Armillaria mellea and Decline of Red Spruce

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ABSTRACT

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Roots of 288 red spruce trees (*Picea rubens*) in mixed hardwood, transitional, and montane boreal forest in New England and New York were excavated and examined for colonization by *Armillaria mellea*. The fungus was associated with declining and dead spruce in all locations. The percentage of roots colonized by the fungus increased with increasing severity of decline symptoms but decreased with increasing elevation. In high-elevation boreal forests, where the decline has been documented to be most intense, 75% of the recently dead and severely declining trees were not colonized by *A. mellea*. Although *A. mellea* is involved in red spruce decline, it is not the major cause of the current regional episode of spruce decline and mortality.

Red spruce (*Picea rubens* Sarg.), a long-lived (300+ yr old), shade-tolerant forest tree (7), has declined in basal area and density within part of its native range in the northeastern United States (6,9,16). Decline intensity is positively correlated with elevation and is most prominent in the transitional and montane boreal forests (9). The primary cause of the decline has not been determined, although several biotic and abiotic stress factors and pathogens have been suspected, including acid deposition and *Armillaria mellea* (Vahl.: Fr.) Kummer (9).

A. mellea is a native root pathogen (14) that preferentially attacks stressed trees (8). Primary stress agents, such as phytophagous defoliating insects (22,23) air pollution (4,5,18), or drought (3), can increase host susceptibility to *A. mellea*. Changes in sugars, amino acids, and other metabolites in roots of stressed trees predispose them to infection by *A. mellea* and stimulate its growth (21,23). Infected trees exhibit dieback, culminating in mortality (8).

The purposes of this investigation were to determine the incidence and extent of colonization of red spruce by *A. mellea* and to relate these measures to elevation and decline.

MATERIALS AND METHODS

Nine study sites were chosen in Massachusetts, New Hampshire, New York, and Vermont on the basis of previous documentation of decline of red spruce (9). Study sites in order of sampling were Styles Peak, Peru, VT; Camel's Hump, Huntington, VT; Mt. Mansfield, Stowe, VT; Mt. Washington, Gorham, NH; Mt. Cushman–Hubbard Brook Forest, Thorton, NH; Mt. Greylock, Williamstown, MA; Paul Smiths' College, Paul Smiths, NY; Whiteface Mountain, Wilmington, NY; and Hunter Mountain, Hunter, NY. At each site, a transect was established along the contour in each vegetation zone. Not all zones were represented at each site because of differences in latitude and elevation. Transect 1 (elevation $<$750 m) was in a northern hardwood forest in which spruce occurs as scattered groups or individuals. Transect 2 (elevation 750–950 m) was in a transitional forest between the hardwoods and the conifer forest. Transect 3 (elevation 950–1,150 m) was in a montane boreal forest composed primarily of balsam fir (*Abies balsamea* L.) and red spruce. The objectives of the sampling were to determine the extent of colonization by *A. mellea* on roots of red spruce in various stages of decline. Each transect consisted of five plots at least 50 m apart. Each plot consisted of four dominant or codominant trees: one healthy tree with a full crown and green foliage, one mildly declining tree with a thinning crown and some dying of branch tips, one severely declining tree with a very thin crown and dieback of branches and/or top, and one recently dead tree with fine twigs and necrotic needles still present.

A plot was defined by the first recently dead tree sighted along a given transect and a tree in each of the three other decline categories that was closest to the dead tree. The next plot was defined by the next dead tree along the transect at least 50 m from the previous plot. After sampling the first two sites (10 plots), we determined that if *A. mellea* was not found on dead and severely declining trees within a plot, it was not found on mildly declining or healthy trees in the same plot. Therefore, at the two upper-elevation transects, if *A. mellea* was not present on any of the roots of the dead or severely declining trees in a plot, no mildly declining or healthy trees were excavated.

For trees that were excavated, all main lateral roots were uncovered to at least 1 m from the bole. After noting the presence of rhizomorphs of *A. mellea* on root surfaces, the roots and root collar were debarked to detect mycelial fans. The total number of roots, number of roots with rhizomorphs, and number of roots with mycelial fans were recorded.

Soil samples were collected from the forest floor and A2 horizon at each transect. Soil pH was measured with an Orion Research Model 611 pH meter after mixing equal parts (by volume) of distilled water and soil.

Relationships summarized in the analyses of data were 1) percentage of roots infected versus decline category, 2) percentage of roots infected versus elevation, and 3) percentage of trees with at least one root infected versus elevation.

