THE INCIDENCE AND SEVERITY OF *HETEROBASIDION ANNOSUM* (FR.) BREF. IN LOBLOLLY PINE (*PINUS TAEDA* L.) UNTHINNED PLANTATIONS AND SEED ORCHARDS

by

Roger Stuart Webb

Dissertation submitted to the Graduate Faculty
of the Virginia Polytechnic Institute and State University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

Plant Pathology

APPROVED:

S. A. Alexander, Co-Chairman

J. M. Skelly, Co-Chairman

D. F. Amos

J. D. Gregory

L. J. Miller

January, 1980

Blacksburg, Virginia

ACKNOWLEDGEMENTS

The author wishes to express his sincerest appreciation to the following individuals and organizations for their contributions to this dissertation:

Drs. Samuel A. Alexander and John M. Skelly for their expertise, guidance and unfaltering enthusiasm which was invaluable to the completion of the various experimental studies and final preparation of this manuscript;

Dr. Lawrence I. Miller for his assistance and especially his philosophical advice relative to the analysis of plant disease;

Dr. Dan F. Amos for his involvement and analysis of edaphic factors inherently important in the etiology of root disease;

Dr. Jimmy D. Gregory for his invaluable experience in subsoiled loblolly pine seed orchards and his willingness to advise and contribute to this project.

The Chesapeake Corporation, Virginia Division of Forestry and Union Camp Corporation for their contributions of personnel, research areas and heavy machinery critical to the successful completion of the original research objectives;

The Southern Forest Disease and Insect Research Council and the Virginia Agriculture Foundation for providing graduate research stipends;

for

technical field assistance;

My wife, , for her motivation and understanding without which this opportunity would not have been possible.

TABLE OF CONTENTS

Table of Contents (continued) Page

Table of Contents (continued) Page

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

In his monograph on loblolly pine (Pinus taeda L.), Ashe (1915) described the superior silvical characteristics which contributed to this species' foremost commercial importance in southern forestry:

> Loblolly combines all the essentials for an ideal forest management tree. It seeds profusely and regenerates readily, is adapted to nearly all types of soil, grows rapidly, become marketable at an early age, grows densely, making large yields per acre, and produces material for which there is a general demand at a fair and increasing price.

The value of loblolly pine to the forest industry is underscored by its relative abundance since within the 14 states comprising the natural range of this species, the loblolly-shortleaf pine (P. echinata Mill.) type occupied 27 percent of the total commercial forest land (Wahlenberg, 1960). In Virginia, loblolly pine predominates in the Coastal Plain and is the primary timber management species comprising about 40 percent of the total softwood growing stock (Knight and McClure, 1978).

However, the preeminence of pines, particularly loblolly pine, in the southern forest industry is threatened by a combination of inadequate pine regeneration and subsequent hardwood encroachment. Although the South's net annual cubic volume growth of softwood currently exceeds the harvest by 45 percent and the sawtimber growth exceeds the cut by 30 percent, in Coastal Plain areas of Virginia, southeastern Georgia and northern North Carolina the sawtimber cut now exceeds net annual growth (Williston, 1979). Areas of Alabama, Arkansas, Mississippi and Texas are in similar jeopardy.

Central to this problem are the small individual landowners who hold almost 73 percent of all southern commercial timberlands. Marlin (1978) in Louisiana and Porterfield and Moak (1977) in Mississippi both reported that only about half of the landowners surveyed believed timber production to be the prime use of their land. Also, many landowners are not making the financial investments in site preparation and planting of pines necessary for regeneration following harvest. As Knight (1978) emphasized, the result has been a sharp decline in the total southern acreage planted to pines. Specifically, he cites the net loss of about seven million acres in pine forest types in the South over a recent 10-year period. Knight and McClure (1978) noted a concurrent 24 percent decline in pine acreage with a 15 percent increase in hardwood acreage in Virginia over the period 1957-77. This amounted to an approximate annual loss of 53,000 acres of pine types, particularly loblolly pine.

Over the next 30 years, the abundant supply of hardwood will account for more than 90 percent of the prospective increase in Virginia's timber supplies (Knight and McClure, 1978). In contrast, the expected softwood supply will increase only modestly, mainly due to a projected decline of approximately 242,800 ha of planted pines, especially loblolly pine. Thus, pine plantations will become increasingly important sources of available softwood and their proper establishment and management will be critical in assuring a continuing softwood supply. Knight and McClure (1978) stated that the growth per acre of loblolly pines in Virginia could be increased 50 percent through improved timber management, particularly by using genetically improved seedling stock and managing these plantations for maximum fiber production using optimum thinning schedules.

One aspect of improved pine timber management is the clonal seed orchard which is the production area for genetically improved seed and currently accounts for 41 percent of the total annual federal, industrial and state nursery seedling production in the South (Lantz, 1979). The value of these seed orchards to a consistent program of improved softwood regeneration is inestimable. Porterfield (1979) reported that genetically improved loblolly pine yields in Virginia at age 25 were 15 percent greater than yields from unimproved loblolly plantations. Simply restated, genetically improved loblolly pine plantations attained a similar fiber yield at age 22 than did unimproved plantations at age 25. Relative to present value differences, harvesting the younger, genetically improved plantations would yield twice the financial return than if the harvest of unimproved plantations were simply postponed the additional three years.

The second aspect of improved timber production is the optimum management of tree growth throughout the entire rotation of the plantation. When pine plantations are initially established, the seedling stocking density is typically far in excess of the level for optimal fiber production. As the saplings compete for increasingly limited nutrients and growing space, superior growth and natural pruning of lower, shaded limbs are stimulated. Eventually this competition reduces annual increment growth and thinnings are implemented to remove inferior trees and release residual stock to increase diameter growth. Thus, choosing the correct schedule for thinning involves minimizing growth reduction while maximizing the time necessary for expression of superior growth and development.

As pine plantation management assumes increasing importance, so does the potential impact of Heterobasidion annosum (Fr.) Bref., the major

root- and butt-rotting fungus of southern pines. Rishbeth (1951) demonstrated that freshly-cut pine stump surfaces, such as those provided by thinnings, could be readily colonized by airborne basiodiospores of this fungus. Subsequent development within the root system and spread to nearby trees through root grafts and contacts would promote disease development, especially in plantations. Bradford et. al. (1978) reported 85 percent of 350 loblolly pines in 14 thinned plantations in Virginia were colonized by H. annosum. Similarly, Belanger and Brender (1968) noted 65 percent mortality seven years after thinning 19-year-old loblolly pine plantations in Georgia. Bradford et. al. (1978a) demonstrated that, in addition to mortality, H. annosum also caused a 19 percent growth loss in colonized loblolly pines in thinned plantations in Virginia.

However, Powers and Verrall (1962) ignored unthinned loblolly and slash pine plantations in their southwide survey since the absence of thinning was assumed to preclude H. annosum development. Furthermore, by relying upon the presence of basidiocarps as sole evidence of colonization, the impact of the pathogen in thinned plantations was greatly underestimated. This unfortunately determined the official U. S. Forest Service policy towards H. annosum as unimportant in unthinned plantations and causing only slight damage in thinned plantations. It was not until years later that studies involving bulldozer excavation of root systems reported significantly higher incidence and severity levels (Skelly, et. al., 1974; Bradford, et. al., 1978b).

Hendrix and Kuhlman (1964) and Hodges (1968) have reported the probable occurrence of direct root colonization under natural conditions by H. annosum basidiospores which multiplies the threat of growth loss and mortality not only in thinned plantations, but in unthinned plantations and clonal seed

orchards as well. Cordell (personal communication) described high incidence levels of H. annosum in a loblolly pine seed orchard in Tennessee. Perhaps the creation of subterranean wounds from root pruning operations has enhanced the potential for H. annosum colonization.

The objectives of this study are designed to address the aforementioned problems, specifically:

1. Evaluate H. annosum incidence and severity in unthinned loblolly pine plantations in Virginia.
2. Evaluate H. annosum incidence and severity in loblolly pine seed orchards in North Carolina and Virginia, particularly with regard to colonization of subsoiled roots.
3. Investigate the potential for direct colonization of loblolly pine root segments by H. annosum basiodiospores.

REVIEW OF LITERATURE

Clarification of Nomenclature

Since its original description, the fungus now known as Heterobasidion annosum (Fr.) Bref., the cause of annosum root and butt rot, has undergone numerous nomenclatural revisions, i.e., Polyporus annosum (Fr.) (1821), Trametes radiciperda Hartig (1874), Fomitopsis annosa (Fr.) Karst. (1881), Fomes annosus (Fr.) Cke. (1885), Placodes annosus (Fr.) Quel. (1888), H. annosum (Fr.) Bref. (1889), H. annosus (Fr.) Bref. (1889), and Ungulina annosa (Fr.) Pat. (1900). Unfortunately, four binomials, i.e., F. annosa, F. annosus, H. annosum, and H. annosus, still persist in the literature and a final determination of the correct epithet is required.

The fungus F. annosa produces a characteristic brown rot in its hosts while the other fungus, known variously as F. annosus, H. annosum and H. annosus, is a white-rotter and thus the former is considered a completely different organism. Fomes fomentarius (L. ex Fr.) Kickx. is the type-species for the genus Fomes while the type-species for the genus Heterobasidion is H. annosum. These two polypores differ both macroscopically, i.e., different-colored contexts and basidiocarp forms, etc., and microscopically, i.e., different hyphae, hyphal systems and basidiospore shapes. Also, F. fomentarius has not been observed to produce an asexual stage either in nature or in culture unlike H. annosum which readily produces its imperfect stage Spiniger meineckellus (A. J. Olson)

Stalpers, formerly Oedocephalum lineatum Bakshi, in culture, under the bark of certain hosts in the western United States and in bark beetle galleries. Thus, these two fungi are sufficiently different and warrant separation into two distinct genera, Fomes and Heterobasidion, the latter of which contains the causal agent of annosum root rot. Pertinent characters distinguishing F. annosa, F. annosus and H. annosum are described in Table 1.

Further confusion surrounds the generic term Heterobasidion which has been incorrectly transliterated and should instead be Heterobaseidion. Applying current taxonomic principles, this generic term should be latinized to Heterobasidium, a homonym for which precedence has already been established (Donk, 1960). However, Heterobasidium is a nomen confusum (Ainsworth and Bisby, 1961) and is therefore unavailable as a valid generic term so the original term Heterobasidion is still considered appropriate.

Within the genus Heterobasidion, Donk (1960) and Domanski et. al. (1973) have both reported the fungus in question as H. annosus which is incorrect since the gender of this generic term is masculine instead of neuter and accordingly, requires the masculine specific term, annosum (T. O. MacAdoo, personal communication). Hence, the correct bionomial is Heterobasidion annosum (Fr.) Brefeld (Pegler and Waterston, 1968).

Physical Description of the Fungus

1. Perfect Stage

Since Brefeld (1889) erected the genus Heterobasidion prior to the International Botantical Code requirement for a Latin description, none was available (O.K. Miller, personal communication).

Table 1. Pertinent morphological characteristics which distinguish *F. annosa*, *F. annosus* and *H. annosum*.

Characteristics	*F. annosa*	*F. annosus*	*H. annosum*
Rot color	Brown	White	White
Context color	White	Brown	White
Hyphal system	Trimitic	Trimitic	Dimitic
Perennial basidiocarp	Yes	Yes	Yes
Cystidia present	No	No	No
Generative hyphae with clamps	Yes	Yes	Yes

Heterobasidion annosum produces sexual fruiting structures known as basidiocarps, conks or sporophores whose shape and size are highly variable and ultimately determined by the specific location and environmental conditions where these structures occur on the host (Mook and Eno, 1961). Imbricate basidiocarps form on colonized hosts above the duff layer or within the duff when the litter is not packed. When forming underground on colonized roots, compact effused-reflexed mycelial masses develop. Resupinate basidocarps often occur on exposed root surfaces in subterranean cavities provided by leaning or wind-thrown hosts. Finally, the initial external appearance of the fungus on colonized wood is in small hemispherical masses or button conks. If mild temperatures and adequate moisture persist, these button conks may develop into imbricate basidiocarps.

The characteristically corky-to-woody basidiocarp texture makes it difficult to tear. The dimensions of the applanate pileus may range up to 10 X 12 X 3 cm with the light brown glabrous upper surface becoming darker with age (Lowe, 1957). The conk undersurface is sulcate from the loose attachment of the annual tube layers at their margins while the current year's pore layer is white and becomes golden-brown with age. The pores are angular-to-round and average 2-to-4 mm in diameter (Mook and Eno, 1961).

The basidiospores are thin-walled, hyaline, ovoid-to-elliptical, slightly apiculate and range in size from 3.5 - 5.7 X 3.5 - 4.5 um (Pegler and Waterston, 1968). Occasional guttulate contents may be observed. The small clavate basidia typically have four basidiospores each approximately 9 - 13 X 5 - 7 um. The dimitic hyphal system of the

basidiocarp has both generative and skeletal hyphae. The generative hyphae are thin-walled, hyaline, branched and 1.5-3.0 um in diameter with simple septa. The skeletal hyphae are unbranched, thick-walled, hyaline, 1.5-5.0 um in diameter and are aseptate. Cystidia are absent.

2. Imperfect Stage

Since the erection of the genus Oedocephalum by Preuss (1851), the conidial stages of several ascomycetes and numerous basidiomycetes, including H. annosum, have been lumped into this genus on the basis of general conidiophore morphology. Stalpers (1974a) has recently revised this genus based upon easily distinguishable differences in conidiophore morphology between the ascomycetous and basidiomycetous subgroups. The ascomycetous conidiophore is typically septate, simple and swollen into a globose vesicle covered with conidia. Following conidial discharge, the vesicle remains warty from the presence of residual sterigmata. However, the basidiomycetous conidiophore is aseptate and gradually widens towards its apex and is denticulate following conidial discharge. These and other differing cultural characteristics supported separation of the ascomycetous subgroup, which remained in the genus Oedocephalum, from the basidiomycetous subgroup which was transferred into the new genus Spiniger described by Stalpers (1974b):

> Coloniae fere celeriter vel lente crescunt, albidae vel ochraceae vel brunneae. Hyphae hyalinae, tenui-tunicatae, septatae, fibulatae vel efibulatae, ramosae; deinde hyphae crassi-tunicatae adesse possunt. Conidio-phora erecta, solitaria vel 2-4 gregaria, simplicia vel ramosa, hyalina, septata an non, sensim dilatata ad apicem conidiferum. Pars conidiiferum. Pars conidiifera polyblastica, a stipite non delimitata, dentibus conidii-feris conicis vel cylindricis, 1.5-7 um longis praedita. Conidia unicellularia, levia vel ornamentata, hyalina, forma varia, basi apiculata an non.

> Colonies on malt-agar growing moderately rapidly to very slowly, cover the Petri dish in 3 to more than 6 weeks, whitish, later often with ochraceous or brownish tinges. hyphae hyaline, thin-walled, septate, branched, clamp connections may be present. After 2-4 weeks thick-walled or skeletal hyphae may occur. Conidiophores erect, solitary or up to 4 originating from the same cell, simple or branched, hyaline, septate or aseptate, gradually widening apically into the polyblastic conidiogenous region. Conidiogenous region not separated from the non-conidiogenous region, covered with conical to cylindrical denticles (1.5-7 um long) on which the conidia are borne. Conidia one-celled, smooth-walled or ornamented, hyaline, globose to cylindrical, apiculate or not.

Within this new genus, Stalpers (1974b) described the asexual stage of H. annosum which he termed S. meineckellus (A. J. Olson) Stalpers. The condia are subglobose to pyriform and are approximately 4.5-8 X 3.6 um. The conidiogenous vesicle is 7.5-18 um wide. Hyphal clamp connections are rare and the color of the hyphal mat ranges from white to buff to light yellow, becoming brown with age. Colony odor ranges from none to faint to noxious.

Host Range

Since the first description by Hartig (1974) of H. annosum as a destructive root- and butt-rotter of European conifers, the recorded host range has broadened considerably to include many other gymnosperms as well as numerous hardwood and herbaceous hosts. A current list of reported hosts of H. annosum appears in Table 2. The most economically important host in the southern United States, loblolly pine (Pinus taeda L.), was first described as susceptible to this pathogen by Hartley (1910) but the parasitic relationship was not established until Lightle (1960) isolated the fungus from colonized lateral roots of planted loblolly pine in Mississippi.

Table 2. Reported hosts of H. annosum.

Host	Common Name	Country of Observation	Economic Damage	Reference
Filicinae				
Pteridium aquilinum (L.) Kuhn	Bracken fern	Great Britain	Minor	Rishbeth (1950b)
Angiospermae				
Acer sp.	Maple	Great Britain	Minor	Wilson(1927)
A. macrophyllum Pursch.	Bigleaf maple	United States	Minor	Zeller(1935)
A. negundo L. var. pseudo-californicum	Boxelder (var. pseudocalifornicum)	Denmark	Minor	Wagn(1978)
A. pseudoplatanus L.	Sycamore maple	Yugoslavia	Minor	Marinkovic(1978)
A. tataricum. L.	Tatarian maple	Denmark	Minor	Wagn(1978)
Aesculus indica L.	Buckeye	Pakistan	Minor	Hussain(1952)
Alnus glutinosa (L.) Gaertn. A. incana (L.) Moench.	European alder	Great Britain; Norway	Minor	Wilson(1927) Roll-Hansen(1940)
Amelanchier spicata L.	Serviceberry	Denmark	Minor	Wagn(1971)
Berberis vulgaris L.	European barberry	Yugoslavia	Minor	Marinkovic(1978)
Betula spp.	Birch	Germany; Poland	Minor	Hartig(1874);Garbowski (1926)
B. alba L.	European white birch	Norway	Minor	Jorgenson(1954)
B. dahurica Pall.	Dahurian birch	France	Minor	Delatour(1977)
B. pendula Roth.	European white birch	Great Britain	Minor	Rishbeth (1950b)
B. pubescens Ehrh.	European white birch	Europe	Minor	Spaulding(1961)

Table 2. Reported hosts of H. annosum (continued).

Host	Common Name	Country of Observation	Economic Damage	Reference
Castanea dentata (Marsh.) Borkh.	American chestnut	United States	Minor	Baxter (1941)
Carpinus betulus L.	European hornbeam	Denmark	Minor	Wagn (1971)
Cercocarpus sp.	Mountain-mahogany	United States	Minor	Tegethoff (1973)
Cornus sanguinea L.	Red dogwood	Yugoslavia	Minor	Marinkovic (1978)
Corylus avellana L.	Filbert	Great Britain	Minor	Wilson (1927)
Cotoneaster bullatus Bois.	Cotoneaster	Denmark	Minor	Wagn (1971)
Crataegus intricata Lange	Entangled hawthorn	Denmark	Minor	Wagn (1978)
C. monogyna Jacq.	English hawthorn	Great Britain	Minor	Rishbeth (1950b)
C. oxyacantha L.	Hawthorn (May)	Great Britain	Minor	Wilson (1927)
Diospyros virginiana L.	Persimmon	United States	Minor	Baxter (1941)
Empetrum nigrum L.	Black crowberry	Norway	Minor	Jorstad and Roll-Hansen (1943)
Fagus spp.	Beech spp.	Germany	Minor	Hartig (1874)
F. crenata L.	European beech (crenate variety)	Europe	Minor	Spaulding (1961)
F. sylvatica L.	European beech	Great Britain	Minor	Rishbeth (1950b)
Fraxinus americana L.	White ash	United States	Minor	Punter and Cafley (1968)
F. excelsior L.	European ash	Great Britain	Minor	Wilson (1927)
F. pennsylvanica (Marsh). var. lanceolata (Burkh.) Sarg.	Green ash (var. lanceolata)	Denmark	Minor	Wagn (1978)
Kalmia latifolia L.	Mountain laurel	United States	Minor	Cordell et. al. (1970)

Table 2. Reported hosts of H. annosum (continued).

Host	Common Name	Country of Observation	Economic Damage	Reference
Laurus nobilis L.	Laurel	France	Minor	Parrot (1946)
Ligustrum vulgare L.	Privet	Yugoslavia	Minor	Marinkovic (1978)
Liquidambar styraciflua L.	Sweetgum	United States	Minor	Miller (1943)
Lonicera tatarica L.	Tatarian honeysuckle	Denmark	Minor	Wagn (1978)
Malus sylvestris Mill.	Apple	United States	Minor	Sinclair (1960)
Nothofagus obliqua (Mirb.) Blume	Beech (Southern Hemisphere)	Great Britain	Minor	Grieg (1974)
Nyssa sylvatica Marsh.	Blackgum	France	Minor	Delatour (1977)
Pachistima myrsinites Raf.	Pachistima	United States	Minor	Tegethoff (1973)
Physocarpus amurensis (Maxim) Maxim	Ninebark	Denmark	Minor	Wagn (1978)
Populus balsamifera L.	Balsam poplar	United States	Minor	Baxter (1941)
P. X berolinensis Dipp.	Laurel-leaved X Lombardy poplar	Denmark	Minor	Wagn (1978)
P. balsamifera L. var. subcordata	Balsam poplar (var. subcordata)	Denmark	Minor	Wagn (1971)
P. candicans Ait.	Balm of Gilead	Denmark	Minor	Wagn (1978)
P. canescens (Ait.) Sm.	Gray poplar	Norway	Minor	Jorgenson (1954)
P. X canadensis Moench.	Eastern cottonwood X Eastern black poplar	Denmark	Minor	Wagn (1978)
P. nigra L.	Black poplar	Great Britain	Minor	Rishbeth (1950b)
P. tremuloides Michx.	Quaking aspen	Sweden	Minor	Lagerberg (1937)
P. trichocarpa Hook	Black cottonwood	United States	Minor	Weir (1917)

Table 2. Reported hosts of H. annosum (continued).

Host	Common Name	Country of Observation	Economic Damage	Reference
Prunus avium L.	Sweet cherry (Mazzard)	Great Britain	Minor	Wilson (1927)
P. cerasifera Ehrh.	Myrobalan plum	Denmark	Minor	Wagn (1971)
P. mahaleb L.	Mahaleb cherry	Denmark	Minor	Wagn (1971)
P. padus L.	European bird cherry	Great Britain	Minor	Wilson (1927)
P. serotina Ehrh.	Black cherry	Great Britain	Minor	Rishbeth (1957)
Purshia tridentata DC.	Bitterbrush	United States	Minor	Tegethoff (1973)
Pyrus communis L.	Common pear	Norway	Minor	Jorgenson (1954)
Quercus alba L.	White oak	United States	Minor	Hansbrough (1953)
Q. borealis Michx.	Northern red oak	Great Britain	Minor	Rishbeth (1957)
Q. cerris L.	European turkey oak	Yugoslavia	Minor	Marinkovic (1978)
Q. falcata Michx.	Southern red oak	United States	Minor	Driver and Dell (1961)
Q. gambelii Nutt.	Gambel's oak	United States	Minor	Baxter (1941)
Q. ilex L.	Holly oak	Great Britain	Minor	Wilson (1927)
Q. leucotrichophora L.	None	Europe	Minor	Spaulding (1961)
Q. petraea (Muttuschka) Lieblein	Durmast oak	Norway	Minor	Jorgenson (1954)
Q. prinus L.	Chestnut oak	United States	Minor	Baxter (1941)
Q. robus L.	English oak	Great Britain	Minor	Wilson (1927)
Q. velutina Lam.	Black oak	United States	Minor	Anonymous (1961)
Rhamnus frangula L.	Glossy buckthorn	Denmark	Minor	Wagn (1978)

Table 2. Reported hosts of H. annosum (continued).

Host	Common Name	Country of Observation	Economic Damage	Reference
Rhododendron ponticum L.	None	Great Britain	Minor	Wilson (1927)
R. maximum L.	Great rhododendron	United States	Minor	Cordell et. al. (1970)
Rhus copallina L.	Shining sumac	United States	Minor	Driver and Dell (1961)
R. toxicodendron L.	Poison ivy	United States	Minor	Miller (1943)
Rosa glauca Pourr.	Glaucous rose	Denmark	Minor	Wagn (1971)
R. multiflora Thunb. ex Murr.	Multiflora rose	Denmark	Minor	Wagn (1971)
R. rugosa Thunb.	Rugose rose	Norway	Minor	Jorgenson (1954)
R. virginiana Mill.	Virginian rose	Denmark	Minor	Wagn (1971)
Salix spp.	Willow spp.	Norway	Minor	Jorgenson (1954)
S. acutifolia Willd.	None	Denmark	Minor	Wagn (1971)
S. alba L.	White willow	Denmark	Minor	Wagn (1971)
S. dasyclados Wimm.	Osier	Denmark	Minor	Wagn (1978)
S. purpurea L.	Purple willow	Denmark	Minor	Wagn (1971)
S. repens L.	Creeping willow	Norway	Minor	Jorgenson (1954)
S. X smithiana Willd.	Purple willow X Goat Willow	Denmark	Minor	Wagn (1971)
S. viminalis L.	Basket willow	Denmark	Minor	Wagn (1978)
Sarothamnus scoparius (L.) Wimmer ex Koch	Scotch broom	Great Britain	Minor	Rishbeth (1957)
Sorbus aria Crantz	White beam-tree	Great Britain	Minor	Wilson (1927)

Table 2. Reported hosts of H. annosum (continued).

Host	Common Name	Country of Observation	Economic Damage	Reference
S. aucuparia L.	European mountain-ash	Norway	Minor	Jorgenson (1954)
S. intermedia (Ehrh.) Pers.	Mountain-ash	Norway	Minor	Jorgenson (1954)
Spiraea douglasii Hook	Douglas' spiraea	Denmark	Minor	Wagn (1978)
S. X vanhouttii (Briot) Zab.	VanHoutte's spiraea	Denmark	Minor	Wagn (1971)
Syringa josikaea Jacq.	Hungarian lilac	Denmark	Minor	Wagn (1971)
S. vulgaris L.	Common lilac	Denmark	Minor	Wagn (1978)
Ulex europaeus L.	Gorse	Great Britain	Minor	Rishbeth (1948)
Ulmus americana L.	American elm	United States	Minor	Punter and Cafley (1968)
U. glabra Huds.	Scotch elm	Norway	Minor	Jorgenson (1954)
U. montana With.	Wych elm	Norway	Minor	Jorgenson (1954)
U. pumila L.	Siberian elm	Norway	Minor	Jorgenson (1954)
Vaccinium myrtillus L.	Bilberry	Norway	Minor	Roll-Hansen (1940)
Gymnospermae				
Abies alba Mill.	Silver fir	Denmark	Major	Bornebusch and Holm (1934)
A. amabilis (Douglas) Forbes	Pacific silver fir	United States	Major	Buchanan (1940)
A. balsamea (L.) Mill.	Balsam fir	United States	Major	Stoddard et. al. (1939)
A. cephalonica Loudon	Greek fir	Great Britain	Major	Grieg (1974)
A. cilicica L.	Cilician fir	France	Major	Delatour (1977)
A. concolor (Gordon) Engelmann	White fir	United States	Major	Wagener and Cave (1946)

Table 2. Reported hosts of H. annosum (continued).

Host	Common Name	Country of Observation	Economic Damage	Reference
A. faxoniana Rehd and Wils.	Faxon fir	China	Major	Ch'en and Ch'iu (1959)
A. fraseri (Pursh) Poir.	Fraser fir	United States	Minor	Cordell and Astin (1965)
A. georgii L.	George fir	United States	Major	Teng (1940)
A. grandis Lindl.	Grand fir	Great Britain	Major	Anderson (1921)
A. lasiocarpa (Hook) Nutt.	Subalpine fir	United States	Major	Baxter (1941)
A. magnifica A. Murr.	California red fir	United States	Major	Wagener and Cave (1946)
A. magnifica var. shastensis Lemm.	Shasta red fir	United States	Major	Baxter (1941)
A. mariesii Mast.	Maries fir	Japan	Minor	Aoshima (1954)
A. nobilis (Dougl.) Lind.	Noble fir	Great Britain	Major	Holmes and Buszewicz (1957)
A. nordmanniana (Steven) Spach	Nordmann fir	Denmark	Major	Bornebush and Holm (1934)
A. pindrow Royle	Himalayan silver fir	India	Major	Hole (1927)
A. pinsapo Boiss.	Spanish fir	Spain	Minor	Spaulding (1961)
A. recurvata Mast.	Recurved fir	China	Minor	Ch'en and Ch'iu (1959)
A. sachalinensis Mast.	Sakhalin fir	Japan	Major	Sasaki and Yakota (1956)
A. sibirica Ledeb.	Siberian fir	U.S.S.R.	Major	Minin (1959)
A. veitchii Lindl.	Veitch fir	Japan	Minor	Aoshima (1954)
Araucaria cunninghamii Ait. ex D. Don	Hoop pine	Australia	Major	Walters (1967)
Cedrus atlantica Manc.	Atlas cedar	France	Minor	Jacamon and Lanier (1961)
C. deodara (Roxb.) Loud.	Deodar cedar	India	Major	Bagchee (1952)
Chamaecyparis lawsoniana (A.Murr.) Parl.	Port-Orford cedar	Great Britain	Major	Rishbeth (1950b)

Table 2. Reported hosts of H. annosum (continued).

Host	Common Name	Country of Observation	Economic Damage	Reference
C. thyoides (L.) B.S.P.	Atlantic white-cedar	United States	Major	Korstian and Brush (1931)
Cryptomeria japonica Hassk	Japanese cryptomeria	Japan	Minor	Spaulding (1961)
Cupressocyparis leglandii (Jacks and Dallimore)	Legland cypress	Great Britain	Minor	Grieg (1974)
Cupressus arizonica Greene	Arizona cypress	France	Minor	Delatour (1977)
C. sempervirens L.	Italian cypress	Italy	Minor	Morlondo (1970)
Cycas revoluta L.	Sego palm	France	Minor	Bourdot and Galzin (1927)
Juniperus communis L.	Common juniper	Germany	Major	Hartig (1874)
J. occidentalis Hook.	Western juniper	United States	Major	Tegethoff (1973)
J. osteosperma (Torr.) Little	Utah juniper	United States	Major	Tegethoff (1973)
J. rigida Sieb. and Zucc.	Juniper	France	Major	Delatour (1977)
J. sabina L.	Savin	U.S.S.R.	Major	Negrutskii (1960)
J. virginiana L.	Eastern redcedar	United States	Major	Hartley (1910)
Larix decidua Mill.	European larch	Great Britain	Major	Hiley (1919)
L. eurolepis Henry	Hybrid larch	Great Britain	Major	Grieg (1974)
L. gmelinii (Rupr.) Litvinov	Dahurian larch	Norway	Major	Jorgenson (1954)
L. gmelinii var. olgensis (Henry) Ostenf and Syrach-Larsen	Dahurian larch (var. olgensis)	Norway	Major	Jorgenson (1954)
L. laricina (Du Roi) K. Koch	Tamarack	France	Major	Huet (1937)
L. leptolepis (Sieb. and Zucc.) Gord.	Japanese larch	Great Britain	Major	Anderson (1921); Bakshi(1950)
L. occidentalis Nutt.	Western larch	U.S.; Norway	Major	Weir (1917);Roll-Hansen(1940)

Table 2. Reported hosts of H. annosum (continued).

