Biology, Ecology, and Epidemiology of *Heterobasidion annosum*[1]

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Abstract: Pertinent literature on the biological aspects of annosus root disease is reviewed. Key features of the life cycle of Heterobasidion annosum such as stump infection, stump colonization, host-parasite relations, and interactions of various physical and biological factors are discussed in relation to forest stands in the western United States. This review suggests our knowledge of the pathology of this disease is limited on most affected tree species. Further research on various aspects of the life cycle of this fungus is essential to minimizing losses to this disease.

The literature on Heterobasidion annosum (Fr.) Bref. before 1970 contains over 1,000 titles dealing with various aspects of the fungus and the disease it causes (Hodges and others 1971; Koenigs 1960). A preliminary literature review conducted by Otrosina estimates at least 850 titles dealing with H. annosum have been published during the period 1970 to 1988. This paper is not intended to be a review and will not attempt to address all aspects of the biology of H. annosum; it will highlight pertinent research on the biological and ecological relationships as they pertain to the pathology of pine and true fir in the western coastal states of the United States. The disease as it relates to other hosts in other geographic areas is discussed elsewhere in these proceedings.

STUMP SUSCEPTIBILITY AND INFECTION

The most crucial stage in the disease cycle of H. annosum is the entry or invasion of the fungus into the stand where it can then move from tree to tree through roots. The primary mode of stand entry in pines is through freshly cut stump surfaces (Begs 1963) (fig. 1). We believe that stump infection is important in fir as well, though there are other modes of entry in Abies (fig. 2). Stump surfaces act as ideal semi-selective media for germination of deposited basidiospores of the fungus. Susceptibility of stump surfaces of various hosts has been studied by a number of investigators (Rishbeth 1951; Yde-Andersen 1962; Cobb and Barber 1968). The general consensus of these studies is that stumps of most susceptible species can remain receptive to invasion by the fungus for up to 45 days, depending upon season and host species. On the other hand, Cobb and Schmidt (1964) found eastern white pine (Pinus strobus L.) stumps to be highly susceptible for only a few days after felling. In the western United States, ponderosa pine (Pinus ponderosa Laws.) stumps may remain susceptible for at least 4 weeks, although susceptibility drops markedly after 1 to 2 weeks (Cobb and Barber 1968). Susceptibility of stumps also was greater in the autumn than in the spring. This was attributed to higher resin content of cut stump surfaces in the spring-felled trees than in those felled in the fall. Not all susceptible tree species are colonized through stump surfaces at the same rates or conditions as ponderosa pine. For example, spore inoculation studies of incense cedar (Calocedrus decurrens (Torr.) Florin) suggest substantially more resistance to colonization under the same conditions that allow ponderosa pine stumps to be colonized (Hunt and others 1974).

Temperature is an important factor in determining successful infection of stump surfaces by H. annosum. The optimal temperature for growth of the fungus in pure culture is 23-26 C for a wide variety of host and geographic origins of isolates (Cowling and Kelman 1964). The fungus is also capable of considerable growth at lower temperatures, averaging 21 percent of optimum at 8 C. In general, the fungus does not grow at temperatures above 32 C. The upper temperature limit has important implications regarding stump infection in certain climates. Ross (1969) found basidiospores and conidia of the fungus to be inactivated after 60 minutes at temperatures above 45 C. There is an apparent difference in temperature effects between mycelia and spores. Actively growing mycelia can become inactive or killed at temperatures above 35 C (Gooding 1964). In California, stumps in ponderosa pine stands may be exposed to temperatures greater than 35 C during the summer months. For example, Cobb and Barber (1968) noted ambient temperatures greater than 33 C during a study involving artificial inoculation of stumps, but they detected stump

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infection by H. annosum during this period of high temperature. They so found that sumps exposed to direct solar radiation in stand openings were infected at the same level as stumps under more closed canopies. In the southeastern United States, recommendations for controlling annosus root disease in southern pine stands revolve around thinning stands in the warm summer months, during which ambient temperatures are above the 35 C inactivation point for the fungus (Ross 1973). Studies conducted by Cobb and Barber (1968), Gooding (1964), and Rose and others (1980) suggest high stump temperatures may not be the sole factor responsible for lowering rates of stump infection. Gooding (1964) studied survival of H. annosum in inoculated bolts of loblolly pine (Pinus taeda L.) incubated at various temperatures. He was unable to recover the fungus from bolts incubated at 35 C and above that were not surface sterilized before inoculation. On surface sterilized bolts, however, the fungus was reisolated at temperatures up to 40 C. These results suggest microbial activity at the stump surface plays some synergistic or interactive role in stump infection at higher temperatures. Rapid replacement of H. annosum by Trichoderma viride Pers. ex Fr. in a greenhouse inoculation study was attributed to high soil temperatures (Towers and Stambaugh 1968). Also, T. viride may act together with other fungi such as the saprotrophic colonizer Phlebia (Peniophora) gigantea (Fr.) Masses to inhibit H. annosum (Curl and Arnold 1964). The stump infections observed in California during the hot, dry summer months may indicate differences in kinds and quantity of microorganisms present on stump surfaces between climatic and geographic regions. The warm, humid climate of the southeastern United States tends to favor fungi such as Trichoderma and Phlebia, where they can often be observed fruiting on stump surfaces. However, these fungi are rarely observed in this manner in California.

