RELATIONSHIPS AMONG ARMILLARIA ROOT DISEASE, JACK PINE BUDWORM, AND JACK PINE FOREST ECOSYSTEMS

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ABSTRACT

Armillaria root disease is one of the most important tree diseases in Canada. Its importance in natural forest ecosystem development has not been well studied. Armillaria root disease in western Canadian jack pine is commonly caused by *Armillaria ostoyae*. A hypothesis that Armillaria root diseased jack pine trees may develop abnormally large cone crops that sustain endemic jack pine budworm populations is presented. With jack pine budworm defoliation the fungus is able to advance within the root system and insure its survival. Jack pine stands benefit from Armillaria root disease-jack pine budworm defoliation mortality as it reduces competition for resources.

INTRODUCTION

Tree pathogens and the tree diseases that they incite have been traditionally viewed and studied as competition or as a nuisance to forest management. Consequently, in the past little study has been devoted to what role tree disease plays in the forest ecosystem; several recent reviews have addressed this issue (Van der Kamp 1991; Dickman 1992; Castello et al. 1995). Van der Kamp (1991) argued that root diseases such as Armillaria root disease (ARD) and laminated root rot could create forest communities that he considered to be root disease climaxes. Castello et al. (1995) have put forth a hypothesis that "pathogens regulate, and in turn are regulated by, patterns and processes in forest ecosystems".

This paper provides a hypothesis of how a tree disease, Armillaria root disease, regulates and is regulated in a jack pine (*Pinus banksiana* Lamb.) forest ecosystem with special reference to jack pine budworm (JPBW) (*Choristoneura pinus* Freeman).

JACK PINE

Jack pine is found throughout Canada's boreal forest on a variety of sites; best growth is exhibited on well-drained soils (Hosie 1969). It is a pioneer species that, in the boreal forest, is reliant on fire for natural regeneration. Jack pine grows in pure, even-aged stands but can also be found in mixed hardwood/conifer stands (Hosie 1969).

ARMILLARIA ROOT DISEASE

Armillaria root disease (ARD) is one of the most common and important tree diseases in Canada and the United States (Wargo and Shaw 1985; Hiratsuka 1987; Myren 1994). It has been studied for well over a century because of its perceived impact on forest and agricultural crops. Its importance as a forest pathogen has often been questioned; however, little attention has been paid to what role ARD plays in forest stands and its effect on other parts of the forest ecosystem.

BIOLOGY

In Canada ARD is found in all forest regions and on a wide variety of host species. Prior to 1978, Armillaria root disease was thought to be incited by the fungus *Armillaria mellea* (Vahl:Fries) Kummer, a member of the Agaricales; however, recent research has shown that many more *Armillaria* species exist and are capable of causing disease in trees (Watling et al. 1991). There are nine *Armillaria* species in Canada with *Armillaria ostoyae* (Romagn.) Herink being the most widespread and pathogenic to conifers (Morrison et al. 1985; Mallett 1992; Myren 1994). Some of these nine species are found only in eastern or western Canada and may be specific to only certain forest regions (Mallett 1992). In Canada *Armillaria ostoyae* (Romagn.) Herink and *Armillaria sinapina* Bérubé and Desserault are two of the most cosmopolitan species found on both conifer and hardwood hosts (Mallett 1992).

Armillaria species are necrotrophic pathogens that can cause wood decay as well as mortality in trees. They are soil-borne fungi that spread from tree to tree by means of rhizomorphs (cord-like structures made up of hyphae) and/or by root to root contact. The importance of basidiospores, produced from mushrooms, in the disease cycle is not well known (Redfern and Filip 1991). Tree roots can be infected at any age, but generally infection begins to occur in young conifers when the roots become a large enough target, around age five. Once in the host root, a characteristic white mycelial fan is formed beneath the bark tissues.

PATHOGENICITY

Armillaria species vary in their pathogenicity (ability to cause disease). This has led some forest managers to erroneously conclude that *Armillaria* is a secondary pathogen that only attacks weakened trees. Host stress and environmental conditions no doubt play a role in ARD, but the amount of stress and the exact environmental conditions necessary for infection and disease development vary from one *Armillaria* species to the next. Conditions that may induce host stress include abiotic factors such as light, drought, and temperature or biotic factors such as insects, and animals.