Host	Common Name	Country of Observation	Economic Damage	Reference
L. sibirica Ledeb.	Siberian larch	Norway	Major	Roll-Hansen (1940)
Libocedrus decurrens Torr.	Incense-cedar	Great Britain	Major	Anderson (1921)
Metasequoia glyptostroboides Hu and Cheng	Dawn redwood	Netherlands	Major	Broekhuizen and Zwart(1966)
Picea abies (L.) Karst.	Norway spruce	Germany	Major	Hartig (1874)
P. asperata Mast.	None	France	Major	Delatour (1977)
P. cembra L.	None	Norway	Major	Roll-Hansen (1940)
P. contorta L. var. latifolia	None	Norway	Major	Roll-Hansen (1940)
P. engelmannii Parry	Engelmann spruce	United States	Major	Shope (1931)
P. glauca (Moench) Voss	White spruce	Norway	Major	Jorgenson et. al. (1939)
P. glehnii Mast.	Saghalin spruce	Japan	Major	Spaulding (1961)
P. jezoensii Sieb. and Zucc.	Jeddo spruce	Norway	Major	Roll-Hansen (1940)
P. likiangensis (Franch.) Pritz	None	China	Major	Teng (1940)
P. morinda Link	Himalayan spruce	India	Major	Hole (1927)
P. omorika (Pancic) Purkyne	Serbian spruce	Great Britain	Major	Grieg (1974)
P. orientalis (L.) Link	Oriental spruce	Great Britain	Major	Grieg (1974)
P. pungens Engelm.	Blue spruce	Norway	Major	Roll-Hansen (1940)
P. retroflexa Mast.	None	France	Minor	Delatour (1977)
P. rubens Sarg.	Red spruce	Europe	Major	Spaulding (1961)
P. sitchensis (Bong.) Carr.	Sitka spruce	Canada	Major	Bier et. al. (1946)

Table 2. Reported hosts of H. annosum (continued).

Host	Common Name	Country of Observation	Economic Damage	Reference
P. smithiana (Walt.) Boiss.	Himalayan spruce	India	Major	Spaulding (1961)
Pinus banksiana Lamb.	Jack pine	United States	Major	Bega (1962)
P. brutia Ten.	Calabrian pine	United States	Major	Bega (1962)
P. canariensis Smith	Canary pine	United States	Major	Bega (1962)
P. caribaea Morelet	Caribbean pine	United States	Major	Bega (1962)
P. cembra L.	Swiss stone pine	Norway	Major	Jorstad and Roll-Hansen (1943)
P. cembra L. var. sibirica	Swiss stone pine (var. sibirica)	U.S.S.R.	Major	Negrutskii (1963)
P. clausa (Chapm.) Vasey	Sand pine	United States	Major	Ross (1968)
P. contorta Loud.	Lodgepole pine	Norway	Major	Jorgenson et. al. (1939)
P. contorta Loud. var. latifolia S. Wats.	Lodgepole pine (var. latifolia)	Norway	Major	Jorstad and Roll-Hansen (1946)
P. coulteri D. Don	Coulter pine	United States	Major	Bega (1962)
P. densiflora Sieg. and Zucc.	Japanese red pine	United States	Major	Bega (1962)
P. echinata Mill.	Shortleaf pine	United States	Major	von Schrenk (1898)
P. edulis Engelm.	Colorado pinon pine	United States	Major	Tegethoff (1973)
P. elliottii Engelm. var. elliottii	Slash pine	United States	Major	Powers and Boyce (1961)
P. flexilis James	Limber pine	China	Major	Teng (1940)
P. griffithii McClelland	Himalayan white pine	India	Major	Hussain (1952)
P. glabra Walt	Spruce pine	United States	Major	Bega (1962)
P. halepensis Mill.	Aleppo pine	United States	Major	Bega (1962)

Table 2. Reported hosts of H. annosum (continued).

Host	Common Name	Country of Observation	Economic Damage	Reference
P. jeffreyi Grev. and Balf.	Jeffrey pine	United States	Major	Olson (1941)
P. lambertiana Dougl.	Sugar pine	United States	Major	Wagener and Cave (1946)
P. leiophylla Sch. and Deppe	Smooth-leaved pine	United States	Major	Bega (1962)
P. massoniana Lamb.	Masson pine	United States	Major	Bega (1962)
P. montezumae Lamb.	Montezuma pine	United States	Major	Bega (1962)
P. monticola Dougl.	Western white pine	United States	Major	Weir and Hubert (1919)
P. mugo Turra	Swiss mountain pine	United States	Major	Bega (1962)
P. mugo var. rostrata (Ant.) Hoopes	Swiss mt. pine (var. rostrata)	Europe	Major	Spaulding (1961)
P. mugo var. rotundata (Link) Hoopes	Swiss mt. pine (var. rotundata)	Europe	Major	Spaulding (1961)
P. muricata D. Don	Bishop pine	United States	Major	Bega (1962)
P. nigra Arn.	Austrian pine	United States	Major	Lowe and Mook (1960)
P. nigra var. calabrica Schneid.	Calabrian pine	Great Britain	Major	Rishbeth (1950b)
P. nigra var. maritima (Ait.) Melville	Corsican pine (var. maritima)	Great Britain	Major	Grieg (1974)
P. nigra (Ant.) Aschers. and Graebn. var. poiretiana	Corsican pine (var. poiretiana)	Europe	Major	Spaulding (1961)
P. palustris Mill.	Longleaf pine	United States	Major	von Schrenk (1898)
P. pinaster Ait.	French maritime pine	United States	Major	Bega (1962)
P. pinaster Ait. var. gigantea	French maritime pine (var. gigantea)	United States	Major	Bega (1962)
P. pinea L.	Italian stone pine	United States	Major	Bega (1962)
P. ponderosa Laws.	Ponderosa pine	United States	Major	Bega (1962)

Table 2. Reported hosts of H. annosum (continued)

Host	Common Name	Country of Observation	Economic Damage	Reference
P. ponderosa Engelm. var. scopulorium	Ponderosa pine (var. scopulorium)	United States	Major	Mielke and Davidson (1947)
P. pseudostrobus Lindl.	False Weimouth pine	United States	Major	Bega (1962)
P. radiata D. Don	Monterey pine	United States	Major	Bega (1962)
P. remorata Mason	Bishop pine	United States	Major	Bega (1962)
P. resinosa Ait.	Red pine	United States	Major	Welch and Stone (1953)
P. rigida Mill.	Pitch pine	United States	Major	Stoddard et. al. (1939)
P. roxburghii Sarg.	Chir pine	United States	Major	Bega (1962)
P. rudis Endl.	None	Great Britain	Major	Tinsley et. al. (1967)
P. sabiniana Dougl.	Digger pine	United States	Major	Bega (1962)
P. sibirica Mayr	Siberian pine	U.S.S.R.	Major	Negrutskii (1963)
P. strobus L.	Eastern white pine	United States	Major	Clinton (1907, 1934)
P. sylvestris L.	Scots pine	Germany	Major	Hartig (1874)
P. taeda L.	Loblolly pine	United States	Major	Hartley (1910)
P. torreyana Parry	Torrey pine	United States	Major	Bega (1962)
P. virginiana Mill.	Virginia pine	United States	Major	Jones (1961)
P. X attenuradiata Stockwell and Righter	Knobcone pine X Monterey pine	United States	Major	Bega (1962)
Pseudotsuga menziesii (Franco) Mirb.	Douglas-fir	Great Britain	Major	Rishbeth (1950b)
Sequoia gigantea (Lindl.) Decne.	Giant sequoia	United States	Major	Baxter (1941)
S. sempervirens (D. Don) End.	Redwood	United States	Major	Baxter (1941)
Taxus baccata L.	English yew	Norway	Minor	Jorgenson (1954)

Table 2 Reported hosts of H. annosum (continued).

Host	Common Name	Country of Observation	Economic Damage	Reference
Thuja occidentalis L.	Northern white-cedar	United States	Minor	Baxter (1941)
T. plicata D. Don	Western red cedar	United States	Major	Buckland (1946)
Tsuga canadensis (L.) Carr.	Eastern hemlock	United States	Major	Kauffman (1917)
T. heterophylla (Raf.) Sarg.	Western hemlock	United States	Major	Rhodes and Wright (1946)

Geographical Range

Although distributed worldwide, H. annosum incidence and severity are greater in the temperate zones than in either tropical or subtropical areas (Bega, 1963). As indicated in Figure 1, this is particularly true in the northern temperate areas of Asia, Europe and North America (Anonymous, 1968).

Growth Characteristics

Although no distinct physiological races of H. annosum have been reported (Etheridge, 1955), different isolates may exhibit highly variable characteristics when grown in culture (Bega and Hendrix, 1962; Cowling and Kelman, 1964; Gooding et. al., 1966). Bega and Hendrix (1962) reported great cultural variability in asexual sporulation, growth rate, and colony type and margin from 100 monobasidiospore isolates from a single H. annosum basidiocarp. Etheridge (1955) reported cellulose utilization and mycelial production were optimal at 23 C for three North American isolates but three European isolates exhibited maximal growth at 25 C. However, statistical analysis of cellulose utilization failed to significantly distinguish between the cultures of either geographical origin and he concluded that naturally-occurring strains of H. annosum did not exist.

Cowling and Kelman (1964) compared optimal temperatures for maximal cultural growth of 46 H. annosum basidiocarp tissue isolates from various parts of the world with that of 48 monobasidiospore isolates from North Carolina. While individual growth rates of both monobasidiospore and basidiocarp isolates varied widely, mean growth rates did not differ significantly. A temperature optimum of 24.0-24.5 C was observed for isolate types while the majority of isolates ceased to grow at temperatures

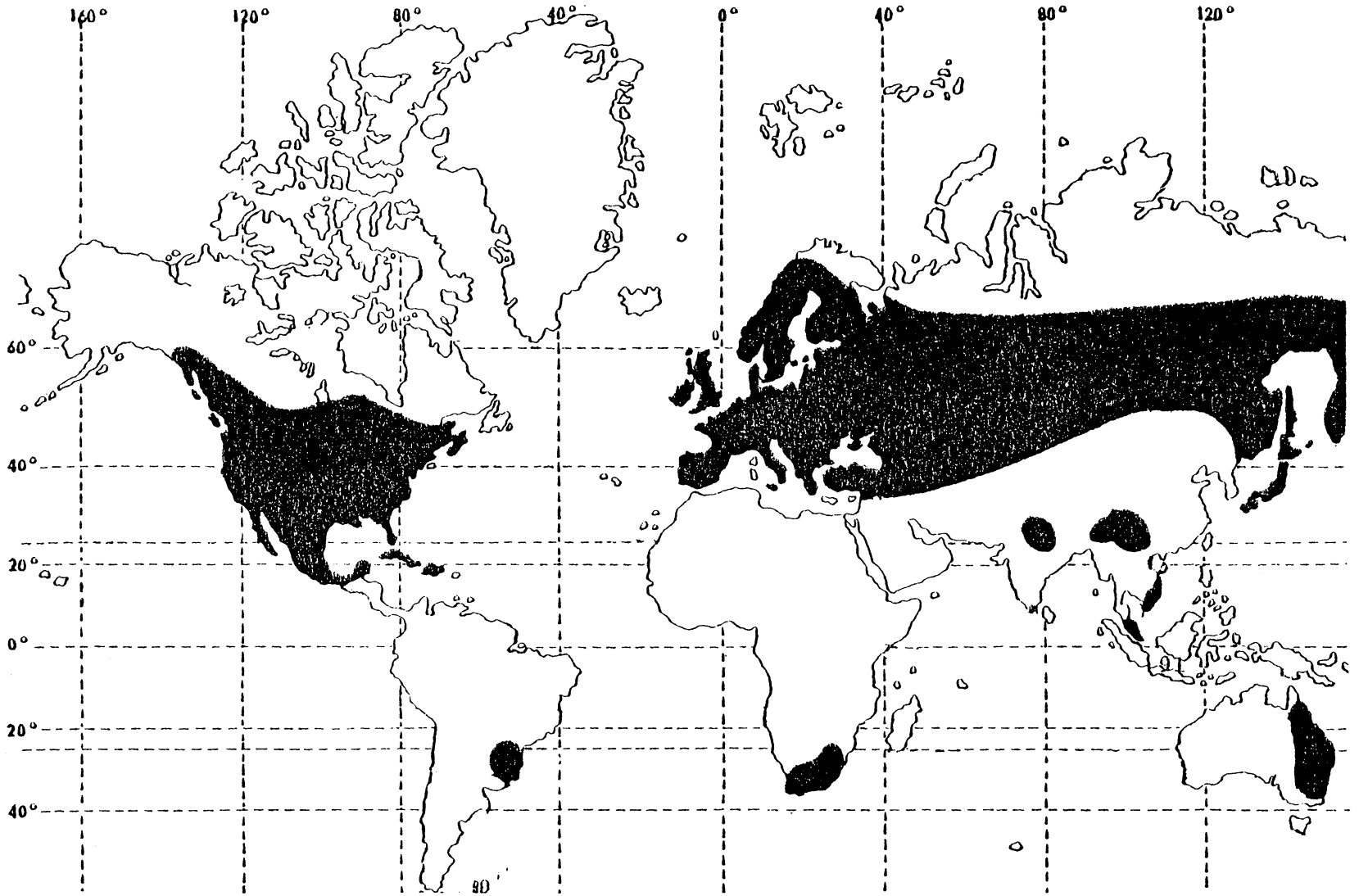


Figure 1. Geographical range of H. annosum root and butt rot (after Anonymous, 1968).

greater than 32 C or less than 2 C. They concluded that H. annosum temperature optima were under rigid genetic control and were resistant to selection pressures which would adapt these optima to local temperature conditions. Even at 8 C, the isolates averaged 21 percent of the optimum growth which emphasized the destructive potential of this fungus in temperate conifer forests.

Gooding (1964) demonstrated that H. annosum mycelia in loblolly pine bolts were killed at temperatures exceeding 40 C and that such naturally-occurring high temperatures may reduce fungal activity within colonized stumps. Gooding et. al. (1966) investigated the effect of temperature on growth rate and mycelial inactivation in fresh five-to-six-year old loblolly pine stem sections. Actively growing mycelia in wood chips taken from inoculated stem sections were killed after exposure to 40 C for less than two hours. Since stump surface temperatures equal or exceed 40 C for at least two hours on more than half the days from May to August, summer thinning in the southeastern United States is suggested as a means of reducing stump colonization levels.

Ross (1969) inoculated loblolly pine stem discs with either conidia or basidiospores and incubated at 45 C and 90 percent relative humidity. One conidial isolate was inactivated after 40 minutes and the remaining five isolates as well as all the basidiospore isolates were killed after 60 minutes. These temperature and relative humidity conditions reflect normal levels occurring during the summers in the Southeast and further support summer thinning as a means of reducing H. annosum colonization of freshly-cut stumps.

Gunderson (1961) investigated the ecological adaptation of H. annosum to low oxygen and high carbon dioxide tensions typical of colonized pine roots and stems. Linear growth rates of nine isolates revealed uninhibited mycelial growth under both aerobic and microaerophilic, but not anaerobic, conditions. A slight increase in carbon dioxide pressure stimulated growth which was subsequently inhibited at higher concentrations.

Colonization Measurement

Utilization of a reliable diagnostic technique becomes critically important with a root-rotting fungus such as H. annosum where the symptoms of incipient and advanced decay, resin soaking and stringy rot, respectively, are subterranean and not easily observed. The superficial diagnostic method, i.e., basidiocarp occurrence, used in the first southern survey was unsatisfactory and greatly underestimated H. annosum incidence (Powers and Verrall, 1962). Subsequently, progressively more intensive and sophisticated methods were developed (Ginns and Gillespie, 1962; Cordell and Stambaugh, 1966; Dimitri, 1970; Alexander and Skelly, 1974; and Skelly and Alexander, 1974).

Following initial reports of southern pine mortality attributed to H. annosum (Lightle, 1960; Driver and Dell, 1961), an intensive survey of loblolly and slash pine plantations from Virginia through eastern Texas was initiated by the United States Forest Service (Powers and Verrall, 1962). Diagnosis of H. annosum incidence in this survey relied upon the presence of basidiocarps at the base of host trees despite the authors' concession that such reproductive structures may not be visible at the time of inspection. Also, crown decline as indicative of H. annosum advanced decay was determined to be unreliable since apparently healthy

trees with full green crowns may actually contain extensive rot. Hodges (1974) suggested the failure of most H. annosum basidiocarps to survive in the southeastern United States for more than one year in the moist duff layer was due to decomposition by other fungi, especially Trichoderma species, and insects.

Ginns and Gillespie (1962) cultured H. annosum from increment cores removed from the base of several living eastern white pines with fading crowns in West Virginia. This informal survey was the basis for a more extensive survey in North Carolina by Cordell and Stambaugh (1966) in which 54 loblolly, 223 eastern white and 15 red pines in 0.04-0.08 ha plots on plantations known to contain H. annosum were similarly examined. The imperfect stage of the pathogen was isolated with 94 percent frequency from increment cores removed from the root collar of each sign-bearing tree while 15 percent of the non-signbearing trees were latently colonized.

Dimitri (1970) compared H. annosum isolations between stem discs and multiple increment cores removed at a height of 50 cm from each of 256 71-year-old spruces. The imperfect stage was cultured from 85 percent of the discs but only 40 percent of the increment cores and he concluded the increment core technique to be unreliable in determining butt rott in old-growth spruce stands.

Artman et. al. (1969) evaluated the effectiveness of borax and urea in preventing H. annosum colonization of loblolly pine stumps following first thinning. Eighty three-year-old stumps from their control plots were sampled and one increment core from each stump's root collar zone as well as from each lateral primary root was removed. Each root was split longitudinally and six chips excised and plated onto ortho-phenyl phenol medium.

The increment cores were similarly incubated. The root halves were rematched, wrapped in moist paper and incubated in plastic bags at room temperature. The imperfect stage was isolated from 40 to 45 percent of the root chip and split root cultures, respectively, but from only 15 percent of the increment core cultures.

Morris and Frazier (1966) developed a soil hazard rating scale for potential H. annosum colonization of thinned loblolly pine stands in Virginia. Depth and texture of the A horizon and height of the water table were compared to the percentage of conk-bearing stumps in 11 thinned natural and 40 thinned plantations. Sample plots were located on both predominantly sand (Coastal Plain) and predominantly clay (Piedmont) soils. Among sandy loam, loamy sand and sandy soils a significant relationship was observed between increased stump colonization, as indicated by the presence of basidiocarps, and increased damage to the residual stand. However, the unreliability of conk presence coupled with only suspected mortality by H. annosum were serious shortcomings of this technique which failed to provide valid results on finer-textured soils. Clays and clay loams were designated low hazard for H. annosum, loams and silt loams were intermediate, and sandy loams, loamy sands and sands were high hazard soils if greater than 25 cm deep. The exceptions were those high hazard soils with clay hardpans less than 25 cm from the surface and these soils would then become intermediate or low hazard. Also, where a perched water table existed for two or more months a year, as indicated by standing surface water or soil mottling less than 45 cm deep, that soil was classified as low hazard regardless of texture. They reported, however, that two high hazard Coastal Plain sites had much less

mortality than expected, despite the occurrence of conks on 50 percent of the stumps, and this was attributed to the time of thinning and presence of clay in the A horizon.

W. J. Stambaugh (personal communication) has been unable to substantiate hazard ratings at various sites on the Duke forest in the North Carolina Piedmont with observed loblolly pine mortality from H. annosum. Rishbeth (1951) reported more frequent colonization and greater ectotrophic hyphal growth by H. annosum on pine roots in alkaline soils in Great Britain than in acidic soils. Skelly et. al. (1974) excavated 50 loblolly pines in Virginia and concluded that annosum root rot severity may vary more than incidence on these sites. Kuhlman (1974) compared 348 and 255 loblolly pine stump root systems on a low and high hazard site, respectively, in the southeastern United States for frequency of root contact and H. annosum colonization. The incidence was similar for stumps on either site but severity was greater among those stumps on the high hazard site. Alexander and Skelly (1972) cultured samples from colonized loblolly pine roots and increment cores from low and high hazard sites and their results, while supporting the reliability of the soil hazard rating scale, described varying incidence levels on specific sites.

Morris (1970) estimated volume loss from loblolly pines killed by H. annosum following initial thinning of high hazard sites in Virginia. Relying only upon the presence of basidiocarps as evidence of colonization and the examination of only dead trees in assessing H. annosum incidence and severity suggest his volume loss figure of 1.81 cu m per 0.4 ha per year for the nine years after first thinning is extremely conservative.

Alexander and Skelly (1974) selected one 0.02 ha plot in each of five thinned loblolly pine plantations to compare percent recovery of the imperfect stage between the increment core method and a two-root sampling technique. Two roots were selected from opposite sides of each sample tree and a 15 cm increment core was removed from the root collar zone of both roots. After incubating on ortho-phenyl phenol medium for two weeks at 21 C, percent recovery of the imperfect stage revealed an insignificant correlation with the occurrence of conks or crown condition of sample trees. Each plot was subsequently revisited and all previously examined roots were severed at the root collar. Chips from the excised roots were similarly incubated and subsequently yielded the imperfect stage from 32 percent of the trees sampled while only 10 percent of the trees exhibited the pathogen using the increment core method.

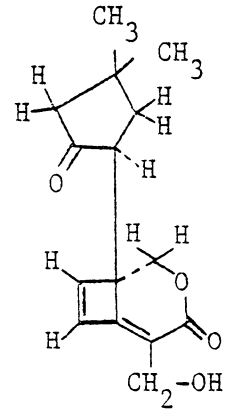
The most intensive method of evaluating H. annosum incidence and severity was developed by Skelly et. al. (1974). Entire root systems of 25 loblolly pines on each of two loamy sand and two sandy clay loam sites in Virginia were excavated with a bulldozer and residual soil was removed with hand tools. Colonization by H. annosum was determined by visual inspection of the roots for the presence of symptoms, i.e., resin soaking or stringy rot. The average disease incidence was 71 percent on the loamy sand and 76 percent on the sandy clay loam sites which greatly exceed those incidence levels reported from previous surveys where inferior, less intensive survey techniques were used.

Mechanism of Fungal Parasitism

Shain (1967) and Woeste (1956) reported the death of xylem parenchyma cells in advance of H. annosum hyphal invasion which suggested the presence

of a vivotoxin. Hyppel (1969) inoculated aqueous extracts of bark-free ground root tissue of silver fir and Norway spruce with H. annosum mycelium and noted when the concentrations of the extracts from silver fir were increased, the mycelial yield decreased. When the extract concentrations from Norway spruce were increased, however, the mycelial yield also increased which supported the concept of an inhibitory factor present in silver fir but not in Norway spruce.

Kepler et. al. (1967) were the first to describe the chemical structure of the vivotoxin produced by H. annosum which they termed fomannosin. The structure was unusual in two respects: (1) this was the first report of a sesquiterpene containing the cyclobutene moiety, and (2) the isoprene units were not joined in the usual head-to-tail sequence. The structure of fomannosin is described by the following:



Bassett et. al. (1967) first detected fomannosin in liquid culture filtrates after 42 days when mycelial dry weight was at a maximum. Since the concentration of this toxin increased in progressively older cultures they suggested its production was linked to mycelial aging or senescence. When a lateral root or terminal shoot of 12 two-year-old potted loblolly

pine seedlings were wound-inoculated with 0.088 mg of pure fomannosin in 25 ul of water, all developed symptoms of localized necrosis and/or systemic killing. Only those seedlings partly killed formed the resin-soaked reaction zones as described by Jorgenson (1961) and Shain (1967).

Wenzel and Diaz-Palacio (1970) artifically induced drought in a Norway spruce stand by covering the surface with plastic sheeting which resulted in a 32 percent decrease in soil water. Analysis of innner bark from these drought-stressed trees revealed a lower concentration of fungistatic substances which demonstrated a reduced fungistatic effect. They suggested enhancement of H. annosum colonization may occur during periods of soil water stress from decreased host fungistasis. This concurs with Towers (1966) and Towers and Stambaugh (1968) who reported increased H. annosum colonization of inoculated loblolollly pine stumps and seedlings, respectively, when soil moisture stress was induced.

Root Colonization Sequence

Peek et. al. (1972a) described the colonization mode and subsequent deterioration of uninjured spruce root bark by H. annosum. Cracks in the outer cork layers of the root bark were first penetrated by hyphae. Where an intact cork layer was encountered, the hyphae created boreholes enzymatically through the pits and degraded the pit membranes yet did not extensively decay the cell walls. They concluded the bark tissue was merely a transition zone whose penetration was necessary for subsequent colonization of the root xylem.

In a subsequent report, Peek et. al. (1972b) described the colonization sequence of spruce root wood following bark colonization by H. annosum.

Under natural conditions, the hyphae spread directly from colonized root bark into the phloem rays and subsequently into the wood rays. From there the hyphae grew laterally into adjoining tracheids where xylem degradation was initiated by delignification of latewood tracheids. Earlywood tracheids were not delignified as easily while parenchymatous epithelial and ray cells were highly resistant to enzymatic breakdown. Where H. annosum hyphae contacted tracheid walls, degradation was initiated by the diffusion of ectoenzymes within the S_2 lamellae of the cell wall in the direction of cellulose microfibril orientation. The amorphic encrusting substances were subsequently hydrolyzed and the S_1 layer, which apparently resisted fungal enzyme diffusion, was then similarly decayed.

Dual Aspects of Colonization

Early reports of H. annosum severity (Hartley, 1910; Lightle, 1960; Driver and Dell, 1961) described host mortality and were the impetus for renewed interest in the pathogen and its impact on southern pines. However, the aspects of growth reduction in colonized trees was not addressed until Burdekin (1972) investigated losses in a Scots pine plantation in England. He reported that in three of four 0.1 ha plots, the volume losses due solely to dead trees did not account for the total loss and suggested that growth reduction from colonized living trees was significant and may have equalled that from killed trees.

Alexander and Skelly (1973) reported that H. annosum-colonized loblolly pines in low and high hazard plantations exhibited 19 and 6 percent reduction, respectively, in diameter growth compared to noncolonized trees in the same plantations. This was attributed to a reduced growth

rate caused by H. annosum colonization. Similarly, Ferrell and Smith (1976) demonstrated reduced diameter and height growth in H. annosum-colonized sapling white fir.

Froelich et. al. (1977) found that among 65 planted slash pine, those trees with less than 50 percent of their roots colonized by H. annosum exhibited little or no reduction in diameter and height growth after six years. However, among trees with greater than half their roots colonized, d.b.h was reduced 20-30 percent during the fourth through the sixth years of the study and height growth decreased 40 percent after six years. These results concur with those of Powers and Skelly (1975) for loblolly pine in Virginia.

Bradford et. al. (1978) excavated 350 plantation loblolly pine root systems with a bulldozer and annual increment growth for healthy ($\leq$1 percent root mass colonized) and diseased ($\geq$1 percent root mass colonized) trees was compared for each of the last five years prior to excavation. They reported an approximate growth loss of 4 percent for each of the last five years or a 19 percent reduction for the entire period.

Host Resistance to Colonization

Rennerfelt and Nacht (1955) investigated the resistance mechanism of coniferous heartwood against invasion by insects and fungi. Two fungi-toxic compounds were identified as constituents of pine heartwood, pinosylvin (trans-3,5-dihydroxystilbene) and pinosylvin monomethyl ether (3-hydroxy-5-methoxystilbene). Other heartwood constituents were not concluded to be fungicidal.

Lyr (1960) described pinosylvin monomethyl ether as a respiratory uncoupling agent which was toxic to fungal mycelium. Pinosylvin was suggested to act in a similar manner.

Jorgenson (1961) discovered that both fungal colonization and mechanical damage induced the formation of pinosylvin and its monomethyl ether in the sapwood of 15-to-40- year old red pine stems and roots. These two phenolic compounds are usually present only in pine heartwood and never undamaged sapwood. However, these were identified in red pine sapwood cells which were slowly dying, either from dessication or aeration, and their formation was suggested as a pathogenic defense reaction. These pinosylvins were not present in root cells rapidly killed by H. annosum but only in those roots which had been colonized for more than one year.

Shain (1967) demonstrated the formation of a resinous phenol-enriched reaction zone developing between healthy loblolly pine sapwood and sapwood colonized with H. annosum. This reaction zone occurred in all 16 naturally-colonized and 72 artificially-inoculated loblolly pines and pinosylvin and its monomethyl ether were extracted from these zones but not from uncolonized sapwood. The production of these two fungitoxic compounds was believed to occur within dying parenchyma cells of the reaction zones. This was considered a nonspecific defense reaction against H. annosum attack.

Gibbs (1968) studied the resistance to annosum root and butt rot by selected coniferous species. An approximate 3-cm length of each selected conifer root was removed and replaced with a beech block of similar size inoculated with H. annosum. After replacing the soil, these roots were incubated for 14 months and analyzed for the lengths of proximal and

distal colonization. Pines were less colonized (0.2-1.8 percent than spruces (4.2-12.2 percent) which were more resistant to decay than Douglas fir (2.2-23.5 percent). The decreasing effectiveness of the resin duct systems of the latter two conifers was suggested as the cause of the differential susceptibility. Furthermore, mycelial growth did not occur in either spruce or Douglas-fir outer sapwood but rather in the central xylem where more functionless resin ducts would be expected to occur. Similarly, butt rot was greatly reduced among the pines due to both copious resin flow and the presence of pinosylvin and its monomethyl ether. Susceptibility to annosum butt rot was directly related to the failure of host resin mobilization which, in turn, was determined largely by water availability and thus upon soil texture. Prior (1975) reported that the genus Pinus is the only member of the Coniferales with a fully interconnecting resin duct system which would allow rapid and abundant resin production.

Wallis (1961) variously inoculated Scots pine roots in situ using H. annosum-colonized beech blocks and, after incubating seven months, found approximately 20 percent root mortality. He reported that mycelia grew an average 26 cm from the point of inoculation in those roots killed during the course of the study yet only 3 cm in roots which remained alive. He suggested an active resistance mechanism was functioning in those living roots.

