those originally inoculated with *T. terrestris* (810).

Various fungi, including P. tinctorius, have been found to prevent infection by some fungal root pathogens. Various protective mechanisms may be involved. The mantle of the mycorrhizal fungus may function as a mechanical barrier to pathogen entry; antibiotics may be produced by the mycorrhizal fungus and/or by nondiffusable fungal inhibitors from cortex cells of the roots in response to mycorrhizal development; chemotactic attraction by mycorrhizae may be low to zoospores in comparison with nonmycorrhizal, unsuberized roots (821, 1315). Seedlings mycorrhizal with Laccaria laccata, Suillus luteus, P. tinctorius and other mycorrhizal species were resistant to infection when incubated with zoospores of Phytophthora cinnamomi Rands (802). Although nonmycorrhizal roots of loblolly pine are just as susceptible as shortleaf pine to artificial infection by P. cinnamomi, loblolly pine shows less susceptibility to P. cinnamomi infection and littleleaf disease development. Differences in specific mycorrhizal associations between the two species may be involved (821). Mortality from Rhizoctonia solani is reduced on seedlings with P. tinctorius mycorrhizae. The mycorrhizae must be formed on the seedlings prior to infection in order for the protective mechanism to be effective (1315).

Inoculation

Inoculation of seedlings with a specific fungus can be used to help prepare the mycorrhizae for particular site conditions in order to achieve the best growth of the pine. Most of the research done on inoculation of loblolly pine has been with P. tinctorius, testing it for its ability to be introduced into fumigated soil, to persist and spread after outplanting, and to find the most efficient and satisfactory method of inoculation (816, 1017, 810, 817). Other tests involve determining the fertility of the growth medium under which the roots are most receptive to the inoculum, and the effect of containers on establishment of natural mycorrhizae (823, 1159).

Containerized seedlings that are outplanted without prior inoculation with mycorrhizal fungi develop mycorrhizae, but not as uniformly as bare root stock. The container presents a physical barrier to mycorrhizal infection. Mycorrhizal development is crucial to first-year survival, so the container must degrade quickly to allow invasion of mycorrhizal fungi (1159).

On the other hand, the growth medium of containers and nursery beds can be infested with inoculum so that seedlings are established with mycorrhizae before outplanting. Trees can be inoculated with P. tinctorius both by basidiospores and by mycelia. Colonization by mycelial inoculation is more rapid and vigorous than by spores (816). Basidiospores of P. tinctorius require about 4 months to develop sufficient mycorrhizae to stimulate seedling growth. This time lag could allow colonization of the roots by other species. However, spores can be successfully used to inoculate loblolly pine seedlings either by infestation of the growth medium or by dusting the roots directly (1017, 810).

Soil fumigation generally retards the rate and extent of mycorrhizal establishment in the nursery. Development of the Hartig nets may occur within 3 weeks on roots of loblolly pine growing in untreated soil, but is delayed a week or more on fumigated soil, depending on the intensity of the fumigation (283). In order to artificially infest the soil with *P. tinctorius*, however, fumigation is necessary. Ineffective fumigation can result in high soil populations of pathogenic fungi and plant-parasitic nematodes, and colonization of the roots by indigenous mycorrhizal fungi (816).

Two years after outplanting loblolly pines with root systems successfully inoculated with *P. tinctorius* on sites in North Carolina, the *P. tinctorius* had persisted, although *T. terrestris*, *C. graniforme* and a *Rhizopogon* sp. were occupying more and more of the new short roots. The mycorrhizae of seedlings inoculated with vegetative mycelia of *P. tinctorius* had more tips, persisted longer, reproduced better, and stimulated more seedling growth than the mycorrhizae developed from basidiospores (817).

Development

Mycorrhizae appear in numbers on loblolly pine seedlings 1 1/2 to two months after germination of the seed or planting of the seedling, both on sites where naturally occurring mycorrhizal fungi are allowed to develop and on sites where the soil is infested with *P. tinctorius* inoculum (578, 119, 617). By the second week after planting, however, 40% to 60% of the primary lateral roots have growing tips on dichotomous short branches. Growth of dichotomous roots and subsequent visible mycorrhizal development begins on the laterals near the soil surface and progresses downward (119).

Growth stimulation of loblolly pine by *P. tinctorius* on the artificially infested soil was not of significant increment in comparison with nonmycorrhizal control seedlings until the fourth month of growth. In the fifth month, 47% of the total feeder roots were mycorrhizal. A similar figure was obtained for natural infection on an upland pine site. The percentage of mycorrhizal roots on the loblolly seedlings was somewhat less on an upland hardwood site. These upland soils were shallow clay loams with a disturbed A horizon over a heavier clay B horizon having considerable gravel content. The mycorrhizal development on pines growing on soils of the Coastal Plain that consisted of shallow sand to clay underlain by a sandy B horizon leveled off after the fourth month, with 20% of the short roots mycorrhizal (1159).

Ectendomycorrhizae

Very little information is available concerning ectendomycorrhizae on loblolly pine. Two types of ectendomycorrhizae have been recorded on 11-year-old loblolly pine in two plantations in North Carolina. Together, the two types occupied about 6 or 7% of the total mycorrhizal surface area. Fertilization treatments did not greatly affect the percentage of surface area occupied by these ectendomycorrhizae relative to the effect on other types of mycorrhizae (833).

Non-infectious

Early mortality of loblolly seedlings after seeding can be extremely high if the soil has been compacted or puddled by heavy equipment. On these soils the few fortuitous survivors were able to send the radicle into a crack in the soil. A major portion of the mortality that occurs soon after germination can be attributed to the failure of the radicle to become anchored (938, 500). Loosening of compacted soils improves establishment substantially (500).

Loblolly pine tends to be more windfirm than shortleaf pine on soils with a heavy subsoil and poor internal drainage. This is attributed to the deeper rooting of loblolly pine (170).

Spot die-out may occur on these types of soils where erosion has been severe. In natural stands and, more commonly, in plantations affected by this disease, spots that are roughly circular in shape and 0.1 to 2 acres in diameter die out when the trees are between 12 and 20 years of age. The die-out is not associated with any injurious organism, but is associated with very high soil moisture, sheet erosion of the surface soil, dense subsoils, reducing conditions and poor aeration. The symptoms become apparent about the tenth year due to increased intensity of competition upon canopy closure (1227, 255).

Trees growing on shallow, poorly developed soils over impervious parent material are subject to greater drought stress than trees on deeper soils. Entire stands up to 15 years of age may succumb on such soils with less than 16 in (41 cm) effective rooting depth (168).

Calcium deficiency causes a retardation of cell division in root tips, but has less effect on cell enlargement. The root tips of loblolly growing in Ca-deficient solution appear blunt and, in some cases, swollen and bulbous. The xylem is lignified nearer to the apex than it is in roots supplied with adequate Ca due to the fewer cells separating meristem from the lignified xylem (290). A zinc deficiency also results in short, swollen roots. Shortleaf pine, which has a higher Zn requirement than loblolly, appears to be more affected by the lack of Zn in water culture than loblolly pine (521).

Loblolly pine is sensitive to high levels of sodium fluoride and lead chloride when applied to the soil. The higher concentrations, in the range from 2×10^{14} M to 2×10^{-2} M, reduced root system development. Under lead treatments the roots were blackened. In this experiment, red maple appeared more sensitive to fluoride treatments than the pine, and lead treatments affected both species more than fluoride treatments (292).

Relative to three other pine species, loblolly pine is very tolerant of high salinity. In an experiment with automatically-irrigated sand cultures, several plants of loblolly pine survived 100% "sea water" while red pine did not survive beyond the 40%

level. Pinus thunbergii was rated salt-tolerant but not quite as tolerant as loblolly pine, and Pinus radiata was classed with red pine as salt-sensitive. The needles of salt-sensitive species had higher concentrations of ions, particularly sodium and chlorine, than salt-tolerant species. The ion concentration in the needles rises sharply at the highest salinity level in which all plants of a given species survive (213).

Insects

The larvae of Phyllophaga spp. feed on the roots of loblolly pine seedlings as well as many other tree species (606, 1250). Death results when the entire secondary root system and a portion of the taproot cambium are consumed. The damage is sublethal if the cambium of the taproot is left mostly intact. The grubs feed in the top 6 to 8 in (15 to 20 cm) of soil (1250).

Pales weevil, Hylobius pales (Herbst), shows attraction to root bark for oviposition, but older adult beetles show less affinity for feeding on root bark than newly emerged adults. Elimination of other food sources during site preparation is thought to be the reason for the severity of attack on pine seedlings, which were the least preferred food in the tests (581).

Nematodes

The following species of nematodes have been demonstrated to be parasitic on loblolly pine: Criconemoides xenoplax Raski, Helicotylenchus dihystera (Cobb) (H. nannus Stein.), Hemicycliophora vidua Raski, Hoplolaimus galeatus (Cobb) (=H. tylenchiformis Daday), Meloidodera floridensis Chitwood, Hannon & Esser, Pratylenchus brachyurous (Godfrey), Trichodorus christiei Allen, Tylenchorhynchus claytoni Steiner, and Xiphinema americanum Cobb (1018, 1013, 1014).

The lance nematode, Hoplolaimus, causes internal destruction and loss of mycorrhizal roots by collapsing the cortical cells as it migrates through the root (1018, 1016). The pine cystoid nematode, Meloidodera, becomes sedentary with its head in the vascular cylinder, inducing the formation of giant cells and hyperplasia of surrounding cortical cells (1018). The stubby-root nematode, Trichodorus, does not deform the cells but prevents root elongation by feeding at or near the tips of fine roots. The loss of fine roots results in a reduction in surface area, the magnitude of which is not reflected in the root weight loss (1015). Nematodes that are indigenous to the outplanting site are a more serious threat to pine growth than those species transported from the nursery in or on planting stock (1011).

Applications of Aldrin to protect seedlings against pales and pitch-eating weevils decreased nematode populations in sterilized soil. Both stylet-bearing and non-stylet nematodes were affected. There was a corresponding increase in the amount of mycorrhizal growth with the applications of Aldrin (702).

Post-emergence damping-off of loblolly pine is caused by *Rhizoctonia solani* Kuehn, *Fusarium* spp. and *Sclerotium bataticola* Taub. In the South, the combination of warm temperatures and the fungi *S. bataticola* and *Fusarium* spp. appears to produce the black root rot disease (533). The symptons first appear at about the age of 2 months, with a slight enlargement and blackening of the distal portion of the taproot and deeper laterals. These roots show reddish brown areas that become blackened and roughened, appearing about one month after the onset of the disease. Death of the roots is rapid as the infection progresses up the root system. By midsummer the lower part of the taproot and most of the lateral roots may be dead (534). Above the dead portion of the taproot numerous new roots are formed, possibly as a result of stimulation by indoleacetic acid produced by *S. bataticola* (533). These roots may succumb to the disease as well, and more new roots proliferate (534).

The amount of literature on *Fomes annosus* (Fr.) Cke. is voluminous, and much of the research conducted on one or more species of Southern pines applies to the other Southern pines as well. Several recent summaries and handbooks have been published (see 688). This account pertains only to *F. annosus* on loblolly pine in relation to other tree species.

Although isolated cases of the occurrence of *F. annosus* on loblolly pine had been reported previously, not until 1960, in Mississippi and central Alabama, was damage to loblolly stands recorded (158, 732).

Loblolly pine is among the least resistant pines to attack by *F. annosus*. In experiments with inoculations of stemwood and rootwood, stemwood of loblolly, shortleaf, slash, and eastern white pines was less resistant than stemwood of red, Virginia and longleaf pines, and eastern red-cedar (932). More roots of loblolly pines were infected 6 months after artificial inoculation than of longleaf or slash pines (536). The fungus grew at a faster rate on loblolly and slash pine roots than on roots of longleaf pine. In the field, disease centers in loblolly pine or slash pine stands spread more rapidly than disease centers in longleaf pine stands (538). The same relationships held for loblolly, shortleaf, slash, Virginia and longleaf pines in one test of seedling mortality, although a second test showed no significant differences in mortality between loblolly, slash and longleaf seedlings. Average mortality for all the pines tested ranged from 64% to 82% (681, 685).

No genetically related resistance to *F. annosus* by loblolly pine has yet been demonstrated (686, 55).

Loblolly pine is subject to the littleleaf disease which involves the pathogen *Phytophthora cinnamomi* (Rands) in combination with unfavorable soil conditions. The disease occurs mostly on trees more than 20 years of age or greater than 3 in (8 cm) DBH (595). The diseased root systems are characterized by exfoliation of the bark which produces brown patches, large pitchy cankerlike lesions, and dieback of roots (595). A critical percentage of dead roots occurs somewhere between 18% and 34%, beyond which the root system can not adequately maintain the top in healthy condition (254).

Loblolly pine is not as susceptible to littleleaf disease as shortleaf pine. The susceptibility is related to resistance to infection by P. cinnamomi, the tolerance of the tree to poor soil drainage and aeration, and the vigor of the tree (1356, 1354).

