History

Annosus Root Disease in Europe and the Southeastern United States: Occurrence, Research, and Historical Perspective'

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Abstract.--The history of annosus root disease in Europe and the southeastern United States is reviewed in prefacing the focus of this symposium on the disease as it occurs in the western United States. The topic is developed mostly from world literature on the disease published since mid-1970. The occurrence of annosus root disease in both plantations and natural stands of conifers is discussed, with particular emphasis on disease range, host-pathogen variability, and environmental influences. Concluding attention is given to re-examination of the U.S.D.A. Forest Service guidelines for management of annosus root disease in the southeastern United States in the light of current understanding and the continuing need for improved technology transfer.

The "death circle" in Hartig's (1894) textbook description of annosus root disease nearly a century ago has become an all too familiar sight in conifer stands throughout the north temperate region. Even then, he recognized tree-to-tree spread of Trametes radiciperda Hartig (equals Heterobasidion annosum (Fr.] Bref.) via root contacts, but it was not until more than 50 years later when Rishbeth (1951) made the connection by showing the potential for disease initiation through plantation thinning and basidiospore colonization of fresh-cut stumps, thereby reaching adjacent trees. This mode of spread has accounted for a long history of damage in Europe where losses occur as: (1) mortality of residual stems in young conifer plantations, following and related to the extent and number of thinnings (Greig 1984) and (2) wood loss from butt and heart rot of old-growth timber, particularly Norway spruce (Picea abies Karst.), on previously cut-over lands (Dimitri 1973). The total loss from such impacts has been estimated for the countries of the European Economic Community alone at $35 million annually (Dimitri 1973).

In the eastern United States and Canada, where H. annosum has been known mycologically since the 1980's (Ross 1975), disease occurrence was not recognized until the late 1940's as plantations reached thinning age at an increasing number of locations (Kuhlman and others 1976). A major research effort, spearheaded by the USDA Forest Service, soon followed, especially in the southeastern United States, where vast monocultures of fast-growing, densely planted southern pines required frequent thinning and thus were considered vulnerable. As studies evolved, it became evident that the mode of spread in the principal southern hard pines conformed to that of Pinus spp. in Europe (Kuhlman and others 1976), whereas butt rot and windthrow of live stems are more common in eastern white pine (P. strobus L.), western hemlock (Tsuga heterophylla [Raf.] Sarg.) (Edmonds and others 1984), and perhaps other less resinous species, much like that of spruce in Europe. Additional data on disease impact showed significant reduction in height and trunk diameter growth in loblolly pine (P. taeda L.) (Alexander and others 1975, Bradford and others 1978) and slash pine (P. elliottii Engelm. var. elliottii) (Froelich and others 1977) during the few years preceding tree death.

In the last two decades in the United States, the emphasis in research on H. annosum has shifted almost exclusively to the western states where the pathogen attacks a broad array of tree species in a variety of environments and where its potential in second-growth forest management is a mounting concern because of the historical record of the disease elsewhere. Now, after the passage of nearly 100 years, more than cursory attention, and two bibliographies (Koenigs 1960, Hodges and others 1971), the literature base on the disease is conservatively estimated at 1800 research papers and reports.

The focus of this paper is drawn primarily from the literature published since the mid-1970's, as identified by the last IUFRO (International Union of Forest Research Organizations) conference solely devoted to annosus root rot (Kuhlman 1974), the eastern states status report by Ross (1975), and the disease management recommendations of Kuhlman and others (1976). These accounts basically closed the ledger on USDA Forest Service research on the disease in the eastern United States. With research continuing so actively in the west ever

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since, there is ample justification for naming this symposium "... in Western North America." Citations to western work herein, however, will be selectively limited in deference to this being the historical review topic of Smith (1989) that immediately follows in this symposium.

