

Is *Heterobasidion annosum* Poorly Adapted to Incite Disease in Cool, Wet Environments?¹

Charles G. Shaw, III²

Abstract: An argument is advanced to suggest that infection and damage caused in coniferous forests by *Heterobasidion annosum* are markedly less severe, and survival of the fungus less common, under cool, wet conditions than in other climates. This premise is supported by the author's incisive insights, experience in southeastern Alaska, and data from this area and from other sources. In general, frequent rains reduce the population of airborne spores and wash many of them from stump surfaces. Cool temperatures reduce evaporation of water which helps to maintain a high moisture content in stumps that hinders development of *H. annosum*. This cool, wet condition also lowers overall metabolic rates and reduces the availability of oxygen, which further inhibits infection by, and survival of, *H. annosum* in stumps. In contrast, primarily saprophytic *Armillaria* spp. survive under these same conditions and, through rather rapid colonization of stumps and roots, limit the opportunity for whatever colonies of *H. annosum* do become established to spread and incite disease in surrounding trees.

Heterobasidion annosum (Fr.) Karst. damages numerous coniferous tree species growing under various, primarily temperate, environmental conditions in many localities around the world (Pegler and Waterston 1968). It is the purposely provocative premise of this paper, however, that damage from this organism is markedly less in cool, wet environments than in those characterized by either warm and wet (the southeastern United States), warm and dry (the east side of the Sierra Nevada mountains and south-central Oregon), or cool and dry climates (interior Scandinavia).

I developed this hypothesis of limited impact from annosus root disease in cool, wet environments after years of often being cold and sopping-wet while doing fieldwork in southeastern Alaska. That work revealed limited infection by, and survival of, *H. annosum* in

stumps of Sitka spruce (*Picea stichensis* (Bong.) Carr.) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.)--and no damage caused in standing trees (Shaw 1981a, 1989). Additional data to support the hypothesis were selectively obtained from other sources.

THE SITUATION IN SOUTHEASTERN ALASKA

Over 160,000 ha of old-growth Sitka spruce/western hemlock forest have been clearcut harvested on the mainland and islands of southeastern Alaska (W. Farr, 1989, Research Mensurationist, Juneau Alaska, Personal Communication). Young stands of these species have regenerated naturally into the clearcut areas, generally with adequate stocking and vigorous growth (Harris 1974). At age 15-20 years, many of these stands are precommercially thinned--an operation that creates numerous stumps that may serve as infection courts for root disease fungi.

Spores of *H. annosum* and *Armillaria* spp. are relatively common in these young stands, even though basidiocarps of *H. annosum* are rare (Shaw 1981a,b), as are infections of large and small stumps of both of those tree species (Shaw 1981a, 1985, 1989, Tait and others 1985). In contrast, stumps frequently are colonized by *Armillaria* spp. (Shaw 1981a, 1985, 1989, Tait and others 1985), probably by contact of their roots with rhizomorphs or infected roots rather than by spores (Wargo and Shaw 1985). Nevertheless, few surrounding trees die.

Butt and stem decay are common in old-growth trees in the area. In old, affected stands, gross timber volumes have often been reduced by one-third or more (Farr and others 1976) by rot caused primarily by hymenomycetes--*H. annosum*, *Armillaria* spp., and *Phaeolus schweinitzii* (Fr.) Pat (Kimmey 1956). Even in these old-growth forests, however, sporophores of *H. annosum* are rare--as noted by Kimmey on an herbarium collection form filed at the Forestry Sciences Laboratory in Juneau, Alaska. In addition, T. Laurent (1981, forest pathologist, Juneau Alaska; personal communication) found no basidiocarps of *H. annosum*, although decay caused by it was common, during the dissection of 1776 trees to measure cull volumes at 67 locations in southeastern Alaska (Farr and others 1976). Several basidiocarps previously collected in southeastern Alaska and identified as those of *H. annosum* (Cooke 1955, Cooke and Shaw 1952) have been reexamined and found to be

¹ Presented at the Symposium on Research and Management of Annosus Root Disease in Western North America, April 18-21, 1989, Monterey, CA.