Driver and Ginns (1966) described a procedure for mass screening southern pines for resistance to annosum root rot. Pines exhibiting no mortality or crown decline symptoms after occupying known H. annosum colonization centers for at least five years would be assumed to have resisted colonization under favorable field conditions. Cuttings removed

from those trees suspected of having resistance would be grafted onto seedlings of the same species and maintained in field plantings at a 3 X 3 m spacing for later use as seed orchards. Also, seed from open-pollinated cones would be collected from these "resistant" trees for production of 1-0 seedlings to be outplanted in established H. annosum colonization centers. Evaluation of these saplings at five, eight, and 10 years after planting would confirm suspected resistance. Ladeischikova et. al. (1975) similarly suggested breeding "disease-free" or "resistant" Scots pine within or adjacent to H. annosum colonization centers. However, these techniques have several shortcomings: (1) exposure and resistance to the pathogen is assumed if no symptoms appear after a trial period but no consideration is given to the possibility of disease escape, (2) early evaluation of saplings outplanted on colonization cneters may not allow sufficient time for disease expression should colonization occur, and (3) without root system excavation the question of resistance cannot be substantiated.

Grieg (1978) has reported several species in which resistance to H. annosum has been described, i.e., Abies alba. A. grandis, Betula pendula, Chamaecyparis lawsoniana and Pseudotsuga menziesii. In Russia, the use of mixed plantations of P. sylvestris, Q. rubra, Caragana arborescens and B. verrucosa has been recommended to reduce losses from H. annosum although these resistant species may neither be as well-adapted to the particular site or as productive as the more susceptible hosts.

Kuhlman et. al. (1976) suggested using longleaf pine to regenerate high hazard sites in the southeastern United States since this species appears to be more resistant than shortleaf or loblolly pine to H. annosum mortality.

Experimental evidence has demonstrated interspecific host resistance to H. annosum colonization. Platt et. al. (1965) evaluated root and stem decay resistance of eight coniferous species to H. annosum after incubating 12 weeks in soil-block chambers. Eastern redcedar exhibited greatest resistance, red, Virginia and longleaf pines were intermediate, and shortleaf, slash, loblolly and eastern white pines were least resistant to decay. Kuhlman (1969) wound-inoculated seedlings of 10 tree species with each of 10 isolates of H. annosum which were examined after four month's incubation for percent mortality. Yellow poplar and American sycamore exhibited low mortality (1 percent) while resistance varied among the remaining species, i.e., slash (82 percent), shortleaf (80 percent), loblolly (74 percent), Virginia (72 percent), longleaf (65 percent) and eastern white 64 percent) pines, Fraser fir (67 percent) and eastern redcedar (28 percent). In a subsequent experiment using similar inoculation methods, Kuhlman (1972) failed to obtain significant intraspecific variation among 10,000 seedlings from almost 300 families of loblolly pine. McGauley and Hubbes (1976) used H. annosum colony diameter upon the surface of stem wood discs taken from 13 pine species as a measure of relative decay resistance. The most resistant species were pitch pine and several related hybrids, i.e., pitch X slash, pitch X monterey and pitch X loblolly, while the least resistant species were Japanese red, Scots and Japanese red X Scots pines. Von Weissenberg (1975) inoculated four

clones of 2-0 Norway spruce seedlings with H. annosum and while no differences in resistance to spread were evident after five weeks, one clone exhibited significant (p=0.10) resistance after 13 weeks. However, he emphasizes that the observed relative resistance may not exist at a more advanced age when the greatest economic damage occurs.

Chemical Control Methods

The role of the freshly-cut conifer stump in the etiology and epidemiology of H. annosum is critically important in effecting control. Thus, efforts to devise chemical control methods have emphasized immediate stump surface treatments to protect the residual or regenerated stand. Two strategies have been developed with regard to chemical control: (1) the application of a fungicidal barrier to kill the pathogen as it develops on the stump surface and (2) the utilization of nitrogenous compounds to promote the growth of microorganisms antagonistic to H. annosum.

Failure to control stump colonization may seriously threaten regenerated conifer stands. Grieg and Pratt (1976) noted that in 24 second-rotation stands of Sitka spruce in Great Britain colonized by H. annosum, the pathogen was isolated from 30-to-62 year-old stumps from previous conifer plantings. Thus, H.annosum can exist in conifer stumps for extremely long periods and increase the levels of disease incidence among subsequent conifer rotations.

Immediately after thinning, Rishbeth (1951) covered 21-year-old Scots pine stumps with either paint, creosote or a four-to-five inch soil layer. After one year the four creosoted and painted stump plots averaged 4 percent H. annosum colonization while the four control and three soil-covered stump plots averaged 36 and 51 percent colonization, respectively,

based upon isolation of the asexual stage from the stump surface. Rishbeth concluded this was further evidence for stump surface colonization by airborne spores and suggested the incidence of H. annosum in a few of the painted and creosoted stumps resulted from faulty application of the protectants or from the development of surface cracks due to stump dessication.

In a subsequent study, Rishbeth (1959) observed that prompt creosoting of freshly-cut pine stumps prevented colonization by airborne spores of H. annosum. An immediate and heavy coating of 50 Scots pine stumps almost completely inhibited colonization after incubating 15 months as determined by isolation of chips from the stump surface. Immediate light applications and heavy applications after one hour proved ineffective. He described several disadvantages of creosoting; (1) limited penetration of surface wood, (2) incomplete stump surface coverage during application, (3) eventual surface cracking which exposed unprotected interior stump tissues and, (4) exclusion of wood-rotting basidiomycetes which delayed decomposition and instead prolonged stump susceptibility to subterranean colonization. Thus, if H. annosum is present within the root system at the time of thinning and subsequent stump creosoting, other competitive microorganisms would be effectively excluded and development of the pathogen will be enhanced. He concluded that where pine stump root systems were either grafted or in contact with roots colonized by H. annosum, stump creosoting may be useless for control purposes and even stimulatory to disease spread.

Chemicals other than creosote have proved toxic to H. annosum and, at least superficially, have prevented colonization of freshly-cut stump surfaces. Some of these include ammate, pentachlorophenate and urea (Berry and Bretz, 1964), fomesan (Gunderson, 1963), sodium nitrite

(Gunderson, 1967), diquat, formaldehyde, ammonium sulfate, ammonium sulfamate, potassium nitrate, sodium bicarbonate and sulfuric acid (Phillips and Grieg, 1970). Morrison and Johnson (1975) have reported stump surface protection in Canada using zinc chloride but further testing was considered necessary.

It can not be emphasized too strongly that evaluation of these chemical treatments for prevention of H. annosum stump surface colonization has been based solely upon the isolation of conidial stage of the fungus from wood or discs of wood at the stump surface. Excavation and inspection of entire stump root systems have been totally neglected and the mere failure to isolate S. meineckellus from the chemically-treated stump surface does not preclude possible extensive colonization throughout the root system. This possibility was clearly demonstrated by Skelly et. al. (1974).

Realizing the problems associated with creosoting, Rishbeth (1959) treated 100 Scots pine stumps immediately after cutting with solutions of formalin (13 percent), disodium octaborate (20 percent), ammonium sulfamate (40 percent) or creosote. Only the disodium octaborate treatment significantly prevented stump surface colonization (81-100 percent effective) as determined by isolation of the S. meineckellus stage from stump discs 8 to 10 months following treatment. Driver (1963) reported effective stump control in a 14 year-old slash pine plantation using only a 10 percent concentration of disodium octaborate. Isolations from 30 stump discs 10 to 12 weeks after treatment yielded no H. annosum and he suggested even a 5 percent concentration of the commercial detergent, Borateem, should give acceptable control. In Virginia, Artman et. al.

(1969) reported greatly reduced percentages of sporophore-bearing stumps (1.4-5.8 percent) following treatment with borax relative to the untreated controls (54.8-56.5 percent). Graham (1971) noted that less than 1 percent of borax-treated Jeffrey and ponderosa pine stumps in California were surface-colonized four weeks after artificial inoculation with H. annosum. More than 61 percent of the control stumps similarly inoculated became colonized during the same period. Borax has also been reported as effectively protecting freshly-cut stumps of white fir (Smith, 1970), shortleaf pine (Berry and Bretz, 1964) and western hemlock (Edmonds, Driver and Russell, 1969).

Weidensaul and Plougher (1966) described the mode of action of boron in treated stumps. In addition to the rapid mortality and dessication of stump tissues, they discussed the probable toxicity of the borate ion to H. annosum. Basidiospores of P. gigantea would not germinate on stump tissue treated with only 0.01 percent boron even after one year. They suggested that the initially high boron concentration is greatly reduced by leaching to a level below that toxic to basidiomycetes within several months following application and failure of H. annosum colonization would probably be due to exclusion by competitive microorganisms.

Hodges (1974) investigated the costs incurred in treating loblolly pine stumps with borax in a pulpwood thinning on moderate-to-high hazard sites in the southeastern United States. Losses during a five-year period from H. annosum mortality were $10.40 per acre and the treatment cost of $3.00 per acre was reported to be both economically justifiable and a wise investment. However, he reported borax treatment on low hazard clayey Piedmont and poorly-drained Coastal Plain soils would be of doubtful value.

Biological Control

Competition from certain saprophytic fungi may prevent successful stump colonization by root pathogens such as H. annosum due to rapid depletion of stump food reserves. Rishbeth (1952) first demonstrated the biological control potential of P. gigantea in reducing H. annosum colonization of freshly-cut pine stumps. Thirteen percent of the 15 stumps treated with a suspension of H. annosum basidiospores and P. gigantea oidia were successfully colonized by the parasite after one year while 78 percent of the 18 stumps treated only with the pathogen were colonized.

Meredith (1959) confirmed P. gigantea was one of only a few fungi capable of naturally colonizing freshly-exposed pine stump surfaces. An increased frequency of stump colonization by H. annosum during the warm and dry months of early spring and summer was correlated with decreased spore production by the more drought-sensitive P. gigantea. This periodic decrease in competitive pressure for stump surface colonization was suggested as the cause of increased stump colonization by the parasite. He emphasized the need for artificial inoculation of P. gigantea basidiospores, particularly during periods of low natural inoculum levels, to promote adequate control.

Rishbeth (1963) demonstrated successful control of H. annosum by P. gigantea in stumps of both dominant and suppressed Corsican and Scots pines, the most prevalent conifer species in East Anglia. He observed slower colonization of Corsican pine stumps and noted that stumps of suppressed trees of both species were colonized faster than those of dominant trees. Soil type apparently exhibited no influence on stump

colonization of either host species by P. gigantea. Host specificity was noted when 32 year-old European larch stumps inoculated with P. gigantea revealed only slight sapwood and no heartwood colonization after six months, whereas H. annosum had often become naturally established via airborne spores.

Hodges (1964) described the replacement capability of P. gigantea in roots of naturally colonized loblolly pine stumps. Ten months after cutting, H. annosum was isolated from 58 percent of the sampled roots while P. gigantea was present in 20 percent of these roots. After 12 months, the pathogen was recovered from only 23 percent of the roots while almost half contained P. gigantea which had apparently entered through freshly-cut stump surfaces and replaced H. annosum.

Artman and Stambaugh (1970) combined oidia and S.A.E. 30 chain saw reservoir oil to achieve simultaneous tree-felling and H. annosum stump control. The oidia-oil suspensions were successfully stored for 33 days and oidia germinated readily after exposure to temperatures ranging from 25 to 86 C. However, the percent isolations of H. annosum and P. gigantea between the treated and control loblolly pine stumps after ten month's incubation were not significantly different. Inoculum quality and concentration were suspected as causes of the inconsistent results. In two of the five test plots however, 99 percent inoculation success was achieved via chain saw application of oidia while H. annosum was rarely isolated (1 percent). In a subsequent study, Artman and Sharp (1971) brushed recently-felled eastern white pine stump surfaces with a similar oidia-oil mixture and after 10 months, 12 of 13 stumps exhibited P. gigantea colonization while no H. annosum was recovered from increment core sections cultured on ortho-phenyl phenol medium.

In Great Britain plastic sachets consisting of P. gigantea basiodiospores suspended in liquid have been successfully used in pine stump protection trials (Webb, 1973). These packets are mixed with five liters of water to which a marker dye is added. Six-to-twelve months following application, basidiocarps should appear on the inoculated stumps and these stumps should be completely decayed within three-to-five years. This method is now used in over 62,000 ha of pine forests in East Anglia.

Fungi other than P. gigantea have been successfully tested for potential stump control of H. annosum and are listed in Table 3.

Stump Removal

Grieg and Low (1976) applied six treatments for annosum root rot control, i.e., (1) tree poisoning with frill injections of 40 percent sodium arsenite, (2) stump poisoning with surface applications of 40 percent sodium arsenite, (3) tree girdling at the ground line, (4) removal of entire standing trees and thinned stumps, (5) removal of entire standing trees only, and (6) controls. The treatments were conducted in a 12 ha stand of 25-year-old Scots pine which had been thinned seven-years earlier and at that time was exhibiting 17 percent mortality due to H. annosum. Mortality due to H. annosum was evaluated using the presence of basidiocarps at the base of trees or fungal pustules on the roots. The two stump removal treatments had similar but significantly less percent mortality (27 percent) than the remaining four treatments.

Grieg and McNabb (1976) described a method of stump removal using a Massey-Ferguson hydraulic digger which individually removed even large stumps with minimal root breakage. About 400 stumps were removed per

Table 3. Fungi other than *P. gigantea* successfully tested for potential stump control of *H. annosum*.

Fungus	Reference
Nonmycorrhizal	
Hematostereum sanguinolentum	Grieg (1978)
Nematoloma capnoides	Grieg (1978)
Polystictus versicolor	Grieg (1978)
Scytalidium sp.	Ricard and Laird (1970)
S. album	Klingstrom and Johansson (1973)
S. aurantiacum	Klingstrom and Beyer (1965)
Trichoderma sp.	Dennis and Webster (1971)
T. viride	Sierota (1976)
Mycorrhizal	
Actinomyces spp.	Federov and Stajcenko (1968)
Amanita muscaria	Korotkov (1975)
Bacillus sp.	Orekhov (1974)
Boletaceae (*Clitocybe* spp.)	Eghbaltalab, Gay and Brucket (1975)
Boletus variegatus	Krupa and Nylund (1972)
Gomphidium glutinosus	Froidevaux and Amiet (1974)
Rhizopogon vinicolor	Zak (1971)

0.5 ha at a cost of $80.00 and cost-benefit analysis of stump removal expense versus losses due to H. annosum revealed a savings of $120.00 in discounted revenue when destumping was implemented.

Koch (1974a, b) reported the development of a complete tree harvester which sheared lateral roots of 15-year-old pines on clay soils and then lifted the stems and taproots up through the tubular shear. A 20 percent increase in fiber yield from 15 to 30 year-old slash pine was estimated and this procedure would reduce site preparation costs for subsequent stand regeneration.

Kuhlman et. al. (1976) suggested that stump removal would prevent or restrict the development of new H. annosum colonization centers since the few lateral roots left in the soil could not provide sufficient food substrates for sustained fungal growth. I would suggest that further experimental evidence is needed before final conclusions can be drawn. Twarowska (1966) reported stump removal as the most successful means of reducing annosum root rot among residual pine stands in the Soviet Union. However, Kazadaev (1957) cited the failure of complete removal of all colonized roots as a major drawback of this technique in checking further spread of this disease.

Trenching

Hartig (1894) recommended trenching to localize H. annosum colonization but this technique had two serious shortcomings: (1) it would be economically impractical over large areas and (2) correct location of the trench to protect uncolonized trees would be subject to much guesswork since trees with incipient colonization may appear no different from

healthy trees. Rishbeth (1952) reported that attempts to halt the spread of H. annosum by root contacts and grafts in East Anglian pine plantations were unsuccessful and the technique was not recommended as a practical control method.

Control Through Alternate Cropping

Kelley and Curl (1972) applied various cultural treatments to slash pine plots known to contain H. annosum and which had been clearcut. The plots were (1) burned, (2), burned and disked and (3) burned, disked and seeded (one plot each) with either lupine, oats or rye.. A natural slash pine stand comprised the control. One year after treatment, an evaluation revealed that conidia germinated well (45-98 percent) on sterilized soil from all three treatments except on soil obtained from oats and rye plots in April which apparently exhibited much inhibition. No germination of conidia occurred on nonsterilized soil collected in either January or August though some occurred on soil collected in April. Germination inhibition was highest on oat- and burned-plot soils while microorganisms antagonistic to H. annosum were more prevalent in the oat- and rye-plot soils. They concluded that since H. annosum was a poor saprophyte upon soil organic matter, these various cropping and burning practices may have been of little value in actual disease control. However, soil fungistasis may have increased which may have prolonged H. annosum spore dormancy.

Grieg (1962) cited two traditional reasons for regenerating cut-over conifer sites with hardwood-conifer mixtures as a means of reducing H. annosum colonization: (1) some of the hardwood fungal flora was considered antagonistic to the pathogen and (2) the hardwood-conifer mixtures reduced

the frequency of root contact between conifers which subsequently minimized the likelihood of subterranean disease transmission. The examination of 240 thinned mixed-conifer stumps revealed that colonization by H. annosum, as determined by the presence of basidiocarps or isolation of the imperfect stage from incubated root tissue, may occur on sites where Armillariella mellea inhabited stumps of a previous hardwood crop, colonized thinned conifer stumps or existed in the soil as rhizomorphs. They suggested that A. mellea competed with H. annosum both in the initial colonization of freshly-cut stump surfaces and later by preventing transfer of H. annosum through root grafts and contacts.

Summer Thinning

Gooding, Hodges and Ross (1966) inoculated 5-to-6 cm diameter stem sections from 5-to-6 year-old loblolly pines and observed the effect of temperature on the growth rate of a single H. annosum isolate. Actively-growing mycelium was killed in less than two hours at 40 C and since stump surface temperatures equal or exceed this level for the same period on more than half the days from May to August in the southeastern United States, summer thinning was suggested as a possible control measure. Reduced levels of stump colonization by H. annosum under these conditions were attributed to three factors: (1) reduced basidiospore production, (2) thermal inactivation of spores prior to stump infection and (3) seasonal effects, i.e., altered stump and root physiology and increased dessication and breakdown of stump tissue. Their conclusions were supported by Ross and Driver (1966).

Mason (1969) investigated the behavior of two species of Ips beetles following a summer thinning in a loblolly pine plantation in Tennessee. Beetles invading the thinned area colonized fresh slash instead of live trees and the newly-emerging progeny dispersed to new areas. He concluded that summer thinning of southern pine pulpwood stands would pose a hazard to residual healthy trees.

Fumigation

Houston and Eno (1969) reported that soil fumigation with methyl bromide along a path near living red pines resulted in root mortality in a continuous band from 1.5 to 2.1 m wide. However, H. annosum survived in some resin-impregnated areas of fumigated roots. Another shortcoming of this method is its impracticality over vast forested areas.

Houston (1975) created fumigation-killed root barriers around 11 H. annosum colonization centers in red pine plantations in four northern states. After four years, the pathogen had apparently crossed only two of the colonization barriers as determined by sign and symptom appearance outside the original barrier zones. In each instance, he suspected that the apparently healthy tree next to the fumigation zone was colonized by H. annosum at the time of treatment but he admitted that the absence of signs and symptoms was unreliable in evaluating "disease-free" trees and subsequently the location of zones for fumigation involved much speculation.

Fallowing

Curschman (1960) reported that when conifer sites which once exhibited severe H. annosum colonization were replanted with various conifer species following 50 years of agricultural production, mortality and growth

reduction decreased for pole-sized trees. He suggested that an increase in antagonistic soil fungi was responsible though fallowing would not be feasible where intensive short-rotation forestry was practiced.

Subsoiling

Subsoiling is a means of deep tillage whereby the subsoil is fractured and loosened but not uplifted or mixed with the surface soil. The subsoiler is generally a metal blade attached to usually a tractor or bulldozer and oriented perpendicularly to the surface of the soil. This blade is forced into the soil to a desired depth and as the vehicle moved forward a narrow trench is created as the subsoil is disturbed. Four advantages from subsoiling have been claimed: (1) increased permeability of the soil profile, (2) increased drought resistance since the water-holding capacity of the soil is supposedly increased, (3) expansion of roots into a greater volume of soil and, (4) increased annual crop yields. However, these claims have been readily renounced and these contradictions arose when subsoiling was conducted in unsuitable soils which provided no long-term advantages (Wells, 1956).

The actual porosity of the subsoil determines the need for subsoiling and subsequent alteration of subsoil permeability. Where a porous subsoil is mechanically disturbed, annual crop yields are usually reduced (Raney, et. al., 1955), but if they are increased, the minimal gains were insufficient to cover the expense of subsoiling (Winters and Simonson, 1951). Benefits to aeration and permeability from subsoiling finer-textured clays are minimal since this subsoil is not usually dry enough to be sufficiently fractured (Diebold, 1954) and the subsoiler trench would fill in from

illuviation and swelling of clays following the next abundant wetting (Sanders, 1947). However, subsoiling would be beneficial to permeability and root growth if a clay layer were present in the profile since several years at least would be required for it to reform (Martinez and Lugo-Lopez, 1952). Yet, this expensive procedure could be avoided by plowing at different depths or by chisel plowing (Diebold, 1954).

Coty et. al. (1975) and Reicosky et. al. (1976) investigated the effects of subsoiling compact A_2 horizons on water stress and yield of millet and sweet corn. Millet and corn yields on sandy sites subsoiled prior to planting were comparable to yields from nonsubsoiled but irrigated areas. However, when these sandy sites later underwent drought stress, yields from subsoiled areas were less due to the reduced waterholding capacity of the subsoil. Also, preplant subsoiling resulted in only a small increase in root volume as this procedure disrupted only a limited portion of the total soil cross-sectional area available for root penetration.

Originally, subsoiling was applied as a preplant treatment to ameliorate soil conditions which would restrict the production of annual crops. Later, subsoiling was implemented as a preplant treatment for perennial crops. Savage, et. al. (1968) subsoiled sandy clay loam acreage prior to planting peach seedlings (Coronet variety) and reported a 45 percent increase in growth after three years and a 58 percent increase in yield after eight years compared to similar trees planted on nonsubsoiled areas. Furthermore, when a portion of the orchard was subsoiled one year after planting, no significant growth or yield increases were observed for trees on these twice-subsoiled sites when compared to trees on sites

subsoiled prior to planting only. Also, subsoiling was reported to increase moisture loss from lower soil depths.

Root pruning is an unavoidable consequence of subsoiling after planting. Cline and Bradt (1969) reported that growth and yield of sweet cherry trees were consistently less when the soil was subsoiled and this were attributed to root pruning. Cline (1968) observed that subsoiling reduced the yield of sweet cherry but not Montmorency cherry or peach planted on a Vineland fine sandy loam. He stated that since Montmorency cherry probably had a less extensive root system, root pruning from subsoiling would not be as frequent as with sweet cherry and hence, growth and yield of the former would not be as adversely affected.

Subsoiling in loblolly pine seed orchards on predominantly clay soils arose not from research but from final desperate attempts to reverse tree decline caused by mechanical compaction of the soil (C. B. Davey, personal communication). Prior to this, extra fertilization and extra irrigation were attempted but were unsuccessful. After subsoiling, declining trees on these clayey, compacted soils dramatically responded by regaining their "vigor" and once again produced flowers, cones and seeds. Based on this circumstantial evidence, subsoiling was recommended in seed orchards on lighter soils where compaction was not a problem in the hope of similarly stimulating increased flower production. However, subsoiling declining trees on clay sites to restore "normal" cone and seed productivity should not imply that subsoiling apparently healthy trees on coarse-textured soils would raise cone and seed productivity above "normal" levels. This latter argument has become a controversial issue in the application of subsoiling in pine seed orchards.

Dewers and Moehring (1970) investigated the effect of seasonal water stress on the potential cone crop of 13-year-old seed orchard loblolly pines in Texas. Five soil water treatments were applied in the spring of 1967: (1) irrigation(April 1 to September 30), (2) irrigation (April 1 to June 30) then drought (July 1 to September 30), (3) drought (April 1 to September 30), (4) drought (April 1 to June 30) then irrigation (July 1 to September 30) and, (5) natural rainfall (April 1 to September 30).

These five treatments were replicated eight times and the root system of each replicate was situated at the center of a 16 square-foot zone. A polyethylene barrier three feet deep restricted lateral root growth and water movement. Polyethylene sheeting was arranged around each tree to shed rainfall. The soil was a deep sand which overlayed clay deposits at a depth of eight feet. During the first week of April of the following year, conelets were counted and the only treatment which significantly increased conelet numbers was irrigation (April 1 to June 30) followed by imposed drought (July 1 to September 30). They concluded a period of soil water deficiency stimulated cell differentiation towards initiation of reproductive tissue and recommended the application of this treatment in Texas during the late summer or early autumn.

This one report however, should not be accepted in support of subsoiling sandy sites for increased cone production without first examining several deficiences in the experimental design: (1) only several clones were replicated and these were field-grafted onto loblolly pine seedling rootstock of unknown genetic constituency, (2) no pruned roots were examined for their ability to heal in this droughty environment which could have been compared to cone yields in future years, (3) the timing of

root pruning (prior to April 1) differs greatly from conventional industry schedules (late June-July), (4) drought-induction by the pruning of root tips is contrary to the principles of pine root water conduction as outlined by Kramer (1932, 1946), and Kramer and Bullock (1966), and (5) since no treatment was conducted without the pruning of roots, no adequate control group was available for any truly conclusive comparisons. Furthermore, the converse argument for the production of significantly greater numbers of conelets, i.e., abundant soil moisture through irrigation in the early spring, was totally disregarded in the discussion. It seems plausible that if more reproductive structures are desired, then more moisture, not less, during a critical developmental period may be required.

Shoulders (1973) reported that abundant rainfall in all months of the year was associated with maximum flowering of longleaf pine yet abundant rainfall from May to July reduced the flowering of slash pine in Louisiana and Mississippi. Bengston (1969) reported that irrigating a slash pine plantation in Florida throughout the year at rates which overcame seasonal soil moisturedeficits reduced female flowering in the 24 clones tested. Lowery (1966) analyzed the meteorological requirements for abundant cone production in Douglas-fire in western Oregon and Washington by correlating records of cone crop sizes with mean monthly temperature and total monthly precipitation over a 48 year period. He concluded that the occurrence of an abundant cone crop in a given October required a warm January during the same year, above-average rainfall during March and April one-and-one-half years before harvest and a cool July two years prior to harvest.

Three principal methods have been tested within tree improvement programs to stimulate increased flowering: (1) mechanical disruption of the tree's translocative and root systems by strangulation, girdling or root pruning, (2) fertilization and (3) the use of flower-regulating hormones (Bergman, 1968). However, the physiological mechanisms altered by these various treatments to stimulate flower production are unclear and, particularly in the case of root pruning or subsoiling, are complex and somewhat contradictory.

Bergman (1968) emphasized this complexity by outlining relevent genetic, environmental and cultural factors which affect seed orchard yields:

I. Genetic variation in pollen and cone production
   - A. Primary differences in flowering ability per se
   - B. Flowering cycle; differs with species
   - C. Differences in number of ovules per cone
   - D. Differences in flowering patterns, such as cones being produced singly or in clusters
   - E. Variation in reaction to treatments such as fertilization and irrigation
   - F. The occurrence of lethal genes which influence the empty seed percentage

II. Influence by environment
   - A. The geographic location of the seed orchards
   - B. The local placement of the seed orchard, especially soils and air drainage
   - C. The space allocated to trees in the orchard

III. Management activities

A. Fertilization

B. Treatment with hormones

C. Irrigation

D. Sodding and cultivation

IV. Clone arrangement in the orchard

A. The degree of similarity between clones in time of flowering

B. The empty seed percentage as influenced by genes and synchronization of flowering among clones.

To this list should be added the additional genetic variant of scion - rootstock compatibility and its combinatorial effects upon flower production. This feature has been completely overlooked in the design of clonal seed orchards and though scions have been meticulously catalogued for clonal identification, no similar care was taken in the selection of rootstocks for grafting. All clonal seed orchards then are the result of clonal scions grafted onto rootstocks of unknown genetic constituency and the resultant floral behavior should not be assumed necessarily to be identical among scions of the same clone.

Colby (1935) observed striking differences in fruitfulness and growth when scions of several apple varieties were each grafted onto different clonal apple rootstocks. Vyvyan (1955) reported that among the apple varieties tested, the rootstock has a greater influence on tree size than did the scion. Ahlgren (1962) performed interspecific grafting among Balkan (P. koraiensis Sieb. and Zucc.), red and Swiss stone pines and reported that survival, growth and total flower (male and female) production

of all species were significantly higher on eastern white pine rootstocks. However, certain differences among species' flower production were also noted: (1) Swiss stone pine produced more female strobili when grafted onto red pine rootstocks but more male strobili when on eastern white pine rootstocks and (2) Balkan and Korean pines produced more female strobili when grafted onto eastern white pine rootstocks. Allen (1967) grafted combinations of loblolly, shortleaf and slash pine scions and rootstocks and reported that scions grafted onto rootstocks of faster growing species demonstrated an appreciably greater height growth than the controls. However, reduced growth occurred when scions of faster growing species were grafted onto rootstocks of slower growing species. Unfortunately, the effect of these various scion - rootstock combinations upon flowering was not investigated.

Subsoiling was first implemented in desperation on predominantly clay sites to revive seed orchards declining from soil compaction caused by routine orchard traffic (C. B. Davey, personal communication). The subsoiled root tips typically healed successfully in these moist soils and produced numerous adventitious roots which readily grew into the less physically restrictive environment of the subsoiler trenches. This effectively increased the volume of soil available for root development and the subsoiled trees responded vigorously as evidenced by the increased production of foliage and flowers the following year. As a technique for ameliorating compacted soils and at least temporarily restoring "normal" growth, subsoiling has proved very effective (R. Wasser, personal communication). Kaufman (1968) observed eight year-old- root-pruned slash pines in Florida growing on a Eulonia soil series which consisted of a surface

layer of fine sand underlain by a clay subsoil. The rapid regrowth of roots severed by cultivation was due probably to the wetter soil environment aiding the healing of these wounded roots. Conversely, Larson and Whitmore (1970) noted that red oak (Q. rubra L.) seedlings did not regenerate new roots when placed under soil moisture stress.

Dewers and Moehring (1970) suggested that moisture stress during late summer in Texas stimulated the cessation of loblolly pine vegetative growth and initiated the formation of ovulate primordia. However, on Kalmia sandy loam soils in southeastern Virginia Wenger (1957) reported that cultural measures to stimulate cone production of loblolly pine must be implemented before late June. Tree improvement programs in this region typically recommend subsoiling loblolly pine seed orchards in mid-to-late July to theoretically increase moisture stress and initiate ovulate primordia. He also noted that the amount of rainfall between early spring and midsummer would influence flower production more so than at any time of the year. His analysis of May-to-July rainfall and its interaction with yearly loblolly pine seed crops was highly significant in influencing seed crop variation two years later. He summarized his study by describing the two effects of soil moisture on loblolly pine flower production: (1) available soil moisture affects the volume of nutrients absorbed which may account for annual seed crop variations and (2) movement of nutrients within the tree also is water-dependent and moisture stress in growing root tips may adversely affect floral initiation. Increasing soil moisture levels through irrigation during the spring was recommended to increase flower production.