The inoculum potential of the fungus in the form of airborne spores (largely basidiospores) is another important determinant of stump infection. Spore deposition rates have been measured almost everywhere annosus root disease is a problem. Edmonds and others (1984) found deposition rates in precommercially thinned stands of western hemlock (Tsuga heterophylla (Raf.) Sarg.) to be up to 8 times greater (up to 19,577/m^2/hr) in

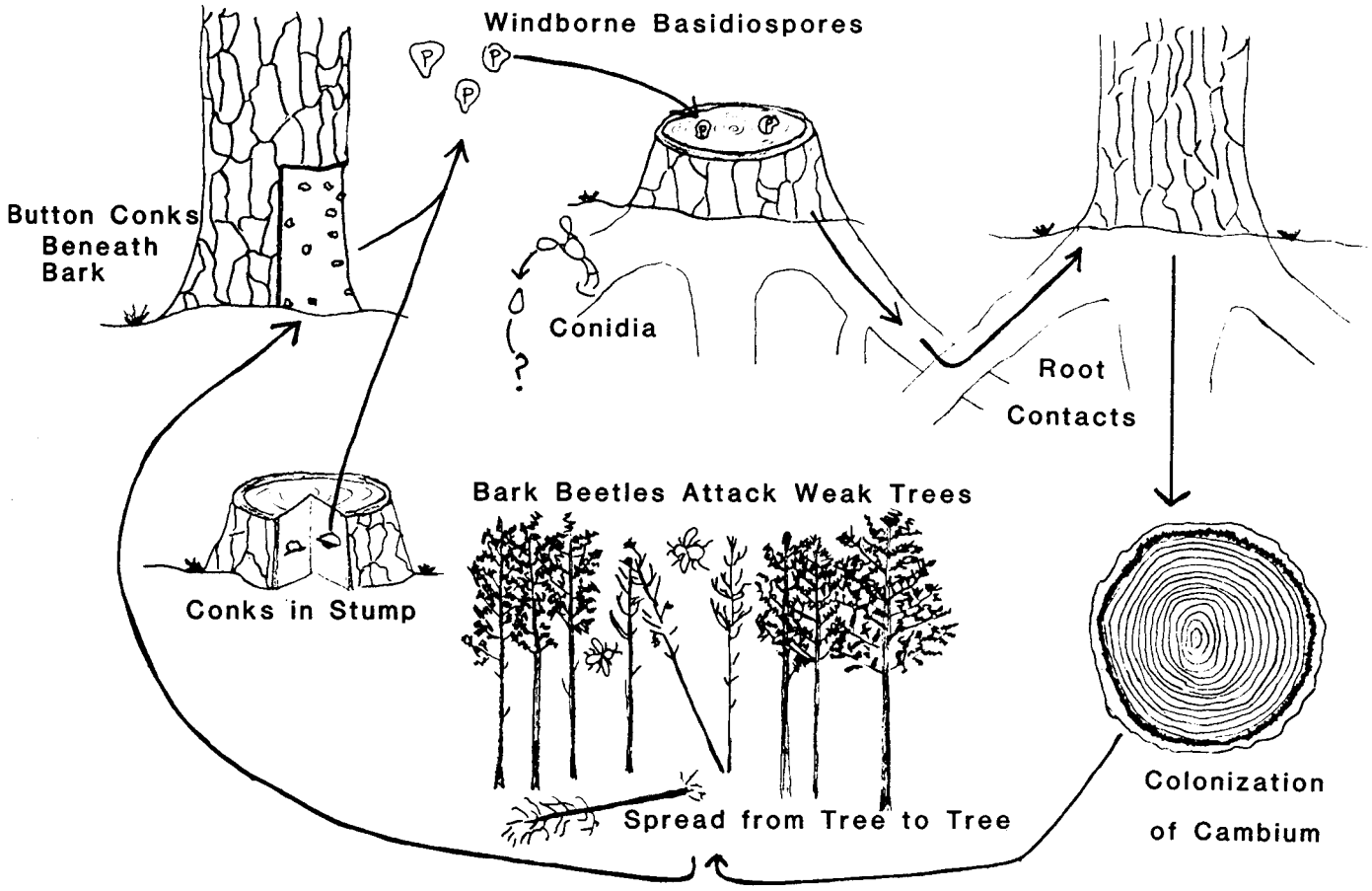

Figure 1--Infection cycle of Heterobasidion annosum in Pinus.