Loblolly pine is less susceptible to damage of the root tips by P. cinnamomi than shortleaf pine; it appears to have more vigor in regenerating new roots after an attack. Aeration of the soil probably does not greatly affect pathogenicity of P. cinnamomi (1354, 811). Rather, the tolerance of the roots to poor soil aeration is a greater factor in resistance to littleleaf disease (1356, 1354). Loblolly pine, as noted earlier, can withstand conditions of poor aeration with less stress than shortleaf pine (1354, 481). Loblolly pine is somewhat better suited to sites that encourage littleleaf disease in shortleaf pine.

Phymatotrichum omnivorum (Shear) Dugg., which causes cotton root rot of shelterbelt trees in Oklahoma and Texas, attacks loblolly pine as well (1227).

Stereum sanguinolentum Alb. & Schw. ex Fr. caused extensive root and stem rot on loblolly pine in South Africa (754). Cylindrocladium clavatum caused root disease in Brazil, attacking loblolly pine up to 15 years of age (539).

EFFECTS OF PLANTING METHODS

Experiments have been made subjecting seedling roots to various treatments before planting in order to improve survival, growth, or resistance to pests. Soaking seedling roots in solutions of indolebutyric acid generally increased root volume, but there was no consistent relationship between root volume and concentration of the acid. Mortality increased markedly following treatment with concentrations above 20 mg l^{-1} (796). The insecticide Orthene^R (o,S-dimethyl N-acetyl phosphoramidothioate) can be applied by dipping the roots in order to control pales weevil. Greenhouse-grown seedlings were protected from the weevil damage for 60 to 90 days with dosages of 0.1 to 0.3 g active ingredient per seedling (1263). Milled pine bark as the growing medium for containerized seedlings promotes good development of the secondary roots and mycorrhizae (1017).

Much experimentation has been directed toward finding a way to reduce mortality of bare-root stock resulting from exposure at the time of planting. Bare-root stock can withstand 30 min. of exposure, more or less, depending on the weather conditions, without reducing the survival (1094). Roots dipped in clay suspensions are protected from dessication for about twice as long or more (1095, 1157). Soaking the roots in water also extends the allowable period of exposure, but not as long as a clay dip. The treatments do not protect the seedlings from drought once they are planted. Amendments to the clay can provide additional nutrients. Using clays of high CEC satuarated with a single cation appears to be ficial to the early growth of seedlings (1157). Coating the roots with a 1% solution of alginate (B-D-mannurono-pyranose), a hygroscopic gelatinous substance, has a similar effect in protection of seedling roots from dessication (749). Both clay and alginate coated seedlings have exhibited better vigor than untreated seedlings in the first growing season (1095, 749).

Planting depth affects survival and growth of seedlings. Shallow planting with a portion of the root system exposed is extremely detrimental to their survival and growth (1094, 1201). The effect of deep planting, however, is variable. On well drained soils the seedlings grow normally, or top growth may be stimulated, an effect that is apparent for at least two years after planting (1094, 463). Survival is not affected (1094). No roots form above the root collar on the buried stem (1094, 463). On poorly drained or eroded soils the effect of deep planting is detrimental. Since no roots grow on the stems, deep planted seedlings have no adequate source of nutrients on thin topsoils or anchorage in soils with a high water table (463, 1201).

The form of the root system on direct-seeded pines differs from that of planted pines. The root systems of direct-seeded seedlings have vertical taproots with laterals developed on all sides growing out from the taproot almost perpendicularly. The original root systems of planted trees are more irregular. Almost all have twisted, intertwined roots in the upper 3 in. (8 cm) or so, regardless of the method of planting. Taproots are often bent, even on carefully planted trees. The center-hole method of planting results in a more spreading root system than slit planting, but the root system is often deformed in comparison with undisturbed seedlings (739).

Subsequent root growth in planted stock may show a tendency to favor the plane of the planting slit (118). Bent roots either turn downwards or new roots develop along the curvature (1201). The lateral root development in seedlings with deformed taproots is extensive, while those with straight roots have strong taproot development and fewer laterals (504). Five or 9 years after planting, signs of deformity were still evident. The radial distribution of laterals was often not even, and intertwined roots were often found near the taproot and soil surface. Severe bending of the roots was still noticeable, and some roots which were twisted around the taproot were being overgrown by it. Overall though, root systems were well developed (738). Whether girdling roots, windthrow, and increased susceptibility to other diseases will become problems in the future is not known.

The size of the seedling before transplanting is not correlated with subsequent root growth (432). However, deformation of the roots upon planting may affect the top growth. The tops of pine seedlings that have been planted so that their roots are twisted show no ill effects due to the deformation. Total survival appears not to be significantly affected, although some deformities may suffer more mortality (507).

Plants with deformed roots may even tend to have larger tops (506, 504). They also have more profuse lateral root development

(504, 507). The bend in the taproot of improperly planted seedlings impedes the translocation of carbohydrates through the phloem, and reducing sugars accumulate immediately above the curvature (505). The growth materials are channeled into lateral roots that are in proximity to the zone of accumulation, resulting in more lateral root surface area than found in straight rooted seedlings (504). The increased growth response that has been observed on occasion may be due to the more extensive exploitation of the surface soil by the lateral roots (507). Some researchers have not observed a correlation of top growth with deformation of the root system (507, 203).

MORPHOLOGY

Distribution in Soil Profile

Little has been written on the rooting habit of sycamore, although Biswell (128) described the root systems of 6-year-old sycamore saplings as "branched widely at all depths....with deeply penetrating laterals....and a strong taproot." Taproot depth of the trees he examined averaged about 7 ft. (2.1 m) on an upland soil. Taproots pursued a nearly vertical course and tapered fairly gradually; one taproot, for example, was 4 in. (10.2 cm) thick at the soil surface, 3 in. (7.6 cm) at a depth of 1 ft. (.3 m), and 0.2 in. (.5 cm) at a depth of 5 ft. (1.5 m). Five or more large primary laterals arose from the first 6 in. (15.2 cm) of the tap-root. These extended up to 9 ft. (2.7 m) from the stem and branched profusely in the surface 6 in. (15.2 cm) of soil. They were supplemented by primary laterals of smaller diameters.

Biswell's saplings also had several major roots arising in the second 6-inch (15.2 cm) soil layer which usually extended obliquely downward 1-2 ft. (.3 -.6 m), then turned almost vertically downward and ultimately reached a depth of 4-6 ft. (1.2-1.8 m). Absorbing rootlets occurred abundantly upon this framework of larger roots, with up to 32 rootlets per inch in the surface soil layer. Except for branches of the first order, laterals were scarce below 25 in. (.6 m). Below this depth many of the primary laterals were free of branches for several inches.

Adventitious Rooting

Slips or cuttings made from young sycamore will readily root and may be used for propogation (795, Fowells 1965, Williams and Hanks, 1976). One study found that 2/3 or more of untreated cuttings normally can be expected to root and survive when outplanted, and that hormone treated seedlings survived at even a slightly higher rate (795). Healthier top growth occurred on cuttings that were made close to the root collars than from other parts of the stem.

SEASONAL GROWTH PATTERN

Planted sycamore in Southern Illinois were found to exhibit no root growth at all during the winter and early spring, although winter growth has been reported for the spevies under milder climatic conditions. Root initiation in the Southern Illinois study (418) for 10-inch plantings of both cuttings and seedlings occurred during the last two weeks of April, whereas 20-inch plantings showed no root development until the first two weeks of May. Rooting occurred first on the old root system of both shallow- and deep-planted seedlings, and on cuttings in the vicinity of injured basal tissue. In all instances root-growth initiation was preceded by bud-break.

ROOT-SHOOT RELATIONS

One study found that the root systems of seedling sycamore penetrated deeper and were more branched under conditions of full light as opposed to partial shade (128).

EXUDATION AND UPTAKE

A determination of the cation exchange capacity of the roots of several tree species revealed that sycamore had a higher C.E.C. than either sweetgum or yellow poplar, but a lower C.E.C. than white pine. The author felt that root C.E.C. could be used as a fairly accurate predictor of soil fertility requirements, with a low C.E.C. reflecting a high fertility requirement. Sycamore's ability to grow on poor strip-mined land in the Central and Northeastern U.S. was cited as evidence of its ability to survive on poor soils, as predicted by its fairly low root C.E.C. in comparison to other central hardwoods (870).

EFFECTS OF EXCESSIVE AND DEFICIENT MOISTURE

Much has been written concerning the ability of sycamore to tolerate flooded conditions, partially because of its wide distribution as a bottomland species. Among all tree species it is considered tolerant or moderately tolerant of flooding (767) (1016). Among bottomland species it is generally rated as intermediate in flood tolerance; one study ranked sycamore 18th out of 38 bottomland trees (482), while another ranked it 8th out of 16 trees (566). The latter study found that all secondary and lower primary roots of sycamore seedlings died after 60 days of growing-season inundation, although many adventitious roots formed. Sycamore also has the ability to recover quite rapidly from growth stunting induced by saturated soil conditions once conditions return to normal (778).

It has been suggested that sycamore's ability to survive flooded conditions is due primarily to rapid adventitious root formation, as opposed to species such as green ash and water tupelo which may have the ability to translocate oxygen and substrate to the roots via the shoot (556) (565) (553). Sycamore has also been rated as intermediate among bottomland hardwoods in its ability to absorb nutrients from saturated soil, presumably mainly through the adventitious roots at or near the soil surface (568).

RESPONSE TO SOIL CHARACTER

Little has been written on this subject with regard to sycamore. Biswell (128) found that the roots of saplings penetrated much deeper in a loess soil than in a clay, although branching was most profuse in the clay soil. Roots were also often distorted in penetrating the hard clay soil.

A comparison of growth in sycamore seedlings and stem cuttings reported that, after one growing season, cuttings produced greater root and top dry matter. Of much greater importance in influencing root development than cutting vs. seedling, however, was depth of planting. Stock planted 20 in. (.5 m) deep produced significantly greater dry root matter than did stock planted 10 in. (.25 m). The overall effect of the higher root surface area of the deeper plantings was a significant increase in both height and diameter growth (418).

MYCORRHIZAE

Only Boletus edulis has been named as a mycorrhizal associate of Platanus spp. (1181). Sycamore seedlings artificially inoculated with the endomycorrhizal fungus Glomus mosseae showed significant improvements in survival and growth over non-inoculated controls. After two years, however, even those seedlings initially nonmycorrhizal at planting had many endomycorrhizae formed by indigenous fungi (810).

DESTRUCTIVE AGENTS

Insects

Sycamore is one of several tree species susceptible to attack by the Japanese Beetle, Popillia japonica Newm., an introduced insect first recorded in New Jersey in 1916. Ornamental nursery stock are particularly susceptible to root damage from the larvae, which overwinter in the soil. The adult beetles can on occasion become serious defoliators. (Baker, 1972).

Larvae of another introduced species, the Japanese Weevil, Pseudocneorhinus bifasciatus Roelofs, also may feed upon the roots of sycamore. The weevil is widely distributed throughout the northeastern states (Baker, 1972).

Nematodes

Nematodes associated with the roots or root zone of sycamore include Hoplolaimus galeatus, Tylenchorhynchus claytoni, Xiphinema americanum (Ruehle, 1967), Criconemoides sp., Helicotylenchus sp., H. dihystera (Cobb) Sher, H. crythrinae (Zimmerman) Golden, Hemicycliophora sp., Meloidogyne sp., Pratylenchus sp., Trichodorus sp. (Ruehle, 1968). None have been associated with damage. Introduction of the sting nematode, Belonolaimus longicaudatus, into pots containing sycamore seedlings, however, was shown to stunt growth in proportion to the nematode population (Hepting, 1971).

Fungi

The only root rot fungi mentioned in the literature in conjunction with sycamore are the shoestring rot, Armillaria mellea, Texas root rot, Phymatotrichum omnivorum, and Corticium *galactinum*. *A*. *mellea* is probably the only one capable of killing trees directly (Hepting, 1971). Sycamore has been rated as intermediate in susceptibility to *P*. *omnivorum* when planted in areas within the range of this fungus. Sycamore has been rated as very susceptible to infection (through artificial inoculation) by *C*. *galactinum* (1175). Sycamore has been shown to be resistant to infection by *Fomes annosus* (681, 685).

Populus deltoides - Eastern Cottonwood

MORPHOLOGY

Development of Form

The root system of mature cottonwood is characterized by a stout, gradually tapering taproot from which arise widespreading lateral roots. The taproot may attain a depth of 10 feet (3 m.). The lateral roots are more or less perpendicular to the taproot. In the first 3 feet (1.0 meter) of soil, some of the laterals grow upward, while on the lower portions of the taproot they tend to grow obliquely downward.