Stephens (1961) subsoiled two eastern white pine plantations, 14 and 22 years old, in July, 1959. Using a spade, each test tree was root-pruned to a depth of 14-18 inches at a radius of four feet while both test and control plots were fertilized at 0, 18, 53, and 158 pounds of nitrogen per acre. An evaluation one year later revealed no flowers were produced on the 14 year-old subsoiled trees among any of the fertilizer treatments. Among the 22 year-old subsoiled trees, only those fertilized at the rate of 53 pounds per acre produced flowers while the controls produced no flowers and he concluded that subsoiling was stimulatory to floral induction. Further inspection of his data revealed that among the 22 year-old trees, the same trees which produced 141 cones in 1960, one year after subsoiling, had produced 175 cones in 1958, one year prior to subsoiling. Also, 13 trees which remained barren in 1960 had produced a total of 104 cones in 1958. These contradictions when coupled with the complete lack of flowers on the 14 year-old subsoiled trees seem to suggest his conclusion was incorrect and that additional factors as outlined by Bergman (1968) may have strongly influenced flower production, more so that the mere act of subsoiling. Finally, he noted an almost complete absence of male strobili on subsoiled trees one year after subsoiling which obviously would have serious implications for uninterrupted superior seed production.

Hoekstra and Mergen (1957) in Florida on a Blanton sandy soil claimed to have demonstrated stimulation of early flowering by subsoiling six year-old slash pines which had not previously flowered. Root-pruned and control trees were included in each of three treatments: (1) no stem injury, (2) wire strangulation and (3) partial girdling. Only the first

treatment will be discussed as only this is applicable to subsoiling as conducted in tree improvement orchards. A 3-12-6 fertilizer was applied at rates of 0, 5, 10 and 15 pounds per tree and was continued at six-week intervals. Test trees were subsoiled with an axe at a radius of two feet in April, 1954, and in February, 1955, all female flowers were counted on the upper three whorls of each tree. Female flowers were produced on one of 36 control trees which had been fertilized at the 15 pound rate. Only two of 36 subsoiled trees, one fertilized at 5 and the other at 15 pounds, exhibited female flowers. For trees which had not previously flowered, the occurrence of flowers on only two medium-to-heavily-fertilized subsoiled trees seems hardly to warrant unqualified support of root-pruning as a means of inducing early floral induction. Unfortunately, no mention was made of rainfall during the test period or whether male strobili were observed.

Gregory (1975) observed the effect of subsoiling on female flower production in two loblolly pine seed orchards, one of which was the same Union Camp seed orchard test area where the current study was performed. Clones in this orchard were selected from Coastal Plain sources in North Carolina and Virginia. After subsoiling in late July, 1973, female flower counts were conducted in late April of 1974 and 1975 and cones were counted in September, 1974, and August, 1975. In 1974, the average number of female flowers per tree was greater in the subsoiled plots than in the control plots yet these differences were statistically insignificant ($p=0.05$). The difference in female flower crop means for 1975 between subsoiled and control plots was less than in 1974 and was also insignificant. Subsoiling apparently did not affect the one-year-old cones present when the trees

were initially subsoiled but the number of cones per subsoiled tree in 1975 averaged twice the number for the controls. However, this difference was also statistically insignificant ($p=0.10$). At the VDF loblolly pine seed orchard on a predominantly clay soil in the Virginia Piedmont, the subsoiling treatments produced similarly insignificant differences between female flower and cone production when compared to the controls. The lack of success from subsoiling at both seed orchards was attributed to several factors: (1) tree age and size, (2) size of the root systems and the number of roots subsoiled and (3) highly significant clonal variation in female flower production.

At the end of July, 1975, Greenwood (1977) in Oklahoma subsoiled on all four sides the lateral roots of 14 grafted first generation superior loblolly pines using a Vermeer Tree Spade. Despite this drastic treatment, subsoiled trees when evaluated two weeks later differed from the controls in water potential by only about minus one bar which did not suggest subsoiling had created prolonged moisture stress. The effects of subsoiling on the stimulation of strobili production were resoundingly negative. The only parameter to increase on the subsoiled trees relative to the controls was the percentage of branches forming female strobili, 16 versus 8 percent, respectively. Otherwise, the number of branches bearing male strobili decreased. The number of clones producing male strobili was reduced from 6 of 7 among the controls to 2 of 7 among the subsoiled trees. Of crucial importance though, was the actual reduction in the number of female and male strobili produced from the subsoiled trees.

MATERIALS AND METHODS

Due to declining pine plantation acreage, the use of genetically improved seed from superior loblolly pine seed orchards and the optimal management of existing and future plantations for maximum fiber production are critically important in assuring a continuing supply of softwood. Thinning increases the risk of H. annosum development by deposition of basidiospores which may colonize freshly-cut stump surfaces and spread by root contacts and grafts to residual trees. Powers and Verrall (1962) relied upon basidiocarp occurrence to determine H. annosum incidence but this was an invalid survey technique (Hodges, 1974a) and greatly underestimated the presence of the pathogen. Moreover, their study completely ignored unthinned plantations. Similarly, no information exists on the potential for colonization of seed orchard loblolly pine subsoiled roots. Evaluation of H. annosum impact in unthinned loblolly pine plantations and loblolly pine seed orchards, and the potential for direct colonization of roots by percolated basidiospores were the objectives of this study.

I. Unthinned Loblolly Pine Plantation Survey

According to Morris and Frazier's (1966) soil rating scheme for expected levels of H. annosum, five high and four low hazard unthinned loblolly pine plantations were selected. High hazard plantations were located in the Coastal Plain while three low hazard plantations were

selected from the Piedmont of Virginia. The remaining low hazard plantation, Union Camp (UC) #306, was located in the Coastal Plain. Stand history, location and hazard rating data are presented in Table 4. Two circular 0.02 ha plots were established in each plantation except in UC #219 and #306 where two pairs of plots were installed. Location of plot centers was such that no plot perimeter was located less than two chains (48 m) from any natural or man-made stand disturbance, i.e., mortality due to bark beetle infestations or woods road excavations. Loblolly pines within these plots were subsequently selected, excavated and their root systems rated according to Bradford et. al. (1978b).

II. Loblolly Pine Seed Orchards Survey

The Chesapeake Corporation (West Point, Va.), Union Camp Corporation (Murfreesboro, N. C.) and the Virginia Division of Forestry (VDF) (New Kent, Va.) each provided a loblolly pine seed orchard for use in this study. All three seed orchards had been subsoiled both between- and within-rows and, in addition, the Union Camp test area was further subdivided into three treatments, i.e., deep subsoiling (38 cm average depth), shallow subsoiling (18 cm average depth) and no subsoiling (control) (Gregory, 1975). The VDF orchard had been subsoiled in 1971 and again in 1976 while the Union Camp Corporation and Chesapeake Corporation orchards were subsoiled in July, 1973,and July, 1974, respectively.

Loblolly pine seed orchard trees were selected on the basis of healthy-versus-declining crowns and subsoiled-versus-nonsubsoiled root systems, the latter applicable only to the Union Camp orchard. From each orchard 10 trees were chosen according to each of the following categories:

Table 4. History, location, hazard rating and soil analysis of unthinned loblolly pine plantations.

Plot	History	Physio-graphic Region	Annosum root rot Hazard Rating	% Sand	% Silt	% Clay	pH	% Organic Matter	Calcium*	Magnesium*	Phosphorus*	Potassium*
C6601-1	Old-field plantation	Coastal Plain	High	83	6	11	4.5	1.2	L	L	L	L
C6601-2	Old-field plantation	Coastal Plain	High	84	4	12	4.3	1.2	L	L	L	L
J15-1	Old-field plantation	Piedmont	Low	38	16	46	4.8	1.2	L	H	L	L
J15-2	Old-field plantation	Piedmont	Low	36	13	51	5.1	0.9	L	H	L	M
J28-1	Old-field plantation	Piedmont	Low	29	11	60	4.8	0.5	L	H	L	L
J28-2	Old-field plantation	Piedmont	Low	34	11	55	5.0	0.9	M	H	L	L
RQ23-1	Old-field plantation	Piedmont	Low	26	23	51	5.1	0.9	M	H	L	L
RQ23-2	Old-field plantation	Piedmont	Low	29	22	49	5.2	0.7	L	H	L	L
UC4-1	Old-field plantation	Coastal Plain	High	87	8	5	5.3	0.7	L	L	L	L
UC4-2	Old-field plantation	Coastal Plain	High	85	8	7	4.9	0.9	L	L	M	L
UC39-1	Old-field plantation	Coastal Plain	High	86	4	10	5.1	0.5	L	L	M	L
UC39-2	Old-field plantation	Coastal Plain	High	76	3	21	4.8	0.6	L	L	M	L
UC219-1	Old-field plantation	Coastal Plain	High	89	3	8	5.1	0.5	L	L	M	L
UC219-2	Old-field plantation	Coastal Plain	High	91	4	5	5.6	0.5	L	L	M	L
UC219-3	Old-field plantation	Coastal Plain	High	76	6	18	6.6	0.5	L	L	H	L
UC219-4	Old-field plantation	Coastal Plain	High	86	4	10	5.7	0.7	L	L	M	L
UC223-1	Old-field plantation	Coastal Plain	High	87	5	8	4.8	0.4	L	L	M	L
UC223-2	Old-field plantation	Coastal Plain	High	86	5	9	4.8	0.5	L	L	L	L
UC306-2	Old-field plantation	Piedmont	Low	19	61	20	4.3	0.7	L	L	L	L
UC306-3	Old-field plantation	Piedmont	Low	27	60	13	4.2	0.8	L	L	L	L
UC306-4	Old-field plantation	Piedmont	Low	26	54	20	4.2	0.6	L	L	L	L
UC306-5	Old-field plantation	Piedmont	Low	25	53	22	4.2	0.4	L	L	L	L

*L = low; M = moderate; H = high.

(1) healthy crowns/subsoiled root systems and (2) declining crowns/subsoiled root systems. At the Union Camp orchard an additional five trees were selected from each of the following categories: (3) healthy crowns/non-subsoiled root systems and (4) declining crowns/nonsubsoiled root systems. Thus, categories 3 and 4 constituted the control groups in the Union Camp study.

Trees in all four categories were scheduled by orchard personnel for roguing during the summers of 1977 (Union Camp and VDF) and 1978 (Chesapeake). Poor progeny testing or poor seed production were primarily the reasons for roguing these particular trees. Explicit care was taken to avoid tree selection where symptoms of obvious graft incompatibility were present, i.e., graft over-growth or basal fluting. Also, trees within each category were selected from as many different available clones as possible. No more than two trees of the same clone were chosen in any one category to circumvent the confounding influence of clonal type on root reaction to subsoiling. Furthermore, superior loblolly pine scions were originally grafted onto "wild" loblolly pine or pond pine (Union Camp only) root stock and the probability of the same clonal scion grafted onto the same "clonal" root stock would have been extremely low. Only loblolly pines which had been grafted onto loblolly pine root stock were selected for root system excavation and analysis. To avoid this similar clonal influence, trees exhibiting fusiform rust galls were also avoided.

Following seed tree selection, certain above-ground parameters were measured, including total height, height-to-live-crown, d.b.h., and crown rating (healthy, declining or dead). A photograph of each tree prior to excavation was taken and each stem was then cut at d.b.h.and a radial section removed for growth analysis. The number of cones was recorded.

Previous subsoiler trenches were located approximately 1.5 m from the base of the trees, both between- and within-rows. However, the original between-row trenches at the VDF orchard were located about 0.9 m from the tree bases.

A backhoe was used to excavate a new trench on each of the four sides of a selected tree in the same general areas as the original trench. This insured that subsequent root system removal would include subsoiled primary root tips with a minimum of breakage or loss. These new trenches were dug to a depth of about 1.2 m and each root system loosened by rocking the stump with the bucket of the backhoe. A chain was attached to the bucket and wound around the base of the stump after which the root system was uplifted and swung clear of the pit for closer observation. While suspended, the roots were cleaned of residual soil using hand picks, each root system photographed and then the primary roots were measured for root collar diameter and the length of healthy and colonized or resin-soaked tissue. For each tree, the resinous primary root sections were severed, placed in a plastic bag and stored immediately on ice for subsequent transfer to the laboratory.

Prior to cultural isolation the severed resinous primary root portions were washed to remove surface soil, scraped with a knife to remove bark and locate the colonization margins and the exposed colonized tissue flame-sterilized briefly (1-2 sec.) with 95 percent ethanol. Using a sterile wood chisel (0.6 cm blade), several chips approximately one cm^3 in size were removed from each colonization margin and each was randomly plated on one of four isolative media. Two general (PDA, 2 percent MEA) and two selective (Hendrix-Kuhlman, OPP) media were used to promote maximum

isolation efficiency from the resinous root chips. After incubating 10 days, pure culture transfers were conducted and subsequently analyzed for the occurrence of S. meineckellus.

III. Root Inoculation Study

According to Keller (1974), the exterior surface of H. annosum basidiospores is covered with echinulate projections. This anatomical feature is useful in distinguishing these spores from the smooth-walled conidia of S. meineckellus (Scurfield and Da Costa, 1969). However, this technique has not previously been applied in distinguishing these spores from spores of other fungi as they develop on inoculated root surfaces.

Eighteen suberized primary root segments approximately 2-3 cm long and 1-2 mm wide were septically cut from potted three-year-old loblolly pines, placed in a covered flame-sterilized watchglass and inoculated with 4 ml of a H. annosum basidiospore solution (824,000 spores/ml). These spores were collected one week earlier by placing several sterile petri plates for 24 hours under the partially exposed root system of a leaning eastern redcedar exhibiting numerous imbricate H. annosum basidiocarps. These plates were recovered and stored on ice for removal to the laboratory where the contents were washed with sterile distilled water into several sterile dropper bottles and placed under refrigeration. To test viability prior to inoculation, several mls of the spore suspension were incubated overnight at 24 C on 2 percent malt extract agar medium and subsequently observed for the abundant production of germ tubes.

Initially, 30 g of dextrose were dissolved in 400 ml of distilled water after which 8.56 g of sodium caccodylate were added and the pH adjusted to 7.4 with several drops of 1N sulfuric acid. A separate

2 percent gluteraldehyde solution was prepared by adding 16 ml of 50 percent gluteraldehyde to 384 ml of distilled water. A 1:1 dilution of the dextrose-sodium caccodylate and 2 percent gluteraldehyde solutions was then prepared (800 ml total) and refrigerated in the dark until used. At intervals of 0.5, 3, 5, 8, 11 and 14 days three inoculated root segments were transferred to the dextrose-sodium caccodylate-gluteraldehyde fixative for 12 hours. Following fixation, each root segment was progressively dehydrated according to a standard ethanol-acetone sequence during which each was submerged for five minutes in sequential solutions of 40, 70, 80, 95 and 100 percent ethanol-distilled water (v/v) and then in solutions of 40, 80, 95, and 100 percent acetone-ethanol. Root segments were then stored in 100 percent acetone in screw-cap vials until prepared for scanning electron microscopy. Each dehydrated root segment received a thin coating (approximately 200 Å) of a 60 percent gold-40 percent palladium mixture using a Denton Vacuum Evaporator model DV515 (Denton Vacuum Corp., Cherryhill, N. J.). Coated segments were then observed using the AMR 900 scanning electron microscope (Advance Metals Research Corp., Bedford, Mass.) with an electron beam of 100 uamps and a standard operating potential of 20,000 volts.

RESULTS

I. Unthinned Loblolly Pine Plantation Survey

Plot parameters

Nine loblolly pine plantations in Virginia were selected for intensive investigation in this study. Two 0.02 ha circular plots were installed in each plantation except for UC219 and UC306 where, due to their large areas, four plots were installed. Twelve of the plots were located on sites which, according to the soil classification scheme of Morris and Frazier (1966), were determined to be high hazard for annosum root rot. These plots were located in King and Queen, Isle of Wight and Southampton counties. The remaining 10 plots were located on low hazard sites in Buckingham (Cumberland State Forest) and Southampton counties. The UC306 plantation exhibited a high sand content in the upper 30 cm of soil but was classified as low hazard due to an underlying clay layer which created a perched water table. Average soil textural and elemental analysis for high and low hazard unthinned loblolly pine plantations is described in Table 4. Except for the textural hazard differentiation, all plots were similar with regard to acidic pH values (4.2 to 5.6 range), low percent organic matter (0.4 to 1.2 range) and generally low levels of calcium, magnesium, phosphorus and potassium.

Tree and site index parameters

Average tree and site index parameters for high and low hazard plots in unthinned loblolly pine plantations are presented in Table 5. Site

Table 5. Tree and site index parameters for 22 plots in unthinned loblolly pine plantations.

Plot	No. trees	Average DBH (cm)	Average height (m)	Average Height-to-live crown (m)	Stand age (yr.)	Site Index (Base age 25)	Average crown rating	Average shigometer total
C6601-1	25	7.0	18.3	11.7	13	92	3.6	-
C6601-2	27	7.2	17.5	10.8	13	90	3.4	-
UC4-1	25	9.5	27.1	19.0	21	95	3.2	110.3
UC4-2	25	10.1	26.5	17.7	18	93	3.3	126.0
UC39-1	25	8.7	26.1	19.1	23	86	4.0	135.6
UC39-2	25	8.4	25.8	18.1	23	86	3.8	110.0
UC219-1	39	6.1	18.0	12.5	19	64	3.7	137.4
UC219-2	47	6.0	16.2	11.8	19	62	3.9	137.4
UC219-3	27	7.7	24.1	16.2	19	83	3.5	108.7
UC219-4	32	7.3	24.3	18.0	19	83	3.4	101.8
UC223-1	26	7.7	18.2	13.7	16	74	4.0	136.1
UC223-2	25	7.4	19.6	14.4	17	75	3.9	122.5
J15-1	40	5.3	14.9	10.3	13	71	3.9	181.8
J15-2	36	4.9	14.2	9.7	13	71	3.6	181.1
J28-1	44	5.7	14.4	10.0	15	63	3.7	179.5
J28-2	37	6.2	15.0	9.3	15	64	3.4	183.2
RQ23-1	41	5.1	13.6	9.0	17	54	3.2	176.5
RQ23-2	42	5.4	16.5	11.0	17	64	3.2	188.1
UC306-2	18	9.9	24.6	17.0	44	45	3.2	75.2
UC306-3	14	12.3	26.5	18.5	45	53	3.2	99.6
UC305-4	11	10.7	26.4	17.1	44	53	3.0	114.8
UC306-5	17	10.1	24.9	17.6	44	45	3.1	102.6
Averages	30	7.1	19.3	13.3	22	71	3.5	144.3
All *H. annosum* colonized trees	39	9.1	24.1	17.0	19	72	3.6	116.7
All non-colonized trees	609	6.9	19.0	13.1	22	70	3.5	146.2

indices for all trees averaged 71 at a base age of 25 years while the range was from 45 to 92. Thus, these plots ranged from intermediate to excellent site quality for growth of loblolly pine.

The average loblolly pine excavated exhibited a codominant, green crown, a d.b.h. of 7.1 cm, a height of 19.3 m, was 22 years old and had a total Shigometer value of 144.3. Compared to noncolonized trees which also exhibited codominant, green crowns, the average H. annosum-colonized loblolly pines exhibited a larger diameter (9.1 cm d.b.h.), greater height (24.1 m) and a lower total Shigometer value (116.7) which fell within the range (100-120) associated with trees of greater "vigor".

Disease incidence

The incidence of annosum root rot on high and low hazard sites in unthinned loblolly pine plantations is presented in Table 6. Twenty-nine of the 348 trees (8.3 percent) located on high hazard sites were colonized with H. annosum as determined by cultural isolation of the asexual stage of the fungus from symptomatic tissue, i.e., resinous or stringy decayed roots. Only 5 (1.4 percent) of these trees were colonized on greater than one percent of the total root system mass which was indicative of serious incidence. Only 2 trees, both of which were located in UC4-2, exhibited H. annosum basidiocarps at the time of excavation. On low hazard sites, 10 of 300 trees (3.3 percent) were colonized by H. annosum with 2 (0.7 percent) of these exhibiting colonization on greater than one percent of the total root system mass. Basidiocarps were not observed on any trees in the low hazard plots.

Table 6. Incidence of annosum root rot in unthinned loblolly pine plantations.

Annosum root rot hazard	Plot	No. trees	Total no. trees colonized	No trees colonized 1%	Percent no. trees colonized	No. trees with conks
High	C6601-1	25	0	0	0	0
	C6601-2	27	0	0	0	0
	UC4-1	25	2	0	8	0
	UC4-2	25	9	4	36	2
	UC39-1	25	2	0	8	0
	UC39-2	25	3	0	12	0
	UC219-1	39	0	0	0	0
	UC219-2	47	2	1	4	0
	UC219-3	27	4	0	15	0
	UC219-4	32	2	0	6	0
	UC223-1	26	2	0	8	0
	UC223-2	25	3	0	12	0
Totals		348	29	5		2
Averages					8.3	
Low	J15-1	40	0	0	0	0
	J15-2	36	1	1	3	0
	J28-1	44	0	0	0	0
	J28-2	37	0	0	0	0
	RQ23-1	41	0	0	0	0
	RQ23-2	42	0	0	0	0
	UC306-2	18	2	0	11	0
	UC306-3	14	4	1	29	0
	UC306-4	11	0	0	0	0
	UC306-5	17	3	0	18	0
Totals		300	10	2		0
Averages					3.3	

Disease severity

Annosum root rot severity data for high and low hazard sites in unthinned loblolly pine plantations are presented in Table 7. On high hazard sites, 5 of 348 trees were colonized greater than one percent. Four of these were located in UC4-2 and the root systems were decayed an average 34 percent by length. The remaining tree occurred in UC219-2 and was colonized 25 percent by length. Of the characteristic symptoms attributed to H. annosum colonization, these trees on high hazard sites exhibited primarily resin soaking which was indicative of incipient decay associated with recent colonization.

On low hazard sites, only 2 of 300 trees (0.7 percent) were colonized greater than one percent. The root system of one tree located in J15-2 was decayed 84 percent by length while the root system of the remaining tree, located in UC219-2 was colonized 68 percent by length. These two trees exhibited symptoms of stringy decay which indicated prolonged colonization by the fungus, extending over a period of at least several years.

Insignificant growth reduction

Radial increment growth for each excavated loblolly pine was electronically recorded to an accuracy of 0.01 mm using an Addo-X dendrochronograph. Differences in mean radial increment growth between H. annosum-colonized and noncolonized trees were subsequently statistically analyzed using the Duncan's Multiple Range test. The results of this analysis are presented in Table 8. Assuming radial increment growth to be the resultant expression of all environmental and physiological effects, the only variable

Table 7. Severity of annosum root rot in unthinned loblolly pine plantations.

Annosum root rot hazard	Plot	No. trees measured (colonized > 1%)*	Total measured root length(m)	Total length decayed tissue	Percent decayed root length
High	C6601-1	0	0	0	0
	C6601-2	0	0	0	0
	UC4-1	0	0	0	0
	UC4-2	4	49.2	16.2	34
	UC39-1	0	0	0	0
	UC39-2	0	0	0	0
	UC219-1	0	0	0	0
	UC219-2	1	14.1	3.6	25
	UC219-3	0	0	0	0
	UC219-4	0	0	0	0
	UC223-1	0	0	0	0
	UC223-2	0	0	0	0
Totals		5 / 348	63.3	20.2	
Average					32
Low	J15-1	0	0	0	0
	J15-2	1	5.2	4.4	84
	J28-1	0	0	0	0
	J28-2	0	0	0	0
	RQ23-1	0	0	0	0
	RQ23-2	0	0	0	0
	UC306-2	0	0	0	0
	UC306-3	1	22.9	15.6	68
	UC306-4	0	0	0	0
	UC306-5	0	0	0	0
Totals		2 / 300	28.1	20.0	
Average					71

*Based upon visual estimation of decay symptoms on >1% of the total root system mass.

Table 8. Duncan's Multiple Range analysis of mean radial increment growth (mm) for H. annosum - colonized and noncolonized loblolly pines from colonized unthinned plantations.

	J15-2		UC4-1		UC4-2		UC39-1		UC39-2		UC219-2		UC219-3		UC219-4		UC223-1		UC223-2		UC306-2		UC306-3		UC306-5	
Year	C[1]	NC[2]	C	NC	C	NC	C	NC	C	NC	C	NC	C	NC	C	NC	C	NC	C	NC	C	NC	C	NC	C	NC
1976	1.7	1.5	1.0	1.4	1.7	1.4	1.1	1.3	1.6	1.1	1.1	0.8	1.0	1.3	0.9	1.2	0.5	0.8	0.7	0.6	1.0	0.6	0.5	0.8	0.6	0.7
1975	1.4	1.7	0.9	1.4	1.2	1.4	0.9	1.1	1.0	0.9	0.6	0.5	0.7	0.8	0.6	0.9	0.3	0.6	0.5	0.5	0.7	0.5	0.4	0.6	0.5	0.7
1974	1.8	2.0	1.2	1.5	1.7	1.4	1.4	1.1	1.6	0.9	0.9	0.8	0.9	1.0	0.4	1.0	0.3	0.7	0.5	0.6	0.6	0.5	0.3	0.6	0.4	0.6
1973	2.5	2.4	1.5	1.3	1.8	1.2	0.9	1.1	1.1	0.8	1.1	0.8	0.8	1.0	0.7	1.0	0.8	0.7	0.6	0.6	0.8	0.6	0.4	0.7	0.7	0.7
1972	2.0	2.7	1.5	1.4	1.7	1.3	1.6	1.3	1.4	1.2	2.1	1.0*	0.9	1.1	0.5	1.1	0.7	0.9	0.8	0.8	0.6	0.7	0.7	0.9	0.5	0.8
1971	2.5	2.8	1.3	1.6	1.7	1.5	2.0	1.5	1.3	1.1	2.6	1.2*	1.1	1.2	0.7	1.2	0.8	1.1	1.0	1.0	1.0	0.7	0.8	1.1	0.5	0.8
1970	2.0	3.3	2.2	1.7	1.7	1.6	1.9	1.5	1.8	1.3	2.9	1.4	1.2	1.3	1.0	1.4	0.9	1.2	1.5	1.1	1.0	0.9	1.1	1.0	0.7	0.8
1969	2.5	3.3	1.9	1.8	1.9	1.9	1.9	1.8	2.1	1.6	3.2	1.6	1.5	1.5	0.9	1.6	1.1	1.4	1.4	1.3	1.0	0.7	1.0	0.8	0.7	0.8
1968	3.1	3.1	2.0	2.1	2.2	2.1	1.9	1.7	1.7	1.6	4.9	1.6*	1.2	1.5	1.2	1.6	1.8	1.5	1.9	1.5	0.9	0.7	0.8	0.8	0.9	0.9
1967	2.9	4.1	1.5	2.0	2.6	2.3	1.8	1.7	1.4	1.6	4.1	1.9	1.5	1.7	1.1	1.8	1.8	1.6	2.4	1.8	0.8	0.7	0.9	0.8	0.6	1.0

* Means are significantly different (p=0.05)

[1] C = trees colonized by H. annosum

[2] NC = healthy or noncolonized trees

in this analysis to differ among the trees was the presence of H. annosum. Therefore, any significant growth reduction among colonized trees would be attributable to root disease caused by this pathogen.

Loblolly pines colonized by H. annosum occurred in 13 of 22 unthinned plantation plots. Duncan's Multiple Range analysis of differential mean radial increment growth between H. annosum-colonized and noncolonized trees revealed no significant ($p=0.05$) difference between these two groups in any of the colonized plots during the 10-year period from 1967 to 1976, with the exception of plot UC219-2. In plot UC219-2, the noncolonized trees grew significantly less than the H. annosum-colonized trees, a complete reversal of what would have been expected, during the years 1968, 1971, and 1972. For all other years, no significant difference in mean annual increment growth between colonized and noncolonized trees in this plot was observed. This particular 10-year period was selected for analysis of radial increment growth since this would represent the predominant growth period for young stands yet represent the most important economic period for older stands about to be thinned or harvested.

II. Loblolly Pine Seed Orchards Survey

Criteria for determining microbial colonization of subsoiled roots

The three criteria for determining whether a primary root had successfully healed following subsoiling were: 1) the presence of wound callus tissue, 2) the formation of adventitious roots proximal to the wound surface and 3) a band of resin soaked tissue at the wound no greater than approximately 6 mm wide. Resinosis was attributed to microbial colonization and this assumption was substantiated by laboratory isolation of over 600 pure fungal cultures from resin soaked roots at all three seed orchards.

Root pruning operations had been confined to only lateral primary roots and upon excavation, these roots were observed to occupy primarily the upper 15 cm of soil. Often these lateral primary roots were located within 3 cm of the soil surface. Consequently, any cultural activities within the upper 15 cm of soil would have direct impact upon these lateral primary roots.

Summary root data for excavated loblolly pines at the Chesapeake Corporation, Union Camp Corporation and Virginia Division of Forestry seed orchards are presented in Table 9. The general trend at all three seed orchards was the consistent association of resin soaked lateral primary roots with root pruning operations as influenced by the surrounding soil texture and the date of subsoiling.

Soil texture differences

Average soil texture data for the three loblolly pine seed orchards are presented in Table 10. All three orchards, based upon random sampling prior to root system excavation, exhibited extremely high sand contents particularly in the upper 15 cm of soil. However, during excavation at the Chesapeake Corporation orchard pockets of grayish clay indicative of waterlogging were observed throughout the test area. Even though this orchard had a high general sand content, the clay fraction imparted a greater moisture-holding capacity to the soil compared to the more drought-sensitive sandy soils at the Union Camp Corporation and Virginia Division of Forestry seed orchards. At both of these latter two orchards the soil texture was sandy throughout the profile extending to the water table which occurred at a depthof approximately 1.5 - 2.0 m. Tap roots at these two orchards, particularly among healthy trees,

Table 9. Summary root data for the Chesapeake Corp., Union Camp Corp. and Virginia Division of Forestry seed orchards.

Orchard	Status	No. Trees	No. Primary Roots	No. Subsoiled Primary Roots	% No. Subsoiled Primary Roots	% No. Resin Soaked Subsoiled Primary Roots	% Primary Root Resin Soaked Length
Chesapeake Corp.	Declining/subsoiled	10	67	22	33	41	10
	Healthy/subsoiled	10	78	14	18	0	0
Union Camp Corp.	Declining/control	5	13	*	*	*	17
	Healthy/control	5	64	*	*	*	0
	Declining/subsoiled	10	192	152	79	71	18
	Healthy/subsoiled	10	152	115	76	70	8
Virginia Division of Forestry	Declining/subsoiled	10	130	17	13	94	55
	Healthy/subsoiled	10	197	11	6	82	0.7

* Not applicable to control group

Table 10. Average seed orchard soil texture analysis for three soil samples collected at each of three depths.

