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Multiple diseases impact survival of pine species planted in red pine stands harvested in spatially variable retention patterns

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ABSTRACT

Increasing the diversity of species and structure of red pine (*Pinus resinosa*) is often a management goal in stands simplified by practices such as fire suppression and plantation management in many areas of the Great Lakes Region. One approach to diversification is to convert predominantly even-aged, pure red pine stands to multi-cohort, mixed-species forests through variable overstory retention at harvest. Based on limited empirical evidence, pathologists have advised against this multi-cohort approach in stands where pathogens causing damaging shoot blight diseases are established. We examined disease incidence among planted red, jack (*Pinus banksiana*), and white pine (*Pinus strobus*) in a variable retention harvest and understory woody vegetation removal (brushing) experiment in northern Minnesota. The experiment included four overstory treatments (dispersed and two aggregated overstory retention treatments and a control, $N = 4$) that were split by an understory brushing treatment (yes or no). Prior to harvest in 2003, the fungal pine pathogens *Diplodia pinea*, *Sirococcus conigenus* and *Armillaria solidipes* (syn. *Armillaria ostoyae*) were common on the study site. Within 6 years after harvest, these pathogens reduced the survival of planted red, white and jack pine, potentially interfering with long-term management objectives. Across all treatments, shoot blight incidence was generally higher in dead red and jack pine than white pine seedlings and was predominantly caused by *D. pinea*. The disease killing white pine seedlings was predominately *Armillaria* root rot. Overstory treatment affected the percentage of jack and white pine seedling mortality attributable to shoot blight, but not the more susceptible red pine, with greater overstory retention resulting in greater disease incidence. Understory brushing had no effect on the incidence of shoot blight on seedlings. We expect disease to continue to influence stand structure and composition across all treatments. Our study results highlight the need for forest managers to assess long-term risk of potentially damaging pathogens in red pine stands prior to harvest and use that information to guide decisions regarding silvicultural practices to increase age and species diversity.

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1. Introduction

In Minnesota, Wisconsin and Michigan, there is growing interest in restoring complex structure and composition in red pine (*Pinus resinosa*) stands managed for wood and fiber (Abella, 2010; Palik and Zasada, 2003). Prior to settlement, red pine was often a component of mixed forests that also included, in lower abundance, white pine (*Pinus strobus*), jack pine (*Pinus banksiana*) and various deciduous species (Frelich and Reich, 1995). Moreover, evidence indicates that red pine dominated forests sometimes consisted of two and three age-cohorts, a result of fire and wind disturbances (Palik and Zasada, 2003; Fraver and Palik, 2012) that naturally regenerated red pine, other pine species and hardwoods.

Compared to these historical conditions, many current red pine stands have a simplified stand structure and composition. Natural regeneration of red pine is inconsistent (Farnsworth, 2002). Red pine has been extensively replanted after clearcutting across the Great Lakes Region. Resulting stands are often single cohort and near monotypic in composition. This simplified stand structure avoids shoot blight diseases that damage red pine seedlings and saplings growing in multi-cohort stands. Forest pathologists currently advise against planting red pine in or near diseased stands (Bronson and Stanosz, 2006; O'Brien, 1973; Ostry et al., 1990, 1999, 2002).

Prior to the 1960s, red pine regeneration was relatively free of major diseases on most sites. Eyre and Zehngraff (1948) wrote "Where red pine occurs naturally in fairly extensive stands such as in Minnesota, it has always been considered one of the most insect- and disease-resistant trees." In the 1960s after several fungal pathogens were inadvertently spread throughout the region on nursery stock, damage and losses of second growth red pine began to occur (Palmer et al., 1988; Stanosz et al., 2005). Pathogen spread and disease development were aided by large areas of red pine

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monocultures, limited genetic variability within the host, site and environmental stress factors, and perhaps, the absence of fire.