² Research Plant Pathologist and Project Leader, U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

those of Fomitopsis pinicola (Swartz: Fr.) Karst (R. Gilbertson, 1981, mycologist, University of Arizona; personal communication). During 9 years of collecting in southeastern Alaska, I gathered basidiocarps of H. annosum only once (Shaw and Florance 1979) and, even with a monetary bounty inducement, all students except one found none. Thus, the source of the airborne spore inoculum that does exist remains an enigma (Shaw 1981a, b). Perhaps conidia are involved (Florance and Shaw 1988, Shaw and Florance 1979).

As indicated, the results of several studies in southeastern Alaska showed limited stump colonization by H. annosum--an event which is considered to be a necessary precursor to development of damaging levels of disease caused by H. annosum in managed, young stands of Sitka spruce and western hemlock. Because of this situation, I have concluded (Shaw 1989) that, in southeastern Alaska, there is little likelihood that H. annosum will damage young, managed stands of Sitka spruce and western hemlock within the planned 90- to 120-year rotation. The question, however, still remains--Why not?

ENVIRONMENTAL CONDITION OF STUMPS

My data (Shaw 1981a, 1985, 1989) and those of Morrison (1976, Morrison and others 1986) indicate that H. annosum becomes a less common inhabitant of thinning stumps with movement northward along the west coast of North America. With movement north, lower temperatures (Farr and Harris 1979) and higher precipitation (Farr and Hard 1987) probably reduce the aerial spore population of H. annosum (Reynolds and Wallis 1966). The frequent and often heavy rains also are likely to wash many spores from stump surfaces. In Scotland, near the latitude of southeastern Alaska, Redfern (1982) suggests that infection of Sitka spruce stumps may be limited by high rainfall, and that on sites with high rainfall, H. annosum is absent from stumps with a high moisture content. These results resemble those found in southeastern Alaska where rain is common on any date (Farr and Hard 1987) and where the moisture contents (on a percent dry weight basis) of Sitka spruce and western hemlock stumps are often well over 100 percent (Shaw 1989).

Perhaps the high moisture content of these stumps reduces the availability of O_2 to a level that inhibits growth of H. annosum--a reason suggested for the lack of growth by H. annosum in white fir wetwood (Worrall and Parmeter 1983). The low temperatures common in southeastern Alaska could further affect fungal utilization of the limited O_2 available because they would lower overall metabolic rates of the pathogen and inhibit the evaporation of water from stump surfaces.

In vitro studies indicate that H. annosum (Worrall and Parmeter 1983), Armillaria spp.

(Smith and Griffin 1971, Worrall and others 1986), and an array of other wood-decaying fungi (Jensen 1967, Scheffer 1986, Worrall and Parmeter 1983) can grow at extremely low levels of available O_2 . Extrapolation of these in vitro results to decay of stumps in situ may not, however, be appropriate. Availability of O_2 in woody substrates is complicated by the patterns of water and air distribution in cell walls and pores, and how this distribution is affected by decay, moisture content, temperature, and other microenvironmental factors (Boddy 1983).

The moisture content of wood at which no air spaces would remain can be calculated if the specific gravity (SG) of the species in question and that of solid wood substance are known. I made such theoretical calculations, using 1.5 for the SG of solid wood substance, a value that is rather constant regardless of tree species (Wangaard 1950), and a range of values between 0.34 and 0.44 for the SG of wood from young Sitka spruce and western hemlock trees in southeastern Alaska (Farr 1973). These calculations indicate that, at a moisture content between 161 percent and 227 percent (depending on SG), all pore spaces in these woods would be water-filled and thus unavailable for air. Many stumps in southeastern Alaska have moisture contents that high (Shaw 1989).

The results of in vitro studies indicate that decay by certain fungi is inhibited in Sitka spruce wood at moisture contents around 150 percent and that decay stops near 190 percent (Boyce 1961)--a value within the theoretical range (as calculated above) for all available wood pore spaces to be water-filled. Redfern (1989) suggests that at moisture saturation levels somewhere between 70 and 80 percent, Sitka spruce wood is unsuitable for growth of H. annosum. Using a SG of 0.36, this 70 percent saturation level corresponds to a moisture content of 147 percent, a value that is exceeded in many of the stumps in southeastern Alaska, particularly Sitka spruce (Shaw 1989). Even though in southeastern Alaska, H. annosum frequently failed to colonize stumps with a moisture content below that necessary for total occupancy of the pore spaces by water, these calculations appear to support the contention that the reduced availability of O_2 may limit colonization of wet, cool stumps by H. annosum.