Seed Orchard	Depth (cm)	Percent Sand	Percent Silt	Percent Clay
Chesapeake Corp.	0-15	90	3	7
	16-30	87	4	6
	31-45	83	3	14
Union Camp Corp.	0-15	88	9	3
	16-30	88	8	4
	31-45	86	6	8
Virginia Division of Forestry	0-15	89	5	6
	16-30	89	4	7
	31-45	89	6	5

extended into the upper water table with fibrous roots commonly developing at the distal ends of the tap roots at the tap root - water table interface.

Chesapeake Corporation seed orchard

Tree data for declining/subsoiled and healthy/subsoiled loblolly pines at the Chesapeake Corporation seed orchard are described in Tables 11 and 12, respectively. As expected, the declining trees were generally shorter, grew slower, had smaller crowns and exhibited less feeder root development than healthy trees at the same orchard. A clonal variation in cone and conelet production was observed in both declining/subsoiled (0 to 226 range) and healthy/subsoiled (0 to 36 range) trees.

At the Chesapeake Corporation orchard, about 33 percent (22 of 67) of all excavated lateral primary roots of declining trees were subsoiled (Table 13). Of these subsoiled roots, 41 percent exhibited resinosis indicative of microbial colonization. Resin soaked tissue comprised 10 percent of the total lateral primary root length. However, not all subsoiled roots became resin soaked and, conversely, some root systems exhibited considerable resin soaking in the absence of any subsoiled lateral primary roots.

Healthy/subsoiled trees at the Chesapeake Corporation seed orchard displayed a complete lack of resinosis among subsoiled lateral primary roots (Table 14). About 18 percent (14 of 78) of these roots had been subsoiled yet none became resin soaked which was apparently due to the successful healing of all severed root tips.

Table 11. Tree data for declining/subsoiled loblolly pines at the Chesapeake Corp. seed orchard.

Clone	Height (m)	Height m-to-Live Crown	DBH (cm)	Crown*	Feeder Root Rating**	Feeder Root Amount***	Feeder Root Width (cm)	No. Cones and Conelets
D 4-18 I 145	7.3	3.6	10.7	0	1	1	86.4	18
D 4-18 N 146	7.3	2.5	13.2	0	1	1	91.4	4
I 20-506 H 146	3.6	1.8	4.1	0	0	0	12.7	0
J 20-513 S 157	5.5	2.9	7.6	0	0	0	20.3	4
M 20-529 O 165	6.2	2.5	7.6	0	0	0	20.3	9
N 14-35 J 156	8.0	2.5	7.6	1	2	2	154.9	12
N 14-35 W 143	9.1	2.2	12.7	1	0	0	119.4	22
O 4-6 D 160	10.2	2.2	19.1	1	2	1	182.9	223
O 4-6 O 147	9.4	2.2	15.2	1	1	1	63.5	76
P 20-542 B 160	7.6	2.2	8.1	1	1	1	58.4	5

* Crown rating: 0=small; 1=intermediate; 2=large

** Feeder Root Rating: 0=none present; 1=present only on primary roots; 2=present on primary and secondary roots

*** Feeder Root Amount: 0=small; 1=intermediate; 2=large

Table 12. Tree data for healthy/subsoiled loblolly pines at the Chesapeake Corp. seed orchard.

Clone	Height (m)	Height m-to-Live Crown	DBH (cm)	Crown*	Feeder Root Rating**	Feeder Root Amount***	Feeder Root Width (cm)	No. Cones and Conelets
A 4-19 Q 167	11.3	2.9	16.3	2	1	1	132.1	0
A 4-19 S 157	12.0	2.9	19.3	2	2	2	144.8	0
C 20-501 F 168	10.5	2.5	17.3	2	2	2	109.2	30
H 14-66 N 168	9.8	2.5	15.2	2	2	2	67.2	5
N 14-35 I 67	11.6	2.9	17.8	2	2	1	109.2	2
N 14-35 U 159	11.3	2.9	18.0	2	2	2	119.4	1
O 4-6 B 158	11.6	2.9	20.3	2	2	2	109.2	0
P 20-535 W 153	11.3	2.9	27.9	2	2	2	104.1	36
P 20-542 G 161	10.9	2.9	19.1	2	2	2	160.0	0
R 20-542 Q 161	10.2	2.9	17.8	2	2	2	116.8	0

* Crown rating: 0=small; 1=intermediate; 2=large

** Feeder Root Rating: 0=none present; 1=present only on primary roots; 2=present on primary and secondary roots

*** Feeder Root Amount: 0=small; 1=intermediate; 2=large

Table 13. Root data for declining/subsoiled loblolly pines at the Chesapeake Corp. seed orchard.

Clone	No. Primary Roots	No. Subsoiled Primary Roots	No. Resin Soaked Subsoiled Primary Roots	% No. Resin Soaked Subsoiled Primary Roots	Primary Root Length (m)	Primary Root Resin Soaked Length (m)	% Primary Root Resin Soaked Length (m)
D 4-18 I 145	9	3	2	67	14.5	1.0	7
D 4-18 N 146	8	5	0	0	16.7	0	0
I 20-506 H 146	1	0	0	0	0.8	0.5	63
J 20-513 S 157	9	0	0	0	11.9	8.4	71
M 20-529 O 165	4	1	1	100	3.7	0.7	19
N 14-35 J 156	10	6	0	0	20.7	0	0
N 14-35 W 143	6	5	5	100	13.2	0.2	2
O 4-6 D 160	6	1	0	0	9.7	0	0
O 4-6 O 147	5	1	1	100	9.6	0.1	1
P 20-542 B 160	9	0	0	0	11.1	0	0
Totals	67	22	9		111.9	10.9	
Averages				41			10

Table 14. Root data for healthy/subsoiled loblolly pines at the Chesapeake Corp. seed orchard.

Clone	No. Primary Roots	No. Subsoiled Primary Roots	No. Resin Soaked Subsoiled Primary Roots	% No. Resin Soaked Subsoiled Primary Roots	Primary Root Length (m)	Primary Root Resin Soaked Length (m)	% Primary Root Resin Soaked Length (m)
A 4-19 Q 167	6	2	0	0	9.7	0	0
A 4-19 S 157	8	0	0	0	8.0	0	0
C 20-501 F 168	12	1	0	0	18.3	0	0
H 14-66 N 168	7	0	0	0	9.4	0	0
N 14-35 I 67	9	3	0	0	15.9	0	0
N 14-35 U 159	7	2	0	0	8.9	0	0
O 4-6 B 158	8	5	0	0	16.3	0	0
P 20-535 W 153	5	1	0	0	8.5	0	0
P 20-542 G 161	10	0	0	0	13.7	0	0
R 20-542 Q 161	6	0	0	0	10.3	0	0
Totals	78	14	0		119.0	0	
Averages				0			0

Union Camp seed orchard

Tree data for declining/control, healthy/control, declining/subsoiled and healthy/subsoiled loblolly pines at the Union Camp Corporation seed orchard are presented in Tables 15, 16, 17, and 18, respectively. Declining trees, both control and subsoiled, were comparatively shorter, grew slower, exhibited smaller crowns and less feeder root development than the healthy/control and healthy/subsoiled trees, respectively. One exception, however, was greater cone and conelet production among the declining/control and declining/subsoiled trees compared to the healthy/control and healthy/subsoiled trees, respectively.

The declining/control trees were, of course, not subsoiled yet these pines demonstrated resinosis on 17 percent of the total primary root length (Table 19). Healthy/control loblolly pines exhibited similar numbers of primary roots and total primary root lengths compared to the declining/controls but the former group exhibited no resin soaked primary roots (Table 20). This suggests that resinosis may be a general root response mechanism to microbial colonization which may be facilitated indirectly by a gradual reduction in host vigor due perhaps to graft incompatibility or, more directly, by the production of subterranean wounds by subsoiling.

Approximately 80 percent of the lateral primary roots of declining/subsoiled trees at the Union Camp Corporation orchard were subsoiled and of these, 71 percent demonstrated resinosis, lack of adventitious root formation and failure of wound callus formation characteristic of microbial colonization (Table 21). Among the healthy/subsoiled trees, 76 percent of the lateral primary roots were subsoiled and 70 percent of

Table 15. Tree data for declining/control loblolly pines at the Union Camp Corp. seed orchard.

Clone	Height (m)	Height m-to-Live Crown	DBH (cm)	Crown*	Feeder Root Rating**	Feeder Root Amount***	Feeder Root Width (cm)	No. Cones and Conelets
H-12 2-65	9.8	3.3	12.7	1	1	0	53.3	34
N-11 14-513	7.3	2.5	11.7	1	0	0	20.3	20
N-14 2-10	4.7	1.5	5.8	1	0	0	0.0	12
O-8 2-20	10.2	2.5	15.5	1	1	0	38.1	99
O-13 2-39	9.8	2.2	17.3	1	1	2	182.9	51

* Crown rating: 0=small; 1=intermediate; 2=large

** Feeder Root Rating: 0=none present; 1=present only on primary roots; 2=present on primary and secondary roots

*** Feeder Root Amount: 0=small; 1=intermediate; 2=large

Table 16. Tree data for healthy/control loblolly pines at the Union Camp Corp. seed orchard.

Clone	Height (m)	Height m-to-Live Crown	DBH (cm)	Crown*	Feeder Root Rating**	Feeder Root Amount***	Feeder Root Width (cm)	No. Cones and Conelets
C-9 2-17	12.0	2.5	22.2	2	2	2	114.3	0
H-9 2-21	13.4	2.5	20.3	2	2	2	157.5	0
H-14 2-60	11.3	2.5	15.5	2	2	2	137.2	6
L-10 2-53	12.4	2.5	15.2	2	2	2	154.9	6
L-13 2-12	12.0	2.9	17.3	2	2	2	144.8	20

* Crown rating: 0=small; 1=intermediate; 2=large

** Feeder Root Rating: 0=none present; 1=present only on primary roots; 2=present on primary and secondary roots

*** Feeder Root Amount: 0=small; 1=intermediate; 2=large

Table 17. Tree data for declining/subsoiled loblolly pines at the Union Camp Corp. seed orchard.

Clone	Height (m)	Height m-to-Live Crown	DBH (cm)	Crown*	Feeder Root Rating**	Feeder Root Amount***	Feeder Root Width (cm)	No. Cones and Conelets
E-5 2-3	7.3	1.8	11.2	1	0	0	55.9	15
J-17 2-33	9.8	2.2	16.3	1	0	1	78.7	15
L-17 2-5	10.2	2.5	15.0	1	2	1	83.8	58
L-21 2-61	8.4	2.9	13.0	1	0	0	61.0	3
M-16 2-58	7.6	2.2	10.9	1	1	1	40.6	7
N-17 2-21	7.6	1.8	10.1	1	1	0	25.4	5
N-21 2-33	7.3	2.2	14.7	1	1	0	27.9	33
O-16 2-39	8.5	1.8	13.7	1	1	1	66.0	23
Q-18 2-5	10.2	2.9	15.7	1	1	1	33.0	31
T-17 2-18	7.6	2.5	14.0	1	0	0	27.9	37

* Crown rating: 0=small; 1=intermediate; 2=large

** Feeder Root Rating: 0=none present; 1=present only on primary roots; 2=present on primary and secondary roots

*** Feeder Root Amount: 0=small; 1=intermediate; 2=large

Table 18. Tree data for healthy/subsoiled loblolly pines at the Union Camp Corp. seed orchard.

Clone	Height (m)	Height m-to-Live Crown	DBH (cm)	Crown*	Feeder Root Rating**	Feeder Root Amount***	Feeder Root Width (cm)	No. Cones and Conelets
B-5 2-39	11.6	2.5	20.6	2	2	2	226.1	6
B-6 2-12	12.4	2.5	21.6	2	2	2	198.1	12
B-18 2-53	13.4	2.5	20.6	2	2	2	182.9	25
D-2 14-513	7.3	2.2	14.7	2	2	2	101.6	3
I-2 2-24	12.4	2.9	23.4	2	2	1	99.1	0
J-18 2-22	11.6	2.5	20.8	2	2	2	109.2	11
K-20 14-513	13.4	2.9	19.1	2	2	2	167.6	17
M-2 2-61	7.3	2.5	18.5	2	2	1	104.1	1
M-18 2-3	13.4	2.5	21.1	2	2	2	109.2	7
P-19 2-12	11.3	2.5	14.2	2	2	1	45.7	11

* Crown rating: 0=small; 1=intermediate; 2=large

** Feeder Root Rating: 0=none present; 1=present only on primary roots; 2=present on primary and secondary roots

*** Feeder Root Amount: 0=small; 1=intermediate; 2=large

Table 19. Root data for declining/control loblolly pines at the Union Camp Corp. seed orchard.

Clone	No. Primary Roots	No. Subsoiled Primary Roots	No. Resin Soaked Subsoiled Primary Roots	% No. Resin Soaked Subsoiled Primary Roots	Primary Root Length (m)	Primary Root Resin Soaked Length (m)	% Primary Root Resin Soaked Length (m)
H-12 2-65	8	N/A	N/A	N/A	24.3	1.8	7
N-11 14-513	13	N/A	N/A	N/A	17.7	5.0	28
N-14 2-10	10	N/A	N/A	N/A	12.8	0.7	6
O-8 2-20	14	N/A	N/A	N/A	24.2	4.5	19
O-13 2-39	12	N/A	N/A	N/A	20.9	4.8	23
Totals	57	-	-		100.2	16.8	
Averages				-			17

Table 20. Root data for healthy/control loblolly pines at the Union Camp Corp. seed orchard.

Clone	No. Primary Roots	No. Subsoiled Primary Roots	No. Resin Soaked Subsoiled Primary Roots	% No. Resin Soaked Subsoiled Primary Roots	Primary Root Length (m)	Primary Root Resin Soaked Length (m)	% Primary Root Resin Soaked Length (m)
C-9 2-17	10	N/A	N/A	N/A	17.9	0	0
H-9 2-21	16	N/A	N/A	N/A	24.3	0	0
H-14 2-60	13	N/A	N/A	N/A	17.6	0	0
L-10 2-53	12	N/A	N/A	N/A	18.2	0	0
L-13 2-12	13	N/A	N/A	N/A	32.0	0	0
Totals	64	-	-		110.0	0	
Averages				-			0

Table 21. Root data for declining/subsoiled loblolly pines at the Union Camp Corp. seed orchard.

Clone	No. Primary Roots	No. Subsoiled Primary Roots	No. Resin Soaked Subsoiled Primary Roots	% No. Resin Soaked Subsoiled Primary Roots	Primary Root Length (m)	Primary Root Resin Soaked Length (m)	% Primary Root Resin Soaked Length (m)
E-5 2-3	17	3	3	100	18.2	0	0
J-17 2-33	13	13	8	62	18.6	0	0
L-17 2-5	26	22	15	68	34.3	5.3	16
L-21 2-61	18	18	11	61	23.3	0	0
M-16 2-58	28	21	14	67	38.7	0	0
N-17 2-21	21	12	10	83	28.9	2.5	9
N-21 2-33	15	13	13	100	17.3	15.4	89
O-16 2-39	22	20	14	70	29.3	7.8	27
Q-18 2-5	23	21	12	57	23.7	8.7	37
T-17 2-18	9	9	8	89	12.6	3.9	31
Totals	192	152	108		244.9	43.6	
Averages				71			18

these demonstrated symptoms of microbial colonization (Table 22). However, these healthy/subsoiled pines exhibited resinosis on 8 percent of the total primary root length while the declining/subsoiled pines demonstrated resinosis on 18 percent of the total primary root length.

Virginia Division of Forestry seed orchard

Tree data for declining/subsoiled and healthy/subsoiled pines at the Virginia Division of Forestry seed orchard are described in Tables 23 and 24, respectively. The declining trees were also shorter, smaller in diameter and had smaller crowns and reduced feeder root systems compared to the healthy trees. Declining/subsoiled trees produced many more cones and conelets than did the healthy/subsoiled trees.

Compared to the other two seed orchards, the percentage of lateral primary roots actually subsoiled at the Virginia Division of Forestry orchard was greatly reduced. Among declining/subsoiled trees, 13 percent (17 of 130) of the lateral primary roots were subsoiled and of these, 94 percent developed resinosis from microbial colonization of root wounds created during subsoiling (Table 25). Despite the low number of primary roots subsoiled, resinosis was symptomatic on 55 percent of the total primary root length. Among the healthy/subsoiled trees, only about 6 percent (11 of 197) were subsoiled yet 82 percent of these became colonized (Table 26). Though the incidence of microbial colonization was high, the severity was greatly reduced as resinosis occurred on only 0.7 percent of the total lateral primary root length.

Table 22. Root data for healthy/subsoiled loblolly pines at the Union Camp Corp. seed orchard.

Clone	No. Primary Roots	No. Subsoiled Primary Roots	No. Resin Soaked Subsoiled Primary Roots	% No. Resin Soaked Subsoiled Primary Roots	Primary Root Length (m)	Primary Root Resin Soaked Length (m)	% Primary Root Resin Soaked Length (m)
B-5 2-39	13	12	9	75	18.4	1.7	9
B-6 2-12	14	11	8	73	21.1	3.6	17
B-18 2-53	10	10	7	70	12.2	0	0
D-2 14-513	12	10	7	70	18.3	2.0	11
I-2 2-24	10	4	3	75	13.2	1.4	11
J-18 2-22	11	10	6	60	18.3	3.9	21
K-20 14-513	24	6	5	83	37.5	0.8	2
M-2 2-61	18	16	12	75	25.8	2.8	11
M-18 2-3	26	26	16	62	43.7	0.7	2
P-19 2-12	14	10	7	70	20.7	0.8	4
Totals	152	115	80	70	229.2	17.7	
Averages							8

Table 23. Tree data for declining/subsoiled loblolly pines at the Virginia Division of Forestry seed orchard.

Clone	Height (m)	Height m-to-Live Crown	DBH (cm)	Crown*	Feeder Root Rating**	Feeder Root Amount***	Feeder Root Width (cm)	No. Cones and Conelets
B 6-10 R10 T4 66	9.4	2.9	5.1	1	0	0	48.3	52
B 6-10 R17 T16 66	8.0	2.5	13.1	1	0	0	27.9	54
C 506 R13 T26 66	7.3	2.5	16.8	1	1	1	119.4	2
C 532 R9 T26 66	7.3	1.8	10.2	0	0	0	22.9	1
C 532 R14 T13 66	6.5	2.2	13.2	1	1	1	55.9	24
L 517 R4 T32 66	10.5	3.3	15.2	1	1	1	106.7	4
O 14-48 R13 T14 66	5.8	2.2	9.9	1	1	1	40.6	2
P 521 R6 T31 66	8.4	2.9	16.3	1	0	0	17.8	41
P 521 R10 T24 66	7.3	2.5	14.4	1	1	0	33.0	2
Q 524 R11 T5 66	7.6	2.5	11.9	1	1	1	40.6	1

* Crown rating: 0=small; 1=intermediate; 2=large

** Feeder Root Rating: 0=none present; 1=present only on primary roots; 2=present on primary and secondary roots

*** Feeder Root Amount: 0=small; 1=intermediate; 2=large

Table 24. Tree data for healthy/subsoiled loblolly pines at the Virginia Division of Forestry seed orchard.

Clone	Height (m)	Height m-to-Live Crown	DBH (cm)	Crown*	Feeder Root Rating**	Feeder Root Amount***	Feeder Root Width (cm)	No. Cones and Conelets
A 6-7 R6 T42 66	10.5	2.9	18.9	2	2	2	154.9	0
C 532 R8 T28 66	11.3	2.5	22.5	2	2	1	83.8	0
C 532 R8 T43 66	10.2	2.6	18.5	2	2	2	121.9	0
D 14-513 R5 T8 66	10.2	2.2	21.0	2	2	2	124.5	0
D 14-513 R5 T40 67	10.5	2.5	20.1	2	2	2	223.5	0
E 512 R9 T15 66	10.5	2.5	20.6	2	2	1	63.5	1
F 511 R6 T13 66	11.3	3.3	19.8	2	2	1	66.0	1
H 508 R13 T10 66	9.8	2.9	16.3	2	+	+	+	0
J 510 R8 T21 66	12.0	2.5	22.4	2	2	2	106.7	0
S 526 R9 T14 66	11.3	2.4	20.6	2	+	+	+	2

* Crown rating 0=small; 1=intermediate; 2=large

** Feeder Root Rating: 0=none present; 1=present only on primary roots; 2=present on primary and secondary roots

*** Feeder Root Amount: 0=small; 1=intermediate; 2=large

\+ Feeder root system damaged during excavation

Table 25. Root data for declining/subsoiled loblolly pines at the Virginia Division of Forestry seed orchard.

Clone	No. Primary Roots	No. Subsoiled Primary Roots	No. Resin Soaked Subsoiled Primary Roots	% No. Resin Soaked Subsoiled Primary Roots	Primary Root Length (m)	Primary Root Resin Soaked Length (m)	% Primary Root Resin Soaked Length (m)
B 6-10 R10 T4 66	17	1	1	100	19.3	8.2	43
B 6-10 R17 T16 66	8	4	4	100	11.3	7.8	69
C 506 R13 T26 66	14	0	0	0	20.8	19.0	91
C 532 R9 T26 66	13	0	0	0	5.0	4.4	88
C 532 R14 T13 66	17	3	3	100	23.9	13.3	56
L 517 R4 T32 66	6	2	2	100	6.1	4.2	69
O 14-48 R13 T14 66	12	2	2	100	11.9	5.6	47
P 521 R6 T31 66	17	0	0	0	23.8	6.4	27
P 521 R10 T24 66	13	0	0	0	8.1	8.1	100
Q 524 R11 T5 66	13	5	4	80	15.7	2.6	17
Totals	130	17	16		145.9	79.6	
Averages				94			55

Table 26. Root data for healthy/subsoiled loblolly pines at the Virginia Division of Forestry seed orchard.

Clone	No. Primary Roots	No. Subsoiled Primary Roots	No. Resin Soaked Subsoiled Primary Roots	% No. Resin Soaked Subsoiled Primary Roots	Primary Root Length (m)	Primary Root Resin Soaked Length (m)	% Primary Root Resin Soaked Length (m)
A 6-7 R6 T42 66	24	1	1	100	33.7	0	0
C 532 R8 T28 66	23	0	0	0	20.3	0	0
C 532 R8 T43 66	23	1	1	100	44.3	0	0
D 14-513 R5 T8 66	20	0	0	0	29.6	0	0
D 14-513 R5 T40 67	21	2	2	100	39.7	0.3	0.8
E 512 R9 T15 66	16	0	0	0	18.1	0	0
F 511 R5 T13 66	13	1	1	100	25.2	0.1	0.2
H 508 R13 T10 66	15	3	2	67	23.1	0	0
J 510 R8 T21 66	25	2	1	50	33.9	1.3	4
S 526 R9 T14 66	17	1	1	100	17.5	0.3	1
Totals	197	11	9		285.4	2.0	
Averages				82			0.7

Impact of subsoiling on loblolly pines

Two effects were noted when the pines at all three seed orchards were subsoiled. The long-term impact of subsoiling was the prolonged and persistent microbial colonization of root wounds which had failed to heal. However, the immediate effect of subsoiling was growth reduction which may have appeared to be unimportant in trees not managed for total fiber production yet any reduction in rate of growth may be construed as a reduction in vigor which may adversely affect a tree's wound - healing capacity following subsoiling. Since subsoiling occurred during the month of July at each orchard, approximately half of the growing season remained during which the trees would express the effect of subsoiling upon growth rate. If adverse environmental conditions occurred, i.e., low soil moisture levels and high temperatures, then the likelihood of reduced radial increment growth would be increased.

At the Chesapeake Corporation seed orchard, mean radial increment growth among the declining trees had lagged behind that of the healthy trees since the orchard was established (Table 27). In 1972 and 1973, the difference in radial increment growth rates was significant and in 1974 when the trees were initially subsoiled, the healthy trees demonstrated a dramatic reversal in radial increment growth rate (Figure 2). The declining trees continued their reduced rate of annual growth and subsoiling appeared to have negligible effect on reducing growth rates of these already slow-growing trees. While the healthy trees demonstrated a severe growth reduction after they were subsoiled, this was not manifested in increased resinosis probably due to the consistently wetter soil environment afforded by the soils at the Chesapeake Corporation orchard which would have aided root wound recovery.

Table 27. Mean radial increment growth (mm) for declining and healthy subsoiled loblolly pines at the Chesapeake Corp. loblolly pine seed orchard.

Year	Mean annual increment growth (mm)	
	Healthy/ Subsoiled	Declining/ Subsoiled
1967	4.4	4.6
1968	3.7	6.0
1969	4.1	4.2
1970	7.1	4.6
1971	9.2	5.6
1972	9.7	5.4*
1973	10.5	3.7*
1974	11.4	4.4*
1975	9.6	3.9*
1976	8.8	3.2*

* Means significantly different (p=0.05)

Figure 2. Mean radial increment growth (mm) for declining/subsoiled and and healthy/subsoiled loblolly pines at the Chesapeake Corp. seed orchard.

At the Union Camp Corporation seed orchard, the relationship of growth reduction to subsoiling as affected by droughty soil conditions was more clearly demonstrated. Beginning in 1967, six years prior to subsoiling, the declining and healthy trees which were to be subsoiled exhibited greater mean increment growth than did their declining and healthy controls, respectively (Table 28). For the period 1968 to 1972, the healthy-to-be-subsoiled trees consistently demonstrated the greatest annual growth while the healthy/control and declining-to-be-subsoiled trees exhibited intermediate growth rates and the declining/control trees always grew the slowest. When the orchard was subsoiled in 1973, this ranking abruptly changed as the healthy/controls began growing faster than the healthy/subsoiled trees and the declining/controls grew faster than the declining/subsoiled trees (Figure 3). Duncan's Multiple Range analysis showed that by 1976 all four groups were growing significantly different ($p=0.05$) in the following order: 1) healthy/controls, fastest, 2) healthy/subsoiled, slower, 3) declining/controls, more slowly, and 4) declining/subsoiled, slowest.

At the Virginia Division of Forestry seed orchard located on similar droughty soil conditions, the annual rates of growth for declining and healthy trees were similar until the orchard was subsoiled in 1971 (Table 29). After 1971, the declining/subsoiled trees experienced a dramatic reduction in radial increment growth compared to the healthy/subsoiled trees whose positive growth rate was only slowed somewhat (Figure 4). It must be emphasized that only about 6 percent of the lateral primary roots of the healthy group at this orchard had been subsoiled and this probably was insufficient to cause significant growth reduction among this particular group of trees. In 1972, both groups began

Table 28. Duncan's Multiple Range analysis of mean radial increment growth(mm) for healthy and declining subsoiled and control loblolly pines at the Union Camp Corp. seed orchard.

1967			1968			1969			1970			1971		
Group*	Rank**	Mean	Group	Rank	Mean	Group	Rank	Mean	Group	Rank	Mean	Group	Rank	Mean
HSS	A	4.3	HSS	A	5.7	HSS	A	8.8	HSS	A	10.0	HSS	A	11.8
HC	A	3.3	DSS	A	4.9	HC	AB	6.6	DSS	B	6.6	HC	AB	11.3
DSS	A	3.3	HC	A	3.0	DSS	B	4.7	HC	B	6.0	DSS	BC	8.1
DC	A	2.8	DC	A	2.9	DC	B	3.7	DC	B	4.5	DC	C	6.1

1972			1973			1974			1975			1976		
Group	Rank	Mean	Group	Rank	Mean	Group	Rank	Mean	Group	Rank	Mean	Group	Rank	Mean
HSS	A	11.6	HC	A	11.1	HC	A	9.0	HC	A	8.5	HC	A	8.8
HC	A	10.9	HSS	A	10.6	HSS	A	8.9	HSS	A	7.7	HSS	B	6.7
DSS	A	9.7	DC	A	9.7	DC	A	7.3	DC	B	4.7	DC	C	3.4
DC	A	8.5	DSS	A	8.6	DSS	B	3.8	DSS	C	2.5	DSS	D	1.4

*HSS = healthy/subsoiled
HC = healthy/control
DSS = declining/subsoiled
DC = declining/control

** Ranks with different letters represent significantly different means (p=0.05)

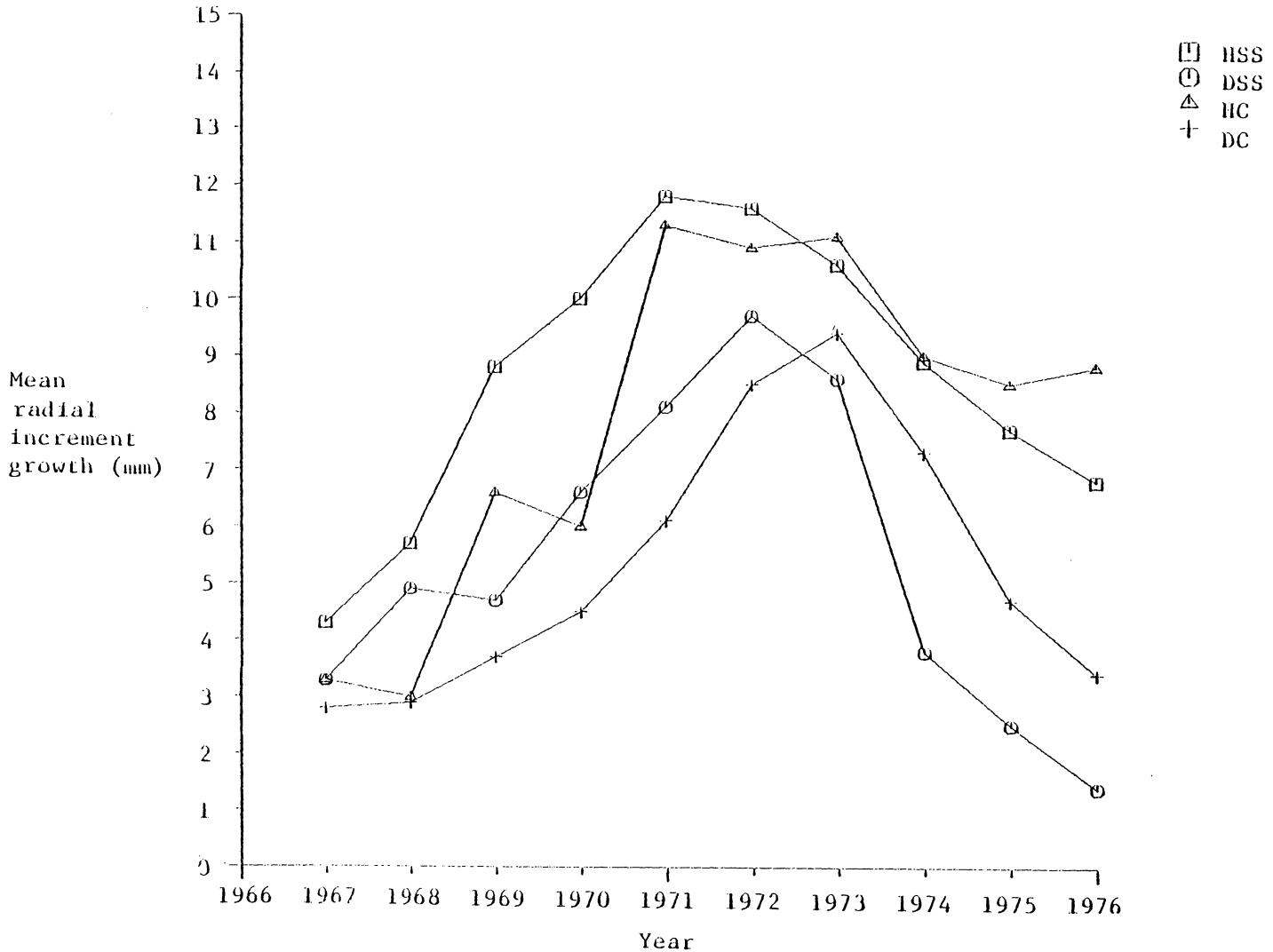


Figure 3. Mean radial increment growth (mm) for declining and healthy subsoiled and control loblolly pines at the Union Camp. Corp. seed orchard.