Understory red pines are particularly vulnerable to *Sirococcus conigenus* (Ostry et al., 1990) and *Diplodia pinea* (Nicholls et al., 1977) that cause shoot blights. These fungi can co-occur on the same tree and even on the same shoots of red pine, increasing the potential for damage (Haugen et al., 1998; Stanosz and Smith, 2007). Outbreaks of *S. conigenus* have been associated with wet spring weather, shade and periods of high humidity (Ostry et al., 1990), while *D. pinea* outbreaks are common among trees under moisture stress or on trees wounded by hail or various shoot insects (Nicholls and Ostry, 1990). Both shoot blight diseases are most severe on red pine regeneration under, or adjacent to, infected overstory red pines that are the sources of fungal inoculum (Haugen et al., 1998). Logging debris such as colonized branches and cones are also sources of *D. pinea* inoculum and spores from these sources can result in shoot blight disease on red pine regeneration in the absence of an overstory (Oblinger et al., 2011; Munck and Stanosz, 2010).

Although white pine is more resistant to shoot blights (Ostry et al., 1990; Waterman, 1943), regeneration success of white and jack pine on many sites is affected by disease. White pine blister rust, caused by *Cronartium ribicola*, is a major consideration in managing white pine on many sites within the region (Ostry et al., 2010). Armillaria root and butt rot impacts all pines, particularly trees stressed by other biotic and abiotic agents and partial stand harvests (Wargo and Harrington, 1991). The pine–oak gall rust (syn. eastern gall rust) caused by *Cronartium quercuum* f. sp. *banksianae* is especially damaging to jack pine on sites where its oak (*Quercus*) alternate hosts are present. Jack pine is also damaged in stands where the autoecious, pine–pine gall rust (syn. western gall rust) caused by *Peridermium harknessii* (syn. *Endocronartium harknessii*) is present (Anderson, 1965).

An operational-scale variable retention harvesting experiment designed to increase structural and compositional diversity of simplified red pine stands (Palik and Zasada, 2003) provided us a unique opportunity to examine the incidence and effects of several pine diseases in relation to silvicultural treatments. The treatments were designed to establish a two-cohort age structure and introduce compositional diversity by planting three pine species and differed in the spatial arrangement of retained overstory trees with and without the removal of understory woody shrubs.

Prior to this study, little empirical evidence of the impact of these regeneration diseases on a large scale existed, but were inferred from small research plots or informal observations. This study was undertaken to provide forest managers with more thoroughly-tested guidance on silvicultural practices to avoid damaging diseases in red pine stands managed to increase species and structure diversity. The objective of this study was to evaluate the effect of various silvicultural treatments of red pine on diseases and mortality of red, white and jack pine seedlings. We formally tested three hypotheses: (1) spatial patterns of overstory retention affect the incidence of shoot blight, *Armillaria* and gall rust diseases; (2) the incidence of diseases and seedling mortality will differ between understory removal and understory control treatments; and, (3) red pine stands affected by shoot blights present an opportunity for restoration of eastern white pine because of its resistance to shoot blight diseases.

2. Methods

2.1. Study area and treatments

This study is part of a larger red pine variable retention experiment with researchers examining the effects of different spatial patterns of overstory retention on regeneration, productivity, and plant and songbird communities. The study area has a cold temperate climate with mean annual temperatures of 3.9° C and mean annual precipitation of 70.0 cm. Surficial geology consists of outwash and ice contact landforms characterized by deep sand parent materials. Soils are excessively to well-drained nutrient poor loamy sands. The native plant community is classified as FDn33-northern dry-mesic mixed woodland (MN DNR, 2003). This ecosystem is dominated by red pine in the overstory, with lesser amounts of eastern white pine, jack pine, red maple (*Acer rubrum*), trembling aspen (*Populus tremuloides*), big tooth aspen (*Populus grandidentata*), paper birch (*Betula papyrifera*), balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), northern red oak (*Quercus rubra*) and bur oak (*Quercus macrocarpa*). The understory was dominated by beaked hazel (*Corylus cornuta*) and serviceberry (*Amelanchier* spp.). Study stands were estimated to be approximately 85-years-old at the time of treatments, were broadly even-aged and had naturally regenerated after early 20th century logging and wildfires.