First year cootonwood seedlings on sandflates in central Oklahoma possessed a taproot 12 to 18 inches long (30 to 46 cm.), and five to ten lateral roots 24 or more inches in length (63 cm.). Growth during the second season was much greater, several roots attaining a length of 10 feet (3m.) (1236).

The length of the upper laterals ranges from a few inches to many feet. One tree in North Dakota is described having a lateral root 75 feet (23 m.) long. Lower laterals tend to be shorter. The laterals branch into succeedingly finer rootlets, the greater part of these being near the surface. The greatest proportion of roots are in the first 3 feet (1.0 meter) or soil (128,1332).

Adventitious Rooting & Root Suckering

Root Suckers in cottonwood will develop both from periderm tissue (as in aspen) and if roots are damaged, from cambium exposed at the cut ends of lateal root segments. Stem cuttings from cottonwood suckers were, in one study, generally superior in rooting capacity to those from aspen (1040).

ROOT-SHOOT RELATIONS

Root bark percent is inversely correlated with the vigor of the crown, and can be used for early selection of trees. Root bark percent is the relative area of the root cross-section occupied by bark. It is a clonal characteristic independent of the growth of an individual ramet on a fairly uniform site. No difference has been detected between root bark of seedling roots and that of adventitious roots (1028).

EFFECTS OF EXCESSIVE AND DEFICIENT MOISTURE

The best development of cottonwood seedlings and cuttings occurs on soils having a water table maintained at the lower portion of the normal root zone. Roots will not grow far into the free water below the water table (173). The cortex of taproots growing into saturated sand is brown, swollen, and without starch, as compared to healthy white cortex with an abundance of starch in taproots growing on drained sand (1236). Moisture levels near saturation are least favorable for growth. Lack of aeration in this situation seems to be the main cause of root mortality (Brendemuehl, 1958, 173).

An adaptation of cottonwood to meet temporary flood situations is the ability to develop adventitious roots. An extensive adventitious root system develops on seedlings by the thirtieth day under saturated soil conditions. All of the original roots except the primary roots die when flooded for 30 days. (566) If nonsaturated conditions are restored, the adventitious system continues to develop, and the chlorotic condition of the crown is relieved (565). Adventitious roots also form if the base of the tree is buried in soil, as occurs from fluvial depositions of sediment after high water (1305).

Under a 60 day period of saturated soil conditions, nutrient absorption by cottonwood seedlings is greater than under well-watered, nonsaturated conditions. Dry weight, ash content, and absorption of nitrogen, phosphorus, potassium, calcium, and magnesium are all greater. Possible reasons for the better uptake could be: (1) waterlogging may decrease acidity through reduction of nitrogen to ammonia, thus increasing the availability of certain elements over short time periods, (2) over longer periods managanese and iron may become more available, and (3) the development of the adventitious root system augments aeration.

In comparison with other hardwood species, cottonwood seedlings are classed as intermediate in tolerance to flooding since (although dry weight and nutrient absorption are increased) the original root system is unable to survive in entirety (568).

Mature cottonwood will not thrive on sites where flooding during a six-month growing season exceeds approximately 60 days (482). It can survive one entire season of flooding very well, but succumbs after the second year of continuous flooding (104, 455). Some individuals, however, may survive permanent inundation for 4 years (1333).

Cottonwood on upland sites is fairly resistant to drought, probably more resistant than cottonwood growing along waterways. This resistance is thought to be due to deeper penetration of the root system on dry sites (128,15). When grown under moisture stress, shoot-to-root ratios of cuttings are smaller (358).

MYCORRHIZAE

Cottonwood has both ectotrophic and endotrophic mycorrhizae (748,122). *Lepista nuda* (Bull. ex Fr.)Cke. and *Cenococcum* *graniforme* (Sow.)Ferd. & Winge form ectotrophic mycorrhizae with cottonwood. The fungus which forms endotrophic mycorrhizae is a species of *Endogene* (1221).

DESTRUCTIVE AGENTS

Non-infectious

Survival of cottonwood planting stock is not affected by exposure of roots to drying by sun and wind if the stock is planted while still dormant. After budbreak, survival declines rapidly with the length of exposure. The mortality after budbreak is heavier than for other hardwood shelterbelt species (171).

In comparison with other shrub and tree species, cottonwood is moderately tolerant of soil-applied salts (871).

Insects

The cottonwood borer, *Plectrodera scalator* (Fab.), attacks the root collar and main roots of cottonwood trees in the southeastern region of the United States. Roots are girdled or structurally weakened. The larvae of the beetle mine out long tunnels and irregular cavities in larger roots. Taproots may be completely hollowed. The larvae hatch from eggs laid in niches cut in the bark at the base of the tree, and tunnel downward into the inner bark and later into the wood. The borer pupates within the root, and only the adults emerge into the open air. An attack is usually undetected until breakage occurs. Sometimes piles of frass ejected from bark openings can be found at or slightly above the groundline at the base of the tree (863).

Nematodes

The dagger nematode, *Xiphinema americanum* Cobb is pathogenic on cottonwood, contributing to premature decline in shelterbelt trees in the Great Plains region. The nematodes strip the root system of its feeder roots (Malek, 1975). Other nematodes associated with the roots or root zone of cottonwood include *Criconemoides* sp., *Helicotylenchus dihystera* (Cobb) Sher, *H. erythrinae* (Zimmerman) Golden, *Hoplolaimus* sp., *Meloidogyne* sp., *Rotylenchus* sp. (Ruehle, 1968).

Fungi

Fungi known to cause root rot in live cottonwood are *Clitocybe tabescens* Bres., *Corticum galactinum* (Fr.) Burt., *Pymatotrichum omnivorum* (Shear)Dugg., *Pleurotus ostreatus* (Fr.)Quel.,and *Polyporus lucidus* Leys. ex Fr. (863, 386). *C. tabescens* occurs in the southeastern United States. White, fan-shaped mycelial mats grow between the bark and the wood on the roots and root collar, causing decay (863). P. omnivorum is prevalent only in the southwestern United States (Taubenhause, 1936). P. ostreatus causes a white flaky rot, and P. lucidus causes a soft, spongy, white rot with black spots (863).

Bacteria have been associated with shake--tangential or radial separation in xylem tissues of the lower trunk--of cottonwoods in the North Central Region of the United States. The bacteria are found in the roots, root collar and lower trunk of cottonwood trees with an otherwise healthy appearance (1235).

Populus tremuloides Michx. - Quaking Aspen
and
Populus grandidentata Michx. - Bigtooth Aspen

MORPHOLOGY

Development of Form

Little information is available on initial development of roots on aspen seedlings since, under natural conditions, reproduction usually occurs by means of suckering from a parent root. In studies of aspen seedlings grown in nurseries, maximum depth reached by the roots during the first season's growth was usually less than six inches. Definite taproots were present only rarely, and the early root system was characterized as fibrous and branching. The lateral roots produced during the first season did not exceed 16 inches in length (269).

During the second year the seed-origin aspen root system becomes much more extensive, with laterals reaching to six feet or more, while stem height will usually be from two to four feet. The system also becomes more woody and less fibrous during this period. Adventitious roots begin to develop near the root collar and extend laterally in the superficial soil (793). Overall, seedling root growth of aspen was found, in one study, to exceed all of its common associates except pin cherry (*Prunus pennsylvanica* L.).

Rate of root spread for mature bigtooth aspen in Indiana was reported to average about 1.0 meter per year on average sites, and 1.3 on good sites (334).

Distribution in Soil Profile

The typical aspen root system is wide-spreading and shallow, with most roots confined to the upper two feet (30.5cm) of soil (62, 350). In many cases nearly all of the lateral roots are in the top 6 inches (15.2cm) of soil (296). Three to five strongly developed laterals originate from the tree base and normally branch within two feet (30.5cm)(793). One or two of these main laterals may be distinctly larger than the rest; these are the original roots upon which the tree formed as a sucker (62). In shape, the laterals are nearly cylindrical, and taper only very slightly after initially tapering rather abruptly to a diameter of about 1 inch (2.5cm)(1027). The laterals may extend for 30 meters or more, often pursuing an undulating course with respect to the soil surface (62, 424, 77). Sinker roots from the lateral system may descent six to eight feet (1.83-2.44m) below the surface and frequently follow old root channels (77, 296). Their development provides firm anchorage while also establishing a contact with vital subsoil moisture (296). At their lower extremity the sinker roots are spread into dense fan-shaped mats (296).

Adventitious Rooting

Suckers or sprouts usually originate on portions of a lateral root very close to the ground surface, usually less than eight inches (20.3cm); this frequently occurs where two very shallow roots cross and the upper is brought very near the surface. Sprouts may also originate from the root collar of stumps, but this is infrequent (61). Diameter of a parent root is not necessarily with its depth in the soil (424). Some of the smaller diameter laterals (sometimes called branch roots) appear to be devoted primarily to reproduction, since they run for long distances near the surface with little change in diameter, and with practically no feeding rootlets (62). Most sprouts arise from roots less than 2.5 centimeters (1 inch); sprouts arising from larger roots do not survive long (Perala, 1978). Growth of a sprout from such a root results in a rapid thickening near the point of attachment and the development of many feeding rootlets. These rootlets normally remain active until the death of the parent tree, at which time they rot off (62). The vast majority of suckers originate from sucker buds formed in the same season, although dormant buds are often more numerous on a root (1027, 523).

Suckers normally remain connected to their parent tree even after developing their own root system. One study of bigtooth aspen found that the parent root still accounted for about half of the annual stem growth in 25-year old suckers (1349). Another reported that severance of the parent root connection was frequently fatal to suckers up to age 25, even though roots originating from the sucker were left intact (303). Live connections between 65-year old trees are not uncommon (793). In addition, dead stumps with live root systems are often joined to living trees through the parent roots (304). In some cases a sprout will not develop any roots of its own, other than its connection to the parent root; this is uncommon, however (424).

The capacity of aspen roots to produce suckers is stimulated by severing the root from the parent tree or cutting the parent stem. New suckers may simply assimilate part of the parent root, especially the portion outward from the new stem, into their individual systems.

Light intensity apparently affects the early growth of suckers more than it affects their actual initiation. One greenhouse study found that suckering was as abundant at 25% of full sunlight as at full sunlight if soil temperature was the same (1027).

There is evidence of significant variation in suckering capacity within the lateral roots of individual clones (1039). One study found that sucker production increased from the distal to the proximal ends of an individual lateral root; there was no evidence, however, of such a gradient within individual root segments. This was interpreted as indicating that aging was not a prime factor regulating suckering within lateral roots.

Comparisons with Other Species

A comparative study of the root systems of trembling and bigtooth aspen growing under various conditions showed that bigtooth generally had deeper, less branched roots, and also fewer adventitious roots, than did trembling aspen (793). Another study found that the lateral roots of bigtooth aspen occupied the total A horizon more completely than the roots of trembling aspen, whose laterals were generally shallower. This was interpreted as an adaptation by bigtooth aspen to sites which are periodically moisture-deficient, on which it may thus have competitive advantage over trembling aspen (356).

A comparison of root suckering ability among four species of Populus (P. tremuloides, P. angustifolia, P. balsamifera, and P. deltoides) revealed the following: a) sucker cuttings from the poplars were generally superior in rooting capacity to those from the aspen, b) places where suckers originated on root segments were more variable in the poplars than in the aspen, and c) lateral root formation from preexisting and newly initiated meristems on root segments was common in the poplars but rare in the aspen (1040).

Root suckering as a result of stem girdling is apparently more easily induced in P. grandidentata than in P. tremuloides (357).

SEASONAL GROWTH PATTERN

Most researchers report that the ability of aspen roots to produce suckers is lowest during the early summer months (1038, 1037, 1042, 1163, Zehngraff, n.d.). This is probably a result of low root carbohydrate reserves during spring and early summer, when a high proportion of photosynthate is being channeled to developing shoots and leaves (1042). Some studies have shown, however, that the effects of cutting at different seasons may be obscured within three or four years, since most of the sprouts from areas that initially sprout densely eventually die from suppression (1027, 1163). There is also some evidence that suckers on spring-collected root cuttings establish independent root systems more often (or more rapidly) than those on fall cuttings (1163).

Aspen roots were found to be most sensitive to sucker-inhibiting phenoxy substances, such as 2,4,5-T, during the summer months.

ROOT-SHOOT RELATIONS

The formation and development of adventitious shoots on aspen roots is a complex phenomenon involving several growth-regulatory substances, including auxins, cytokinins, giberellins, B inhibitors, and possibly others (1034, 522, 1035, 1037, 1038). The presence or absence of these substances under natural conditions is at least partially related to the presence of stem apices. When apical dominance is altered by cutting stems within an aspen clone, numerous suckers arise from the buds initiated in the periderm of roots.

Existing aspen suckers may inhibit the initiation and especially the development of additional suckers if growth conditions (light, temperature, etc.) are less than ideal. This probably involves competition for nutrients (older sprouts are better competitors) in addition to the previously mentioned growth substances (1034, 357).