Table 29. Mean radial increment growth (mm) for declining and healthy subsoiled loblolly pines at the Virginia Division of Forestry seed orchard.

Year	Mean annual increment growth (mm)	
	Healthy/ Subsoiled	Declining/ Subsoiled
1967	2.8	3.6
1968	4.7	4.4
1969	7.1	5.8
1970	10.2	7.4
1971	12.0	10.4
1972	12.4	8.7*
1973	10.7	6.8*
1974	11.2	5.0*
1975	9.6	3.8*
1976	8.0	2.6*

* Means significantly different (p=0.05)

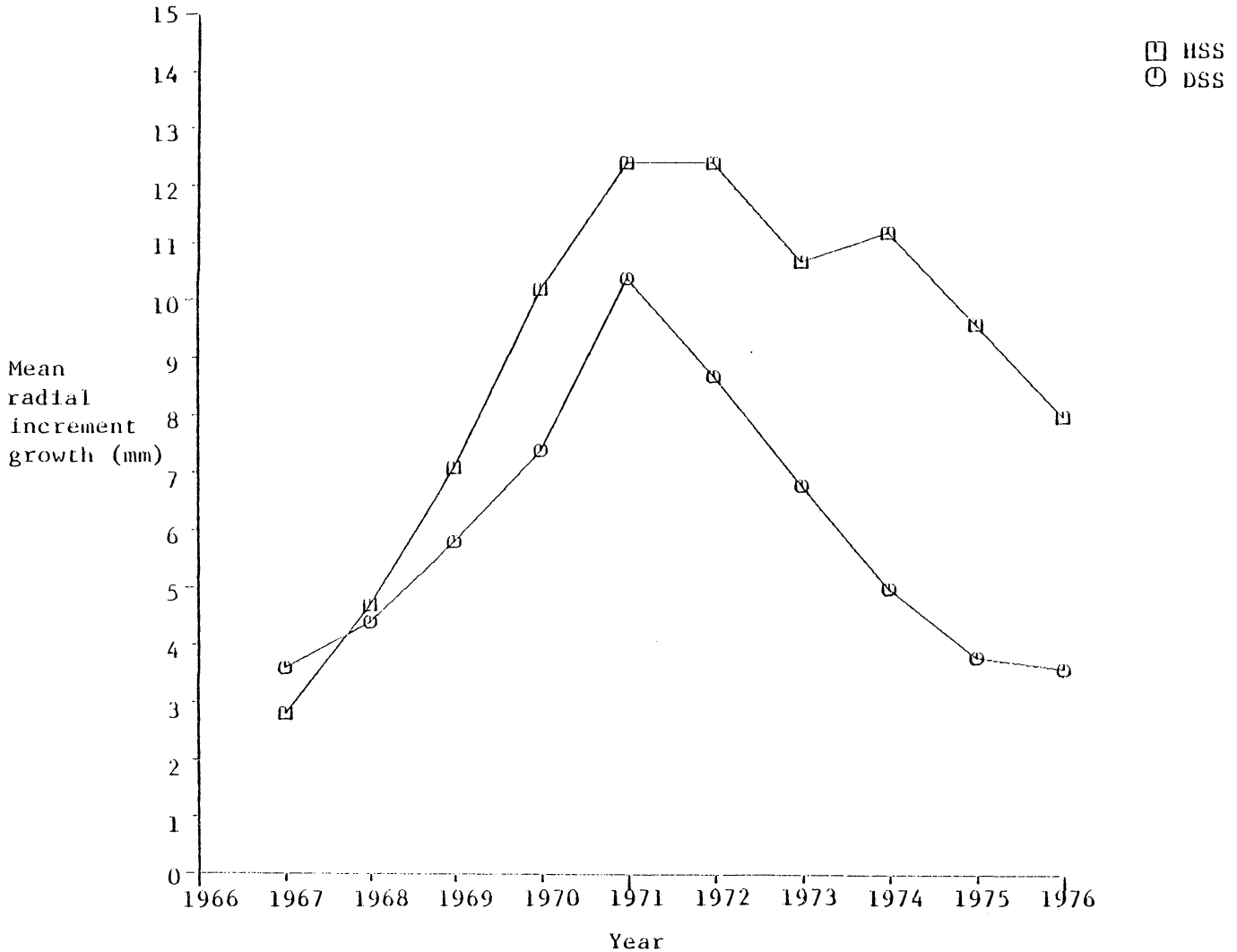


Figure 4. Mean radial increment growth (mm) for declining/subsoiled and healthy/subsoiled loblolly pines at the Virginia Division of Forestry seed orchard.

a trend of progressively reduced radial increment growth with declining/subsoiled trees growing significantly less ($p=0.05$) than the healthy/subsoiled trees as demonstrated by Duncan's Multiple Range analysis.

Temperature and weather data

A United States Weather Service recording station at West Point, Virginia provided rainfall and temperature data for the nearby Chesapeake Corporation and Virginia Division of Forestry seed orchards. In Table 30, data acquired through the Hydrological Information Storage and Retrieval System (HISARS) revealed that the highest average monthly temperatures for the period 1967-1976 had occurred during July. More importantly, when the Virginia Division of Forestry orchard was subsoiled in July, 1971, the average monthly rainfall was greatly reduced from the previous month's level by 55 percent which would have created low soil moisture levels, especially in the upper 15 cm of this very sandy soil (Table 31). Since ambient temperature was high while rainfall was low, available soil moisture should have been low, especially in the upper 15 cm of soil, where extremely harsh edaphic conditions must have existed at the time of subsoiling.

In July, 1974, when the Chesapeake Corporation orchard was subsoiled the average monthly maximum temperature was still high (Table 30), but the average monthly rainfall (Table 31) was almost as high or higher as that of the previous three months. Adequate rainfall when combined with the greater moisture-holding capacity of the soil at this orchard should have maintained a consistently moist edaphic environment to enhance root wound recovery following subsoiling. Healthy/subsoiled trees exhibited no resinosis and had successfully healed all pruned roots while declining/

Table 30. Average monthly maximum temperature (F) for 1967-1976 recorded at West Point, Virginia.

	Month*						
Year	March	April	May	June	July	August	September
1967	60.4	72.9	75.1	84.4	86.6	84.7	77.8
1968	63.5	69.8	76.1	85.5	87.7	89.1	82.0
1969	54.9	72.8	79.5	86.6	88.5	85.4	79.8
1970	53.9	68.9	81.6	87.4	87.3	88.7	86.8
1971[1]	57.3	71.5	77.1	86.4	87.2	85.4	81.7
1972	59.1	69.2	74.5	81.3	86.8	85.8	80.7
1973	62.3	68.8	76.5	85.9	88.8	88.4	84.2
1974[2]	64.0	74.1	78.3	82.1	88.6	85.3	79.9
1975	58.2	65.6	79.9	85.9	86.4	90.1	78.1
1976	63.4	73.3	75.1	84.2	86.9	84.7	79.9

*Data acquired through the Hydrologic Information Storage and Retrieval System (HISARS).

[1]Virginia Division of Forestry seed orchard subsoiled in July, 1971.

[2]Chesapeake Corp. seed orchard subsoiled in July, 1974.

Table 31. Average monthly rainfall (in) for 1967-1976 recorded at West Point, Virginia.

	Month*						
Year	March	April	May	June	July	August	September
1967	3.47	1.25	3.67	1.64	4.74	8.70	2.72
1968	4.06	2.17	3.23	4.41	4.79	3.23	1.99
1969	2.96	2.39	1.69	3.75	9.22	6.39	3.10
1970	3.89	2.74	1.61	2.46	5.38	1.30	2.30
1971[1]	3.86	1.84	6.14	5.05	2.30	5.75	2.16
1972	3.40	2.91	5.39	6.96	5.68	3.13	3.19
1973	4.12	3.89	3.77	3.39	1.57	4.34	2.74
1974[2]	4.43	1.71	2.88	3.88	3.81	6.84	6.69
1975	8.13	2.78	3.89	4.07	7.38	3.14	13.81
1976	2.57	0.78	3.81	4.96	3.42	1.40	4.68

*Data acquired through the Hydrologic Information Storage and Retrieval System (HISARS).

[1]Virginia Division of Forestry seed orchard subsoiled in July, 1973.

[2]Chesapeake Corp. seed orchard subsoiled in July, 1974.

subsoiled trees demonstrated abundant resin soaking and because of their reduced vigor were probably unable to heal their subsoiled roots as quickly thus providing infection courts for soilborne microorganisms.

When the Union Camp Corporation seed orchard was subsoiled in July, 1973, data acquired also through the HISARS system for a United States Weather Service monitoring station near Murfreesboro, North Carolina, revealed that for the period 1967-1976, July was still the hottest month (Table 32). However, rainfall for this date was reduced about 33 percent from the previous month and when the large number of subsoiled roots were exposed to the hot, dry edaphic conditions root wound recovery must also have been adversely affected (Table 33).

III. Root Inoculation Study

Deposition of H. annosum basidiospores on pine roots following percolation through the upper soil layer has been suggested as a means of direct root colonization. Demonstrating this occurrence would reemphasize the potential threat of this pathogen to southern pines since colonization need not be restricted to wounds or freshly-cut stump surfaces but may occur directly through root surfaces despite the presence of host resistance mechanisms, i.e., root bark and cortex layers, oleoresin production and the formation of pinosylvin and pinosylvin monomethyl ether.

The high concentration of basidiospore solution (824,000 spores/ml) facilitated successful deposition of spores on the inoculated root segments (Figure 5). Using scanning electron microscopy at higher magnifications (4,750 to 10,000X) characteristic echinulate basidiospore wall projections could be observed (Figure 6). These projections which were

Table 32. Average monthly maximum temperatures (F) for 1967-1976 recorded at Chowan, North Carolina.

Year	Month*						
	March	April	May	June	July	August	September
1967	66.0	76.9	76.7	84.3	87.0	85.5	78.9
1968	67.0	72.5	78.6	86.7	89.2	91.7	84.5
1969	55.3	72.5	79.8	86.4	87.7	84.6	79.2
1970	60.3	71.6	80.4	86.0	86.6	87.4	86.0
1971	60.3	73.5	77.3	85.7	86.0	85.5	82.1
1972	60.8	73.8	74.9	81.6	86.3	85.9	81.5
1973[1]	65.7	70.9	78.2	84.9	87.7	86.5	83.8
1974	67.1	75.3	77.0	82.2	86.7	83.7	80.4
1975	61.5	67.6	79.1	85.5	85.5	90.5	80.9
1976	69.4	76.0	76.3	82.5	86.8	83.7	81.4

*Data acquired through the Hydrologic Information Storage and Retrieval System (HISARS).

[1]Union Camp Corp. seed orchard subsoiled in July, 1973.

Table 33. Average monthly rainfall (in) for 1967-1976 recorded at Chowan, North Carolina.

Year	Month*						
	March	April	May	June	July	August	September
1967	1.19	1.10	2.91	4.06	9.14	11.75	3.44
1968	5.52	3.35	7.64	3.81	2.95	0.90	1.69
1969	4.68	4.01	2.10	4.32	7.17	6.25	5.18
1970	3.34	6.93	3.24	3.45	12.00	1.59	1.30
1971	5.53	2.27	4.50	5.48	8.32	5.29	5.26
1972	2.86	2.23	4.85	3.39	6.56	2.94	2.22
1973[1]	4.69	4.23	4.94	3.34	2.32	7.45	1.68
1974	4.35	2.62	6.03	6.07	9.63	9.55	4.60
1975	5.50	4.05	4.04	2.01	7.18	1.06	4.54
1976	2.60	3.13	5.22	3.11	5.89	1.46	6.00

*Data acquired through the Hydrologic Information Storage and Retrieval System (HISARS).

[1]Union Camp Corp. seed orchard subsoiled in July, 1973.

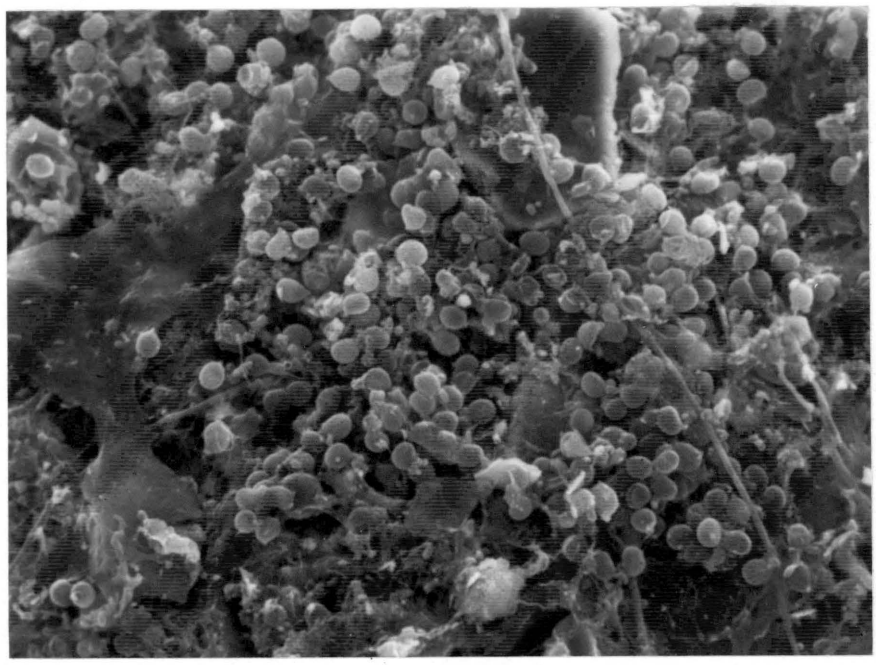


Figure 5. Deposition of H. annosum basidiospores upon the surface of an inoculated loblolly pine root segment (1,000X).

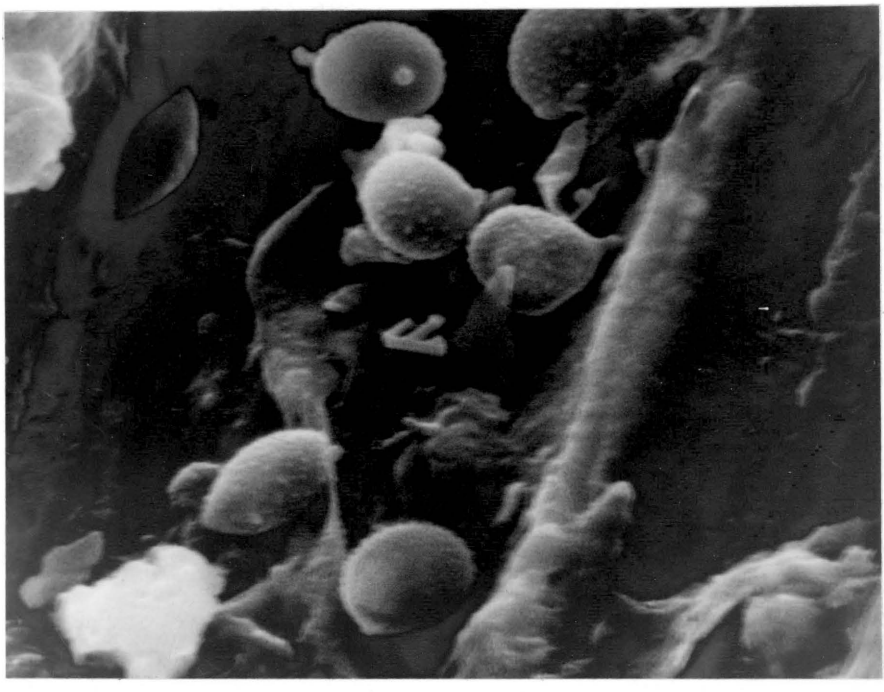


Figure 6. Characteristic echinulate basidiospore wall projections of H. annosum (5,100X).

first described by Keller (1974) served as markers for basidiospore identification and readily distinguished these spores from other root surface microflora (Figure 7).

After incubating for 12 hours on the surface of an inoculated loblolly pine root segment, H. annosum basidiospores typically had not yet germinated (Figure 8). After three days incubation, single germ tubes were observed emerging from the apiculate ends of these basidiospores (Figure 9). After five days, germ tube emergence continued and an appressorial-like structure was occasionally observed at the distal end of the germ tube. In Figure 10, this appressorial-like swelling appeared to develop in response to tactile stimulation even though the substrate was another H. annosum basidiospore. After eight days, two basidiospores on one inoculated root segment had produced germ tubes approximately 25-35 um long but many spores had still not germinated (Figure 11). At higher magnification, one of these germ tubes was observed to have produced an appressorial-like swelling at its distal end where it was in contact with a root surface convolution (Figure 12). Numerous rod-shaped bacteria were also visible upon the surrounding root surface.

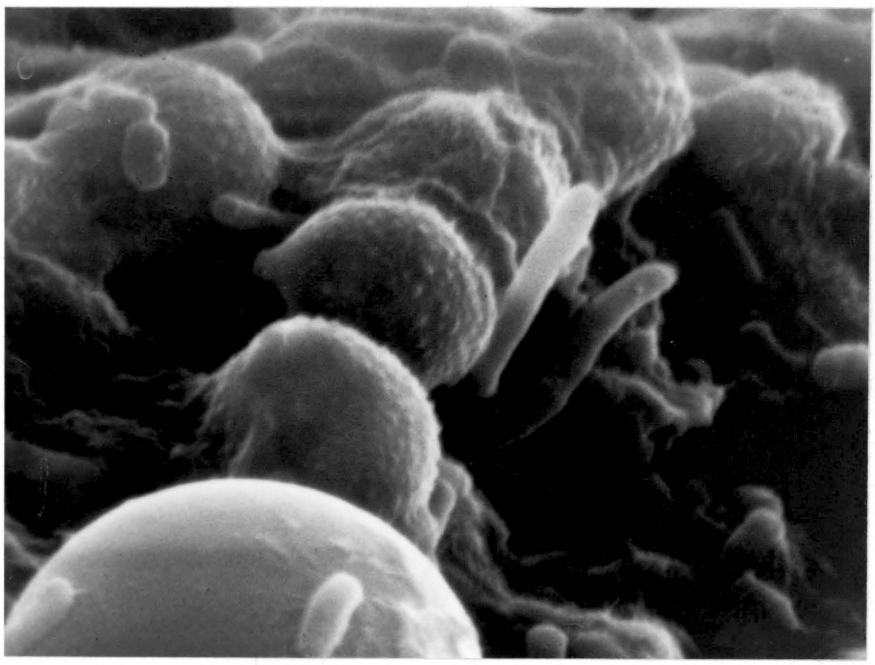


Figure 7. Echinulate basidiospore wall projections distinguish H. annosum basidiospores from other root surface microflora (9,500X).

Figure 8. A basidiospore of H. annosum after 12 hours incubation on an inoculated loblolly pine root segment (10,300X).

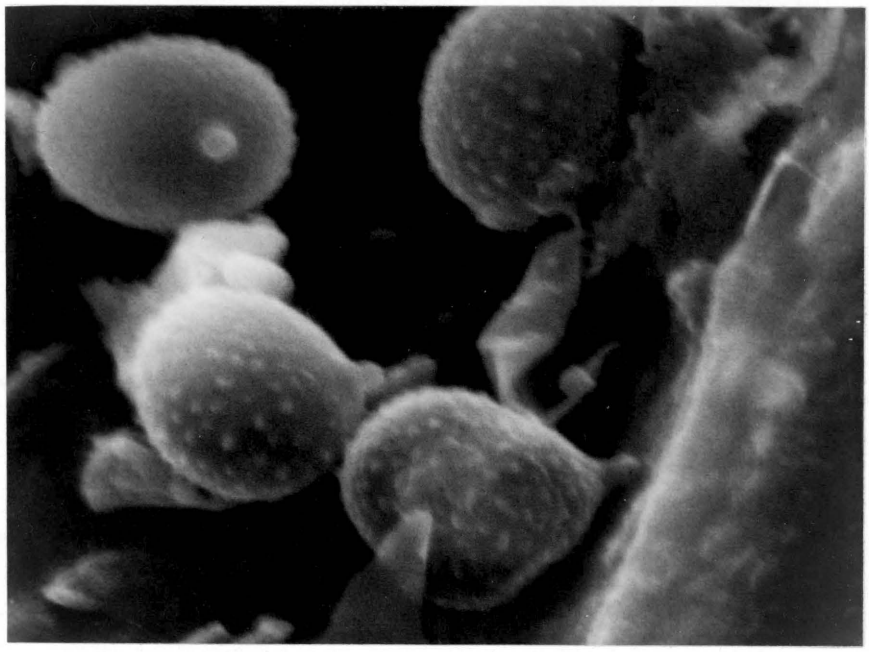


Figure 9. Emerging germ tubes from H. annosum basidiospores after incubating three days on an inoculated loblolly pine root segment (10,000X).

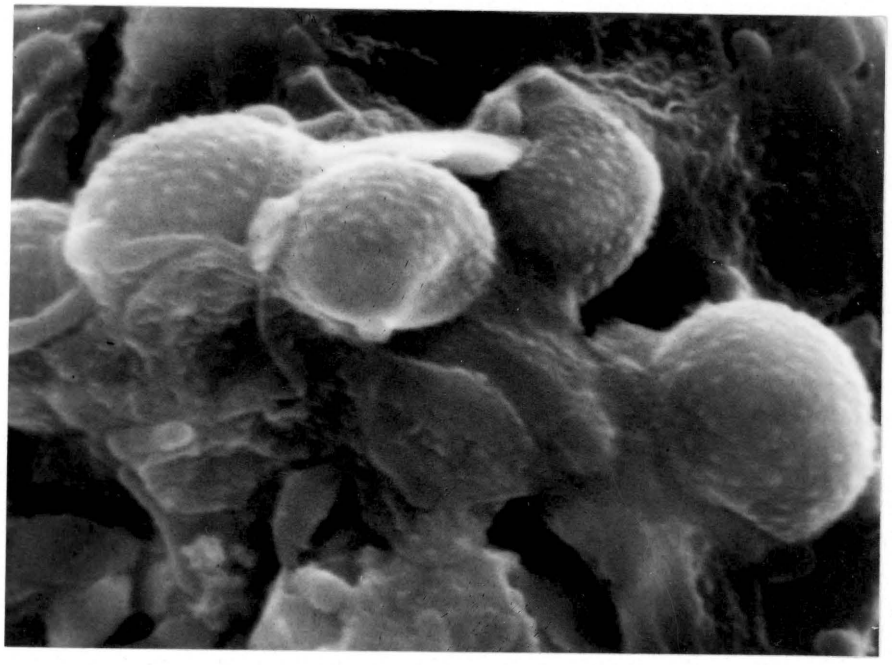


Figure 10. An appressorial-like swelling forms after five days at the distal end of an emerging germ tube of a H. annosum basidiospore (9,500X).

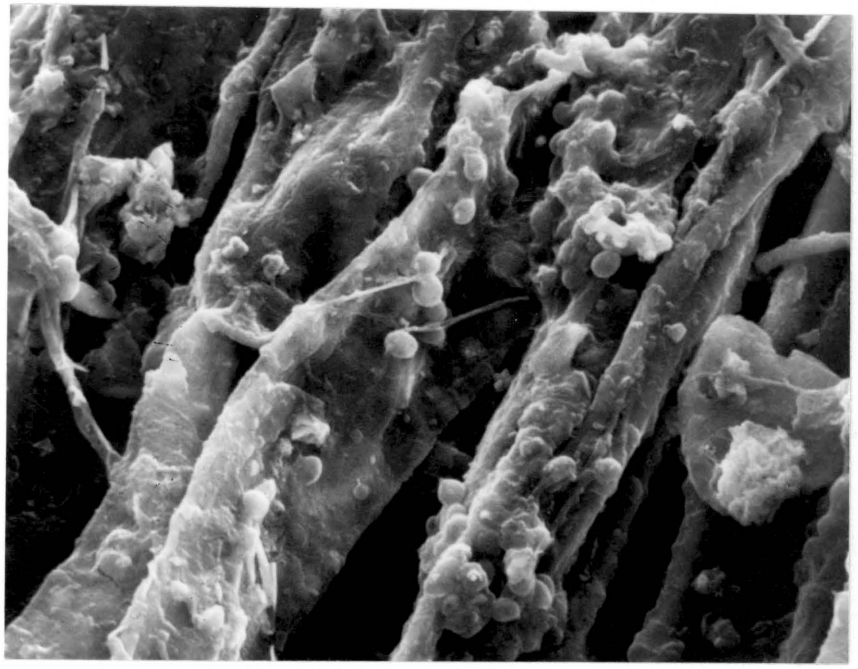


Figure 11. Elongated H. annosum basidiospore germ tubes after incubating eight days on an inoculated loblolly pine root segment (975X).

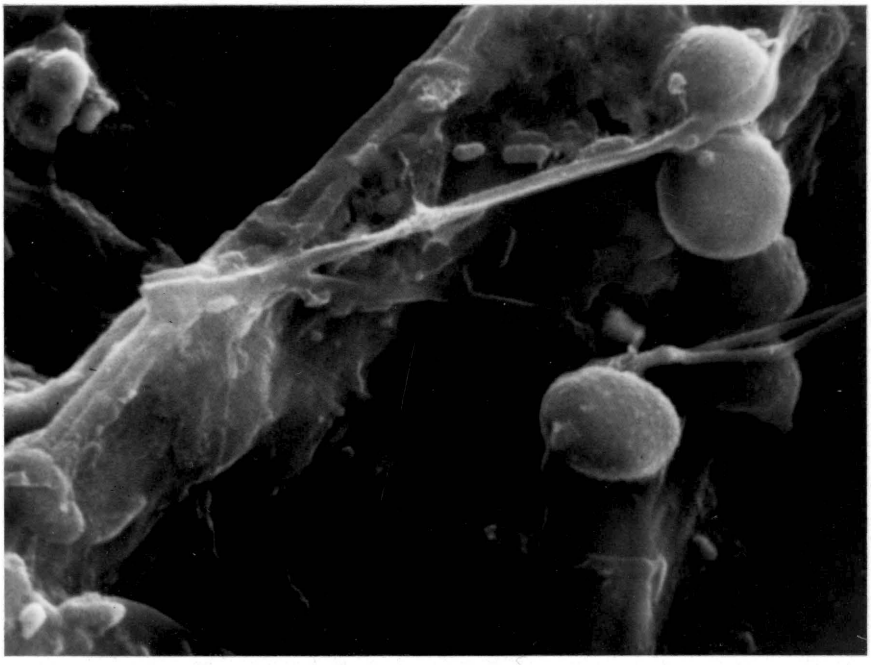


Figure 12. An elongated H. annosum basidiospore germ tube forms an appressorial-like swelling upon contact with the surface of an inoculated loblolly pine root segment after eight days (4,750X).

DISCUSSION

I. Unthinned Loblolly Pine Plantation Survey

Annosum root rot of loblolly pine is a particularly difficult disease to research since the the expression of signs and symptoms is generally so ephemeral that typically the disease develops unnoticed until the host eventually succumbs. Therefore, a requisite for any reliable annosum root rot survey is mechanical excavation of entire tree root systems for intimate and extensive analysis of disease incidence and severity. Perhaps future research will yield a valid predictive model which may replace root system excavation but until then, this technique will remain the most exacting method for surveying annosum root rot.

The purpose of this study was to determine the incidence and severity of H. annosum root rot in selected unthinned loblolly pine plantations and subsoiled seed orchards and relate these results to the possibility of direct root infection by percolated basidiospores of this pathogen.

In the unthinned plantation survey, Chesapeake Corporation, Union Camp Corporation, and the Virginia Division of Forestry supplied the bulldozer and operator as well as the plantation plots for excavation. Their critical assistance in this project and also the seed orchard survey is gratefully acknowledged. Each unthinned loblolly pine plantation was located at least two chains from areas of forest disturbance, i.e., woods, roads, or southern pine bark beetle infestations. In establishing the 22 plots, two stipulations were always enforced; 1) lack of thinning operations as supported by company records and the absence of stumps within the

selected plantation and, 2) the determination of H. annosum root rot hazard according to the soil texture classification of Morris and Frazier (1966). No preconditions existed for the occurrence of the pathogen as determined by signs or symptoms to avoid this bias factor in plantation selection. The ubiquitous nature of H. annosum was assumed and to assure a valid experimental design the only stipulations regarding plantation selection were the avoidance of thinning operations and the particular disease hazard determination.

The trees selected for excavation were consistently asymptomatic for the occurrence of root disease with the exception of 2 trees from the total of 648 which exhibited H. annosum basidiocarps. No crown decline symptoms or leaning or windthrown trees occurred among any of the test plots. The average age of the selected unthinned plantations was 22 years old. A plot area of 0.02 ha was selected as this would provide enough trees i.e., an average of 30 trees per plot, to assure adequate representation of the disease situation in each plantation. This provided enough root systems to excavate and rate efficiently by 2-to-3-man crews in a reasonable period of time. Those loblolly pines colonized by H. annosum were, interestingly enough, taller and with a large diameter and greater "vigor" as indicated by a lack of significant growth differences and the occurrence of lower Shigometer values, than noncolonized trees.

Disease incidence and severity

This survey is unique in that no other systematic study has been attempted to analyze H. annosum incidence and severity in unthinned loblolly pine plantations. These incidence and severity results, therefore,

emanate from the only survey yet conducted among unthinned plantations using the most revealing method of root system analysis. Thus, interpretation of these results must of necessity be more qualitative than quantitative since no other similar survey exists for comparison. In a survey by Bradford et. al. (1978b), bulldozer excavation was utilized but only among thinned loblolly pine natural stands and plantations which represents a very different disease situation from that affecting unthinned plantations.