The study background and design details can be found in Palik and Zasada (2003). Briefly, the study is a split-plot, randomized complete block design consisting of four replicated blocks (approx. 64 ha each) of red pine forest. Four overstory treatments (whole plots, approx. 21 ha each) were split into two understory treatments, for a total of eight treatment combinations. Overstory treatments included an uncut control and three variable retention harvests of different spatial pattern (Fig. 1): a large gap aggregate retention consisting of 0.3 ha gaps cut among residual overstory trees; a small aggregate retention of 0.1 ha gaps cut among residual overstory trees, and an evenly dispersed pattern of retention, resembling a shelterwood regeneration harvest. All variable retention harvests retained a target residual basal area of 13 m^2 ha, regardless of spatial pattern. Harvesting occurred from August 2002 to April 2003. Understory treatments consisted of tree release or "brushing" using brush saws to remove all woody species, predominantly hazel, *Corylus* sp. on one-half of each overstory treatment. Conifers, maples (*Acer* sp.) and oaks (*Quercus* sp.), greater than 0.3 m in height and less than 6.4 cm in diameter were retained. Brushing occurred annually in early June from 2003 to 2009.

In May 2003, red, white, and jack pine 3–0 bareroot seedlings were planted uniformly within all overstory treatments at 2.7×2.7 m spacing between tree seedlings (1329 trees/ha). Seedlings were treated each fall with a commercial blood meal formulation (Plantskydd®) to protect them from herbivory damage. In early 2004, five seedlings of each species were tagged at permanent sample points. Three hundred and twenty permanent sample points (10 per overstory $\times$ understory treatment) were established along transects prior to planting. Number and length of transects were dependent on the size of the treatment unit, but transects were established >50 m from treatment unit boundaries and from other transects. In each overstory $\times$ understory treatment combination, 10 sample points were spaced evenly along transects (25–100 m). Thus, 1600 seedlings of each species were marked for detailed observations (5 seedlings $\times$ 10 points $\times$ 8 treatments $\times$ 4 blocks = 1600 seedlings of each species).

2.2. Pre-treatment stand disease survey

In May 2002, a transect between the 320 research points within the four blocks and designated treatment areas was walked to survey for the presence of major diseases on overstory and any understory pine regeneration. The detection of shoot blight (pathogen species was not determined) in the overstory trees was aided with binoculars.

The areas of root rot centers, identified by the presence of mycelial fans, rhizomorphs, and fruit bodies when present on dead and

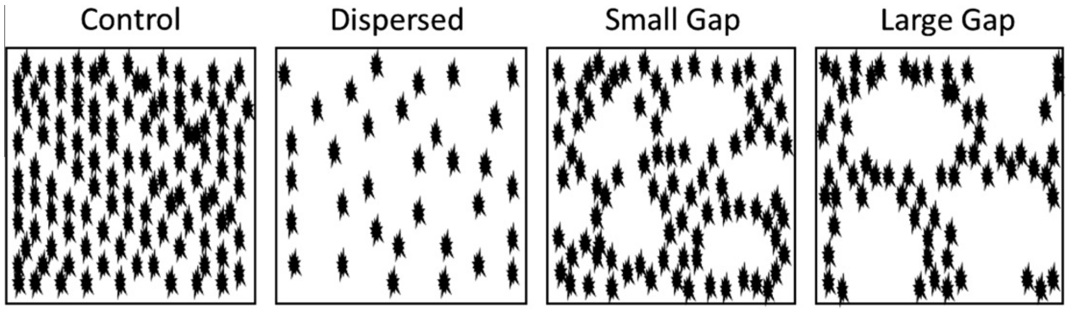

Fig. 1. Idealized illustration of overstory treatments. The control was uncut forest. The dispersed, small gap, and large gap were variable retention harvests of different spatial pattern. Harvested trees were removed evenly in the dispersed, in 0.1 ha groups in the small gap, and in 0.3 ha groups in the large gap. All variable retention harvests retained a target residual basal area of 13 m^2 ha, regardless of spatial pattern.

dying trees, within 30 m of the transect between research points were measured. The tree species infected or killed and the species composition of the regeneration where present were recorded.