Root carbohydrate reserves may have an important role in the production of root suckers. Though they probably do not control the initial number of suckers, carbohydrates become important after the apical meristems become established and large quantities of metabolites are required for shoot growth and development (837, 96). New suckers probably remain totally dependent on root reserves until they emerge at the soil surface. There is some evidence to suggest that clonal differences in initial sucker growth may be due to inter-clonal variations in levels of carbohydrate reserves (1041). In one study, these genetic variations between clones were significant enough to obscure the effects of different cutting treatments (1163).

Effects of Fire

Aspen root suckering is normally stimulated by fire. Repeated burning at intervals as short as three years tends to increase the amount of suckering as long as the original clone is older than two years to begin with (1070). One study found that light burning after cutting resulted in more suckers and better growth during the first year than non-burned areas. It was suggested that this stimulation was primarily due to the increased heat absorption of the blackened surface (1069). In some cases, however, sucker growth may be slowed as a result of burning, although sucker abundance is high (Perala, 1977).

Repeated burning at 1- or 2-year intervals may reduce the abundance and vigor of aspen suckering after as few as three burns (190). Single severe (very hot) burning, unless it results in the death of roots below the half-inch (1.3cm) depth of mineral soil (which is improbable except under conditions of prolonged drought and heavy slash from logging), will generally not significantly diminish root suckering (563). Fires of moderate intensity, conducted after clearcutting in the fall or winter, tend to maxmize sucker abundance and quality (563).

Aspen sprouts which are cut or grazed off annually for three years normally will cease to sprout (61). This is thought to be due to the exhaustion of stored food materials in the roots.

Stimulation of the shallow lateral roots by such activities as trampling (due to grazing) will often induce abundant suckering, even though none of the parent stems are removed. These new sprouts are generally very weak, however, and seldom reach a height greater than a few inches before dying of suppression (61). Management activities such as discing and roller chopping after aspen harvest may result in reduced sucker abundance and vigor, since the stimulation effect is often negated by damage they do to the parent roots (Perala, 1977).

Age of the parent stand affects the amount and vigor of sprouting to some extent. Even in a 110-year old stand, however, sprouting following a clearcut was fairly abundant (12,600 sprouts/acre). One study found that the number of suckers increased with the age of the parent stand from 30 years to a maximum at 70 years, and then began to decrease (645).

UPTAKE

Water and solutes can be translocated over long distances through the xylem of functional root connections between quaking aspen trees within a clone. Water may be translocated through the parent root system from trees growing next to a good supply of water, such as a stream, to other trees growing beyond the riparian zone (1164). This can even occur if the riparian trees are cut, as long as their root systems remain functional. The extent of solute translocation between trees, as well as water translocation, depends on the number of connections within a clone.

A study involving root injections of dye in bigtooth aspen and several other tree species showed that patterns of vertical transport took place in several annual rings of the sapwood, as opposed to only the outermost sapwood (as in several species of oak) (661).

EFFECTS OF EXCESSIVE AND DEFICIENT MOISTURE

Trembling aspen is quite sensitive to both excessive and deficient soil moisture conditions. One study found that aspen site index was highly correlated with soil moisture on a variety of sites (Stoeckeler, 1960).

Shallow water tables within about eight feet (2.44m) of the surface can result in improved growth of aspen, especially on sandy soils. Shallow water tables may reduce growth slightly in loams and heavier soils (Stoeckeler, 1960). Water tables at depths less than two feet (.61m) may reduce growth significantly (Stoeckeler, 1948).

Poor internal drainage and poor soil aeration, as evidenced by strong mottling within 12 inches (.30m) of the surface of relatively fine-textured soils, reduced aspen growth considerably in one study. Sandy soils underlain by heavier soils often support good aspen growth, while sandy soils underlain by coarse gravels often support only very poor, sparsely stocked stands (Stoeckeler, 1960).

With respect to its common associates, trembling aspen is reportedly intermediate in its ability to tolerate prolonged flooding. It is reportedly more tolerant than most conifers (including balsam fir and black spruce), but less tolerant than most of the bottomland hardwoods (12).

RESPONSE TO SOIL CHARACTER

Both depth and lateral extent of aspen rooting are strongly influenced by soil characteristics. For a more detailed discussion of this subject than is presented here, refer to Stoeckeler (1960).

Texture

Under normal conditions, aspen root growth is most rapid in loam or silt-loam soils. At a soil temperature of 18°C, root growth in loam soil (48% sand, 30% silt, 22% clay) was more than three times greater than in either sandy or clay soils (425). A minimum silt plus clay content of 15% is recommended for good growth of bigtooth aspen; trembling aspen requires a slightly higher percentage (Stoeckeler, 1948).

Removal of organic matter as a result of repeated burning may reduce aspen growth significantly, particularly on sandy or loamy-sand soils (Stoeckeler, 1960).

Soil texture, through its influence on moisture-holding capacity and aeration, is probably more important for good aspen growth than are the chemical soil properties (including nutrient content), although texture of course influences nutrient availability.

Temperature

Soil temperature plays a major role in both sucker initiation and root growth (794, 425). One study found that root growth in loam soil at 18°C was nearly double that at 27°C, and more than three times that at 10°C. Soil temperature may actually have a larger influence on sucker stimulation than does the presence or absence of parent stems. One researcher found that prolific suckering occurred on heavily scarified or burned plots (both of which resulted in an increased rate of soil-warming) whether or not the aspen canopy had been removed (794).

Light intensity apparently affects aspen root growth most significantly at certain soil temperatures and in certain soil types. One researcher found that, of three soil types tested at three different temperature (10°C, 18°C, 27°C), light intensity significantly influenced root growth only in loam soil at 18°C (794).

Fertility

As might be expected, root growth is most rapid in soils having relatively high levels of P, N, and K (425). Good growth can still be achieved, however, at fairly low levels of total N and available P (.040% and 29 ppm, respectively)(Stoeckeler, 1960). It is believed that a comparatively high content of mineral nutrients, especially Ca and Mg, contribute to the longer life span, greater growth rate, and lower incidence of heart rot found in aspen growing on certain high quality sites (Stoeckeler, 1960). It is probable that the release of large quanitites of available Ca and Mg as an aftermath of forest fires tends to favor rapid growth of aspen.

Mycorrhizal associations are essential for root establishment and growth of aspen on extremely nutrient deficient soils such as those resulting from mining operations.

It appears that a fairly wide latitude of soil pH, from about 5.3 to 6.5, is permissable for good growth of aspen (Stoeckeler, 1960).

Nitrogen content of the organic soil layer has been shown to be highly correlated with aspen growth (Stoeckeler, 1960).

MYCORRHIZAE

Species of fungi known to form mycorrhizae with trembling aspen include _Cenococcum graniforme_, _Leccinum aurantiacum_, _L. scabrum_ (729), _Pisolithus tinctorius_ (807, 809), _Inocybe_ spp. (1004), _Astraeus hygrometricus_ (1049). _Boletus subglabripes_, _Suillus subaureus_, and _Tylopilus chromapes_ are known to form mycorrhizae with _Populus grandidentata_ in Maine (Homola & Mistretta, 1977).

The fungus _Monotropa hypopithys_ has been reported to form what appear to be mycorrhiza-like associations with aspen roots, but is in fact probably parasitic (680).

Populus is one of the few tree genera known to produce both ecto- and endomycorrhizal associations, and this ability may contribute to its widespread distribution. Only ectomycorrhizae have been reported for _P. tremuloides_, however (1223).

DESTRUCTIVE AGENTS

Non-infectious

Soil compaction from heavy machines or trampling by livestock can reduce suckering and cause root damage to mature trees by lowering soil aeration (Perala, 1977). The potential for compaction is most severe on wet soils having a high clay content, and is minimal on dry sandy soils.

Root growth and development may be significantly reduced on soils contaminated with high levels of Zn and Cd (100 ppm and 10 ppm, respectively), such as those near some smelter sites (614).

Windthrow of aspen is fairly common because of the shallow rooting habit of the trees.

Nematodes

No noteworthy damage to American poplars is known to be due to nematodes (Hepting, 1971).

Insects

Although trembling aspen is attacked by a variety of insects, severe damage is usually limited to the above-ground portions of the plant, particularly the leaves. A number of relatively minor pests affect the below-ground portions.

Mining insects known to damage aspen roots include: the root boring Agrilus, *Agrilus horni* Kerr, the round-headed wood borers *Saperda adsperca* (Lec.) and *Xylotrechus obliteratus* (Lec.), the broad-necked root borer *Prionus laticollis* (Drury), the introduced species of borer *Polydrusus impressifrons* (Gyll.), and the clear-wing moths *Aegeria apiformis* (Clerck) and *A. tibialis* (Harr.).

The aspen root aphid (undescribed species) and white grubs (*Phyllophaga* spp.) are the only surface feeding insects known to cause significant damage to aspen roots and root crowns (449).

Insect galleries extending into the roots of aspen can be identified by the dark zone of discolored wood which surrounds them. Unlike in fungal infections, this dark wood is hard and firm (1045).

For more detail on the root-damaging insects of aspen and their symptoms, refer to (351) and also to Baker (449).

Fungi

Root decay of mature trembling aspen by *Ganoderma applanatum* (Wallr.) Pat. has resulted in locally heavy losses of aspen in the Rocky Mountains, often resulting in affected trees being windthrown. The fungus reportedly infects mostly roots larger than 2.5 inches (6.3cm) in diameter (1002). Trees on moist sites are most likely to be infected (Ross, 1976).

Butt rot fungi affecting trembling aspen include *Pholiota spectabilis* (Fr.) Kummer, *Armillariella mellea* (Vahl. ex Fr.) Karst, and *Pholiota aurivella*. These normally enter the tree through basal wounds, root wounds, and connected roots. They cause a yellow-brown, stringy butt rot that usually extends upward only a few feet. Other butt rot fungi affecting trembling aspen primarily in the Western U.S. include *Collybia velutipes* (Curt, ex Fr.) Kummer, *Pholiota squarrosu* (Fr.) Kummer, *Pleurotus estreatus* (Fr.) Kummer, *Trechispora raduloides* (Karst.) Rogers (Anderson et al., 1977), *Ascocoryne* spp., *Coprinus atramentarius* (Bull. ex Fr.) Fr., *Phialophora* spp., *Libertella* spp., *Talaromyces vermiculatus* (Dang.) C.R. Benjamin, and *Cytospora chrysosperma* Pers. ex. Fr. (Ross, 1976).

It is possible that some types of fungal rot may be spread from one tree to another through the clonal root system, although this is not believed to be common. One study involving *Fomes igniarius* in Minnesota found that the fungus, though prevalent throughout an aspen stand, did not extend any appreciable distance into the root system (1045).

Certain fungal diseases may result in increased root suckering in aspen clones, even though the disease does not affect the roots per se. A study of sucker occurrence in uncut stands indicated that while suckers did not normally arise annually in healthy clones of aspen, they were found each year in clones heavily infected with hypoxylon canker (*Hypoxylon pruinatum*)(355).

The fungus *Diplodia tumefacians* (Shear) Zalasky has been shown to infect the main roots of aspen growing on sites which are periodically flooded (1357). Diseased roots are characterized by their wart-like outline of woody swellings.

A bacterial infection caused by *Agrobacterium tumifaciens* (E.F. Smith and Town.) Conn. produces rough irregular tumors at or near the ground line on aspen saplings (Brinkman and Roe, 1975).

Quercus alba L. - White Oak

MORPHOLOGY

Development of Form

The juvenile root system of white oak is characterized by a long and sturdy taproot which rapidly penetrates below the surface zone (336). If this taproot is somehow injured shortly after germination, a number of fibrous roots often form from near the point of injury.

In one study the average length of the emerging white oak radicle at the end of ten days was 10 cm. A covering of brown, fissured cork extended down the root for about 5 cm at this point. A few scattered secondary roots were observed developing from this corky region. By the fourteenth day the average length of the radicle was 17 cm and formation of secondary roots was profuse, with some branching of secondary roots. All secondary roots originated from the corky region of the radicle. At one month the radicle averaged 26 cm in length; cork formation was very heavy and covered the entire root except the growing tip. The secondary roots were found to have root hairs, but none were found on the primary root (220).

An examination of several one-year-old forest-grown white oak seedlings revealed an average total root length of 7.7 ft (2.3m). Approximately 50 percent of this length was in second-order roots, 41 percent in third-order roots, and 9 percent in the single primary root (660).

Distribution in Soil Profile

Several authors have characterized the root system of mature white oak as deep and widespread (394, 1178, 1135). A prominent taproot is normally present (1178). The main branches of the root system are rather widely spaced, presenting an open appearance (1135). The area immediately surrounding the trunk is often characterized by a dense and highly ramified network of rootlets; these may form a mat at or near the soil surface (184,1135). Most lateral roots do not extend much beyond the limits of the crown perimeter (184). Root concentrations throughout the soil profile have been found to be nearly constant after well-stocked white oak stands reach the age of 30 years (414).