Thirty-nine of 648 trees (6 percent) were colonized with H. annosum with only 7 (1 percent) colonized severely (21 percent of the total root system). Incidence was higher among loblolly pines on high hazard sites (8.3 percent) as opposed to those on low hazard sites (3.3 percent). Only five trees (1.4 percent) on high hazard sites were severely colonized and averaged 32 percent decay by primary and secondary root length. Only two trees (0.7 percent) on low hazard sites were severely colonized and these were decayed an average 71 percent by length. Thus, in terms of sheer magnitude, H. annosum root rot incidence was low among high hazard unthinned loblolly pine plantations and very low among the low hazard plantations. Among high hazard plantations, the few trees which were severely colonized resulted from comparatively recent infections as supported by the consistent association of only resin-soaked root tissue with these colonized trees. Conversely, the two severely colonized trees from low hazard plantations exhibited stringy-decay symptoms indicative of prolonged colonization resulting from perhaps the planting of seedlings in the vicinity of buried, colonized roots which, during normal seedling root growth contacted this inoculum source and infection was initiated.

Progressively-decaying root systems of colonized trees on the low hazard wetter soils would still be able to acquire adequate moisture for growth and thus resistance to H. annosum may, at least partially, be sustained. Thus, a condition of static dynamism may develop between the colonized-yet-resistant host and the invading pathogen on these wetter sites forestalling eventual symptom expression, including mortality. On drier, high hazard sites both pathogen and host would be expected to be adversely affected by periods of low available soil moisture. However, once infection occurred and colonization established, H. annosum would be expected to more rapidly decay its hosts due to the reduced production of fungistatic substances on these drier sites (Wenzel and Diaz - Palacio, 1970). This may explain the comparatively high severity of annosum root rot on high hazard sites which probably resulted from very recent infections. Thus, the effective rate of decay was proportionately greater among colonized trees on high hazard sites.

Insignificant growth reduction

Perhaps the ultimate single determinant of actual impact from H. annosum colonization is its effect upon host radial increment growth. Among those 13 plots containing trees colonized by H. annosum, no significant reduction in radial increment growth occurred during the 10-year period prior to excavation. A significant growth difference occurred in only one plot, UC219-2, with colonized trees growing faster than non-colonized trees during three of the 10 years. The remaining seven years exhibited no significant growth difference between the two groups. One qualification to this analysis would be that since these trees were located

on high hazard sites characterized by recent colonizations, these trees may not have actually been colonized during the three years of significant growth reduction. Instead, these healthy-to-be-colonized trees may have simply been more vigorous than the other noncolonized trees which may explain the significant growth differences.

Thus, the majority of trees in this unthinned plantation survey were not colonized by H. annosum. Of those few trees (7 percent) which were colonized, disease incidence and severity was so minor as to have no immediate impact upon stand growth and development. However, since all selected plantations were of the first generation, H. annosum may yet be a serious management consideration among residual trees once thinning or replanting has occurred. Should a colonized tree be cut during thinning, subsequent disease development within the residual root system would be quickly enhanced. This would create loci of inoculum production within the plantation from basidiocarps produced on these stumps or through the increased availability of subterranean depositories of H. annosum-colonized roots which may contact or graft with healthy root systems and facilitate disease spread. Regenerating pine plantations upon sites occupied by H. annosum-colonized root systems would incur similar increased risks of disease incidence.

The mere report of H. annosum incidence in unthinned loblolly pine plantations is nevertheless very important. The avoidance by Powers and Verrall (1962) of unthinned loblolly and slash pine plantations in their southwide survey due to an erroneously assumed absence of the pathogen was grievously unfortunate. Not only was an early opportunity missed for determining the status of the disease in unthinned plantations, but the

trend was then firmly established which disregarded the significant impact of H. annosum. Subsequent studies which reported increasingly higher levels of the pathogen (Ginns and Gillespie, 1962; Cordell and Stambaugh, 1966; Dimitri, 1970) did not begin to reverse this pathologically incorrect concept until bulldozer excavation was utilized as a survey technique (Skelly et. al., 1974; Bradford et. al., 1978b). Perhaps this report of H. annosum as a management consideration in unthinned loblolly pine plantations on high hazard sites will underscore the importance of the pathogen in this environment.

II. Loblolly pine seed orchards survey

The purpose of this study was to investigate H. annosum incidence and severity in three subsoiled loblolly pine seed orchards and its relation to increased subterranean infection court production. Excavated root systems were evaluated on the basis of whether or not subsoiling had occurred and, if so, what was the incidence and severity of root disease, i.e., H. annosum root rot, among subsoiled primary roots. Sample trees were meticulously selected to avoid clonal repetition and obvious graft incompatibility. The vague concept of latent graft incompatibility as responsible for primary root resin soaking was not of any use in selecting trees based upon above-ground characteristics. Yet this may explain the occurrence of resin soaked roots among declining/control trees in the Union Camp Corporation orchard.

The original impetus for the initiation of subsoiling in seed orchards was a desperate attempt to "revive" orchard trees on finer-textured sites which were "declining" from soil compaction caused by routine traffice in the orchards (C. B. Davey, personal communication). The term "declining"

is of extreme importance since one must distinguish the healthy trees which have experienced successful scion/rootstock grafting but are merely temporarily declining from increased soil compaction as opposed to those trees which never grafted successfully and have been slowly but irreversibly declining ever since their outplanting. As best as can be determined, "declining" trees in those finer-textured orchards must have been those otherwise healthy trees which responded vigorously to the production of subsoiler channels by regenerating numerous adventitious roots. Furthermore, additional credence was attributed to subsoiling not only as a means of restoring vigor but also as a technique to stimulate ovulate primordia formation in a study by Dewers and Moehring (1970). They claimed that subsoiling of loblolly pine lateral primary roots created moisture stress which when applied during mid-to-late summer following irrigation spring to-mid-summer, terminated vegetative growth and stimulated the formulation of ovulate primordia. However, this experimental design was invalid in that no adequate control group was available, i.e., all trees had been subsoiled, and therefore the opposite conclusion was equally as valid, i.e., that irrigation during the spring and early summer was more important in stimulating ovulate primoridia formation. This latter conclusion was supported by Wenger (1957) for loblolly pine in southeastern Virginia. Thus, the current situation has arisen whereby a technique to restore the "vigor" of healthy trees on compacted sites has been universally applied to both healthy and permanently declining trees on finer-as well as coarser- textured soils to predominantly stimulate female flower production. Unfortunately, the validity of this latter practice has never been statistically substantiated (Gregory, 1975; Greenwood, 1977).

Soil texture appeared to have the greatest influence on subsoiled roots to heal and regenerate adventitious roots. Declining/subsoiled loblolly pines on the finer-textured soil at the Chesapeake Corporation orchard experienced less resin soaking (41 percent) indicative of microbial colonization than did trees in the same category on the coarser soils of the Union Camp Corporation and Virginia Division of Forestry orchards, 71 and 94 percent respectively. Furthermore, healthy/subsoiled trees at the Chesapeake Corporation orchard successfully healed each resin soaked subsoiled primary root while similar trees at the Union Camp Corporation and Virginia Division of Forestry exhibited 70 and 82 percent resin-soaking incidence. One interesting occurrence was a surprising amount (17 percent by length) of resin soaking among declining/control (nonsubsoiled) primary roots at the Union Camp Corporation orchard. There existed however, a qualitative difference between the brownish-orange resinous condition which was generally prevalent among the declining/controls as opposed to the concentrated purplish-red resin soaking associated with the declining/subsoiled trees. The former condition would be expected where (latent) graft incompatibility would result in a gradual decline of host "vigor" and the subsequent progressive colonization by soilborne microorganisms. The latter condition is indicative of microbial colonization of unhealed subsoiled root wounds.

Cultural isolation from symptomatic resin soaked roots using two general (PDA and 2 percent MEA) and two selected (ortho-phenyl phenol and Hendrix-Kuhlman) media revealed no H. annosum colonization among either subsoiled or nonsubsoiled root systems. Although disappointing, this was not surprising since the fungus is a poor competitor and numerous other

fungi were simultaneously isolated from the resin soaked samples, i.e., verticicladiella procera, Ovuolariopsis and Monilinia species. The excavation and analysis of these root systems occurred 2-to-5 years after their initial subsoiling which should have been ample time for H. annosum, if ever present at all in the wounded roots, to be replaced by more competitive saprophytic fungi. Isolative failure therefore, must not preclude the possibility of previous incidence yet perhaps a greater hazard to the subsoiled root system would be the effect of low soil moisture as determined by the surrounding soil texture and time of year in which subsoiling occurred.

This study represents the initial attempt to quantify the effect of subsoiling on seed orchard loblolly pines by analyzing radial increment growth. The unavailability of adequate control groups at the Chesapeake Corporation and Virginia Division of Forestry orchards was unfortunate yet similar trends were observed at each orchard following subsoiling, i.e., dramatic radial increment growth reduction among both healthy and declining subsoiled trees. This correlation was further substantiated at the Union Camp Corporation seed orchard where adequate control groups were accessible. At this orchard, healthy and declining trees generally experienced insignificantly different rates of radial increment growth until subsoiling occurred. Then both the healthy/subsoiled and declining/subsoiled trees immediately demonstrated significantly less radial increment growth than did their respective counterparts and this pattern was sustained yearly until the trees were excavated.

Once the declining trees in this study were subsoiled, their radial increment growth was immediately reduced. It seems illogical therefore, to recommend subsoiling as a means of restoring "vigor" to declining trees unless those trees were actually healthy but in a temporary state of

decline from compacted soil conditions. Thus, the practice of subsoiling in sandy soils which typically are subject to similar compaction problems (D. F. Amos, personal communication) could positively affect only healthy trees if significantly reducing radial increment growth indeed enhanced ovulate primoridia formation. This premise is physiologically contradictory and the entire concept of subsoiling demands immediate critical review.

III. Root inoculation study

The purpose of this study was to observe the *in situ* germination and hyphal development of *H. annosum* basidiospores upon inoculated, severed loblolly pine root segments. The sequence of basidiospore percolation, deposition on host roots, germination and subsequent infection has never been observed yet may be the only valid explanation for disease incidence in unthinned pine stands. Furthermore, this sequence may also contribute to increased disease incidence in thinned stands. Demonstration of the likelihood of occurrence would be an initial step in the final determination of the validity of direct basidiospore infection.

Other researchers have reported both the high probability of direct root infection by percolated basidiospores (Kuhlman and Hendrix, 1964) and the recovery of basidiospores from depths up to 50 cm in the soil (Rishbeth, 1951b). One inherent problem plaguing the final determination is an adequate means to demonstrate basidiospore percolation, deposition, germination, and initiation of the infective process. Scanning electron microscopy has greatly aided the solution to this problem in two ways; 1) Keller (1974), using SEM described a reliable method for distinguishing *H. annosum* basidiospores based upon the presence of echinulate surficial projections, and 2) the use of SEM at various intervals following root inoculation could determine the likelihood of disease initiation by the developmental pattern *in situ* of *H. annosum* basidiospores.

The results indicate that H. annosum basidiospores will settle out of aqueous suspension upon the surfaces of severed loblolly pine root segments. Over the course of an 11 day incubation period, a low percentage of basidiospores germinated and produced appressorial-like swellings at the distal ends of their germ tubes. Only one sample basidiospore was observed to have produced an appressorial-like swelling in actual contact with a root surface convolution and initiation of the infective process was assumed to have occurred. Perhaps more appressorial-like structures would have developed if different environmental conditions, i.e., darkness and colder temperatures, existed during the incubation period. Unfortunately, the mere description of contact between a host and what appears to be an appressorium of a known pathogen is insufficient to claim proof of colonization since there is no way of ascertaining whether subsequent resistance mechanisms would have aborted the colonization attempt. However, the likelihood of direct root infection and colonization has been enhanced through the demonstration of an expected progressive sequence of events ending with the production of appressorial-like swellings upon the host surface. Further investigation combining SEM with ultramicrotome sectioning of inoculated root tissue may reveal the establishment of functional appressoria and demonstrate the capacity for direct root infection.

SUMMARY AND CONCLUSIONS

I. Unthinned Loblolly Pine Plantation Survey

Twenty-two 0.02 ha circular plots were installed in nine unthinned loblolly pine plantations in Virginia. Five of these plantations were located on sites classified as high hazard for annosum root rot while the remaining four plantations were located on low hazard sites. Bulldozer excavation of the loblolly pines permitted an extensive analysis of root systems for the incidence and severity of H. annosum root rot which was substantiated by the cultural isolation of the asexual stage of the fungus from resinous and stringy-decayed roots. On low hazard sites, 10 of 300 trees (3.3 percent) were colonized by H. annosum with 2 trees (0.7 percent) severely colonized ($\geq$1 percent of the total root system mass). On high hazard sites, 29 of 348 trees (8.3 percent) were colonized by H. annosum with 5 trees (1.4 percent) severely colonized. On low hazard sites, the colonization symptom was generally stringy decay which indicated an older, more established disease condition as opposed to the colonized trees on high hazard sites which predominantly exhibited resin soaking characteristic of more recent infection and colonization. No basidiocarps were observed on any trees on low hazard plots while only 2 trees exhibited conks on the high hazard sites. Mean radial increment growth differences between H. annosum - colonized and noncolonized trees were analyzed using the Duncan's Multiple Range test and for the 10 year-period prior to excavation no significant growth reduction was observed. Thus, the low

incidence and severity of H. annosum root rot in unthinned loblolly pine plantations combined with the lack of adverse effect upon radial increment growth suggest that the disease is not a primary management consideration, especially on low hazard sites. The disease however, may be of secondary importance in managing first-generation unthinned plantations on high hazard sites due to the subsequent production of inoculum from residual stumps should colonized trees be removed during thinning operations.

II. Loblolly Pine Seed Orchards Survey

The root systems of 20, 20 and 30 loblolly pines at the Chesapeake Corporation, Virginia Division of Forestry and Union Camp Corporation seed orchards, respectively, were excavated with a backhoe to permit intensive analysis of subsoiled roots for incidence and severity of annosum root rot. The absence of wound callus, lack of adventitious root formation and the presence of a resin-soaked band greater than approximately 6 mm wide at the wound surface were three criteria for determining whether a lateral primary root had failed to heal following subsoiling. Soil texture was closely associated with the incidence and severity of general root disease in that the wetter soil conditions at the Chesapeake Corporation seed orchard probably afforded a more amenable environment for the healing of subsoiled roots. Sandy, drought-susceptible soils at the Union Camp Corporation and Virginia Division of Forestry seed orchards were associated with the higher incidence and severity of root disease among subsoiled lateral primary roots. The asexual stage of H. annosum was not successively isolated from resin soaked subsoiled root tissue at any of the three orchards. Duncan's Multiple Range analysis demonstrated

that mean radial increment growth was significantly decreased among healthy and declining subsoiled trees at the three orchards. At the Union Camp Corporation orchard, when healthy and declining trees were subsoiled they exhibited significantly less radial increment growth than their respective control counterparts.

III. Root Inoculation Study

Severed loblolly pine root segments were inoculated with a concentrated suspension of H. annosum basiodiospores which were observed at various intervals (0.5 to 14 days) for growth and development upon the root surface using scanning electron microscopy. Basidiospores of H. annosum were distinguished from other root surface microflora by the presence of numerous surficial echinulate projections. Germination was evident by the production of germ tubes from the apiculate end of the basidiospores. Occasional appressorial-like structures were observed at the distal ends of well-developed germ tubes and at least one appeared to have initiated infection. The capacity of H. annosum basidiospores to deposit, germinate and probably infect loblolly pine root segments was demonstrated. If the results of this in vitro study accurately reflect the in vivo sequence of events, then the potential for H. annosum colonization by direct root infection from percolated basidiospores has been clearly underscored.

LITERATURE CITED

1. Addoms, R. M. 1946. Entrance of water into suberized roots of trees. Plant Phys. 21:109-11.

2. Ahlgren, C. E. 1962. Some factors influencing survival, growth, and flowering of intraspecific and interspecific pine grafts. J. For. 60:785-89.

3. Alexander, S. A. and J. M. Skelly. 1972. Isolation methods and percent recovery of Fomes annosus and incidence on various soil hazard types. Phytopathology 62:667.

4. Alexander, S. A. and J. M. Skelly, 1973. Disease incidence and disease severity in loblolly pine planted over two soil hazard types. Pages 184-91 in E. G. Kuhlman, ed. Proc. Fourth Intl. Conf. on Fomes annosus. U.S.D.A. For. Serv. SE For. Expt. Sta., Asheville, N.C. 189 pp.

5. Alexander, S. A. and J. M. Skelly. 1974. A comparison of isolation methods for determining the incidence of Fomes annosus in living loblolly pine. Eur. J. For. Path. 4:33-38.

6. Alexander, S. A., J. M. Skelly and C. L. Morris. 1975. Edaphic factors associated with the incidence and severity of disease caused by Fomes annosus in loblolly pine plantations in Virginia. Phytopathology 65:585-91.

7. Allen, R. M. 1967. Influence of the root system on height growth of three southern pines. For. Sci. 13:253-57.

8. Anderson, M. L. 1921. Soil conditions affecting the prevalence of Fomes annosus (Trametes radiciperda). Trans. Roy. Scot. Arbor. Soc. 35:112-17.

9. Anonymous. 1961. Fomes annosus root rot. Northeastern Forest Pest Reptr. 1961 (3):8-9.

10. Anonymous. 1968. Fomes annosus (Fr.) Cooke on conifers and deciduous species. CMI Distr. Maps Plant Dis. 271. 2 p.

11. Aoshima, K. 1954. Butt-rot of Abies mariesii and A. veitchii caused by Tyromyces balsameus and Fomitopsis annosa. (Abstr.) Rev. Appl. Mcol. 33:391.

12. Artman, J. D., D. H. Frazier and C. L. Morris. 1969. Fomes annosus and chemical stump treatment in Virginia -- a three-year study. U.S.D.A. Plant Dis. Reptr. 53:108-10.

13. Artman, J. D. and W. J. Stambaugh. 1970. A practical approach to the application of Peniophora gigantea for control of Fomes annosus. U.S.D.A. Plants Dis. Reptr. 54(9):799-802.

14. Ashe, W. W. 1915. Loblolly or North Carolina pine. N. C. Geol. and Econ. Survey Bull. 24, 176 pp.

15. Bagchee, K. 1952. A review of work on Indian tree diseases and decay of timber and methods of control. Indian Forester 78:540-46.

16. Bakshi, B. K. 1950. Fungi associated with ambrosia beetles in Great Britain. Trans. Brit. Mycol. Soc. 33:111-20.

17. Bassett, C., R. T. Sherwood, J. H. Kepler and P. B. Hamilton. 1967. Production and biological activity of fomannosin, a toxic sesquiterpene metabolite of Fomes annosus. Phytopathology 57:1046-52.

18. Baxter, D. V. 1941. Some resupinate polypores from the region of the Great Lakes. XII. Mich. Acad. Sci. Pap. 26:107-21.

19. Bega. R. V. 1962. Tree killing by Fomes annosus in a genetics arboretum. U.S.D.A. Plant Dis. Reptr. 46:107-10.

20. Bega, R. 1963. Fomes annosus. Phytopathology 53(10):1120-23.

21. Bega, R. V. and F. F. Hendrix. 1962. Variation of monobasidiospore isolates of Fomes annosus. (Abstr.) Phytopathology 52(1):3.

22. Belanger, R. P. and E. V. Brender. 1968. Influence of site index and thinning on the growth of planted loblolly pine. Ga. For. Res. Pap. 57, 7 pp.

23. Bengtson, G. W. 1969. Growth and flowering of clones of slash pine under intensive culture: early results. U.S.D.A. For. Serv. Res. Pap. SE-46, 9 pp.

24. Bergman, A. 1968. Variation in flowering and its effect on seed cost. A study in seed orchards of loblolly pine. N. C. State Univ. Sch. For. Res. Tech. Rept. No. 38, 63 pp.

25. Berry, F. H. and T. W. Bretz. 1964. Urea and other chemicals effective against colonization of shortleaf pine stumps by Fomes annosus in Missouri. U.S.D.A. Plant Dis. Reptr. 48(11):886-87.

26. Bier, J. E., R. E. Foster and P. J. Salisbury. 1946. Studies in forest pathology IV. Decay of Sitka spruce in the Queen Charlotte Islands. Canada Dept. Agric. Tech. Bull. 56. 36 pp.

27. Bornebusch, C. H. and F. Holm. 1934. Kultur paa Trametesinficeret bund med Forskellige traearter. Forstlige Forsogsv. Danm. 13:225-64.

28. Bourdot, H., and A. Galzin. 1927. Hymenomycetes de France. Soc. Mycol. France, Paris.

29. Bradford, B., S. A. Alexander and J. M. Skelly. 1978a. Determination of growth loss of Pinus taeda L. caused by Heterobasidion annosus (Fr.) Bref. Eur. J. For. Path. 8:129-34.

30. Bradford, B., S. A. Alexander and J. M. Skelly. 1978b. Incidence and severity of annosus root rot in loblolly pine plantations in Virginia. Eur. J. For. Path. 8:135-45.

31. Brockhuizen, J. T. M., and F. N. Ewart. 1966. [Fomes in Metasequoia]. Ned. Boschbouw. Tijdschr. 38:409-10.

32. Buchanan, T. S. 1940. Fungi causing decay in wind-thrown northwest conifers. J. For. 38:276-81.

33. Buckland, D. C. 1946. Investigations of decay in western red cedar in British Columbia. Can. J. Res., Sec. C, 24:158-81.

34. Burdekin, D. A. 1972. A study of losses in Scots pine caused by Fomes annosus. Forestry XLV (2):189-96.

35. Ch'en, L. -P. and T. -H. Ch'iu. 1961. Fungi of Abies stands in the Ma-erh-kang leskhoz, Szechwan Province. (Abstr.) Rev. Appl. Mycol. 40:192.

36. Cline, R. A. 1968. Soil drainage and compaction effects on growth, yield and leaf composition of cherries and peaches. Hort. Res. Inst. Ont. Rept. for 1967:28-34.

37. Cline, R. A. and O. A. Bradt. 1970. Soil drainage and compaction effects on growth, yield and leaf composition of cherries and peaches. Hort. Res. Inst. Ont. Rept. for 1969:45-52.

38. Clinton, G. P. 1907. Report of the botanist for 1906. Conn. Agr. Expt. Sta. Ann. Rept. 1906, Part 5. p. 307-68.

39. Clinton, G. P. 1934. Plant pest handbook for Connecticut. II. Diseases and injuries. Conn. Agr. Expt. Sta. Bull. 358:153-329.

40. Colby, H. L. 1935. Stock-scion chemistry and the fruiting relationships in apple trees. Plant Phys. 10:483-98.

41. Cordell, C. E. and J. S. Astin. 1965. A new host for Fomes annosus, Polyporus schweinitzii and Fomes pini. U.S.D.A. Plant Dis. Reptr. 49(4):360.

42. Cordell, C. E., and W. J. Stambaugh. 1966. Increment core sampling reveals more Fomes annosus. U.S.D.A. Plant Dis. Reptr. 50(8): 589-92.

43. Cordell, C. E., W. J. Stambaugh, C. E. Affeltranger and J. L. Knighten. 1970. Rhododendron and mountain laurel, new hosts of Fomes annosus in Western North Carolina. U.S.D.A. Plant Dis. Reptr. 54(7):560.

44. Coty, C. W., R. B. Campbell and D. C. Reicosky. 1975. Crop response to chiseling and irrigation in soils with a compact A_2 horizon. Trans. Amer. Soc. Agric. Eng. 18:668-72.

45. Cowling, E. B. and A. Kelman. 1964. Influence of temperature on growth of Fomes annosus isolates. Phytopathology 54:373-78.

46. Crider, F. J. 1933. Selective absorption of ions not confined to young roots. Science 78:169.

47. Curschmann, O. H. 1960. The mortality of pine on agricultural land, and its silvicultural effects. For. Abs. 22:438.

48. Delatour, P. C. 1977. Les hôtes du Fomes annosus (Fr.) Cke. en France. Eur. J. For. Path. 7:188-90.

49. Dennis, C. and J. Webster. 1971. Antagonistic properties of species - groups of Trichoderma. Trans. Br. Mycol. Soc. 57(1):25-39.

50. Dewers, R. S. and D. M. Moehring. 1970. Effect of soil water stress on initiation of ovulate primordia in loblolly pine. For. Sci. 16(2):219-21.

51. Diebold, C. H. 1954. The effects of tillage practices upon intake rates, run-off and soil losses of dry-farm land soils. Soil Sci. Soc. Amer. Proc. 18:88-91.

52. Dimitri, L. 1970. Valuation of butt rot of spruce by boring cores. Pages 13-15 in C. S. Hodges, J. Rishbeth and A. Yde-Anderson, eds. Proc. Third Intl. Conf. on Fomes annosus. (I.U.F.R.O.) U.S.D.A. For. Serv., Washington, D. C. 207 pp.

53. Domanski, S., H. Orlos and A. Skirgiello. 1973. Fungi. U.S.D.A. and N.S.F., Springfield, Va. 330 pp.

54. Donk, M. A. 1960. The generic names proposed for Polyporaceae. Persoonia I:173-302.

55. Driver, C. H. 1963. Further data on borax as a control of surface infection of slash pine stumps by Fomes annosus. U.S.D.A. Plant Dis. Rept. 47(11):1006-09.

56. Driver, C. H. and T. R. Dell. 1961. Observations on Fomes annosus root-rot in natural stands of loblolly and shortleaf pine. U.S.D.A. Plant Dis. Reptr. 42:352-53.

57. Driver, C. H. and J. H. Ginns, Jr. 1966. A method of mass screening southern pines for a resistance to a root-rot induced by Fomes annosus (Fr.) Cke. Pages 421-22 in H. D. Gerhold, J. E. Schreiner, R. E. McDermott and J. A. Winieski, eds. Breeding pest resistant trees. Pergamon Press, New York. 505 pp.

58. Edmonds, R. L., C. H. Driver and K. W. Russell. 1969. Borax and control of stump infection by Fomes annosus in western hemlock. U.S.D.A. Plant Dis. Rept. 53(3):216-19.

59. Eghbaltalab, M., G. Gay and G. Bruchet. 1975. [Antagonism between 15 species of basidiomycetes and 3 pathogenic fungi.] Bull. Mensuel de la Societe Lineenne de Lyon 44(7)203-08, 225-229.

60. Etheridge, D. E. 1955. Comparative studies of North American and European cultures of the root rot fungus, Fomes annosus (Fr.) Cooke. Can. J. Biol. 33:316-28.

61. Fedorov, N. and N. Stajcenko. 1968. [Effect of certain actinomycetes on the growth of Fomes annosus in culture.] Nauch. Dokl. Vyssh. Shkoly Biol. Nauki 1:99-101 (For. Abstr. 29:675).

62. Ferrell, A. T. and R. S. Smith. 1976. Indicators of Fomes annosus root decay and bark beetle susceptibility in sapling white fir. For. Sci. 72:365-69.

63. Froelich, R. C., E. B. Cowling, L. V. Collicott and T. R. Dell. 1977. Fomes annosus reduces height and diameter growth of planted slash pine. For. Sci. 23(3):229-306.

64. Froidevaux, L. and R. Amiet. 1974. [The mycorrhigal fungus Gomphidius glutinosus, a powerful antagonist of Fomes annosus in pure culture. Eur. J. For. Path. 4(4):245-48.

65. Garbowski, L. 1926. Diseases of cultivated plants in Great Poland, Pomerania and Silesia in 1924 and 1925. (Abstr.) Rev. Appl. Mycol. 5:713-14.

66. Gibbs, J. N. 1968. Resin and the resistance of conifers to Fomes annosus. Ann. Bot. 32:649-65.

67. Ginns, J. H. and W. H. Gillespie. 1962. Fomes root rot found in five thinned, native white pine stands in West Virginia. U.S.D.A. Plant Dis. Reptr. 46(10):734.

68. Gooding, G. V., Jr. 1964. Effect of temperature on growth and survival of Fomes annosus in freshly cut pine bolts. (Abstr.) Phytopathology 54:893-94.

69. Gooding, G. V., Jr., C. S. Hodges, Jr. and E. W. Ross. 1966. Effect of temperature on growth and survival of Fomes annosus. For. Sci. 12(3):325-33.

70. Graham, D. A. 1971. Evaluation of borax for prevention of annosus root rot in California. U.S.D.A. Plant Dis. Reptr. 55(6):490-94.

71. Grieg, B. J. W. 1962. Fomes annosus (Fr.) Cke. and other root-rotting fungi in conifers on ex-hardwood sites. Forestry 35(2): 164-82.

72. Greenwood, M. S. 1977. Flower stimulation techniques for loblolly pine (Pinus taeda L.). Third World Consult. For. Tree. Breed. Canberra, Australia, March 21-26, 1977, Vol. II: 1031-1042.

73. Gregory, J. D. 1975. Subsoiling to stimulate flowering and cone production and ameliorate soil conditions in loblolly pine (Pinus taeda L.) seed orchards, Ph.D. dissertation, N. C. State University, Raleigh, N.C. 121 pp.

74. Grieg, B. J. W. 1978. Chemical, biological and silvicultural control of Fomes annosus. Proc. Fifth Intl. Conifer Root Rot Conf. (In Press).

75. Grieg, B. J. W. and J. E. Pratt. 1976. Some observations on the longevity of Fomes annosus in conifer stumps. Eur. J. For. Path. 6:250-53.

76. Grieg, B. J. W. 1974. Fomes annosus: Mortality rates in young trees underplanted among pine. Pages 53-63 in E. G. Kuhlman, ed. Proc. Fourth Intl. Conf. on Fomes annosus. U.S.D.A. For. Serv. SE For. Expt. Sta., Asheville, N. C. 189 pp.

77. Grieg, J. W. and J. D. Low. 1976. An experiment to control Fomes annosus in second rotation pine crops. Forestry 49:147-63.

78. Grieg, B. J. W. and H. S. McNabb, Jr. 1976. Management of F. annosus root rot disease in pine crops in Britain. Iowa State J. Res. 50:287-92.

79. Gunderson, K. 1961. Growth of Fomes annosus under reduced oxygen pressure and the effect of carbon dioxide. Nature (London) 190:649.

80. Gunderson, K. 1963. [A new chemical to control Fomes annosus.] (Abstr.) Rev. Appl. Mycol. 43:383.

81. Gunderson, K. 1967. Nitrite as a nutrient for microfungi of the outer stem cortex of pine and spruce and its toxicity to Fomes annosus. Stud. Forest. Suecica 43, 24 pp.