Samples of blighted shoots, fallen red pine cones (often reservoirs of *D. pinea* inoculum), *Armillaria*-infected wood, and when present, fruit bodies or rhizomorphs of *Armillaria*, were collected to confirm pathogen identity in the laboratory. No attempt was made to distinguish between the shoot blight fungi *D. pinea* and the relatively weak endophyte *Diplodia scrobiculata* (de Wet et al., 2003; Santamaría et al., 2011).

2.3. Post-treatment planted seedling disease sampling

Dead, tagged seedlings were collected and pathogens identified in the laboratory from 2004 to 2007 and in 2009. Shoot blight fungi were identified to species by obtaining diagnostic spores from fruit bodies, if present, on diseased tissues. Aeciospores on a random sample of jack pine rust galls were identified to rust species based on germ tube characteristics in the laboratory (Anderson and French, 1965). The presence of each pathogen on the dead seedlings was recorded.

In 2006, 2007 and 2009 all dead seedlings were sampled for *Armillaria* by plating stem and root tissues on nutrient agar. After obtaining pure cultures from seedlings with evidence of root rot, *Armillaria* species identification was done using diploid–haploid pairings (Korhonen, 1978). Diploid field cultures were paired with haploid tester isolates of *Armillaria solidipes* (syn. *Armillaria ostoyae*) (Burdsall and Volk, 2008), *Armillaria gallica* and *Armillaria sinapina*. Plugs from field cultures were paired with plugs from each tester isolate on nutrient agar and incubated in the laboratory for 2 weeks. In tests with field cultures belonging to the same species as the haploid tester isolate, the fluffy mycelia of the tester isolate converts to the flat mycelia of the field culture.

2.4. Statistical analyses

Response variables (i.e., the number of dead seedlings and the incidence of shoot blight, gall rust or Armillaria root rot on dead seedlings) were not normally distributed. When possible, appropriate Box–Cox transformations (i.e., $y' = [(y + c)^{\lambda} - 1]/\lambda$) were found using Proc Transreg in SAS 9.2. To evaluate the effects of overstory treatment and brushing, the cumulative number of dead seedlings from 2004 to 2007 and 2009 was transformed using $\lambda = -0.5$ and $c = 0.5$. Suitable transformations could not be found for the percentage of dead seedlings with shoot blight or *Armillaria*, and these data were analyzed using non-parametric methods described below. To compare the incidence of shoot blight or *Armillaria* among pine species, the numbers of dead trees and dead trees with shoot blight or *Armillaria* were summed among all overstory and understory treatments within a block. The proportion of dead trees with shoot blight was arcsin(square root(x))-transformed. The proportion of dead trees with *Armillaria* met assumptions of normality and was not transformed.

Most data were analyzed by analysis of variance (Proc Mixed in SAS 9.2) with block and the block-treatment interaction included as random terms. The Kenward–Roger method was used to calculate degrees of freedom, and the Tukey–Kramer method (with $\alpha = 0.05$) was used for multiple comparisons of mean responses (calculated using LSMEANS) among treatments, brushing levels, and their interaction. Similar procedures were used to compare the incidence of shoot blight or *Armillaria* among pine species. Mean values were back-transformed for reporting purposes.

For the percentage of dead seedlings with shoot blight a two-way non-parametric analysis of variance was performed on the rank order of the proportion of infected trees (Proc Mixed in SAS 9.2) with an unstructured covariance. A mean of the ranks were used when values were tied. We report median values of the percentage of dead trees with shoot blight as measures of central tendency.