OCCURRENCE

Host-Pathogen Range

The incidence of H. annosum is greatest where plantation culture and thinning of conifers are practiced and less so in natural stands, due in part to a diminished root-contact potential and the likelihood of intervening non-host species in mixed stands. Judging from the comprehensive host list of Sinclair (1964) and subsequent updatings (Greig 1976, Webb and Alexander 1985), there seem to be few coniferous species that have not been reported as hosts. A number of hardwoods and woody shrubs are also listed, but damage of any consequence is reported only from continental Europe on Alnus and Quercus spp. (Dimitri 1973) and from Great Britain on Q. borealis Michx. and Nothofagus obliqua (Mirb.) Blume underplanted to Pinus spp. (Greig 1974). It remains to be seen whether the findings of H. annosum in several Central American countries (Greig and Foster 1982) and in eastern Australia (Shain and Bolland, in Kuhlman 1974) pose any threat for ultimate spread to extensive exotic plantings of known hosts at various locations in the southern hemisphere, particularly Australia and New Zealand.

Given its broad host range and its long history of disease occurrence (Dimitri 1973, Ross 1975), H. annosum must be considered present throughout the north temperate region wherever local concentrations of host species exist. A facultative parasite, the fungus utilizes many substrates for its survival and reproduction. Basidiospores of H. annosum colonize freshly exposed wood of conifers in newly cut stumps, which are the primary mode of stand access (Rishbeth 1951); in logging slash; in stem wounds, as limited to western hemlock and true firs, Abies spp. (Aho and others 1983); and in roots (Siepmann 1976). While root-contact infection is the common pattern of spread (Rishbeth 1951, Hodges 1969), both the circumstantial evidence of significant levels of root infection in unthinned loblolly pine (Webb and others 1981) and the successful inoculation of roots with conidia in undisturbed natural soil (Kuhlman 1969) supports the view that basidiospore percolation downward in soil accounts for at least some direct root infection, perhaps more than is currently recognized. Fortunately, H. annosum behaves only as a stump saprophyte in the majority of thinnings, and root-contact progression to stand infection does not occur on many sites. Only in the southeastern United States has a high hazard relationship with deep sands (Alexander and others 1975, Kuhlman and others 1976) been used to achieve, albeit limited, advantage in disease management.

H. annosum fruits most consistently in applanate form at duff level on infected trees and 1- to 2-year-old stumps and, in resupinate form, dorsally on slash and root sprung/thrown roots. Basidiocarps, which initially appear as rubbery white pustules, are mostly annual in the south and tend to be perennial further north. Basidiospore inoculum is generally available throughout the year in the south (Ross 1973), in the northeast (Stambaugh and others 1962, Sinclair 1964), and in the northwest (Edmonds and others 1984), but it declines relative to rising summer temperatures, and dwindles to only trace amounts in southernmost latitudes (Ross 1973). Just how uniform this inoculum is over the time and space of disease occurrence has been the subject of much speculation and, until recently, little understanding.

Host-Pathogen Variability

World source isolates of H. annosum have shown some remarkable similarities in culture (Rishbeth 1987) but also notable differences in other physiological characteristics, including virulence, as reported by Worrall and others (1983). The potential for linking virulence (that is, relative disease capacity) of the fungus with host origin became tenable with the discovery in Finland (Korhonen 1978) of two intersterility groups: group S causes butt-rot in Norway spruce and kills young pines in the near vicinity; group P kills pines of all ages as well as young spruce, junipers, and even some hardwoods. Both groups have been identified in the western United States but only P has been detected to date in the east (Harrington and others 1989). The host specificity implications of these findings were applied by Worrall and others (1983) in evaluating observed elevational differences in the incidence of H. annosum in pine (P. ponderosa Dougl. ex Laws)-fir (A. concolor [Cord. & Glend.] Lindl. ex Hildebr.) mixtures in California. Seedling inoculations of both species with isolates from their range showed significant differential interaction between isolate groups and host species; pine isolates were most lethal on pine and least so on fir, while the lethal effect of the isolates from fir was intermediate between the pine extremes on both. Alternative interpretations were explored and the need for further evaluation was indicated.