RESULTS AND DISCUSSION

Roots of dead and declining red spruce trees were colonized by *A. mellea* at all elevations and the severity of decline symptoms was related to the percentage of roots colonized. The percentage of roots colonized increased with increasing decline category (Fig. 1). In the hardwood forests, 2% of the roots of healthy trees were colonized, whereas 86% of the roots of recently dead trees were colonized. A similar relationship was found in both transitional and montane boreal forests, although the percentage of roots colonized in each decline category was lower. No roots of healthy trees and 54 and 32%, respectively, of the roots of recently dead trees were colonized in the transitional and montane boreal forests.

The incidence of infection by *A. mellea* was inversely related to elevation (Fig. 2). Ninety-seven percent of the recently dead trees in the hardwood forests had at least one root colonized, whereas 63% of those in the transitional forests and 39% in the boreal forests had at least one root colonized. The pattern was similar in severely declining trees.

A. mellea was least abundant on red

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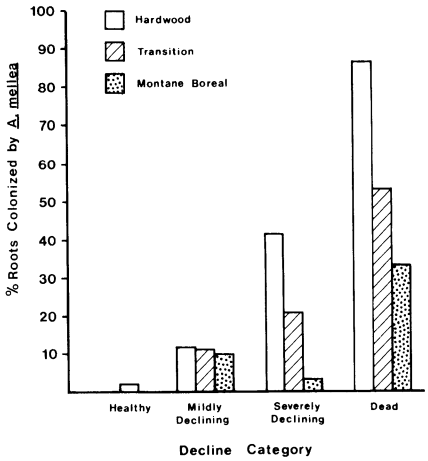

Fig. 1. Percentage of roots of red spruce colonized by *Armillaria mellea* in relation to decline symptoms in three forest communities. Roots were examined to at least 1 m from the bole.

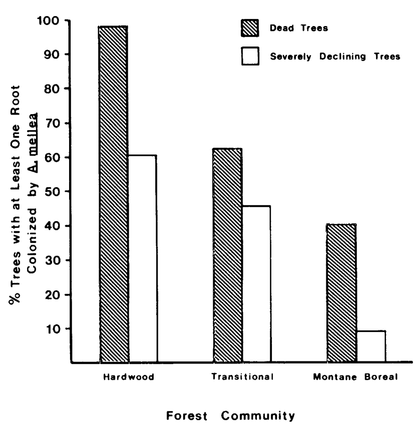

Fig. 2. Percentage of dead and severely declining red spruce colonized by *Armillaria mellea* in three forest communities.

spruce in the montane boreal forests, where the decline is most prevalent (9). In these forests, 91% of the severely declining trees were not colonized by the pathogen, even though they displayed symptoms similar to declining trees at lower elevations. Similarly, 61% of the dead trees sampled in the boreal forest were not colonized. Spruce mortality occurred in the presence or absence of the pathogen.

Because *A. mellea* preferentially attacks stressed trees (8), we expected that most of the severely declining trees within the same plot as a colonized, recently dead tree would also be colonized. This was not the case. In the hardwood and transition forests where *A. mellea* was found on dead trees, only 68 and 60%, respectively, of the severely declining trees within the same plot were colonized. In the montane boreal forest, only 7% of the severely declining trees were colonized when the dead tree in the same plot was colonized. Infrequent colonization of the severely declining, and presumably predisposed, trees indicates that *A. mellea* occurred with spatial heterogeneity in the soil and became less common as elevation increased.

Reasons for the scarcity of the pathogen in the montane boreal forests are only speculative. Factors that may be associated with distribution of *A. mellea* and vary with elevation include soil pH, soil moisture, stand composition, and toxic soil compounds. Soil pH ranged from 3.6 (Mt. Cushman, NH) to 4.6 (Hunter Mountain, NY). Acidity in this range does not inhibit *A. mellea* in culture (2), and there were no discernable patterns between intensity of infection and soil pH at our sites. Evidence has been provided to suggest that rhizomorph growth may be restricted in dry soils (12,13). Moisture content of the forest floor on Camel's Hump Mountain, however, has been shown to increase with increasing elevation (15). The abundance of hardwoods at the lowest elevation sampled may provide *A. mellea* with the greatest quality and quantity of food resources. The natural abundance of this root pathogen is known to be correlated with hardwood occurrence (1). Toxic soil compounds capable of influencing growth or pathogenicity of *A. mellea* may vary with elevation. Lead concentration of forest soils in the Northeast is known to increase with increasing elevation (10). Lead is known to be toxic to the growth and development of numerous fungi (11,17,19,20).

Although *A. mellea* is involved with the decline of red spruce in the northeastern region of the United States, it is not the primary cause of spruce mortality. The association of *A. mellea* with declining trees indicates that the trees are being predisposed to damage by some undetermined biotic or abiotic stress. The fact that trees are dying in the absence of *A. mellea* indicates that the stress is sufficient by itself to cause mortality or that other secondary organisms are interacting with the stress to kill the trees.

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