For the percentage of dead seedlings with *Armillaria* or gall rust a one-way non-parametric analysis of variance was performed by species on the rank order of the proportion of infected trees (Proc Mixed in SAS 9.2) with an unstructured covariance. We only evaluated effects of overstory treatments on the disease incidence in dead seedlings because too few dead seedlings with *Armillaria* or gall rust were present in each of the understory treatments to evaluate the treatment effects. A mean of the ranks were used when values were tied. We report median values of the percentage of dead trees with infection as measures of central tendency.

3. Results

3.1. Pre-treatment stand disease survey

Examination of symptomatic red pine branches along the transect confirmed that shoot blight was generally present on overstory and on the occasional understory red pine throughout the study stands. On diseased shoots examined in the laboratory, conidia of *D. pinea* were detected more often than those of *S. conigenus* and commonly on fallen 1- to 2-year old red pine cones.

A total of 108 Armillaria root rot centers were detected. All recovered isolates paired with haploid tester isolates were identified as *A. solidipes*. Within the study area a total of 20 centers were in the small gap treatment, 32 in the large gap treatment and 27 in each of the dispersed treatment and the control. The centers ranged from one or a few dead overstory red and/or jack pine trees to centers up to 50 m in diameter consisting of many diseased and dying, broken, fallen, and dead standing pine trees. One center contained 26 dead standing red pines averaging 17 cm in diameter. Recruitment of hardwood species such as trembling aspen, paper birch, red maple and red oak were more common in the large natural canopy gaps created by Armillaria root rot than the non-affected portions of the stands.

3.2. Seedling mortality

The total number of jack pine seedlings killed by all causal agents was not affected by overstory treatment ($df = 3, 9$; $F = 1.14$; $P = 0.38$), brushing ($df = 1, 12$; $F = 0.5$; $P = 0.49$), or the interaction of overstory treatment and brushing ($df = 3, 12$; $F = 0.2$; $P = 0.90$). The back-transformed mean number of dead jack pine seedlings ranged from 8 to 14 among treatments.

The total number of white pine seedlings killed by all causal agents was not affected by overstory treatment ($df = 3, 21$; $F = 0.86$; $P = 0.48$), brushing ($df = 1, 21$; $F = 0.59$; $P = 0.59$), or the interaction of overstory treatment and brushing ($df = 3, 21$; $F = 1.4$; $P = 0.29$). The back-transformed mean number of dead white pine seedlings ranged from 3 to 6 among treatments.

The total number of red pine seedlings killed by all causal agents was affected by overstory treatment ($df = 3, 9$; $F = 7.24$; $P = 0.01$), brushing ($df = 1, 12$; $F = 8.5$; $P = 0.01$), and the interaction of overstory treatment and brushing ($df = 3, 12$; $F = 11.9$; $P < 0.01$). More dead seedlings were observed in the control treatment (back-transformed mean = 27.4) than in the dispersed treatment (12.3). The number of dead seedlings in the large gap (18.0) and small gap (20.0) did not differ from the other overstory treatments. Fewer dead seedlings were in plots that were brushed (15.6) than in plots that were not brushed (21.6). Fewer dead seedlings were found in plots within the dispersed overstory treatment and brushed than in any other overstory treatment × brushing combination.

3.3. Shoot blight incidence on dead seedlings

Both *S. conigenus* and *D. pinea* fruit bodies and spores were found on blighted, dead seedlings, sometimes co-occurring on the same seedlings. On the dead seedlings collected throughout the study areas, *D. pinea* predominated over *S. conigenus* (91% vs. 9%). The incidence of shoot blight on dead white pine (back transformed mean = 32.5%) was significantly less than on dead red pine (71.3%) or jack pine (65.0%; $df = 2, 6$; $F = 20.27$; $P = 0.002$). The incidence of shoot blight on dead red pine and jack pine were not significantly different.