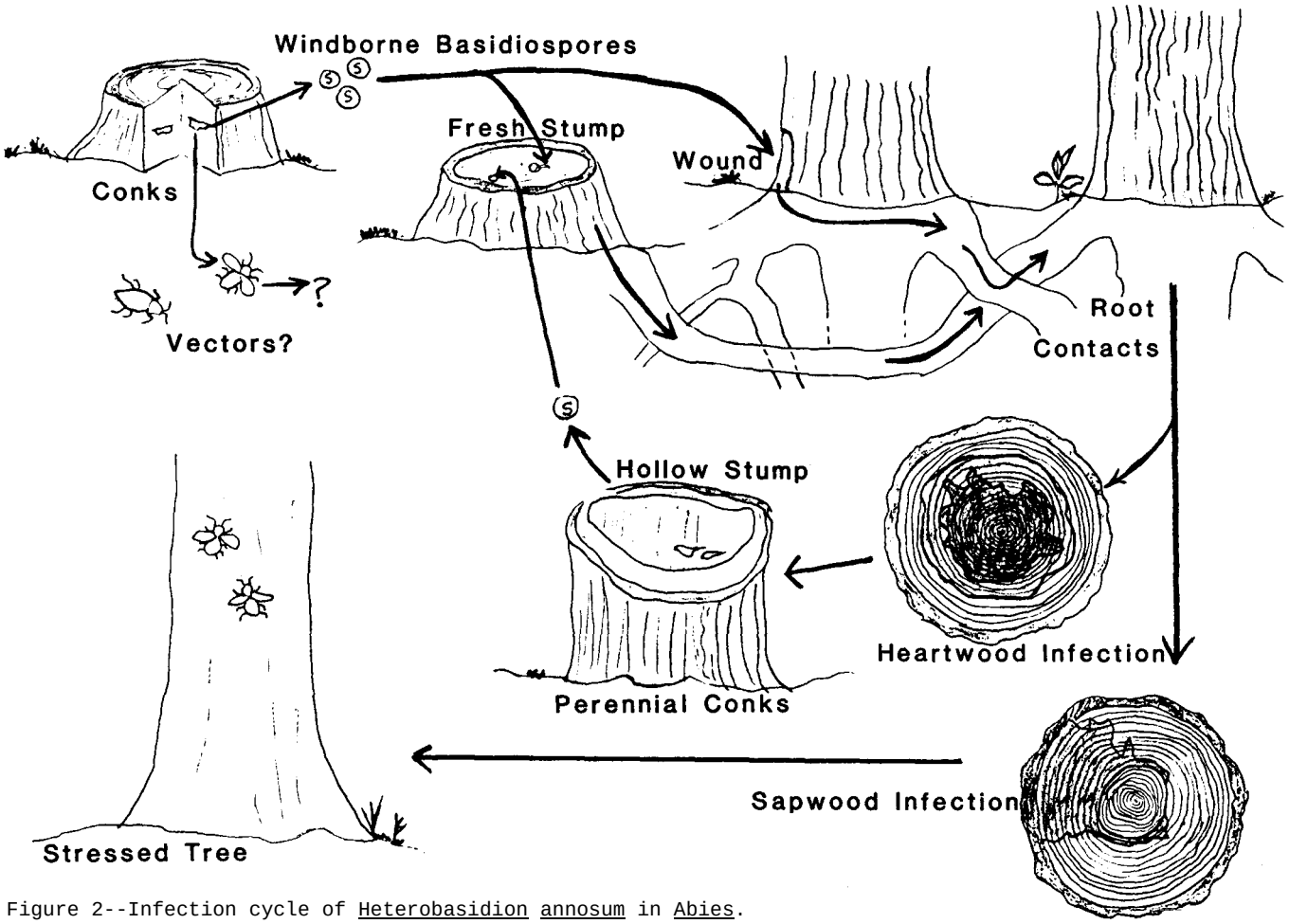

Figure 2--Infection cycle of Heterobasidion annosum in Abies.

precommercially thinned than in commercially thinned stands. In California, spore deposition rates in mixed conifer forests ranged from 3 to 796 spores/m^2/hr, depending on geographic location and season (James and Cobb 1984). Generally, the highest rates occurred in the autumn in these forests whereas in the southeastern United States, greatest spore deposition rates are observed during the winter months (Drummond and Bretz 1967; Ross 1969).

Because H. annosum has an asexual spore state, Oedocephalum lineatum Bakshi (=Spiniger meineckellus (Olson) Stalpers), the question has arisen as to its function in nature, is., whether the asexual conidiospores are an important etiological agent. Kuhlman and Hendrix (1964) found conidial inoculum inferior to basidiospore inoculum as measured by stump colonization 9 months after inoculation with spore suspensions. They did not indicate the relative spore concentrations in their inoculum solutions, but check inoculations on pine disks indicated comparable initial viability of inocula. Conidial inoculum has been used successfully numerous times by others in the study of stump infection and colonization (James and others 1980b). Conidia have been shown to survive in field soils having extremely low water potentials for several months, although survival declines over time to a greater extent in sandy soils than in clay loans (Kuhlman 1969a). The potential for direct root infection by spores of H. annosum exists, and may be responsible for initiation of some root infections, particularly in injured stump roots created after felling (Kuhlman 1969b).