The sexual cycle of H. annosum also was resolved by Korhonen (1978) and later substantiated by Chase and Ullrich (1983): they showed it to be heterothallic, multiallelic, and unifactorial. Armed with this genetic information, Chase and Ullrich (1983), working with monobasidiospore isolates from basidiocarps on red pine (P. resinosa Ait.) in four separate plantations in Vermont, and Stenlid (1985), with direct isolations from the butt of infected trees in a 120-year-old Norway spruce stand in Sweden, were able to detect multiple incompatibility alleles and thus analyzed population structure as patterns of spread. The results from spruce were more definitive for clonal patterns of spread; the largest area was 30 m in diameter and involved 13 trees, whereas the Vermont study suggested that infection centers commonly develop from multiple inoculations, rather than by progressive vegetative extension of the fungus; the disparity is probably explained by the use of markedly different isolate derivations between the two studies. In further broad screening of isolates, Chase and Ullrich (1985) found and reported mutagenesis in H. annosum for the first time; this further confirms the potential for genetic variation in the fungus as suggested by their observations, and those of many others, of the multinucleate condition of hyphal cells. This work also described the most reliable methods yet reported (45 percent success) for promoting the fruiting of H. annosum heterokaryons in culture and their application in routine analysis of genetic criteria.

These recent advances which have resulted in better understanding of, and have stimulated further investigation of, the genetic diversity of H. annosum, may well dampen the search for host resistance. Screening for resistance continues to receive emphasis in Europe, in spite of problems resulting from the methodology and from the long-term nature of the work. Norway spruce has received the most attention in this regard and, without going into detail, Johansson and Unestam (1982) furnish a good review of both old and new approaches for evaluation of and selection for resistance.

Environmental Influence

Whether a given host tree species is inherently susceptible or resistant, the incidence and severity of attack by H. annosum in that host population are mediated by the site characteristics or growth environment. Since soil is the growth medium for root diseases, it is most influential in governing disease development, to the extent with annosus root rot, that some, if not the majority, of stump-colonization sites do not result in disease (Kuhlman and others 1976), nor does the rate of stump colonization always correlate with subsequent disease severity (Ross 1973). Thus, development of reliable predictors for segregating high hazard sites before stand thinning would be operationally advantageous. It would permit focusing disease management efforts only on areas with high potential for spread of the pathogen. Most correlations, to date, have been broadly qualitative and too inaccurate for regionwide application (Kuhlman, in Dimitri 1980).

Soil characterization of annosus root rot has been featured in investigations, first in England and later in the southeastern United States. In England, disease severity is greatest on naturally alkaline (pH > 6) soils or on former agricultural soils, whereas on acid-heathland soils, the disease is less severe and mortality rarely exceeds 5 percent of the planted crop (Greig 1984). In a survey across the entire southeastern United States, high-hazard sites that averaged losses > 5 percent of the residual stand were identified by deep (> 10 inches) sandy or silty soils (Kuhlman and others 1976). Alexander and others (1975), in Virginia, compared high-hazard and low-hazard plots in thinned loblolly pine and found root infection rates of 32.6 and 7.8 percent, respectively; of the 14 soil parameters measured on all plots, only sand, noncapillary pores, and bulk density correlated positively with high disease incidence. The high order of root contacts (2.5X) and resultant root infection (5X) detected in high-hazard versus low-hazard soils by Kuhlman and others (1976) was not detected in this study. Instead, several pockets of infection, with each bounded by uninfected tissue, were found on individual roots. These observations and the results of spore percolation tests and previous mechanical excavation studies that showed 5.7 percent infection of 648 loblolly pines in unthinned stands (Webb and others 1981) suggest that direct root infection by spores may be as important as root infection by way of root contacts. If this is so, high-hazard sands would seem to directly influence root infection more than the relatively protected avenue of vegetative spread within roots. Litter accumulation was not definitive in hazard classification studies (Kuhlman and others 1976); however, the fact that prescribed burning reduced cumulative infection 7 years after stump inoculation with H. annosum in thinned plots by an average of 45 percent of that in unburned plots (Froelich and others 1978), indicates that some factor associated with the litter may play a role in the epidemiology of annosus root disease.

Site hazard also has been used to rate the possible interaction between annosus root disease and predisposition of a host tree to bark beetle attack. Alexander and others (1981) selected plots in Virginia, Texas, and Georgia in which loblolly pine had been recently attacked by the southern pine beetle (Dendroctonus frontalis Zimm.) along with uninfested control plots on high-hazard sites in thinned plantations and on low-hazard sites in unthinned natural stands. They found mean H. annosum colonization of excavated root systems in beetle-infested and uninfested control plots to be 23.1 and 10.9 percent, respectively, and that beetle-infested trees had produced 28 percent less radial growth for the last 1-5 years than otherwise similar trees. They concluded that trees preferred by the beetle were being stressed by H. annosum prior to attack and that this stress resulted in reduced radial growth.