The percentage of dead jack pine seedlings with shoot blight was affected by overstory treatment ($df = 2.79, 10.8$; $F = 4.12$; $P = 0.04$) but not by brushing ($df = 1.0, 7.77$; $F = 1.88$; $P = 0.21$) or the interaction of overstory treatment and brushing ($df = 2.2, 7.77$; $F = 1.11$; $P = 0.38$). Incidence of shoot blight was greater in the control treatment than in the large gap treatment; the percentage of dead jack pine with shoot blight in the dispersed and small gap treatments were not different from any other overstory treatment (Fig. 2).

The percentage of dead red pine seedlings with shoot blight was not affected by overstory treatment ($df = 2.38, 8.64$; $F = 1.26$; $P = 0.34$), brushing ($df = 1.0, 9.67$; $F = 1.09$; $P = 0.32$), or the interaction of overstory treatment and brushing ($df = 2.58, 9.67$; $F = 1.37$; $P = 0.31$). Incidence of shoot blight in dead red pine ranged from approximately 60–80% (Fig. 2).

The percentage of dead white pine seedlings with shoot blight was affected by overstory treatment ($df = 2.68, 10.2$; $F = 4.67$; $P = 0.03$) but not by brushing ($df = 1.0, 9.51$; $F = 1.32$; $P = 0.28$) or the interaction of overstory treatment and brushing ($df = 2.55, 9.51$; $F = 1.87$; $P = 0.20$). Incidence of shoot blight was greater in the control treatment than in dispersed or large gap treatments (Fig. 2).

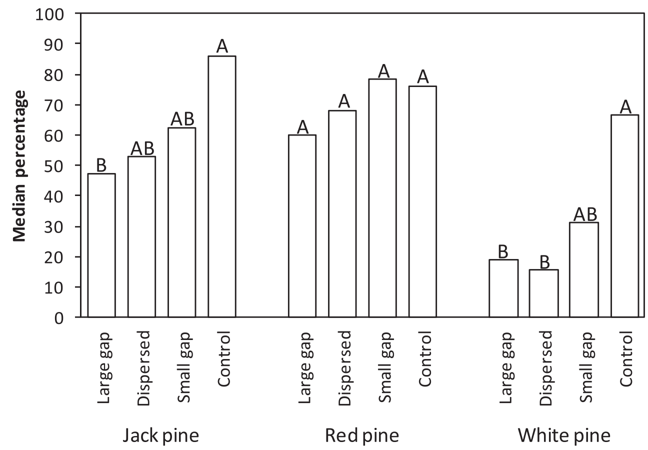

Fig. 2. Effect of overstory treatment on shoot blight incidence in dead pine seedlings from 2004 to 2009. Data for understory treatments are pooled. Values for a species with the same letter are not significantly different ($P > 0.05$). Comparisons among species are not tested.

3.4. Armillaria root rot

Several new symptomatic overstory trees adjacent to root rot centers were noted each year after treatment, evidence that the centers were enlarging. The incidence of *Armillaria* infection from 2006 to 2009 was different among species of dead pine seedlings ($df = 2, 6$; $F = 21.94$; $P = 0.002$). Red pine had a significantly lower percentage of dead seedlings with *Armillaria* (back transformed mean = 27.7%) than jack pine (59.4%) or white pine (73.8%); the percentages of *Armillaria* infection in dead jack pine and white pine were similar.

Overstory treatment affected the incidence of *Armillaria* infection in dead seedlings of jack pine ($df = 1.85, 4.26$; $F = 6.47$; $P = 0.05$), red pine ($df = 2.17, 7.64$; $F = 6.37$; $P = 0.02$) and white pine ($df = 2.34, 7.74$; $F = 4.92$; $P = 0.04$). For jack pine, the proportion of dead seedlings with *Armillaria* was greater in the large gap treatment than in the control; for red pine, in the large gap and small gap treatments than in the control; and for white pine, in the dispersed and small gap treatments than the control (Fig. 3). Very often evidence of more than one damaging agent was present on individual dead seedlings across all treatments so the causal agent responsible for the death of the seedlings could not be determined conclusively.