COLONIZATION

The colonization phase of the infection process refers to the establishment and growth of the fungus through stump and root tissues distally from exposed stump surfaces. Saprotrophic colonization of these woody tissues by the fungus provides the inoculum necessary for infection of adjacent, previously uninfected trees. Not all stump surface infections progress to the point of colonization of the woody root tissues. Factors such as temperature, tree species, climate, type of microflora, and inoculum density can interact to reduce successful stump colonization.

Most of the research regarding stump and root colonization by H. annosum has been conducted on various pine species in different parts of the

world (Driver and Ginns 1969; Rishbeth 1951). Hunt and coworkers (1976) studied stump colonization in the western United States. They investigated factors affecting colonization of ponderosa pine (Pinus ponderosa Dougl. ex Laws.) and to a more limited extent, Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) and sugar pine (Pinus lambertiana Dougl.). Interestingly, they could not study colonization of white fir (Abies concolor (Gord.)Lindl. ex Hildebr.)) because many trees in the study area were found to be infected before felling. Under their experimental conditions, colonization of sugar pine and Douglas-fir stumps lagged behind that of ponderosa pine in the rate at which inoculated stump roots became colonized. They also found colonization of ponderosa pine stumps to be characterized by the formation of "tubes" which are vertically oriented channels formed by disintegrating conductive tissue in the sapwood-bark interface. These tubes, along with beetle galleries containing mycelium, may serve to hasten spread of the fungus to distal portions of large stump roots by providing suitable microsite conditions for unrestricted hyphal growth. Rainwater may also carry conidia formed in tubes or beetle galleries to lower portions of stump root systems. The spores may then germinate and form new infection foci along the sapwood-bark interface. Conidia have been observed in these structures 2.5 to 12 months after inoculation of ponderosa pine stumps and may be an important agent in the early stages of colonization. Such a mechanism can provide for rapid stump root colonization, 0.2 to 0.5 cm/day, as reported by Hunt, et al. (1976), who noted very few root collars becoming infected from the portion of the fungal mycelia growing deeper within the sapwood. Because the fungus moves rapidly along the sapwood-bark interface and because H. annosum can grow readily into bark scales from this interface, rapid spread to adjacent host root systems can be realized through root contacts.

Role of insects in stump colonization

Insects may function in the spread of H. annosum in at least two ways: 1) as vectors transporting propagules of the fungus between stumps and 2) as facilitators in the local spread of the fungus within stump roots.

The black turpentine beetle, Dendroctonus terebrans Oliv., has been shown to carry and transmit H. annosum when various stages of the insect were placed on disks of fresh loblolly pine (Rimes and Skelly 1972). In the western United States, Dendroctonus valens Leconte, closely related to D. terebrans, is associated with trees infected by H. annosum. After detailed study of colonization of stumps and trees by various insects including D. valens, Hunt and Cobb (1982) concluded that insects are not major agents in the dissemination of H. annosum in ponderosa pine. They provided evidence indicating that stump-colonizing insects may introduce fungi such as Phlebia gigantea and Ophiostoma (Ceratocystis) spp. that act as competitors to H. annosum, although none of the introduced fungi colonized stump surfaces enough to reduce colonization by H. annosum.

Within stumps, however, insects may have considerable opportunity to spread the fungus for short distances (several centimeters). Such local spread could be important in aiding rapid establishment of the fungus in larger stump roots, although there is currently no experimental evidence to support this possibility. However, data reported by Hunt and others (1976) and Hunt and Cobb (1982) regarding timing of appearance of conidia in pine stumps and insect colonizers suggest that this topic deserves further study. Virtually no information is available regarding spread of H. annosum by insects in true fir.

SPREAD TO ADJACENT TREES

Role of Root Contacts and Root Grafts

Knowledge of factors affecting spread of this pathogen to adjacent uninfected trees in forest stands is key to our ability to quantify and predict infection rates and losses in these stands. Unfortunately, our knowledge of these factors and how they affect pathogen spread is incomplete, particularly in western forests. It has been known for some time that tree-to-tree spread of the fungus is accomplished through root contacts or root grafts (Rishbeth 1950). Because the fungus readily colonizes the sapwood-bark interface in roots and grows ectotrophically through bark scales, inoculum of the fungus can be potentially available for infection at considerable distances from the site of the initial stump infection. The importance of root contacts or root grafts in the infection process is reflected by the incapability of H. annosum to grow more than a few millimeters through soil (Srago 1973).