Other environmental factors whose interactions with infection of conifers by H. annosum have been reported are air pollutants, as included in Horn's (1985) review. The most comprehensive studies are those of James and others (1980a, 1980b, 1982) and James and Cobb (1982) on the effects of ozone (0_3) on the H. annosum-ponderosa pine/Jeffrey pine (P. jeffreyi Grev. and Balf.) pathosystem in California. They found: a very substantial effect of 0_3 on the rate of increase of H. annosum in the hosts (seedlings) subjected to chronic injury; that surface area and vertical colonization by H. annosum were significantly greater in stumps from severely oxidant-injured host trees; that *in vitro* effects of 0_3 at field dosages on sporulation, spore germination, and growth of H. annosum showed little potential for altering disease epidemiology; and that 0_3 had not influenced the virulence of H. annosum in comparative testing of isolates taken from chronically exposed and pollutant-free sites.

Air pollution aspects in the complex and unresolved etiology of widespread forest decline or "waldsterben" in Europe have focused some attention on the predisposition of trees to forest pests, but primarily bark beetles and defoliators (Baltensweiler 1985). From a disease standpoint, Grzywacz and Wazny (1973), in Poland, sampled the incidence of six forest pathogens along an $S0_2$ gradient that extended 4.3 km from an industrial center and found that all responses followed a sigmoid curve, with H. annosum peaking at 0.5 percent infection 2 km from the source, and for comparison, Armillaria mellea (Vahl.) Quel. peaking beyond at 3.5 km with 1.2 percent infection.

DISEASE MANAGEMENT

Minimizing Losses to *Heterobasidion annosum*

Termination of USDA Forest Service research on annosus root disease in the southeastern United States was summarized by publication (Ross 1975, Kuhlman and others 1976) of recommended practices to control the disease in southern pine plantations, abbreviated as follows:

1. Plant to wider spacings and delay or reduce thinnings
2. Identify site hazard units and focus control procedures on high-hazard sites
3. Thin from April through August south of 34°N latitude (approximately Atlanta, GA); at all other times southward, and at all times northward, use stump protectants when thinning stands on high-hazard sites
4. Treat fresh stumps immediately with dry granular borax, or if biological control is preferred, use Phlebia (equals Peniophora) gigantea (Fr.) Massee
5. No special precautions are needed in replanting sites heavily damaged by H. annosum
6. Plant wisely, using longleaf pine (P. palustris Mill.), for example, because it does well on the deep sands of high-hazard sites and is more resistant to H. annosum than either loblolly pine or slash pine

Wider spacing is still advantageous because it lengthens the time to first thinning and reduces the number of thinnings and the potential for root contact (Kuhlman and others 1976) but as Ross (1975) cautions, plant at as wide a spacing as optimum productivity permits without increasing the hazard from fusiform rust (Cronartium quercuum [Berk.] Miyabe ex. Shirai f. sp. fusiforme). The closer spacing rule (plant sufficiently close to inhibit tree growth and thus rust infection) is no longer considered compatible with the economics of plantation establishment which calls for underutilization of the site, approximately 450 stems/A. at age 5, until trees reach minimum merchantability (Belcher and others 1977, Powers and others 1981). At this rust survival density, spacing would have adjusted at about 10 x 10 ft. (about 3 m^2) which is considered near optimum for productivity in loblolly pine (Shepard 1974).

Site hazard prediction to delineate the need for preventive control of annosus root disease is clearly desirable. However, neither qualitative nor quantitative guidelines have proven adequate to date on a regionwide scale (Kuhlman, in Dimitri 1980). Highly correlative soil parameters in one area, such as Virginia (Alexander and others 1975), do not necessarily apply elsewhere. For example, 25 years of surveillance of H. annosum in approximately 2000 acres of planted loblolly pine on the Duke Forest has seen stump colonization rates, usually in excess of 50 percent, in thinnings on a range of soils, including deep sands, but only two stands have suffered damage, one with 17 percent residual tree infection on a clay loam and the other with 26 percent infection on sand over a clay pan at 1 foot (0.304 m) depth. Both areas were rated intermediate to low hazard for H. annosum according to guidelines then available (Morris and Frazier 1966).