An examination of the root systems of several white oaks ranging in age from 40 to 68 years (6.4 to 7.2 in. d.b.h.; 16.3 to 18.3cm) revealed an average root depth at the stump of 38 inches (1.0m). Mean depth of all lateral roots was 18 in. (.45m), while the average maximum depth of laterals was 36 in. (.9m). Average size of area encompassed by a single root system was 580 square ft. (1135).

A study of the concentration of roots in an even-aged white oak stand in Ohio found that root biomass was highest in the soil horizon termed "first subsoil." The A2 horizon, directly above the first subsoil in the profile, contained the next highest root biomass, while the A1 horizon was third. Average root diameter was greatest in the first subsoil horizon while feeder roots (1/4 in.; cm and smaller) were most numerous in the A1. The concentration of A1 and A2 horizon roots was greatest in the area closest to the trunk whereas root concentration in the subsoil horizons was greatest some 2 to 5 ft. (.6 to 1.5m) out from the trunk. The author speculated that, although one might expect root concentrations at the base of the trunk to be low due to abundant water from stemflow, this is not the case in nutrient-rich surface horizons where variations in moisture are greatest (414).

Comparisons with Other Species

A detailed comparison of the root systems of five oak species in North Carolina revealed that Q. alba was the deepest rooted, third greatest in extent of lateral rooting, and fourth highest in shoot:root ratio. The author concluded from these one other observations that white oak is a "good site" species which is eliminated from poor sites largely becuase of insufficient drought resistance.

One author has classified the initial root system of white oak as "non-plastic", along with such other species as chestnut and water hickory, due to its uniform growth habit as a seedling regardless of soil character (1178).

Another study found that, in comparison with red oak and sugar maple, the root system of white oak was much more massive and contributed a smaller amount of root area in the upper soil horizons (1056).

Grafting

One author reported a 17 percent incidence of root grafts among white oaks based on translocation of dye from treated stumps to surrounding trees. All grafts involved only the treated and one additional tree, with the exception of two trees which were grafted to more than one other tree. The maximum distance between grafted trees was 25 ft. (7.5m) and the average distance was 8 ft. (2.4m) (1094, 613). Another author found root grafting among white oaks to be "uncommon" (690).

Adventitious Rooting and Root Sprouting

Frequent fires and continual grazing of white oak seedlings often results in the formation of root stools under the ground surface. Given adequate protection, these will often sprout abundantly (Fowells, 1965). In some cases, shoots seperated by nearly a meter at ground level may rise from opposite points on the periphery of a large root crown which also supports smaller suckers (1285).

SEASONAL GROWTH PATTERN

One author reported that roots of white oak in Illinois grew rapidly from the time growth resumed in April until about the first of July. Growth decreased from that point until coming to a virtual halt near the end of July. No further growth was detected until September 8 when elongation began again. Growth then continued until November 24, after which no further elongation was detected (780).

ROOT-SHOOT RELATIONS

Since white oak resprouts readily after fire, age of the root systems of some trees may greatly exceed that of the shoots. The root: shoot ratio of such trees may be much greater than for similar trees of seed origin. Smaller, relatively suppressed shoots which do not share a root system with a large shoot may be outweighed by as much as 4 or 5 times by their root systems (1285).

The concentration of white oak roots was found by one researcher to show no perceptible relationship to above-ground volume growth; poorly stocked stands had approximately the same concentration of roots as did well-stocked stands. The importance of this finding is that it supports the concept that the soil can only support up to a certain maximum concentration of roots; thinning basically serves to concentrate the growth potential of any given site onto fewer stems (414).

One researcher found that starch content of white oak roots was lower and more variable than in red oak, especially as distance from the root collar increased. Starch content within roots of both species was found to be inversely related to root diameter (1242).

EXUDATION AND UPTAKE

An investigation of uptake relationships among several tree species showed a greater percentage of white oaks exhibiting uptake in the zone nearest the application point (0-25 ft.;0-7.5m zone) as opposed to the other species. This implies a more intensive network of roots around trunks of white oaks. Further evidence of this rooting habit of white oak was provided by the fact that all white oaks within 18.2 ft (m) of the point of isotope application showed evidence of uptake (184). Another author, however, reported that soil moisture depletion was greater near the trunks of scarlet oaks than near white oaks, implying an even greater trunk-zone rooting intensity in scarlet oak (183).

A study of the movement and respiratory use of ^{14}C-labeled substrate by white oak suggested a rather uniform occupancy of the site by root system. While the speed with which labeled substrate moved into the root system varied considerably, the ultimate allocation was very similar in all six directions tested. Movement of substrate through the system occurred at a rate of app. 0.1 m per day, with 10 to 17 days required for equilibration of the substrate with endogenous pools in the root system (787).

RESPONSE TO COMPETITION

A study of succession on abandoned agricultural lands of the Piedmont Plateau found that, despite the relatively superficial root systems of loblolly pine, root competition in the upper soil is even more intense in the more successionally-advanced pine-oak and oak types than in the loblolly pine type. Acorns of white oak germinate soon after they mature in the autumn and immediately develop a deeply penetrating root system, thus establishing an early defense against possible drought the following summer. The later development of a surface root network by the oak insures that loblolly seedlings, although they may become initially established beneath oak stands, will generally be unable to survive for very long (245).

One author reports that concentraions of roots of all sizes were greater at all depths in white oak-black oak-red oak stands than in post oak-blackjack oak stands. It was emphasized, however, that actual root competition was not assessed (156).

EFFECTS OF EXCESSIVE AND DEFICIENT MOISTURE

A study of the drought resistance of four oak species found that white oak and black oak were approximately equal, with northern red oak less resistant and post oak more resistant in terms of root tissue survival (1060).

White oak was classified by one author as slightly flood-tolerant, with most individuals surviving greater than 50 days but less than 100 days of indundation during the growing season. Nineteen other common Illinois tree species were considered more tolerant than white oak, while only four species were considered less tolerant (104). Another author found that white oak was the third-most flood-intolerant species of 65 tree and shrub species tested in Tennessee (481).

A study of the response of white oak germination to inundation found that only approximately 50 percent of white oak acorns germinated after 12 days of continuous inudation, as compared to 99 percent for the control plantings. After 25 days of flood conditions, only approximately 1 percent of the acorns germinated. The author felt that the restricted range of white oak in Illinois (to areas of streamside forest receiving less than 4 days of potential flood a year) was largely attributable to this sensitivity to moisture conditions during the seedling or sapling stage (103).

RESPONSE TO SOIL CHARACTER

The topography of land does not appear to affect the concentration of white oak roots. The moister sites, lower slopes, and northerly exposures, which are better for white growth in southeastern Ohio, do not support higher concentrations of roots than do the drier sites. The fact that white oak grows faster on the moister sites must mean that the capacity of roots to absorb water and nutrients is less satisfied on the drier sites than on the moister sites (414).

In some areas, the quality of land for growing white oak depends largely upon the depth of the A horizon. A deeper A horizon allows a greater total number of smaller roots to develop and, presumably, this permits larger amounts of water and nutrients to be absorbed. Differences in site quality arise not because roots fail to occupy the soil mass, but because the volume of soil favoring high concentrations of roots can be great or small (414).

One author found that white oak seedlings grown on a silty clay loam soil developed longer tap roots than those grown on a loamy sand. On both soils there was a high percentage of tip rooting, resulting in a widespread, much-branched root system on the seedlings so affected (220).

White oak was mentioned by one author as a species that can obtain significantly more nitrogen from relatively infertile soils than can other species such as yellow poplar and basswood (851).

Treatment of white oak acorns with gibberellic acid prior to planting was found to stimulate stem elongation and leaf production but also inhibit formation of lateral roots and other aspects of root growth. Gibberellic acid-treated white oak seedlings appeared to be less tolerant of soil moisture stress than untreated seedlings (708).

MYCORRHIZAE

Fungi known to form mycorrhizal associations with white oak include *Cenococcum graniforme*, *Russula foetens*, *Scleroderma aurantium*, *Pisolithus tinctorius*, *Penicillium notatum*, *Trichoderma viridae* (242). In general, litle is known of mycorrhizal relationships in the genus Quercus (Hepting, 1971).

DESTRUCTIVE AGENTS

Non-Infectious

White oak has been classified as tolerant of soil salts in the root zone (871).

Among the oaks, white oak seems especially vulnerable to changes in its soil environment. Long-term survival of oaks following soil disturbance is largely determined by the degree of alteration of the A1 horizon, which usually contains the majority of the fine root system. In Illinois, many areas beset by oak decline problems following construction activities showed up to 90 percent mortality within 15 years of the disturbance (573).

White oak has a tendency to develop cracks in the trunk base and exposed roots following sudden severe cold, with the cracks developing a yeast-induced slime flux. Many such cases have been observed in localized areas following unusually severe winters (Hepting, 1971).

White oak is not particularly susceptible to windthrow, although root rot due to *Polyporus dryadeus* and other fungi may seriously weaken the root system and thus increase windthrow hazard (208).

An investigation of lead uptake by tree seedlings found that white oak translocated a large amount of lead from roots to stem, but relatively little to the leaves in comparison with other species tested. The fact that translocation of injected materials in oak species occurs not only upward, but also downward was cited as a possible reason that materials such as lead are held in the roots and stem of oak for longer periods of time (496)

Insects

The oak sapling borer, *Goes tesselatum* (Hald.) is probably the only insect capable of damaging the roots of white oak to a considerable degree. The insect breeds in the base and roots of small white oak saplings from Pennsylvania southward and in parts of the Midwest. Infested trees are characterized by bulb-like swellings around the wounds at the ground line, and may be susceptible to wind breadage (Baker, 1972).

Defoliation of white oak by the gypsy moth (*Lymantria dispar*) is thought to increase vulnerability of the root system to attack by the fungus *Armillaria mellea* (Wargo, 1977).

Nematodes

Nematodes associated with the roots or root-zone of white oak include *Criconemoides* sp., *C. macrodorum*, *Gracilacus capitatus*, *Hemicycliophora sp*. (Ruehle, 1967); *Aphelenhus* sp., *Paratylenchus projectus*. There are no reports of root damage in white oak associated with nematodes, althrough nematodes injury has been reported for several other oak species (Hepting, 1971).

Fungi

The most important vascular disease of white oak and most other members of the genus *Quercus* is oak wilt (*Ceratocystis fagacearum*). The range of the wilt embraces 18 states from Minnesota to Georgia and northward to Pennsylvania. Members of the white oak group often die slowly, a limb at a time, and may even harbor the pathogen without showing any symptoms (Hepting, 1971).

One method of transmission of oak wilt from tree to tree is through natural root grafts. Because of this, trenching around diseased trees to a sufficient depth to sever all root connections with neighboring trees has been occasionally used as a control measure (690, 169). Although the oak wilt fungus is not free-living in the soil, it may be transmitted between root systems in other ways besides by root grafts. Nematodes or other soil fauna that attack the roots may act as vectors in short-distance spread of the fungus (113). Refer to Hepting, 1971 for a more detailed description of the symptoms of oak wilt.

Root rot of white oak may be caused by any of several fungi, including *Corticium galactinum* (attacks pole-sized trees in particular); *Phytophthora cinnamomi* and *P. citricola* (nursery seedlings); *Ustulina vulgaris*; *Armillaria mellea*; several species of Polyporus and a few others, most of which are described in either Hepting 1971, 454, 1173, 272, or 1173.

Quercus rubra L. - Northern Red Oak

MORPHOLOGY

Development of Form

Successful establishment of red oak seedlings is dependent upon the ability of the emerging radicle to penetrate the surface medium and reach mineral soil. Compacted surface layers may result in the acorn being thrown out of position by pressure from the radicle. Red oak radicles will grow along a surface which they cannot penetrate during wet weather, but during dry weather evaporation from the succulent radicle often results in a net water loss and death. Leaf litter is important in preserving the viability of acorns until conditions are favorable for germination (652)

Under favorable conditions in loamy sand soil, the rate of elongation of the hypocotyl during the first month is approximately 1 cm per day. An abundance of much-branched secondary roots are produced during this period, most of which are covered with fine root hairs. By the end of the fourth month many of the branch roots are quite large and covered with cork (220).

Taproot penetration may reach 3.2 ft. (1.0m) or more during the first year. Vertical branching of the tap root is reportedly common (417). Greatest depth of penetration occurs on well-drained soils. It is quite common, however, for the tap root to fail to develop or to turn horizontally due to environmental factors such as excess moisture or the presence of impervious layers. In this case an extensive lateral system may develop, as red oak is moderately flexible in rooting habit (1178,544,220). Regardless of available rooting depth, most red oak seedlings reportedly produce at least one or two important lateral roots the first season (544).

Distribution in Soil Profile

The root system of mature red oak is characterized by a relatively small total number of roots in comparison to its common associates. The proportion of the system composed of fine roots is quite high, although these roots do not usually form a closely woven mass as in some other trees (417). In loamy sand and sandy loam soils, the number of roots is generally highest in the A horizon.