In contrast to acting as a means for inoculum transfer to adjacent trees, root grafting can be responsible for slowing the spread of the disease. There is evidence that progress of infection by H. annosum is reduced in Douglas-fir and western hemlock stumps that have root systems grafted to living residual trees (Morrison and Johnson 1978). Resistance mechanisms of the host could be operating in root systems of grafted stumps. The occurrence and importance of root grafting to disease spread need to be determined in the ponderosa pine, mixed conifer, and true fir type. Such information is necessary in predicting losses from this disease in these forest stands.

Morrison and Johnson (1978) report that Armillaria sp. appears to be an effective competitor against H. annosum in Douglas-fir and western hemlock root systems because in some cases, Armillaria sp. colonized the root systems of trees by rhizomorphs before to felling.

Armillaria colonizes the outer tissues of root systems, thereby reducing opportunity for spread of H. annosum. In contrast, stumps of trees root grafted to residuals may remain alive and receptive to infection for some time, with host resistance excluding opportunistic saprotrophic fungi that may compete with H. annosum.

Observations in California suggest a more complex interaction between H. annosum and Armillaria species in true firs. Armillaria appears to be ubiquitous in Abies, often growing along roots as in oak. In many cases, colonization of fir by H. annosum appears to favor pathogenic colonization by Armillaria, thus enabling both fungi to exist as significant pathogens in true firs. Otrosina (unpublished data) has isolated H. annosum from tissues of firs having abundant rhizomorphs and characteristic rot of Armillaria. The relationships between these two pathogens on true fir need to be studied in detail.

Edaphic factors and disease spread

Rishbeth (1950) noted a relationship between soil pH and severity of root disease caused by H. annosum in Scots pine (Pinus sylvestris L.) plantations in England. He showed that alkaline soils had higher infection rates than acidic soils. The relationship between soil pH and disease severity may not be pronounced in North America, where coniferous forest soils are usually acidic and the disease can be extremely severe.

In searching for easily measured or observed factors associated with severity and non-severity of the disease in the southern United States, Froelich and coworkers (1966) found that severe damage from the disease was associated with a low level of soil organic matter, slightly higher pH (5.65 vs 5.23 in undamaged stands), high sand content or very high clay content, and sparse grass cover. In stands of loblolly pine (Pinus taeda L.) in the piedmont and coastal plain of Virginia, Morris and Frasier (1966) associated sandy soils having an A horizon depth of 30 cm or more and a water table greater than 45 cm with high disease hazard. Alexander and others (1975) also found strong correlations between disease severity and high sand content, low level of organic matter, and low field capacity to be associated with high-hazard sites. There was also evidence of considerable growth loss of infected trees on sites classified as low hazard that approached the growth loss due to mortality on the high-hazard sites. Although these guidelines can serve as a generalized tool for the land manager, there are notable exceptions to these soil/site factors relating to disease hazard (Froelich and others 1977). Stands of loblolly pine in several soil series having low sand content also demonstrate high mortality due to H. annosum. These exceptions indicate our incomplete understanding of these relationships, a situation especially acute in forests of the western United States.

Information on soil microbial activity and disease severity is sparse, although knowledge of these relationships can be important in understanding risk of disease development in conjunction with other soil/site relationships. Few studies have investigated these factors. In the southeastern United States, Veech and Boyce (1964) found lower numbers of soil microfungi, actinomycetes, and bacteria in soils from a severely diseased slash pine (Pinus elliotii Engelm.) plantation than from a relatively unaffected stand. Both stands had similar cultural histories. Also, Adams and others (1964) found more stylet-bearing nematodes under diseased slash pine than in uninfected trees in various sites.

Srago (1973) and Srago and Cobb (1974) studied various soil physical and microbiological factors affecting H. annosum in California. They showed that the fungus was inhibited by soil microorganisms, and that hyphae of the fungus lysed after exposure to microbially active soils, demonstrating the inability of this pathogen to grow more than a few millimeters through the soil. Microbial inhibition may explain reduced spread of the pathogen in certain stands. In other situations, increased populations of soil microorganisms have been observed on severely disturbed sites that have been stabilized by establishment of grasses (Otrosina and others 1984). It is interesting to note that increased organic matter and grass cover are highly correlated with reduced disease severity in pine stands in the southern United States (Froelich and others 1966). Inhibition of H. annosum by the interaction of saprotrophic fungi on different soil substrates has been demonstrated (Curl and Arnold 1964).

Besides possible direct inhibition of H. annosum by soil microbial activity, reduced disease spread in certain stands may be the result of increased decomposition rates of distal portions of root systems of infected stumps. Rapid invasion of distal portions of root systems by saprotrophic fungi can reduce the probability of infection of adjacent uninfected trees by reducing root contacts with infected tissue. These proposed mechanisms are highly speculative, and much research relating soil microbial activity and other soil factors to disease severity in the western United States remains to be done. Knowledge of the factors and mechanisms relating soil characteristics to disease severity has obvious value in the development of predictive models for the land manager.