Differences in pathogenicity may also reflect the niche that a particular *Armillaria* species occupies and how it does this. Species that are primary pathogens such as *A. ostoyae* do not produce rhizomorphs as abundantly as the more opportunistic pathogens such as *A. sinapina* (Mallett, unpublished data). Both species require woody substrate in order to survive and have developed different strategies to obtain the substrate before competing organisms colonize it. Species such as *A.ostoyae* may have evolved a primary pathogenic strategy that puts more energy into the infection process than into producing rhizomorphs. Whereas, *A. sinapina* produces abundant rhizomorphs that form networks over potential host roots but are unable to successfully infect the root until host resistance is in someway compromised. Both strategies allow the fungus immediate access to woody substrate should it become available. Both the primary pathogenic and opportunistic species vary in their virulence (relative ability to cause disease) and hence the amount of damage that they do to the host.

ARD AND INSECT DEFOLIATION

Armillaria root disease has been found to increase in several tree species after defoliation by insects (Wargo and Harrington 1991). It is often viewed that this is typical secondary pathogenic behavior, but this may be dependent upon the *Armillaria* species present. Defoliated trees often become stressed after defoliation, depending upon the tree species and the amount and period of defoliation. This could allow opportunistic *Armillaria* species to infect the root system; however, it is possible that the root system had been infected by a primary pathogenic species of *Armillaria* prior to the defoliation. The resulting ARD somehow altered the host physiology making it attractive to defoliating insects just as *Armillaria* infected conifers are thought to be more attractive to bark beetles (Wargo and Harrington 1991). Defoliation stresses the host, allowing the fungus to capture more woody substrate. An example of this may be the jack pine budworm-Armillaria root disease relationship reported by Mallett and Volney (1990).

ARD AND JACK PINE

Armillaria ostoyae is commonly found in young and mature jack pine stands in the boreal forest of western Canada (Cerezke and Gates 1992; Mallett 1992). The disease can kill single trees or patches of trees known as disease centers. Mortality incidence can vary from nil to 12% depending upon the site and age of the stand (Mallett 1992). Mallett and Volney (1990) showed that there was greater Armillaria root disease in dead and top-killed jack pine than in healthy jack pine following JPBW defoliation. The fungus was present in the root systems of the trees at least at the time of, if not prior, to the defoliation. Jack pine budworm population densities are positively influenced by the production of jack pine pollen cones (Nealis and Lomic 1994). Large jack pine pollen cone crops are produced after drought and on trees with damaged root systems (W.J.A.Volney, pers. com., Canadian Forest Service, Edmonton, Alberta , July 1988). Mallett and Volney (1990) found the highest incidence of ARD in jack pine trees with small root volumes and weights. There was no difference in the number of ARD root lesions nor the number of roots between large and small root volume trees. Armillaria root disease likely damaged the smaller root volume trees and may have caused a stress induced pollen cone crop. Jack pine trees with stress induced pollen crops may therefore provide a food source for endemic JPBW populations during low population density years.

Trees die from ARD during low JPBW population years and during years of JPBW epidemics. Defoliation may induce stress in trees with smaller root systems allowing the fungus to gain more substrate and insure survival. The removal of trees with small root volumes may benefit the jack pine stand as a whole. This is because it would reduce resource competition and, in nutrient poor sites, lead to nutrient recycling.

Armillaria root disease has been found to influence other types of insect populations. Cobb et al. (1974) showed that root rot fungi may predispose conifers to bark beetles, this has been further substantiated by other research work (Cobb 1989). Other researchers have found conflicting findings regarding ARD and spruce budworm (*Choristoneura fumiferana* Clem). Sterner (1970) reported on butt decay in spruce budworm-defoliated balsam fir. He found greater *Armillaria* butt decay in trees that had greater number of years of growth suppression due to defoliation. Roots were examined and sampled from within one foot of the root collar and thus it is possible that ARD that was located further down the roots in less growth suppressed trees was missed. There is no indication of whether the fungus was present in the roots before or after the defoliation. Raske and Sutton (1986) found Armillaria root disease in roots of trees in all defoliation classes of spruce budworm-defoliated black spruce. They noted that the proportion of trees with ARD was greater than 80% in trees with greater than 80% defoliation but for trees in other defoliation categories the proportion with ARD was less than 30%. They interpreted the fungus as being a secondary pathogen. This interpretation may be incorrect because the *Armillaria* species was never identified and there was no indication of whether these infections occurred after the defoliation.

Armillaria root disease and JPBW may help regulate and be regulated by some jack pine forest ecosystems. Undoubtably, there are other factors that influence and will be influenced by the disease and insect populations within such stands. With a greater understanding of how Armillaria root disease and JPBW influence jack pine stands we may be able to develop and apply more strategic forest management plans.

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