The success of summer thinning south of 34°N latitude is predicated on high temperatures reducing spore availability and elevating daytime stump surface temperatures (• 35C) that result in no stump colonization (Ross 1973). Careful monitoring of the weather when opting for summer thinning is recommended by Witcher and Lane (1980) who reported sufficient H. annosum spread to slash pine adjacent to inoculated and control stumps exposed monthly through the year near Aiken, South Carolina, to seriously question the existence of a summer "safe" period. However, the study site is only 30 miles south of 34°N latitude and some inconsistency from year to year might be expected that close to the line.

Chemical stump treatments to prevent stand invasion by H. annosum in first and subsequent thinnings have been widely investigated, but in the southeastern United States, powdered borax is considered the most effective, cheapest, and safest chemical to date (Kuhlman and others 1967). Borax leaches into the top few inches of freshly cut stumps where it remains toxic to H. annosum for up to 2 years, thus allowing sufficient time for competitive soil saprophytes to gain entrance and colonize the declining roots of treated stumps. At demonstrated treatment costs of less than $7.50 per hectare (Hodges 1974), borax use on high-hazard sites is estimated to yield cost: benefit ratios of 1:3 to 1:14 (Kuhlman, in Dimitri 1980).

Use of P. gigantea as an alternative for borax treatment is recommended, especially where a limited amount of H. annosum is already present in the stand, where use of chemicals is undesirable, or with mechanical harvesters (Ross 1973). Discovery of the biocontrol potential of P. gigantea is attributed to Rishbeth in England, where studies on applied biology have led to its operational use in pine thinning (Rishbeth 1979, Greig 1984). Like H. annosum, P. gigantea is a common natural colonizer of pine stumps, but it is an obligate saprophyte with a higher growth rate and range than that of H. annosum (Blakeslee and Stambaugh 1974), which permits it to gain initial dominance over and ultimately to exclude the pathogen in dual colonization of stumps. The mere presence of P. gigantea fruiting on colonized stumps, however, is no assurance of complete root colonization, as shown by Blakeslee (1970) who found at least one root per stump colonized distally by H. annosum in 33 percent of 80 excavated stumps bearing P. gigantea fruiting. This is yet another example of direct root infection by H. annosum, but the potential for spread from one partially occupied root compared to the total stump and root mass would seem to be rather limited. P. gigantea, as oidial suspensions, has been applied successfully in water and chain-saw oil carriers, and most recently, into stumps left from mechanical tree harvesting (Ross and Hodges 1981).

The recommendation that no special precautions are needed in replanting sites heavily damaged by H. annosum has been further substantiated by Kuhlman (1986), who found minimal impact of 6 percent or less at age ten years among trees of seven coniferous tree species planted on two annosus root disease sites 22 years previously. Webb and others (1982) recorded high levels (54-83 percent) of stump colonization by H. annosum on two low-hazard Florida sites after clearcutting and site preparation, but did not find H. annosum in slash pine seedlings 18 months after planting them in those areas. Stump breakdown is quite rapid under the temperature regimes of the southeastern United States, whereas in the northern climates and especially in Europe, H. annosum can persist in stumps for decades and associated stand regeneration seedling losses are not uncommon. For this reason, the feasibility of stump extraction in high-hazard stands is under investigation in England (Greig 1984).

The options for substituting more resistant species in planting high-hazard sites seems rather limited. While longleaf pine is a wise choice based on resistance, its growth rate is not comparable to that of loblolly and slash pine, and this alone may nullify its use.

Finally, in the context of the objectives of this symposium (that is, knowledge and technology transfer), use of the preceding recommendations in southern forestry should pose a challenge to all. A 1974 questionnaire revealed that foresters were not well informed about the procedures for managing annosus root disease (Kuhlman, in Dimitri 1980); then and now, this information was/is available and there is no excuse for not using it.

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