HOST-PARASITE INTERACTIONS

Characteristics of the Infection Process in Living Host Tissues

Next, we will discuss the current information on mechanisms of disease resistance and the host-pathogen interactions potentially affecting it.

Resistance begins to play a role at the point in the disease cycle when the fungus has become established in the stand (figs. 1 & 2). At this point, long-lasting reservoirs of inoculum from previously infected stumps and large root segments are present and serve as sources of infection for adjacent trees. Under conditions present in the western United States, inoculum can remain viable for 60 years in many sites (Morrison and Johnson 1978). There is currently little information on resistance of coniferous tree species to H. annosum root disease or to any other diseases of woody root tissues. Knowledge and use of resistance to this root disease is one of the potential long-term solutions to the problem.

One of the most definitive series of experiments designed to study mechanisms of host response to infection by H. annosum was conducted by Shain (1967, 1971) and Shain and Hillis (1971). They described reaction zone formation in Norway spruce (Picea abies (L.) Karst) and loblolly pine in response to infection by H. annosum and noted similarities and differences between these two species. In loblolly pine, the reaction zone is a nonspecific response to sapwood injury and is qualitatively similar to heartwood formation. The reaction zone moves up the stem or root as the fungus advances, leaving behind the pathological heartwood formed in former sapwood. This pathological heartwood is characterized by death of parenchyma, loss of starch, accumulation of phenols, and increases in oleoresin content. The dynamic, advancing front of the pathogen at the reaction zone is characterized by release of phytotoxic metabolites by the fungus or host, subsequent death of parenchyma, resin accumulation, partial inhibition of fungal advance (possibly a key process in host resistance), metabolism of accumulated fungitoxic compounds by the fungus, and decay of host cells. Unlike loblolly pine, the reaction zone of Norway spruce differs in that there is less accumulation of fungitoxic compounds in spruce heartwood than in pine, possibly explaining the typical heartrot in spruce caused by H. annosum. Spruce reaction zones are not resin soaked as in pine. The other characteristics of reaction zones discussed earlier are similar in both species and serve to slow progress of the pathogen.

H. annosum does not infect living tissues or cells. Living host cells are killed in advance of the fungus either by hypersensitive host reactions or by production of toxic metabolites of fungal origin (Shain 1971). A sesquiterpene, given the trivial name fomannosin, has been characterized from pure cultures of H. annosum (Bassett and others 1967). Pure preparations of this compound were shown to induce reaction zone formation near the point of application that has characteristics similar to those observed during fungal pathogenesis. Fomannosin is apparently produced in senescing cultures of H. annosum as a product of hyphal autolysis, but it has not been detected in host tissues undergoing infection by H. annosum. Oleoresins accumulating in the reaction zone inhibit the fungus (Cobb and others 1968) and may stimulate fungal synthesis and translocation of fomannosin from older mycelium in the food base (Bassett and others 1967). The balance of host defense mechanisms on one hand versus fungal compounds involved in pathogenesis on the other may explain observed variability in tree-to-tree spread as well as the difficulty encountered in experimentally establishing infections by artificial inoculation of larger trees (Shain 1967). That H. annosum usually requires a large food base for infection of living trees makes the study of resistance even more complex. Understanding the interactions among these processes is essential to finding quantifiable disease resistance mechanisms.

Effect of stress on infection

Intuitively, we can state that any factors that diminish the capacity of the host tree to respond to infection will enable more rapid host colonization by the fungus. Several studies involving different types of stress support this statement.

In a study of the effects of photochemical oxidant on susceptibility of ponderosa and Jeffrey pine (Pinus jeffreyi Grev. & Balf.) to infection by H. annosum, James and coworkers (1980b) found greatly increased vertical colonization of stumps to be associated with severe oxidant injury of the host tree before cutting. Their data indicate a sharp decrease in stump colonization rate by the fungus in stands relatively uninjured by photochemical oxidant. Also, James and coworkers (1980a) showed increased susceptibility of roots of oxidant-damaged ponderosa pine to infection by H. annosum. They noted that resin production was greatly diminished in infected roots of trees severely injured by air pollution, an indication of diminished host resistance.

Suppression has also been implicated in increased infection by H. annosum. Shain (1967) reported penetration of the fungus in sapwood of suppressed loblolly pine to be nearly nine times that of non-suppressed trees. The effects of suppression may play an important role in the incidence and spread of H. annosum in many overstocked pine and true fir stands.

Another potentially important factor affecting this root disease is water stress. Towers and Stambaugh (1968) found soil moisture stress decreased the resistance of roots of loblolly pine to infection by H. annosum, but there have been no studies on the effects of drought on spread or infection rates in stands in the west. Moisture is deficient in many soils and stands in the western United States during the hot, dry summer months. Such situations are common in the California Sierra Nevada and can be severe during drought years when the winter snow pack is considerably below optimal. Increased infection and spread can lead to buildup of bark beetle

populations and further mortality of stressed trees (Ferrell and Parmeter, in press).