3.5. Jack pine gall rust

In 2007 jack pine gall rust was first detected in the plots. The incidence of dead seedlings with gall rust through 2009 was affected by overstory treatment ($df = 3, 12$; $F = 3.62$; $P = 0.045$). The incidence of gall rust in the small gap treatment was greater than in the control (Fig. 4). High variability among blocks in the dispersed treatment (incidence ranged from 0% to 92%) and the large gap treatment (14–70%) rendered these treatments no different from any other treatment. Laboratory examination of aeciospores and the frequent presence of seedlings and saplings of red oak, its alternate host, in canopy gaps strongly suggested that *C. quercuum* f. sp. *banksianae* was the causal agent.

4. Discussion

In this study we tested three hypotheses related to disease, variable retention harvesting patterns and understory removal in red

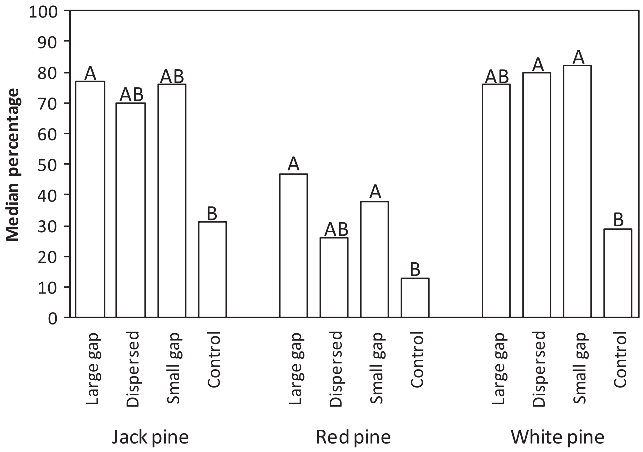

Fig. 3. Percentage of dead seedlings affected by *Armillaria* by treatment and species 2004–2009. Data for understory treatments are pooled. Values for a species with the same letter are not significantly different ($P > 0.05$). Comparisons among species are not tested.

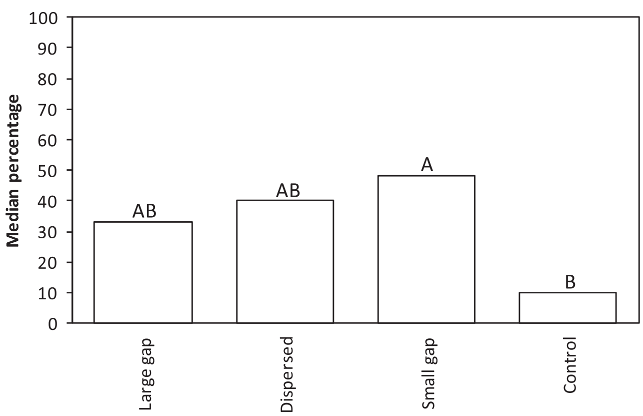

Fig. 4. Percentage of dead jack pine seedlings affected by gall rust by treatment 2004–2009. Symptoms of gall rust were first detected in 2007. Values with the same letter are not significantly different ($P > 0.05$).

pine. Our first hypothesis, that there is a risk for damage by shoot blight diseases in multi-cohort red pine was confirmed and supports previous reports. Although we did not examine the planting stock for latent presence of *D. pinea* (Stanosz et al., 1997), a 2002 survey of the nursery providing the red pine seedlings for this study did not detect the pathogen in the nursery (Stanosz et al., 2005). Results support the recommendation to avoid growing multi-cohort red pine or planting red pine adjacent to red pine stands known to be affected by shoot blights. Successive years of multiple shoot blight damage either killed infected seedlings outright or killed terminal shoots, reducing height increments. This damage may have subjected infected trees to increased stress from competing vegetation and low light levels, perhaps increasing their susceptibility to Armillaria root rot (Wargo and Harrington, 1991).