Lateral roots of red oak may angle downward 20 degrees or more from the horizontal, which is much steeper than many of its associates (908). A tap root is common on soils which do not present obstructions to vertical penetration, such as a high water table or gravel layer(s) (417). The tap root tapers gradually throughout its length and may follow an irregular course, deviating 12 inches (.3m) or more from the perpendicular (128,417).

On well-drained soils, most of the main vertical roots arise from the taproot rather than the laterals. Some of these may penetrate as deeply as the taproot. Branching of roots of all sizes decreases significantly at soil depths greater than 2 ft. (.6m) (128).

The main roots of red oak are mainly devoid of root hairs, while those on first-order laterals are few in mumber and short, usually less than 0.02 mm in length. The second-order laterals appear to complete their growth in length before producing root hairs; then hairs grow thoroughout their whole length, often even, from the extreme root tip (979).

Comparisons with Other Species

On sandy loam soils the lateral roots of red oak were found to be much deeper than those of red maple, yellow birch, and trembling aspen; and slightly deeper than those of white pine and red pine (762).

In a comparison of white pine, red pine, norway spruce, white ash, and red oak, oak had the lowest total number of roots in two soil types. Lateral branching, however, was more extensive in red oak than in some other species, particularly white ash. Small roots in red oak were more numerous but not as long as in white ash (417).

The root system of red oak on deep loam soils was much better developed than shellbark hickory of the same age. Red oak showed a stronger tendency to produce a taproot than basswood, but a somewhat weaker tendency than either bur oak or shellbark hickory (544).

Red oak reportedly has more roots per unit volume than most of the other oaks. However, it does not have the mat of small roots near the surface that is characteristic of chestnut and white oak (1135).

A comparison of four hardwood species on loam soils showed that northern red oak was, on the average, deeper rooted than sugar maple but shallower rooted than chestnut oak or white oak. None of the trees had a well developed tap root (1135).

A comparison of 5 oak species showed that the average root extent (an approximation of root area) of northern red oak seedlings was significantly greater than that of all other species on a sandy loam soil (156).

Grafting

Intraspecific root grafting in northern red oak is reportedly common (1135).

Adventitious Rooting and Sprouting

Northern red oak sprouts readily and prolifically from suppressed buds near the base of trees which are cut or killed by fire. Sprouts that originate at or below ground level and from small stumps are less likely to develop heartwood decay. Sprouts from large stems grow faster than either sprouts from small stems or seedlings, due largely to the respective amounts of root area available.

Seedlings subjected to extreme moisture stress to the point that the shoot is killed may still sprout if some portion of the root system is alive and adequate soil moisture is restored (156).

Adventitious 'aerial' roots may reportedly originate from the stems of stressed or injured trees, though this is uncommon (886)).

SEASONAL GROWTH PATTERN

Studies of northern red oak is Germany have shown that initiation of root growth and shoot growth in the spring occur almost simultaneously. Rate of root growth increased gradually for about 2 weeks, decreased slightly, then increased again until reaching a peak approximately 4 weeks after initiation. Root growth then gradually decreased throughout the summer, almost ceasing completely 10 weeks after initation. Growth then increased again somewhat for a brief (3 - 4 week) period in the fall. Overall, root growth exhibited a more constant growth pattern throughout the year than shoot growth, the vast majority of which was accomplished during a breif 4-week period in the spring (543).

ROOT-SHOOT RELATIONS

Red oak seedlings in one study were found to have an average root-starch content of about 40 percent during the dormant season, which is considerably higher than most reported figures for deciduous-tree species. This may be largely due to the fact that leaf retention of oak extends later into the fall than many of its associates (359).

Hormonal factors originating in the stems are largely responsible for root initiation and growth. This is supported by experiments with red oak seedlings which show that root regeneration occurs on all plants that have some stems, but not on plants which have had their tops severed (359).

RESPONSE TO COMPETITION

Survival of seedling red oak may be significantly affected by root competition with established vegetation. Competition with woody shrubs is generally less intense than competition with ferns or grasses. In one study almost 4 times as many red oak seedlings grown with shrub competition were alive after 5 years as seedlings grown with either grass or fern competition (Scholz, 1955).

EFFECTS OF EXCESSIVE AND DEFICIENT MOISTURE

Northern red oak is reportedly relatively intolerant of flooding during the growing season. One author found that red oak could tolerate 50 days of growing season high water, but usually succumbed after 100 days (104). Another reported that some trees survived 2 years of constant inundation, but few survived much longer (455).

Among the oaks, tolerance to inundation (from most tolerant to least tolerant) is as follows: Q. palustris (pin oak), Q. macrocarpa (bur oak), Q. imbricaria (shingle oak), Q. alba (white oak), Q. rubra (red oak), and Q. velutina (black oak) (104).

As compared to some of its other deciduous associates, northern red oak is more flood-tolerant than black cherry, paper birch, and sassafras, but less tolerant than shagbark hickory, green ash, sycamore, eastern cottonwood, silver maple, and black walnut (104).

Among the oaks, Q. rubra is one of the most sensitive to drought conditions. The roots of red oak were found to be lower in both drought avoidance (ability to postpone dehydration) and drought resistance than the roots of post, white, and black oak (1060). These results may not be well correlated with seedling survival, however, because of the ability of oaks to die back under stress and resprout later. Northern red oak is considered to be more drought-resistant than many of its other deciduous associates (notably sugar maple and basswood), though few comparitive studies have been performed (15,908).

Root regeneration is particularly sensitive to even moderate soil stress conditions. Growing red oak roots can continue to elongate in soil too dry for initiation of new roots; this point was achieved at -4 bars of osmotic potential in one study (-1/3 bar = field capacity; -15 bars = perm. wilt. point).

RESPONSE TO SOIL CHARACTER

The most obvious difference between the root systems of seedling red oak grown on soils of different texture involves the size and number of branch roots. In one study, plants grown in a silty clay loam soil developed branch roots which were long and tapering, while those grown in a sandy soil developed short, thick branch roots which originated close to the primary root tip (39). Another study found that root weight and total root length of red oak seedlings were greatest on a loam soil (as compared to a clay and a clay loam), although maximum root depth was least (336). The clay soils in this case were quite friable.

Distribution of roots in mature red oak also varies with soil texture. One author found an almost equal distribution of roots among the A and B1 horizons on a loamy sand soil, whereas the vast majority of roots on a fine sandy loam soild were in the A horizon.

Roots of the trees on the loamy sand soil also penetrated the B2 horizon (and even deeper) to some extent, whereas virtually no roots could be found in the B2 of the fine sandy loam. It was also found that trees in the loamy sand had a proportionately greater number of roots (especially larger roots) at a greater distance from the stems than was the case on the fine sandy loam (417).

Red oak seedlings grown at four different soil temperatures displayed maximum root and shoot development at 75°F. Root growth was not significantly reduced at 65°F or 85°F, but dropped off sharply at 55°F. Alternating the day to night soil temperature provided no growth advantage over constant temperatures for either roots or shoots (706).

MYCORRHIZAE

Species of fungi known to form ectomycorrhizal associations with northern red oak include *Cenococcum graniforme*, *Clitocybe candicans*, *Cortinarius rubripes*, *Russula emetica*, *Pisolithus tinctorius* (810). *Boletus bicolor* var. bicolor, *Tylopilus rubrobrunneus*, *Boletus griseus*, *Boletus russellii*, *Strobilomyces floccopus*, *Boletellus chrysenteroides* (Homola & Mistretta, 1977). Many other fungi are undoubtedly involved, but experimental proof is thus far lacking.

DESTRUCTIVE AGENTS

Non-infectious

Drought is known to cause stagheading and dieback of oak over extensive areas. Symptoms may not appear until several years after the tree (and roots in particular) are subjected to moisture stress.

The so-called "oak decline" that affects red oak over most of its range has been attributed to a variety of causes, some of them affecting the roots. These include drought, unfavorable soil conditions, *Armillaria* root rot, and insect attack (Hepting 1971).

Northern red oak is classified as tolerant to soil applications of salt (871).

Insects

Northern red oak is relatively free of root damage due to insects. One species of white grub (*Phyllophaga tristis* (Fab.)) and two weevils (*Pseudocneorhinus bifasciatus* Roelofs and *Crytepistomus castaneus* Roelofs may cause damage on occasion, but are normally not a primary cause of mortality. Two beetles of the genus *Prionus* may also damage the roots of red oak; the broad-necked root borer *P. laticollis* (Drury) and the tile-horned Prionus, *P. imbricornis* (L.). Both feed upon roots while in the larval stage (Baker, 1972).

Defoliation of northern red oak by the gypsy moth (Lymantria dispar) is thought to increase vulnerability of the root system to attack by the fungus Armillaria mellea (Wargo, 1977).

Nematodes

Species of nematodes associated with northern red oak include Criconemoides beljaevae, C. macrodorum, Helicotylenches platyurus, Hoplolaimus galeatus, Longidorus elongatus, Xiphinema americanum (Ruehle, 1967), Hoplolaimus coronatus (Hepting 1971).

Fungi

Red oak is highly susceptible to oak wilt, a fungus disease which has resulted in the deaths of thousands of trees from Pennsyvania to Wisconsin and Iowa. Trees often die the same year that they are infected. Spread of oak wilt is accomplished through root grafts and probably by insects, birds, and animals (Sander, 1957). The fungus may pass from an infected tree through root grafts into newly formed sprouts of adjacent stumps of healthy trees beyond the perimeter of the eradication zone (1336).

Red oak seedlings are moderately susceptible to attack by the root rot fungi Phytophthora cinnamomi (Hepting 1971) and P. citricola (454).

A bacteria associated with "shake" has been found to infect red oak growing on poorly drained soils in Wisconsin. The bacteria is believed to enter the tree mainly through root wounds (1235).

In general, root rot of red oak is less prevalent among trees growing on lighter, well-drained soils than among trees on finer textured soils (220).

EFFECTS OF PLANTING METHODS

Environmental controls and planting techniques utilized with red oak bare-rooted stock should be aimed at getting root growth under way before the plants come under moisture stress associated with oaks' rapid shoot elongation. Such techniques might include late winter planting, coupled with efforts such as mulching to increase soil temperature (359).

Certain growth regulators such as Indolbutyric Acid (IBA) have been shown to stimulate root growth in red oak seedlings while suppressing bud growth. Manipulation of IBA applications has been suggested as a way to delay shoot growth in outplanted trees until a sufficient root system has been regenerated (796,197). Gibberellic acid treatments, however, have not proven beneficial in improving seedling survival (1214,708).

Moist soil conditions and freedom from heavy plant competition are considered essential for rapid establishment of planted red oak (707).

Robinia pseudoacacia L. - Black Locust

MORPHOLOGY

Development of Form

Early downward root growth in black locust is quite rapid in comparison with other tree species. Hoffman (1966) found a maximal depth development of 210 cm at the end of the first year of growth, as compared to 188 cm and 149 cm for such taprooted species as bur oak and black walnut, respectively. Average increment of individual black locust roots in this study was 15.2 mm.

Lateral root growth is somewhat slower but relatively constant, resulting in a lateral system that is eventually quite extensive (195).

Distribution in Soil Profile

Black locust has been described as a "heartroot" species, since the extent of lateral and diagonal rooting in mature trees is often nearly as great as rooting depth. Bunger and Thomson (195) found an average depth of penetration of 26 ft. (7.9m) in established shelterbelt black locust in Oklahoma, while the same trees averaged 21 ft (6.4m) in average length of longest lateral root.

Density of fine roots (rooting intensity) is quite high in black locust. Greenhouse-grown, 4-month-old black locust seedlings in one study had approximately 17 times as many roots and about 170 times more root length than did loblolly pine seedlings of the same age (660). Rooting intensity of 20-year-old black locust was not as great, however, as that for similar-aged ash (*Fraxinus* sp.).

Grafting

There is at least one reported instance of intraspecific root grafting in black locust.

Adventitious Rooting & Root Suckering

Black locust readily propogates itself by means of root suckering. The new suckers may form from either adventitious buds on the fine horizontal roots or from dormant buds that occur where branch roots emerge from older roots (Fowell, 1965). Wounding of the roots is not necessary in order to encourage root suckers, although both number and growth rate of suckers may be increased if the parent stems and/or roots themselves are injured (704; Fowells 1965).

Black locust root suckers in Ohio have been reported to encroach on farmlands at rates of up to 10 ft. (3.0m) per year. Areas occupied by trees or dense brush are not normally invaded (704).

Black locust can also be propogated vegetatively by means of transplanting natural spouts, grafting and root cuttings. Large diameter (> 12 mm) root cuttings collected in winter or early spring have been most successful (Fowells, 1965) (1138).