SUMMARY

Numerous factors can affect the development and severity of annosus root disease. Stump susceptibility and infection are influenced by temperature, host species, competing or antagonistic microorganisms, inoculum potential, and the interactions among these and other factors. Successful colonization of woody tissues of stumps and subsequent infection of adjacent trees are determined by interactions of insects, host stress, soil type, soil microbial activity, host species, host-fungus interactions, presence of other root-infecting fungi such as Armillaria, and root grafting or root contacts. Much of our knowledge of these processes in forests of the western United States has been derived from studies conducted on pine species. Little is known about how factors affecting the disease process interact in true fir, and the processes associated with wound and other non-stump originated infections in Abies and other conifer genera. A more complete understanding of biological and ecological relationships between various hosts and H. annosum will allow development of sound silvicultural methods that will minimize losses to this disease.

REFERENCES

Adams, John T; Witcher, Wesley; and Lane, C.L. 1964. Microorganisms in soil from Fomes annosus infected pine stands. USDA Plant Disease Reporter 48:114-118.

Alexander, S.A.; Skelly. J.M.; Morris, C.L. 1975. Edaphic factors associated with the incidence and severity of disease caused by Fomes annosus in loblolly pine plantations in Virginia. Phytopathology 65:585-591.

Bassett, Colin; Sherwood, R.T.; Kepler, J.A.; and Hamilton, P.B. 1967. Production and biological activity of fomannosin, a toxic sesquiterpene metabolite of Fomes annosus. Phytopathology 57:1046-1052.

Bega, Robert V. 1963. Fomes annosus. Phytopathology 53:1120-1123.

Cobb, F. W., Jr.; Barber, H. W. 1968. Susceptibility of freshly cut stumps of redwood, Douglas-fir, and ponderosa pine to Fomes annosus. Phytopathology 58:1551-1557.

Cobb, F.W., Jr.; Krstic, M.; Zavarin, E.; Barber, H.W., Jr. 1968. Inhibitory effects of volatile oleoresin components on Fomes annosus and four Ceratocystis species. Phytopathology 58:1327-1335.

Cobb, F. W., Jr.; Schmidt, R. A. 1964. Duration of susceptibility of eastern white pine stumps to Fomes annosus. Phytopathology 54:1216-1218.

Cowling, Ellis B.; Kalman, Arthur. 1964. Influence of temperature on growth of Fomes annosus isolates. Phytopathology 54:373-378.

Curl, E.A.; Arnold, M. M. 1964. Influence of substrate and microbial interactions on growth of Fomes annosus. Phytopathology 54:1486-1487.

Driver, C.H.; Ginns, J.H., Jr. 1969. Ecology of slash pine stumps: fungal colonization and infection by Fomes annosus. Forest Science 15:2-10.

Drummond, D.B.; Bretz, T.W. 1967. Seasonal fluctuations of airborne inoculum of Fomes annosus in Missouri. Phytopathology 57:340. Abstract.

Edmonds, R.L.; Leslie, K.B.; Driver, C.H. 1984. Spore deposition of Heterobasidion annosum in thinned coastal western hemlock stands in Oregon and Washington. Plant Disease 68:713-715.

Ferrell, George T.; Parmeter, John R., Jr. 1989. Interactions of root disease and bark beetles. (These proceedings).

Froelich, R.C.; Dell, T.R.; Walkinshaw, C.H. 1966. Soil factors associated with Fomes annosus in the Gulf states. Forest Science 12:356-361.

Froelich, R.C.; Kuhlman, E.G.; Hodges, C.S.; Weiss, M.J.; Nichols, J.D. 1977. Fomes annosus in the South - guidelines for prevention. USDA Forest Service, State and Private Forestry, Southeastern Area, Atlanta, Georgia. 17pp.

Gooding, G.W., Jr. 1964. Effect of temperature on growth and survival of Fomes annosus in freshly cut pine bolts. Phytopathology 54:893-894. Abstract.

Himes, W.E.; Skelly, J.M. 1972. An association of the black turpentine beetle, Dendroctonus, terebrans and Fomes annosus in loblolly pine. Phytopathology 62:670. Abstract.

Hodges, Charles S., Jr.; Koenigs, Jerome W.; Kuhlman, E. George; Ross, Eldon W. 1971. Fomes annosus: A bibliography with subject index. Res. Paper SE-84. Asheville, NC: Southeastern Forest Experiment Station, Forest Service, U.S. Department of Agriculture; 75p.

Hunt, R.S.; Cobb, F.W., Jr. 1982. Potential arthropod vectors and competing fungi of Fomes annosus in pine stumps. Canadian Journal of Plant Pathology 4:247-253.