Growth of Armillaria spp. also may be reduced at extremely low levels of available O_2 (Smith and Griffin 1971, Worrall and others 1986). However, three features of stump colonization by this fungus, in contrast to that by H. annosum, could allow Armillaria spp. to survive in O_2 -poor stump wood:

- 1) Typically, H. annosum initially colonizes the more interior portions of stumps, while Armillaria initiates colonization between the bark and wood where more air is likely to be present.

- 2) Rhizomorphs of Armillaria spp., which

are common on interior surfaces of bark on these stumps and in the surrounding soil, can absorb O_2 at their growing tips (Smith and Griffin 1971). Although it is unclear how far back along the rhizomorph such absorbed O_2 might be transported and utilized, certain ions can be transported basipetally within rhizomorphs (Granlund and others 1985, Morrison 1975). Morrison (1976) also suggested that, when *Armillaria* grows from buried wood blocks with a high moisture content (170 percent), which thus have a limited supply of O_2 available in the food base, the O_2 requirement for fungal growth may be met by absorption from the soil atmosphere. Depending on the effective distance of O_2 transport along the rhizomorph, this mechanism may allow for growth of mycelium that is located in an O_2 -poor, wood environment.

3) Growth of *Armillaria* may be stimulated, even at low levels of O_2 (Worrall and others 1986), by ethanol (Weingold and Garroway 1966), which can be a by-product of metabolism in *Armillaria* spp. (Tarry 1968) and other common soil microorganisms often associated with *Armillaria* spp.

The frequent occurrence of *Armillaria* spp. in stumps from southeastern Alaska (Shaw 1989, Tait and others 1985) agrees with data from northern British Columbia (Morrison and others 1986) where 32 percent of the non-pine stumps were infected with an *Armillaria* sp. identified as North American Biological Species (NABS) V (Anderson and Ullrich 1979). The NABS of *Armillaria* spp. in stumps from southeastern Alaska are poorly understood, but NABS V and IX are common in the region (Shaw and Loopstra 1988). Because these two species have limited pathogenic capabilities on coastal species and sites (Morrison and others 1985, Shaw and Loopstra 1988, Wargo and Shaw 1985), their common occupancy of stump wood may deter spread of the limited *H. annosum* that does inhabit stumps, rather than act as an incitant of disease (Greig 1962, Morrison and Johnson 1978, Shaw 1981a, 1989).

WHAT DOES IT ALL MEAN?

Some might consider these ramblings to be rash, data-free analysis. I challenge those active in research on *H. annosum*, however, to critically evaluate the following scenarios, to find the researchable topics, and go at it! *Heterobasidion annosum* is markedly less able to incite disease in managed, young stands growing under cool, wet conditions than in other climates. This situation develops because in a cool, wet environment the airborne population of spores is reduced and many of those that are deposited on stump surfaces are washed away. In addition, low temperatures reduce evaporation of water which helps to maintain a high moisture content in stumps. This condition reduces the availability of O_2 , thereby inhibiting infection by, and survival of, *H. annosum* in stumps. Low temperatures also reduce the

ability of *H. annosum* to utilize the limited O_2 that is available by lowering overall metabolic rates. In contrast, the primarily saprophytic *Armillaria* spp. survive under those conditions and, through rather rapid colonization of stump and root wood, limit the opportunity for whatever *H. annosum* does become established to spread and incite disease in surrounding trees.

An alternate scenario is that *H. annosum* becomes established in aboveground wounds on standing, live trees rather than through contact with roots of infected stumps (Pawsey and Gladman 1965). Such aboveground wounds may offer a dryer, more hospitable infection court than water-logged stumps. They are likely the sites where *H. annosum* became established decades ago in old-growth trees in southeastern Alaska that now contain extensive decay columns caused by *H. annosum*. Even though substantial levels of stump infection are generally considered a prerequisite to development of damaging disease levels in managed, young stands, a preponderance of stem wounds, if infected with *H. annosum*, could be important in disease development. The importance of aboveground wound infection increases when there is an extended time period between thinning and final harvest (that is, 50 or more years), as is anticipated for managed, young stands in southeastern Alaska. Thus, this possibility also needs investigation.

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