SEASONAL GROWTH PATTERN

Lyr and Hoffman (1967) found that, for black locust in Germany, initiation of shoot growth preceded root growth by approximately one week. Root growth began late in May, peaked in mid June, and later peaked again in mid July and early August (though neither of these latter two was as great as the June peak). Root growth ceased around September 25, which was approximately 5 days after the cessation of shoot growth. The following season the pattern was similar, with the exception that root growth peaked at slightly different times and continued (at a very slow rate after September 1) until about October 20, due to favorable autumn weather (543).

ROOT-SHOOT RELATIONS

At a light reduction to 40% of full sunlight, both rooting depth and rooting density of black locust are strongly reduced. At the 40% intensity, one study showed a total length of fine roots of only 39m as compared to 266m for unshaded trees.

EXUDATION

Extracts of black locust have been shown to hinder the growth of some herbaceous plants, notably barley (1323). Another researcher reported that black locust interferes with the development of nearby white pine by limiting the water which the pine can absorb, possibly by means of a toxic excretion (925).

An analysis of the root exudates of four pine species and black locust showed that locusts exudes three amino acids, asparagine, methionine, and tyrosine, which are not exuded by any of the pines. Of these only tyrosine is not common in other legume exudates (1100).

EFFECTS OF EXCESSIVE AND DEFICIENT MOISTURE

Black locust has been classed as intolerant - moderately tolerant to inundation of its root system during the growing season (481,174). Most trees in one study were unable to survive continuous flooding one foot deep for one growing season (174).

In the case of the root development of seedling black locust, one study found that the length of the taproot decreases with diminishing moisture. This was contrasted with ponderosa pine, in which both the taproot and total length of lateral roots increased with diminishing moisture supply (133).

Among common shelterbelt species, black locust was found to be intermediate in its ability to tolerate prolonged drought. Red cedar, asiatic elm, and osage orange were more tolerant than black locust, while honey locust, Russian mulberry, and black walnut were less tolerant (195).

RESPONSE TO SOIL CHARACTER

Soil depth has been shown to largely determine the length of the taproot in black locust. In one study, trees grown in soils with no depth restriction had taproots 5 times longer than trees grown in shallow soils, even though stem height was approximately the same on both soils (133).

On fine-textured soils of the great plains region, black locust was classified by one author as intermediate in rooting depth with most trees reaching depths of 5 to 10 ft (1.5-3m) at age 20. Green ash, American elm, and boxelder were also placed in this category (509).

Black locust is considered to be quite tolerant of saline soil conditions (1064,1200,654). A study of the structure of root systems in various salt-tolerant woody species on soils of different salinity showed that saline horizons prevent the penetration of black locust roots to deep layers of the soil. The maximum depth to which the roots of black locust reach are the layers where the concentration of the soil solution becomes (even periodically) higher than 25-30) g/L. Depending on the moisture conditions and quaitative composition of salts, this corresponds to 0.30-1.00% of salts (841).

Nitrogen-fixing root nodules are characteristic of leguminous species, and tree legumes such as black locust develop large and abundant root nodules. Soil nitrogen increases from 300-600 lbs/acre have been reported under stands of black locust, resulting largely from the high annual turnover of nitrogen from limbs and litter (Fowells, 1965; 588). Increased height and diameter growth and greater foliar nitrogen have been reported for trees associated with black locust cover (Fowells, 1965; 589, 227). The nodules of locust are numerous and effective when nitrogen is deficient, but are innefective and few when certain other soild elements, such as boron, sulphur, and/or magnesium, are deficient (521).

The ability of black locust to grow on relatively infertile soils, combined with its root suckering ability, have made it suitable for use as a colonizer of industrial waste sites (279).

A study of the influence of high soil temperatures on several woody-plant species revealed that growth was reduced significantly after a 4-hour exposure at temperates above 40°c, and that temperatures above 50°c usually resulted in death. Even temperatures of 35°c for 6 hours each day reduced black locust stem growth by 75% (1317). At 33°C length growth of the main root is inhibited, which favors side-root development. Another study, however, found that increases in soil temperature of approximately 5°c above normal for periods of one year or longer (never exceeding 25°c) induced root growth which began 41 days earlier and terminated 44 days later than in control plants. The same study listed 22.5°c as the optimum temperature for root growth of black locust, which is only 3.5°c above the temperature at which lateral root formation begins to be inhibited on the cool end of the scale.

MYCORRHIZAE

Only two fungi have been reported as mycorrhizal associates of black locust, namely Clathrus cancellatus and Gigaspora gigantea (279; Hepting, 1971).

Medve, et al. found that black locust planted on bituminous stripmine soils did not form as many mycorrhizae as many other tree species did, but that survival of locust was still high due to its nitrogen-fixing ability (831). Draft, et al. (279) reported that approximately 66% of black locust growing on coal spoils in Pennsylvania were infected with endomycorrhizae.

DESTRUCTIVE AGENTS

Non-Infectious

One researcher has reported that higher-than-normal applications of some herbicides (calordane, thiosan, allyl alcohol, and others) can adversely affect the N-fixing bacteria associated with locust roots, resulting in decreased nutrient uptake (1232).

Insects

The lesser cornstalk borer, Elasmopalpus lignosellus (Zeller), has damaged black locust seedlings, in nurseries in several southern states. Injury usually occurs at or near the ground line, causing affected seedlings to die or break off at the ground line. Refer to Baker (1972) for more information on this insect.

Black locust seedlings have been shown to be relatively free of damage by white grubs (Phyllophaga), even when grown in seedbeds known to be heavily infested by the larvae (606).

Nematodes

Nematodes associates with the roots or root zone of *Robinia pseudoacacia* include *Meloidegyne* sp., *Paratylenchus projectus*, *Pratylenchus penetrans*, *Tylenchorhynchus claytoni* (Ruehle, 1967)(1148).

Fungi

Except within the Texas root-rot (*Phymatotrichum omnivorum*) belt, Hepting, 1971 states that "there are no important or noteworthy root diseases of black locust in the United States." As with many other hardwoods, *Armillaria mellea* may contribute to the death of black locust already weakened by other causes (Hepting 1971). Black locust has been shown to be only slightly susceptible to root rot by the fungus *Phytophthora cinnamomi* (272).

MORPHOLOGY

Development of Form

Root growth in northern white-cedar seedlings is characterized for the first several years by development of a tap root. The tap root may continue straight downward or may turn horizontally and branch if a favorable soil layer is reached. Depth of seedling penetration is quite great, generally exceeding balsam fir and red spruce but less than white pine on upland sites (859). The tap root system is later replaced by a fibrous system; this replacement occurs earliest on trees growing on wet sites (884). Seedlings which germinate on unfavorable sites, such as stumps or logs with little decay, are often characterized by poorly developed, nearly unbranched root systems (884).

Distribution In Soil Profile

The root system of mature cedar is generally quite shallow, although there is considerable variation among trees on different soil types. One author reports that the lateral roots of cedar are usually only 2 or 3 inches (5.1-7.6 cm) deep, with only a few as deep as 6 inches (15.2 cm) (437). Another reports that the roots of cedar growing along a stream were confined to a layer approximately 30 cm. thick (710).

Cedar rootlets are conspicuous for their red color, are tough, and terminate in translucent root tips of considerable length, up to 10mm. The tips are not enlarged as in some species, but merge gradually with the bark-covered part of the rootlet. The roots can be withdrawn from humus quite easily because they are more or less straight. Because of their nature, cedar roots reportedly do not exclude those of other species, which seem able to grow in nearly the same spot without apparent difficulty (859).

Grafting

Natural root grafting in northern white cedar is reportedly fairly common, especially on the more moist sites (658, 446, 659, 710).

Adventitious Rooting

Northern white-cedar has the ability to produce adventitious roots both from branches (layering) and stems. The former is a common form of reproduction in swamps and on shallow-soiled uplands (884, 939). Adventitious "brace roots" commonly form on the stems of trees growing on shallow or wet soils, presumably serving as an aid in support (884). They are also no doubt important in maintaining sufficient uptake of water and nutrients where the original root system has become buried deeper in the accumulating humus (859). Northern white-cedar rarely develops root suckers, although this has been reported occasionally (Godman, 1958).

Layered stems may or may not develop their own root systems. Stems originating from the branches of windthrown trees commonly are able to obtain water and nutrients from the portion of the root system still in the ground. Stems originating from severed branches may develop completely independent root systems.

A single branch may be covered at several points by moist media and start formation of adventitious roots at all of these points. The adventitious roots in cedar originate from tracheal xylem rays in the stem, rather than from dormant buds as in Picea and Abies (71).

ROOT-SHOOT RELATIONS

A comparison of northern white-cedar, white spruce, black spruce, and balsam fir revealed that dry weight of roots in 4-year old seedlings was greatest in cedar at all light intensities greater than 25% of full. At 13% of full light, however, root weight of cedar was reduced to only .01% of its weight at full light; this was lower than for any of the other species tested (746, 747).

RESPONSE TO COMPETITION

Competition from grasses or sphagnum moss is a fairly significant cause of mortality in seedling white-cedar, although the exact proportion of this which is root competition is unknown (884).

It has been suggested by one author that, despite its shade tolerance, northern white cedar serves as a pioneer species in non-acid swamps. The platform of roots and humus which it builds serves as a place for establishment of white pine, black spruce, and balsam fir. The acid humus and mat of fine rootlets then produced by spruce results in the eventual elimination of cedar, whose roots cannot compete under those conditions (859). It should also be noted, however, that white-cedar is found extensively throughout the acid swamps of the Lake States (884).

EFFECTS OF EXCESSIVE AND DEFICIENT MOISTURE

Studies in Wisconsin have suggested that there are genetic differences between upland and lowland white-cedar involving plasticity of root development and ability to tolerate a certain level of soil moisture. One author found that seedlings from upland sites displayed great flexibility in their root development, producing long root systems in well drained soils and short root systems in saturated soil. Lowland white-cedar seedlings, on the other hand, displayed rather constant root development in both well drained and saturated soils (469). Seedlings from lowland sites were unable to survive for very long on the well drained, sandy soil in which the upland seedlings were growing (878).

Although white-cedar commonly grows on saturated soils, some degree of aeration is critical for survival and reasonable growth. Slow-moving or stagnant ground water tends to reduce the rate of growth and in some cases may kill the entire stand. Draining of swamps has been shown to have a favorable effect upon growth in some cases (Godman, 1958).

On sites with the water table very near the surface the root system of cedar is shallow and widespreading, with a "platform" of much branched roots above the water. The bottoms of root systems on such sites appear flattened as if growing on a smooth ledge (859).

RESPONSE TO SOIL CHARACTER

Much of the variability in the root system of cedar can be attributed to soil moisture conditions. In dry upland soils, especially sands, cedar usually have sinker roots in addition to the laterals. These deep roots include the tap root, when present, and other roots which extend downward from the principal horizontal roots. When growing in swamps, the root system is very shallow, consisting primarily of wide-spreading lateral roots in the top few inches of soil (68).

On rocky sites cedar seems to have greater ability in pushing into crevices and under boulders than most of its associates. This can be seen on trees found clinging to the sides of vertical cliffs (859).

In swamps, root development and vigor generally increases as the depth of the peat decreases and as internal drainage improves. The best peat for growth is generally made up of well-decomposed woody plants or sedges. Poor peat consists of poorly-decomposed moses, reeds, and rushes (Watson, 1936).

The best growth of northern white-cedar occurs on soils of calcareous origin, (Ph 6.5-7.5) though it is by no means limited to these areas. Both root and shoot growth are generally greatest on sandy loam old-field sites (276) (Pirone, 1948).

Unlike most of its coniferous associates, northern white-cedar exhibits very little variation in root wood structure among roots in different soil types or at different soil depths (69).

MYCORRHIZAE

Northern white-cedar is, according to more than one author, the only northeastern conifer that does not have mycorrhizal fungi associated with its roots (884, 859). Homola and Mistretta (1977), however, reported the ectomycorrhizal fungus Leccinum holopus to be common in the cedar swamps of Maine.

DESTRUCTIVE AGENTS

Non-infectious

Swamp stands of northern white-cedar, because of their shallow rooting habit, are susceptible to windthrow and uprooting, particularly in stands that have been partially cut. Roots near the surface may be damaged through trampling by animals and on drier sites are subject to drying from fluctuating water tables. Shallow lateral roots are also easily killed by even light surface fires (276).

Northern white-cedar has been ranked as moderately tolerant of soil applications of salt, although the foliage is very sensitive to salt spray (871, 923, 318).

Insects

The arborvitae weevil, Phyllobius intrusus Kono, an introduced species first recorded on nursery stock in Rhode Island in 1947, feeds on the roots on white-cedar seedlings. It is now known to occur as far west as Pennsylvania. Eggs are deposited in the soil during May and June, and the larvae feed on the roots of the host plant for the remainder of the season. In heavily infested areas, well over 200 larvae may be found on the roots of a single plant, resulting in severe root running (Baker, 1972).