Hunt, Richard S.; Cobb, Fields W., Jr.; Parmeter, John R., Jr. 1976. Fomes annosus stump colonization and fungus development in the California mixed conifer type. Canadian Journal of Forest Research 6:159-165.

Hunt, R.S.; Wilcox, W.W.; Cobb, F.W., Jr. 1974. Resistance of stump tops to colonization by Fomes annosus. Canadian Journal of Forest Research 4:140-142.

James, R.L; Cobb, F.W., Jr. 1984. Spore deposition by Heterobasidion annosum in forests of California. Plant Disease 68:246-248.

James, R.L.; Cobb, F.W., Jr.; Miller, P.R.; Parmeter, J.R., Jr. 1980a. Effects of oxidant air pollution on susceptibility of pine roots to Fomes annosus. Phytopathology 70:560-563.

James R.L.; Cobb, F.W., Jr ; Wilcox, W.W. 1980b. Effects of photochemical oxidant injury of ponderosa and Jeffry pines on susceptibility of sapwood and freshly cut stumps to Fomes annosus Phytopathology 70:704-708.

Koenigs, Jerome. W. 1960. Fomes annosus: a bibliography with subject index. Occasional Paper 181. New Orleans: Southern Forest Experiment Station, Forest Service, U.S. Department of Agriculture; 35 p.

Kuhlman, E.G. 1969a. Survival of Fomes annosus spores in soil. Phytopathology 59:198-201.

Kuhlman, E.G. 1969b. Number of conidia necessary for stump infection by Fomes annosus. Phytopathology 59:1168-1169.

Kuhlman, E.G; Hendrix, F.F. 1964. Infection, growth rate, and competitive ability of Fomes annosus in inoculated Pinus echinata stumps. Phytopathology 54:556-561.

Morris, C.L; Frasier, D.H. 1966. Development of a hazard rating for Fomes annosus in Virginia. U.S. Department of Agriculture Plant Disease Reporter 50:510-511.

Morrison, D.J.; Johnson, A.L.S. 1978. Stump colonization and spread of Fomes annosus 5 years after thinning. Canadian Journal of Forest Research 8:177-180.

Otrosina, W.J.; Marx, D.H.; May, J.T. 1984. Soil microorganism populations on kaolin spoil with different vegetative covers. Reclamation and Revegetation Research 3:1-15.

Rishbeth, J. 1950. Observations on the biology of Fomes annosus with particular reference to East Anglian pine plantations. I. The outbreaks of the disease and ecological status of the fungus. Annals of Botany 14:365-383.

Rishbeth, J. 1951. Observations on the biology of Fames annosus, with particular reference to East Anglian pine plantations II. Spore production, stump infection, and saprophytic activity in stumps. Annals of Botany 15:1-21.

Rose, Sharon L.; Li, Chang-Yan; Hutchins, Anita Stiebrs. 1980. A streptomycete antagonist to Phellinus weirii, Fames annosus, and Phytophthora cinnamomi. Canadian Journal of Microbiology 26:583-587.

Ross, Eldon W. 169, Thermal inactivation of conidia and basidiospores of Fomes annosus. Phytopathology 59:1798-1801.

Ross, Eldon W. 1973. Fomes annosus in the southeastern United States: Relation of environmental and biotic factors to stump colonization and losses in the residual stand. U.S. Department of Agriculture Forest Service Tech. Bull. No. 1459. Asheville, North Carolina. 26p.

Shain, Louis. 1967. Resistance of sapwood in stems of loblolly pine to infection by Fomes annosus. Phytopathology 57:1034-1045.

Shain, Louis. 1971. Response of sapwood of Norway spruce to infection by Fomes annosus. Phytopathology 61:301-307.

Shain, Louis; Hillis, W.E. 1971. Phenolic extractives in Norway spruce and their effects on Fomes annosus. Phytopathology 61:841-845.

Srago, Michael D. 1973. The influence of soil biological and physical factors on the growth of Fomes annosus. Dissertation. University of California; Berkeley: 76 p.

Srago, Michael D; Cobb, Fields W., Jr. 1974. Influence of soil biological factors on the mycelial growth of Fomes annosus. In: Proceedings of the Fourth International Conference on Fomes annosus. Kuhlman E.G; ed. September 17-22, 1973. Athens, Georgia: Southeastern Forest Experiment Station, Forest Service, U.S. Department of Agriculture; pp. 218-226.

Towers, Barry; Stambaugh, W. J. 1968. The influence of induced moisture stress upon Fames annosus root rot of loblolly pine. Phytopathology 58:269-272.

Veech, Joseph A; Boyce, John S. 1964. Soil microorganisms in two Georgia slash pine plantations with annosus root rot. U.S. Department of Agriculture Plant Disease Reporter 48:873-874.

Yde-Andersen, A. 1962. Seasonal incidence of stump infection in Norway spruce by air-borne Fomes annosus spores. Forest Science 8:98-103.