82. Hansbrough, J. 1953. Personal communication to D. S. Welch, Northeastern For. Expt. Sta. Insect and Disease Lab, New Haven, Conn. In Sinclair, W. A. 1964. Root- and Butt-Rot of Conifers Caused by Fomes annosus, with Special Reference to Inoculum Dispersal and Control of the Disease in New York. Cornell Agric. Expt. Sta. Mem. 391, 54 pp.

83. Hartig, R. 1874. Wichtige Krankheiten der Waldbaume. Julius Springer, Berling. 127 pp.

84. Hartig, R. 1894. The diseases of trees (Trans. by W. Somerville, and H. M. Ward.) MacMillan and Co., London. 331 pp.

85. Hartley, C. 1910. Fomes annosus and two species of Gymnosporangium on Juniperus virginiana. (Abstr.) Science 31:639.

86. Hayward, H. E., W. M. Blair and P. E. Skaling. 1942. Device for measuring entry of water into roots. Bot. Gaz. 104:152-60.

87. Hendrix, F. F. and E. G. Kuhlman. 1964. Root infection of Pinus elliottii by Fomes annosus. Nature 201:55-56.

88. Hiley, W. E. 1919. Fungal diseases of the common larch. Clarendon Press, Oxford. 204 pp.

89. Hodges, C. S. 1964. The effect of competition by Peniophora gigantea on the growth of Fomes annosus in stumps and roots. (Abstr.) Phytopathology 54:623.

90. Hodges,, C. S. 1968. Evaluation of stump treatment chemicals for control of Fomes annosus. Pages 43-53 in C. S. Hodges et. al., eds. Proc. Third Intl. Conf. Fomes annosus S. E. For Expt. Sta. USFS Asheville, N. C., 207 pp.

91. Hodges, C. S. 1974a. Symptomatology and spread of Fomes annosus in southern pine plantations. U.S.D.A. For. Serv. Res. Pap. SE-114. 10 pp.

92. Hodges, C. S. 1974b. Cost of treating stumps to prevent infection by Fomes annosus. J. For. 72:402-04.

93. Hoekstra, P. E. and F. Mergen. 1957. Experimental induction of female flowers on young slash pine. J. For. 55:827-31.

94. Hole, R. S. 1927. Mortality of spruce in the Jaunsar forests, United Provinces, Indian Forester 53:434-443, 483-493.

95. Holmes, G. D. and G. Buszewicz. 1957. Forest tree seed investigations. In Great Britain Forestry Comm. Reptr. on Forest Res. for Year Ended March, 1957. p. 17-19.

96. Houston, D. R. 1975. Soil fumigation to control spread of Fomes annosus: results of field trials. U.S.D.A. For. Serv. Res. Pap. NE-327. 4 p.

97. Houston, D. R. and H. G. Eno. 1969. Use of soil fumigants to control spread of Fomes annosus. U.S.D.A. For. Serv. Res. Pap. NE-123. 23 pp.

98. Huet, M. 1937. La maladie du rond (Polyporus annosus . (Abstr.) Rev. Appl. Mycol. 16:145.

99. Hussain, S. M. 1952. Fomes annosus (Fr.) Cke., a common root rot. Pakistan J. For. 2:216-20.

100. Hyppel, A. 1969. Growth of Fomes annosus in the presence of host material from Norway spruce and silver fir. Stud. for. suec. Skogshogsk., No. 68, 16 pp.

101. Jacamon, M. and L. Lanier. 1961. La maladie du rond provoquee par Ungulina annosa (Fr.) Pat. (Fomes annosus Fr.) (Diagnostic et mogens de lutte). Note techn. forestiere No. 3, mars 1961.

102. Jones, T. W. 1961. First report of pine mortality caused by Fomes annosus in Ohio. U.S.D.A. Plant Dis. Reptr. 45:980.

103. Jorgenson, E. 1954. Fomes annosus attack in relation to thinning. Pages 17-18 in Intern. Union Forest Res. Organizations, Sect. 24, Forest Protect., Special Conf. on Root- and Butt-rots of Forest Trees by Fomes annosus. Wageningen. 30 pp.

104. Jorgensen, E. 1961. The formation of pinosylvin and its monomethyl ether in the sapwood of Pinus resinosa Ait. Can. J. Bot. 39:1765-72.

105. Jorgenson, C. A., A. Lund and C. Treschow. 1939. Undersøgelser over rodfordaerveren, Fomes annosus (Fr.) Cke. K. Vet. Landbohøjsk. Aarskr. 1939:71-128.

106. Jorstad, I. and F. Roll-Hansen. 1946. Melding om sykdommer pa skogtraer i arene 1936-1941. (Abstr.) Rev. Appl. Mycol. 25:17.

107. Kahn, A. H. 1960. Fungi occurring on Pinus in Pakistan. Mycopathol. et Mycol. Appl. 13(4):302-20.

108. Kaufman, C. M. 1968. Growth of horizontal roots, height and diameter of planted slash pine. For. Sci. 14(3):265-74.

109. Kauffman, C. H. 1917. Unreported Michigan fungi for 1915-16, with an index to the hosts and substrates of the basidiomycetes Mich. Acad. Sci. Ann. Rept. 19:145-57.

110. Kazadaiv, S. A. 1957. [The infection of pine in Voronezh forests by root fungi and research for the control of dying off.] (Abstr.) Rev. Apply. Mycol 38:231-32.

111. Keller, P. J. 1973 [Ultrastructure of the spore walls of Heterobasidion annosum]. Schweiz. Z. Pilz. 51(7):97-99.

112. Kelley, W. D. and E. A. Curl. 1972. Effects of cultural practices and biotic soil factors on Fomes annosus. Phytopathology 62:422-27.

113. Kepler, J. A., M. E. Wall, J. E. Mason, C. Bassett, A. T. McPhail and G. A. Sim. 1967. The structure of fomannosin, a novel sesquiterpene metabolite of the fungus Fomes annosus. J. Amer. Chem. Soc. 89:1260-61.

114. Klingstrom, A. and L. Beyer. 1965. Two new species of Scytalidium with antagonistic properties to Fomes annosus (Fr.) Cke. Svensk bot. Tidskr. 59(1):30-36.

115. Klingstrom, A. E. and S. M. Johanson. 1973. Antagonism of Scytalidium isolates against decay fungi. Phytopathology 63:473-79.

116. Knight. H. A. 1978. The South is losing its pines. For. Farm. 6:11-13.

117. Knight, H. A. and J. P. McClure. 1978. Virginia's timber, 1977. U.S.D.A. For. Serv. Res. Bull. SE-44, 53 pp.

118. Koch, P. 1974a. Why not take all of me. For. Farmer 33(10):12-13.

119. Koch, P. 1974b. Harvesting southern pine with taproots can extend pulpwood resource significantly. J. For. 72:266-68.

120. Korotkov, G. P. 1975. [Effect of mycorrhizas in reducing the incidence of root fungus]. (Abstr.) Rev. Plt. Path. 54:949.

121. Korstian, C. F. and W. D. Brush. 1931. Southern white cedar. U.S.D.A. Tech. Bull. 251, 75 pp.

122. Kramer, P. J. 1932. The absorption of water by root systems of plants. Amer. J. Bot. 19:148-64.

123. Kramer, P. J. 1946. Absorption of water through suberized roots of trees. Plant Physiol. 21:37-41.

124. Kramer, P. J. and H. C. Bullock. 1966. Seasonal variations in the proportions of suberized and unsuberized roots of trees in relation to the absorption of water. Amer. J. Bot 53(2):200-04.

125. Krupa, S. and J. E. Nylund. 1972. Studies on ectomycorrhizae of pine III. Growth inhibition of two root pathogenic fungi by volatile organic constituents of ectomycorrhizal root systems of Pinus sylvestris L. Eur. J. For. Path. 2:88-94.

126. Kuhlman, E. G. 1969. Variation in susceptibility of some forest tree seedlings to infection by Fomes annosus. (Abstr.) Phytopathology 59:1036.

127. Kuhlman, E. G. 1972. Susceptibility of loblolly and slash pine progeny to Fomes annosus. U.S.D.A. For. Serv. Res. Note SE-176, 7 pp.

128. Kuhlman, E. G. 1974. Variation in infection of loblolly pine roots on high and low hazard sites in the southeastern United States. Pages 179-83 in E. G. Kuhlman, ed. Proc. Fourth Intl. Conf. on Fomes annosus. U.S.D.A. For. Serv. SE For. Expt. Sta., Asheville, N. C. 189 pp.

129. Kuhlman, E. G., C. S. Hodges, Jr. and R. C. Froelich. 1976. Minimizing losses to F. annosus in the southern United States. U.S.D.A. For. Serv. Res. Pap. SE-151, 41 pp.

130. Lagerburg, T. 1937. Nagra synpunkte pa bestandsvard och virksvard. (Abstr.) Rev. Appl. Mycol. 16:145.

131. Lantz, C. W. 1979. Progress report: Improved seedling production in the South. Abstracts 15th South. For. Tree Improv. Conf., p. 8.

132. Larson, M. M. and F. W. Whitmore. 1970. Moisture stress affects root regeneration and early growth of red oak seedlings. For. Sci. 16:495-98.

133. Lauska, A. 1959. [Control of butt rot of pine]. (Abstr.) Rev. Appl. Mycol. 40:147.

134. Lightle, P. C. 1960. Fomes annosus root rot of loblolly pine. U.S.D.A. Plant Dis. Reptr. 44(6):423.

135. Lohr, E. 1966. [Formation of the fruiting body by Fomes annosus in culture.] Bot. Tidsskr. 62:43-45.

136. Lowe, J. L. 1957. Polyporaceae of North America. The genus Fomes. S.U.N.Y. Coll. For. Tech. Pub. No. 80, 97 pp.

137. Lowe, J. H., Jr., and P. V. Mook. 1960. Forest insect and disease conditions in the Northeast - 1959. Publ. U. S. Dept. Agr., For. Serv., Northeastern For. Expt. Sta. Insect and Dis. Lab., New Haven, Conn., 54 pp.

138. Lowery, W. P. 1966. Apparent meteorological requirements for abundant cone crop in Douglas-fir. For. Sci. 12(2):185-92.

139. Lyr, H. 1960. Die Wirkungsweise der Thujaplicine und anderer toxischer Kernholzinhaltsstoffe auf den Stoffwechsel Holzzerstorender. Pilze. Naturwissen schaften 47:499-500.

140. Marinkovic, P. 1978. Fomes annosus in southern Europe. Proc. Fifth Intl. Conifer Root Rot Conf. (In Press).

141. Marlin, C. F. 1978. A study of owners of small timber tracts in Louisiana. La. Agric. Expt. Sta. Bull. 710, 65 pp.

142. Martinez, M. B. and M. A. Lugo-Lopez. 1952. Tillage tools. I. Effect of subsoiling and mole drainage upon the minimum infiltration capacity of a heavy claypan soil of the tropics. (Abstr.) Soils and Ferts. 16:120.

143. Mason, R. R. 1969. Behavior of Ips populations after summer thinning in a loblolly pine plantation. For. Sci. 15(4):390-98.

144. McGauley, B. and M. Hubbes. 1976. Relative susceptibility of selected pure and hybrid pines to Fomes annosus (Fr.) Cke. Eur. J. For. Path. 6:167-176.

145. Meredith, D. S. 1959. The infection of pine stumps by Fomes annosus and other fungi. Ann. Bot. 23:455-76.

146. Mielke, J. L. and R. W. Davidson. 1947. Notes on some western wood-decay fungi. U.S.D.A. Plant Dis. Reptr. 31:27-30.

147. Miller, J. K. 1943. Fomes annosus and red cedar. J. For. 41:37-40.

148. Misin, P. A. 1959 [Reducing the felling age for Abies sibirica in relation to rot damage caused by fungi]. For. Abstr. 22:422.

149. Mook, P. V. and H. G. Eno. 1961. Fomes annosus. What it is and how to recognize it. U.S.D.A. For. Serv. Northeast. For. Expt. Sta. Pap. No. 146, 33 pp.

150. Moriondo, F. 1970. The actual situation of research on the damage caused by Fomes annosus in forest stands in Italy. Pages 91-95 in C. S. Hodges, J. Rishbeth and A. Yde-Andersen, eds., Proc. Third Intl. Conf. on Fomes annosus. (I.U.F.R.O.) U.S.D.A. For. Serv., Washington, D. C. 207 pp.

151. Morris, C. L. 1970. Volume losses from Fomes annosus in loblolly pine in Virginia. J. For. 68(5):283-84.

152. Morris, C. L. and D. H. Frazier. 1966. Development of a hazard rating for Fomes annosus in Virginia. U.S.D.A. Plant Dis. Rept. 50:510-11.

153. Morrison, D. J. and A. L. S. Johnson. 1975. Zinc chloride effectively controls Fomes annosus stump infection. Bi-monthly Research Notes 31(1):5-6.

154. Negrutskii, S. F. 1960. [Fomes annosus on Juniperus sabina]. For. Abstr. 22:267.

155. Negrutskii, S. F. 1963. [Some features of the infection of Pinus sibirica by Fomes annosus.] For. Abstr. 25:266.

156. Negrutskii, S. F. 1963. [Some characteristics of the infection of Pinus cembra var. sibirica by Fomes annosus.] (Abstr.) Rev. Appl. Mycol. 44:165.

157. Nobles, M. K. 1965. Identification of cultures of wood-inhabiting hymenomycetes. Can. J. Bot. 43:1097-1139.

158. Olson, A. J. 1941. A root disease of Jeffrey and ponderosa pine reproduction. Phytopathology 31:1063-77.

159. Orekhov, D. A. 1974. [The biological method of controlling the root fungus (Fomitopsis annosus (Fr.) Karst.] (Abstr.) Rev. Plt. Path. 53:465.

160. Parrot, A. G. 1946. Champignons du pays basque. Bull. Trimestriel Soc. Mycol. France 62:86-102.

161. Peek, R. -D., W. Liese and N. Parameswaran. 1972a. [Infection and deterioration of spruce root bark by Fomes annosus.] Eur. J. For. Path. 2:104-15.

162. Peek. R. -D., W. Liese and N. Parameswaran. 1972b. [Infection and deterioration of spruce root wood by Fomes annosus.] Eur. J. For. Path. 2:237-48.

163. Pegler, D. N. and J. M. Waterston. 1968. Heterobasidion annosum (Fomes annosus). C.M.I. Descr. Path. Fungi and Bact. No. 192, 2 pp.

164. Phillips, D. H. and B. J. W. Grieg. 1970. Some chemicals to prevent stump colonization by Fomes annosus (Fr.) Cooke. Ann. Appl. Biol. 66:441-52.

165. Platt, W. D., E. B. Cowling and C. S. Hodges, Jr. 1965. Resistance of coniferous root wood and stem wood to decay by Fomes annosus. (Abstr.) Phytopathology 55:130-31.

166. Porterfield, R. L. 1979. Southern tree improvement's impact on forest products -- Thoughts on the future. Proc. 15th South. For. Tree Improv. Conf. 15:121-131.

167. Porterfield, R. L. and J. E. Moak. 1977. Timber management for non-industrial forest owners: a matter of perspective? South. J. Applied For. 1:2-6.

168. Powers, H. R., Jr., and J. S. Boyce, Jr., 1961. Fomes annosus on slash pine in the Southeast. U.S.D.A. Plant Dis. Reptr. 45:306-7.

169. Powers, D. W. and J. M. Skelly. 1975. Growth loss due to Fomes annosus in loblolly pine as associated with increasing levels of disease incidence and severity. (Abstr.) Proc. Amer. Phyto. Soc. 2:127.

170. Powers, H. R., Jr., and A. F. Verrall. 1962. A closer look at Fomes annosus. For. Farmer 21(13):8-9, 16-17.

171. Preuss, C. G. T. 1851. Ubersicht untersuchter Pilze, besonders aus der Umgegend von Hogerswerda. Linnaea 24:99-153.

172. Prior, C. 1975. Resin production and susceptibility to Heterbasidion annosum in Corsican pine. Ann. Bot. 39:1103-09.

173. Punter, D., and J. D. Cafley. 1968. Two new hardwood hosts of Fomes annosus. U.S.D.A. Plant Dis. Reptr. 52:692.

174. Raney, W. A., T. W. Edminster and W. H. Allawey. 1955. Current status of research in soil compaction. Soils Sci. Soc. Amer. Proc. 19:423-28.

175. Reicosky, D. C., R. B. Campbell and C. W. Coty. 1976. Corn-plant water stress as influenced by chiseling, irrigation and water table depth. Agron. J. 68:499-503.

176. Rennerfelt, E., and G. Nacht. 1955. The fungicidal activity of some constituents from heartwood of conifers. Svensk. Bot. Tidskr. 49:419-32.

177. Rhodes, A. S., and E. Wright. 1946. Fomes annosus commonly a wound pathogen rather than a root parasite of western hemlock in western Oregon and Washington. J. Forestry 44:1091-92.

178. Ricard, J. and P. Laird. 1970. Current research in the control of Fomes annosus with Scytalidium sp., an immunizing commensal. Pages 104-09 in C. S. Hodges, J. Rishbeth and A. Yde-Andersen, eds. Proc. Third Intl. Conf. on Fomes annosus. (I.U.F.R.O.) U.S.D.A. For. Serv., Washington, D. C., 207 pp.

179. Rishbeth, J. 1948. Fomes annosus Fr. on pines in East Anglia. Forestry 22:174-183.

180. Rishbeth, J. 1950a. Investigations on Fomes annosus attacks in East Anglian pine plantations. In Great Britain Forestry Comm. Rept. on Forest Res. for Year Ended March, 1949. p. 77-78.

181. Rishbeth, J. 1950b. Observations on the biology of Fomes annosus, with particular reference to East Anglian pine plantations. I. The outbreaks of disease and the ecological status of the fungus. Ann. Bot. (N.S.) 14:365-83.

182. Rishbeth, J. 1951a. Observations on the biology of Fomes annosus, with particular reference to East Anglian pine plantations. II. Spore production, stump infections, and saprophytic activity in stumps. Ann. Bot. (N.S.) 15:1-22.

183. Rishbeth, J. 1951b. Observations on the biology of Fomes annosus, with particular reference to East Anglian pine plantations. III. Natural and experimental infection of pines, and some factors affecting severity of the disease. Ann. Bot. (NS.) 15:220-47.

184. Rishbeth, J. 1952. Control of Fomes annosus Fr. Forestry 25:41-50.

185. Rishbeth, J. 1957. Some further observations on Fomes annosus Fr. Forestry 30:69-89.

186. Rishbeth, J. 1959. Stump protection against Fomes annosus. I. Treatment with creosote. Ann. Apply. Biol. 47(3):519-28.

187. Rishbeth, J. 1959. Stump protection against Fomes annosus. II. Treatment with substances other than creosote. Ann. Appl. Biol. 47(3):529-41.

188. Rishbeth, J. 1963. Stump protection against Fomes annosus. III. Inoculation with Peniophora gigantea. Ann. Appl. Biol. 52(1):63-77.

189. Rishbeth, J. 1972. Resistance to fungal pathogens of tree roots. Proc. R. Soc. Lond. B. 181:333-51.

190. Roll-Hansen, F. 1940 [Studies in Polyporus annosus Fr., especially in respect of its occurrence in Norway south of the Dovre Fell.] Meddel. Norske. Skogsforsoksv 71:1-100.

191. Ross, E. W. 1968. Sand pine, a new host of Fomes annosus. U.S.D.A. Plant Dis. Reptr. 52(8):635.

192. Ross, E. W. 1969. Thermal inactivation of conidia and basisiospores of Fomes annosus. Phytopathology 59(12):1798-1801.

193. Ross, E. W. and C. H. Driver. 1966. Relation of temperature and time of cutting to colonization of slash pine stumps by Fomes annosus. (Abstr.) Phytopathology 56:897-98.

194. Sanders, H. G. 1947. An outline of British crop husbandry. Cambridge Univ. Press. 348 pp.

195. Sasaki, T. and S. Yakota. 1958. Wood decay of Abies sachalinensis forest in Tokyo University Forest in Hokkaido. II. (Abstr.) Rev. Appl. Mycol. 37:744.

196. Savage, E. F., R. A. Hagden and W. E. Ward. 1968. The effect of subsoiling on the growth and yield of peach trees. Univ. Ga. Agric. Expt. Sta. Res. Bull. 30. 15 pp.

197. Schrench, H. von. 1898. Notes on some diseases of southern pines. Amer. Assoc. Adv. Sci. Proc. 47:414.

198. Scurfield, G. and E. W. B. Da Costa. 1969. Fine structure of the walls of the conidia of various fungi and of the conidiophore of Fomes annosus. Aust. J. Bot. 17:13-24.

199. Shain, L. 1967. Resistance of sapwood in stems of loblolly pine to infection by Fomes annosus. Phytopathology 57:1034-45.

200. Shape, P. F. 1931. The Polyporaceae of Colorado. Ann. Missouri Bot. Gard. 18:287-456.

201. Shoulders, E. 1973. Rainfall influences female flowering of slash pine. U.S.D.A. For. Serv. Res. Note SO-150. 7 pp.

202. Skelly, J. M., S. A. Alexander and C. L. Morris. 1974. Excavation of entire tree root systems reveals higher incidences of Fomes annosus. Proc. Amer. Phyto. Soc. 1:155.

203. Sierota, Z. H. 1976. Influence of acidity on the growth of Trichoderma viride Pers. ex Fr. and on the inhibitory effect of its filtrates against Fomes annosus (Fr.) Cke. in artificial cultures. Eur. J. For. Path. 6:302-11.

204. Sinclair, W. A. 1960. Unpublished record. In Sinclair, W. A., 1964. Root-and Butt-Rot of Conifers caused by Fomes annosus, with Special Reference to Inoculum Dispersal and Control of the Disease in New York. Cornell Agric. Expt. Sta. Mem. 391, 54 pp.

205. Smith, R. S., Jr. 1970. Borax to control Fomes annosus infection of white fir stumps. Plant Dis. Rept. 54(10):872-75.

206. Spaulding, P. 1930. Some wood inhabiting fungi of Vermont. Vermont Bot. and Bird. Clubs Joint Bull. 14:28-50.

207. Spaulding, P. 1961. Foreign diseases of forest trees of the world. U.S.D.A. Agric. Hdbk. 197. 361 pp.

208. Stalpers, J. A. 1974a. Revision of the genus Oedocephalum (Fungi Imperfecti). Proc. Kan. Med. Akad. Wet., Ser. G 383-401.

209. Stalpers, J. A. 1974b. Spiniger, a new genus for imperfect states of basidiomycetes. Proc. Kon. Ned. Akad. Wet., Ser. C 77(4): 402-07.

210. Stephens, G. R., Jr. 1961. Flower stimulation in Pinus strobus. Proc. 8th NE Forest Tree Improve. Conf., New Haven, Conn., p. 39-42.

211. Stoddard, E. M., A. D. McDonnell and H. W. Hicock. 1939. Fomes annosus on conifers in Connecticut. U.S.D.A. Plant Dis. Reptr. 23:385-86.

212. Tegethoff, A. C. 1973. Known distribution of Fomes annosus in the intermountain region. U.S.D.A. Plant Dis. Reptr. 57(5):407-10.

213. Teng, S. C. 1940. Studies of Chinese timber trees in reference to forest management. Sinensia X:363-95.

214. Tinsley, T. W., D. K. Barrett, and P. G. Biddle. 1967. Forest pathology. (a) Mycology. Commonwealth Forest. Inst., Univ. Oxford, Rep. 42:23-25.

215. Towers, B. 1966. Effect of induced soil moisture stress on the growth of Fomes annosus in inoculated loblolly pine stumps. U.S.D.A. Plant Dis. Reptr. 50:747-49.

216. Towers, B. and W. J. Stambaugh. 1968. The influence of soil moisture stress upon Fomes annosus root rot of loblolly pine. Phytopathology 58:269-72.

217. Twarowska, I. 1966 [Possibility of biological control of Fomes annosus]. (Abstr.) Rev. Appl. Mycol. 46:487.

218. Von Weissenberg, K. 1975. Variation in relative resistance to spread of Fomes annosus in four clones of Picea abies. Eur. J. For. Path. 5:112-17.

219. Vyvyan, M. C. 1955. Interrelation of scion and rootstock in fruit trees. I. Weights and relative weights of young trees formed by the reciprocal unions, as scion and rootstock, of three apple rootstock varieties: M.IX, M. IV, and M. XII. Ann. Bot. 19:401-23.

220. Wagener, W. W., and M. S. Cave. 1946. Pine killing by the root fungus, Fomes annosus, in California. J. For. 44:47-54.

221. Wagn, O. 1971 [Infection experiment with Fomes annosus (Fr.) Cooke in shelter trees. I.] Tedsskr. PlAvl 75(6):766-73.

222. Wagn. O. 1978. Host plants of Fomes annosus in Denmark. Proc. Fifth Intl. Conifer Root Rot Conf. (In Press).

223. Wahlenberg, W. C. 1960. Loblolly pine. Duke Univ. Sch. Forestry, 603 pp.

224. Wallis, G. W. 1961. Infection of Scots pine roots by Fomes annosus. Can. J. Bot. 39:109-21.

225. Walters, N.E.M. 1967. Definite record of Fomitopsis annosa in Australia. Nature (London) 213:532.

226. Webb, P. J. 1973. An alternative to chemical stump protection against Fomes annosus on pines in state and private forestry. Scottish Forestry 27:24-28.

227. Weidensaul, T. C., and N. H. Plaugher. 1966. An evaluation of three stump treatment chemicals for preventing surface infection by Fomes annosus. U.S.D.A. Plant Dis. Reptr. 50(1):22-25.

228. Weir, J. F. 1917. Montana forest tree fungi. I. Polyporaceae. Mycologia 9:129-37.

229. Weir. J. F., and E. E. Hubert. 1919. A study of the rots of western white pine. U.S.D.A. Tech. Bull. 799. 24 pp.

230. Welch, D. S., and E. L. Stone. 1953. Fomes annosus (Fr.) Cke. in coniferous plantations in New York State. U.S.D.A. Plant Dis. Reptr. 37:247-48.

231. Wells, C. B. 1956. The practice of subsoiling-a brief review. J. Aust. Inst. Agric. Soc. 22:247-51.

232. Wenger, K. F. 1957. Annual variation in the seed crops of loblolly pine. J. For. 55:567-69.

233. Wenzel, G. and M. P. Diaz-Palacio. 1970. [The relation between nutrient status of Norway spruce (Picea abies Karst.) and the content of fungal inhibitors in bast.]. Z. Pfl. Ernahr. Bodenk. 127:56-63.

234. Williston, H. I. 1979. The South's pine reforestation problem. J. For. 78(4):234-36.

235. Wilson, M. 1927. The host plants of Fomes annosus. Trans. Brit. Mycol. Soc. 12:147-49.

236. Winters, E. and R. W. Simonson. 1951. The subsoil. Adv. Agron. III:1-92.

237. Woeste. U. 1956. Anatomische Untersuchungen uber die Anfektionswege einiger Wurzelpilze. Phytopathol. Z. 26:225-72.

238. Zak, B. 1971. Characterization and classification of mycorrhizae of Douglas fir. II. Pseudotsuga menziesii + Rhizopogon vinicolor. Can. J. Bot. 49:1079-84.

239. Zeller, S. M. 1935. Some miscellaneous fungi of the Pacific Northwest. Mycologia 27:449-66.

240. Zobel, B. J., J. Barber, C. L. Brown and T. O. Perry. 1958. Seed orchards - their concept and management. J. For. 56(11): 815-25.

The vita has been removed from the scanned document

THE INCIDENCE AND SEVERITY OF *HETEROBASIDION ANNOSUM* (FR.) BREF. IN LOBLOLLY PINE (*PINUS TAEDA* L.) UNTHINNED PLANTATIONS AND SEED ORCHARDS

by

Roger S. Webb

(ABSTRACT)

Studies were conducted to determine the incidence and severity of *Heterobasidion annosum* (Fr.) Bref. root rot in loblolly pine (*Pinus taeda* L.) unthinned plantations and subsoiled seed orchards and to demonstrate the potential for direct root colonization by percolated basidiospores. Twenty-two 0.02 ha circular plots were installed in nine unthinned loblolly pine plantations in Virginia. Five plantations were located on sites classified as high hazard for annosum root rot while four plantations were located on low hazard sites. Bulldozer excavation of the root systems permitted extensive analysis of annosum root rot incidence and severity which was substantiated by isolation of the asexual stage of the fungus from symptomatic resinous and stringy-decayed roots. On low hazard sites, 10 of 300 trees (3.3 percent) were colonized by *H. annosum* with 2 trees (0.7 percent) severely colonized (> 1 percent of the total root system mass). On high hazard sites, 29 of 348 trees (8.3 percent) were colonized with 5 trees (1.4 percent) severely colonized. On low hazard sites, the predominant colonization symptom was stringy decay which indicated an older established disease situation as opposed to colonized trees on high hazard sites which exhibited resin-soaking characteristic of more recent

infection and colonization. No basidiocarps were observed on any trees on low hazard plots while only 2 trees exhibited conks on high hazard sites. Mean radial increment growth differences between H. annosum-colonized and noncolonized trees were analyzed using the Duncan's Multiple Range test and for the 10-year period prior to excavation no significant growth reduction was observed. Due to low incidence and severity of annosum root rot in unthinned loblolly pine plantations and the absence of reduced radial increment growth, the disease is not a primary management consideration, especially on low hazard sites. However, the disease may be of secondary importance in managing first-generation unthinned loblolly pine plantations on high hazard sites due to inoculum production from residual stumps of H. annosum trees removed during thinning. The root systems of 2, 20 and 30 loblolly pines at the Chesapeake Corporation, Virginia Division of Forestry and Union Camp Corporation seed orchards, respectively, were excavated with a backhoe to permit intensive analysis of subsoiled roots for annosum root rot incidence and severity. The absence of wound callus, lack of adventitious root formation and the presence of a resin-soaked band greater than approximately 6 mm wide at the wound surface were three criteria for determining whether a lateral primary root had failed to heal following subsoiling. Soil texture was closely associated with the incidence and severity of general root disease as the wetter soil conditions at the Chesapeake Corporation seed orchard probably afforded a more amenable environment for the healing of subsoiled roots. Sandy, drought-susceptible soils at the Union Camp Corporation and Virginia Division of Forestry seed orchards were associated with the higher incidence and severity of root disease among subsoiled lateral primary roots.

The asexual stage of H. annosum was not successfully isolated from resin soaked subsoiled root tissue at any of the three orchards. Duncan's Multiple Range analysis demonstrated that mean radial increment growth was significantly decreased among healthy and declining subsoiled trees at the three orchards. At the Union Camp Corporation orchard, when healthy and declining trees were subsoiled they exhibited significantly less radial increment growth than their respective control counterparts. Loblolly pine root segments were inoculated with a suspension of H. annosum basidiospores and observed using scanning electron microscopy. Appressorial-like structures occurred at distal ends of elongated germ tubes demonstrating probable direct infection of loblolly pine root segments.