Larvae of the black vine weevil, Brachyrhinus sulcatus (Fab.) also cause some damage to the roots of white-cedar throughout the northern states, although hemlock and yew are the preferred hosts. Eggs are deposited on the ground in trash or among soil particles, under loose bark, or among the leaves of their hosts. The larvae enter the soil and begin feeding on the young rootlets; later, on the cortex of larger roots. Infested roots may be stripped of their bark for several inches, or may be gouged out on one side only. There is one generation per year. Damage in nurseries can be minimized by the rotation of seedbeds or by allowing infested areas to lie fallow while thoroughly cultivating them in alternate years (Baker, 1972; Wilson, 1977).

Larvae of the strawberry root weevil, Brachyrhinus ovatus (L.), a close relative of the black vine weevil, are quite destructive of seedling white-cedar in Lake States nurseries. The overall damage and habits of this insect are similar to those of the black vine weevil, except that the adult is only half as large and lacks the white wing spots of the black vine weevil (Baker, 1972; Wilson, 1977).

Nematodes

Nematodes reportedly associated with the roots of northern white-cedar include Criconemoides bakeri, Longidorus maximus, Rotylenchus robustus (Ruehle, 1967), Pratylenchus penetrans, Tylenchus emarginatus, Paratytenchus projectus (Hepting, 1971), Aphelenchoides parietinus, Aphelenchus avenae, Ditylenchus sp., Helicotylenchus goodeyi, Hoplolaimus tylenchiformis, Paurodontus sp., Pratylenchus pratensis, Trichodorus sp., Tylenchorhynchus claytoni, Tylenchus costatus, Xiphinema americanum (792).

Fungi

The root and butt-rot fungi of northern white-cedar mainly attack old or damaged trees and have not yet proved to be economically important. They include Armillaria mellea, Fomes annosus, F. pini, F. pinicola, Polyporus balsameus, P. schweinitzii, and Poria subacida (Hepting, 1971). Northern white-cedar is reportedly one of the few northern conifers which are resistant to attack by the root-rot fungus Cylindrocladium scoparium Morgan (32, 192, 1089).

Tilia americana L. - American Basswood

MORPHOLOGY

Development of Form

Early root growth of basswood is reportedly quite slow in comparison to some of its associates. Taproot growth is emphasized for most of the first year, but vertical penetration generally will not exceed one ft. (.3m) during the period, and is often considerably less (544, 58).

As growth continues the lateral roots form the greater part of the root system. A 15-ft. (4.6m) sapling growing on a silt loam soil in Wisconsin was found to have four roots 1 to 2 in. (2.5-5.1cm) in diameter. The largest one tended obliquely downward, while the other three ran more or less horizontally. One of the lateral roots was still 1 in.(2.5cm) in diameter at 26 ft. (7.9m) and 1/2 in. (1.3cm) at 34 ft. (10.4m) from the origin. It was also exposed at the soil surface twice in this distance (58).

Distribution in Soil Profile

The root system of mature basswood is shallow and tends to be dominated by wide-spreading lateral roots. Branching is reportedly not as frequent as in most of its associates. The bulk of the absorbing system is generally within the first 2 feet (.61m) of soil, the shallow roots persisting even under conditions of impending drought (58).

Grafting

Self-grafting of roots in individual basswood trees is reportedly common (710, 446). There are no reports in the literature of root grafts between trees.

Adventitious Rooting

Basswood sprouts readily from stumps, but does not produce root suckers. Layering of stems can reportedly be induced (Williams and Hanks, 1976).

SEASONAL GROWTH PATTERN

Root growth in basswood under nursery conditions in Illinois was episodic, extending from May through November. Growth began when soil temperatures were approximately 65^{o}F and was observed to continue at soil temperatures of 50^{o}F. Root growth in the greenhouse continued throughout the year, regardless of the foliage conditions of the shoot. Spring shoot growth in the nursery began before root growth was evident (59).

Another author reports that seedling basswood in Illinois resumed root growth in late April, grew rapidly during May and June, and eventually ceased growth on July 28. Root growth was again detected on September 8 and continued through about November 24, when it ceased again (780).

ROOT-SHOOT RELATIONS

Active root growth in basswood is highly correlated with top growth. In one study, presence or absence of root growth was related to top growth in seedlings differentially chilled and exposed to various photoperiods. Plants of several seedling lots grown under greenhouse conditions without chilling did not renew top growth until mid-summer (58).

Another study reports that girdling of the stem has a marked influence on root growth in basswood, suggesting a dependency on factors transmitted from the shoot. Chlorophyllous stem tissue as well as actual bud and leaf material may play a role in root stimulation (59).

Continuing growth of leafless greenhouse trees through the winter indicates that adequate materials are present in the shoot-root system once growth is initiated. This is also illustrated by the fact that total root growth was found to be equal in undamaged plants and in those debudded once (59).

Root growth in basswood seedlings was found to exhibit compartatively little variation at light intensities from 25-100% of full, but to decrease considerably below 25%. Oven-dry root weight in (grams) of 4-year old basswood was reported to be 8.6%, 17.2, 17.8, and 23.6 at light intensities of 13%, 25%, 45%, and 100% respectively (745).

UPTAKE

One study found that both nutrient and water uptake of basswood seedlings varied considerably with soil temperature. Potassium uptake was 23.7 mg/gm at 16°c, 12.5 mg/gm at 22°c and 17.7 mg/gm at 28°c. Phosphorous uptake ranged from 9.6 mg/gm at 16°c to 8.5 and 8.4 mg/gm at 22°c and 28° c. Water uptake, which was not highly related to leaf number, was always least for the 16° plants. The greatest production of both roots and tops occurred at 28°c. There relationships suggest that nutrient uptake is less limited by low root temperatures than are other metabolic functions which are important for growth (57).

EFFECTS OF EXCESSIVE AND DEFICIENT MOISTURE

Growth of basswood seedlings subjected to flooding for part of a growing season showed earlier than normal bud break, fewer and smaller leaves, some interveinal chlorosis, and greatly enhanced visual hairness on the leaf surfaces. Total growth was highly significantly decreased by flooding; this decrease was most pronounced for root growth. The top-to-root ratio increased from 0.43 to 0.59 with the flooding treatment. At harvest 40% of the flooded plants had actively growing root tips compared to 50% for the control (58).

Another author classified basswood as moderately intolerant to inundation. Most trees did not survive continuous flooding one foot deep for one growing season. Species more flood tolerant than basswood included black locust, shagbark hickory, loblolly pine, sycamore, and boxelder; less tolerant species included sugar maple, yellow-poplar, american beech, black cherry, and white oak (174).

The shallow-rooted basswood is often one of the first tree species to show symptoms of drought injury to the roots, usually in the form of withered leaves or dieback of individual branches (15).

RESPONSE TO SOIL CHARACTER

Basswood exhibits its best growth on sandy loams, loams, and silt loams having clay subsoils, or, lacking these, on soils where the upper 40 inches (1.0m) of the profile consists of fine-textured materials (Fowells, 1965). It may also grow on drier soils such as dune sands, but is generally absent from compacted soils such as of sparsely vegetated abandoned and eroded areas. Basswood regeneration generally will not occur for several years after livestock exclusion from forests, illustrating the importance of porous soil for this species (58).

One author has attributed the rather limited distribution of basswood to its inability to compete for soil nutrients (particularly nitrogen) on infertile soils with such species as white oak and chestnut oak (851).

Although their growth varies considerably, basswood roots do not exhibit the marked differences in succulence and maturation at different soil temperatures that other species reported do, particularly apple and peach (57).

MYCORRHIZAE

Very few fungi have been reported to form mycorrhizae with any species of *Tilia*. *T. americana* is reported to form mycorrhizae with *Cenococcum graniforme*, *Scleroderma aurantium*, *Russula* sp. (Hepting, 1971).

DESTRUCTIVE AGENTS

Insects

Larvae of several beetles are known to feed on the roots of basswood, including the broad-necked root borer, *Prionus laticollis* (Drury), the Japanese Beetle, *Popillia japonica* Newm., and four species of so-called June beetles, *Phyllophaga drakei* (Kirby), *P. prunina* (LeC.), *P. implicata* Horn, and *P. crenulata* (Froel.). Descriptions of these insects and the damage they cause are given in Baker, 1972.

Fungi

No true root rots have been reported for basswood. *Ustulina vulgaris* and *Corticium galactinum* reportedly have a low capacity to rot roots of *Tilia* and other hardwoods (1269; Hepting, 1971).

Tsuga canadensis (L.) Carr. - Eastern Hemlock

MORPHOLOGY

Development of Form

The early root system of hemlock is short and superficial, seldom reaching a depth of more than 5 inches the first season. This undoubtedly relates to hemlock's normal habit of regenerating under a dense canopy, where the largest percentage of available moisture remains in the upper soil layers throughout the growing season (1178). The slender taproot which is formed during the first year is later lost in the development of lateral branches, most of which are quite shallow (407).

Distribution in Soil Profile

The root system of mature hemlock is generally quite shallow, although it is reportedly somewhat flexible depending upon available rooting depth. Lateral branches are large and numerous and may extend for a considerable length (407).

Grafting

Natural root grafts between adjacent hemlock trees have been reported (658). In addition, grafts between hemlock stumps and living trees are reportedly fairly common (903, 893, 285).

Adventitious Rooting

Layering of hemlock in nature is very rare, although it has been noted in a few cases. Natural stump sprouts or root suckers have not been reported.

ROOT-SHOOT RELATIONS

Seedling hemlock grown for 7 years at 4 different light intensities showed that root production (in terms of total weight) was greatest at the 45% light intensity and least at 13%. Root weight at the 100% light level was only slightly greater than at 25%. Hemlock is one of the few northeastern conifers to show appreciable root growth in very low light (747).

EFFECTS OF EXCESSIVE AND DEFICIENT MOISTURE

Early survival of hemlock seedlings depends largely upon continuous availability of moisture in the upper soil horizons throughout the growing season. Experiments have shown that seedlings freed from the moisture-competition of roots from overstory trees will thrive despite dense shade. The root of mature hemlock are also very sensitive to drying out of the surface soil, which in part accounts for the death of trees exposed to increased light through logging or other disturbances (407).

MYCORRHIZAE

Fungi known to form mycorrhizal associations with hemlock include *Cenococcum graniforme*, *Suillus granulatus* (1181), *S. intermedius*, *Tylopilus eximius*, *Boletus edulis*, *B. piperatus*, *B. rubinellus*, *B. radicans*, *B. subvelutipes* (Homola & Mistretta, 1977).

DESTRUCTIVE AGENTS

A decline of hemlock often referred to as post-logging decadence has been at least partially attributed to the change in soil moisture and temperature regimes following opening of the forest. Trees may be affected even though their root area is covered with understory brush (Hepting, 1971).

Hemlock is reportedly quite sensitive to changes in grade around its roots (839).

Because of its shallow rooting habit, hemlock is particularly sensitive to mechanical root damage due to animal trampling or the use of heavy machinery. This type of damage may not be as apparent in hemlock as in other species which produce root suckers from the wounded root (as beech), though it may be just as severe (757).

Prolonged drought may result in heavy mortality of hemlock. The root tips are the first organs to die under moisture stress, followed eventually by starvation of larger roots when they become unable to supply sufficient water to the crown for normal manufacture and translocation of food. With the death of the roots, attacks by disease and insects become more probable (1057).

Hemlock has been rated as very sensitive to soil applications of salt (871, 131).

Hemlock is quite susceptible to windthrow in stands which have been disturbed, or when growing in exposed situations (1123).

The shallow roots of hemlock are easily injured by any fire that burns deeper than the loose surface litter (Fowells, 1965).

Insects

Insects known to cause damage to the roots of hemlock include the black vine weevil *Brachyrhinus sulcatus* (Fab.), the strawberry root weevil *Brachyrhinus ovatus* (L.) the Japanese weevil *Pseudocneorhinus bifasciatus* Roelofs and the pales weevil *Hylobius pales* Herbst.). None are considered to be of significant economic importance.

Nematodes

Nematodes associated with the roots of hemlock include *Hoplolaimus galeatus*, *Paratylenchus nanus*, *Tylenchorhynchus claytoni* (Ruehle, 1967), *Aphelenchoides* spp., *Hemicycliophora* spp., *Pratylenchus* spp., *Tetylenchus* spp., *Tylenchus* *spp.* (1347), *Criconema* sp., *Criconemoides* sp., *Helicotylenchus* sp., *Hemicriconemoides* sp., *Paratylenchus* sp., *Xiphinema americanum*, Cobb, *X. chambersi* Thorne (Ruehle, 1968).

Fungi

The root-rot fungi *Armillaria mellea*, *Fomes annosus*, and *Polyporus schweinitzii* can be pathogenic to hemlock but seldom kill trees (Hepting, 1979).

The fungus *Cylindrocladium scoparium* is reported capable of causing root rot of hemlock in some areas (266, 594).

Other root-rot fungi which may attack hemlock occasionally include *Corticium galactinum* (Fr.) Burt, and *Polyporus balsameus* (1057, 37).