There were differences in shoot blight incidence on dead jack and white pine seedlings among retention treatments. However, there was no difference in shoot blight incidence on dead red pine among treatments, underscoring its high susceptibility. Previous research has shown a gradient of decreasing spore dispersal and infection of seedlings from an inoculum source. Nearly 50% of the first-year nursery seedlings within 15 m of a red pine windbreak infected with *D. pinea* became diseased (Palmer et al., 1988). Based on this research, a recommendation to provide a buffer of at least twice the height of adjacent trees was made to minimize potential risk of infection by rain-splashed spores harbored in the crowns of nearby trees. However, nursery seedlings became infected by inoculum in windbreaks 180 m away (Palmer et al., 1988). Clearly, even the large gap treatment (54 m radius) in this study did not provide a sufficient buffer from the surrounding infected overstory trees to avoid the disease completely. In addition, logging slash and fallen, infected cones on the study site likely provided ample *D. pinea* inoculum within the gaps after thinning.

Examining the effect of brushing alone, our second hypothesis was not confirmed. The percentage of dead pine seedlings affected by shoot blight on brushed plots and the non-brushed plots did not differ. This indicates conditions conducive to infection and shoot blight disease development were not altered by the understory treatment.

Our third hypothesis was confirmed. Eastern white pine seedlings were not seriously damaged by shoot blight disease, with only one or occasionally a few shoots on dead seedlings being affected. It is suspected that most, if not all, of the dead white pine seedlings were killed by *A. solidipes*. In contrast, red pines were far more seriously affected by shoot blight. Red pine stands thus present an opportunity to restore white pine and accomplish the objective of enhancing species diversity in stands that may be at risk for shoot blight damage (Gilmore and Palik, 2006). The success of restoring white pine will, however, depend on managing to avoid damaging agents such as white pine blister rust, Armillaria root rot, animal herbivory and competing vegetation (Ostry et al., 2010).

The high incidence of Armillaria root rot within the stands underscores the importance of this pathogen in red pine ecosystems. The occurrence of over 100 active root rot pockets within the study areas indicate that this pathogen is well-established in these stands and together with shoot blight will continue to have an increasing impact on pine population dynamics in the future (Fig. 5). More dead jack and white pine seedlings across all treatments were infected by *Armillaria* than red pine. More dead seedlings of all species were infected by *Armillaria* in the gap treatments than in the control treatment (Fig. 3). The higher incidence of dead seedlings affected by *Armillaria* in the gap treatments was most likely the combination of preexisting root rot centers within these areas and new stumps that provided additional food bases for the fungus. It is expected that the thinning in and around Armillaria root rot pockets will contribute to the future enlargement of these centers which may steer the succession of affected red pine stands towards a greater hardwood component (McLaughlin, 2001).

Small woody plants and small woody debris can be sources of *Armillaria* inoculum in red pine stands (Kromroy et al., 2005). Harvest entry and partial cutting in stands can intensify Armillaria root and butt rot by temporarily stressing released trees, increasing susceptibility of wounded trees and increasing stumps that serve as food bases for the pathogen (Wargo and Harrington, 1991). *A. solidipes* may increase structure and species diversity, but pine may not be as large a component in these affected stands in the future as these centers continue to enlarge. In addition, red oak regeneration in the resulting canopy gaps served as the alternate host for jack pine gall rust that can be lethal.

5. Conclusions

Shoot blights caused by *S. conigenus* and *D. pinea* are diseases that present risks primarily to the health of red pine regeneration in multi-cohort stands. In the past, before the wide-spread establishment of these shoot blight diseases, as many as five age classes of red pine regeneration were present in a 120-year-old red pine stand following periodic cutting over 20 years (Eyre and Zhengraff,

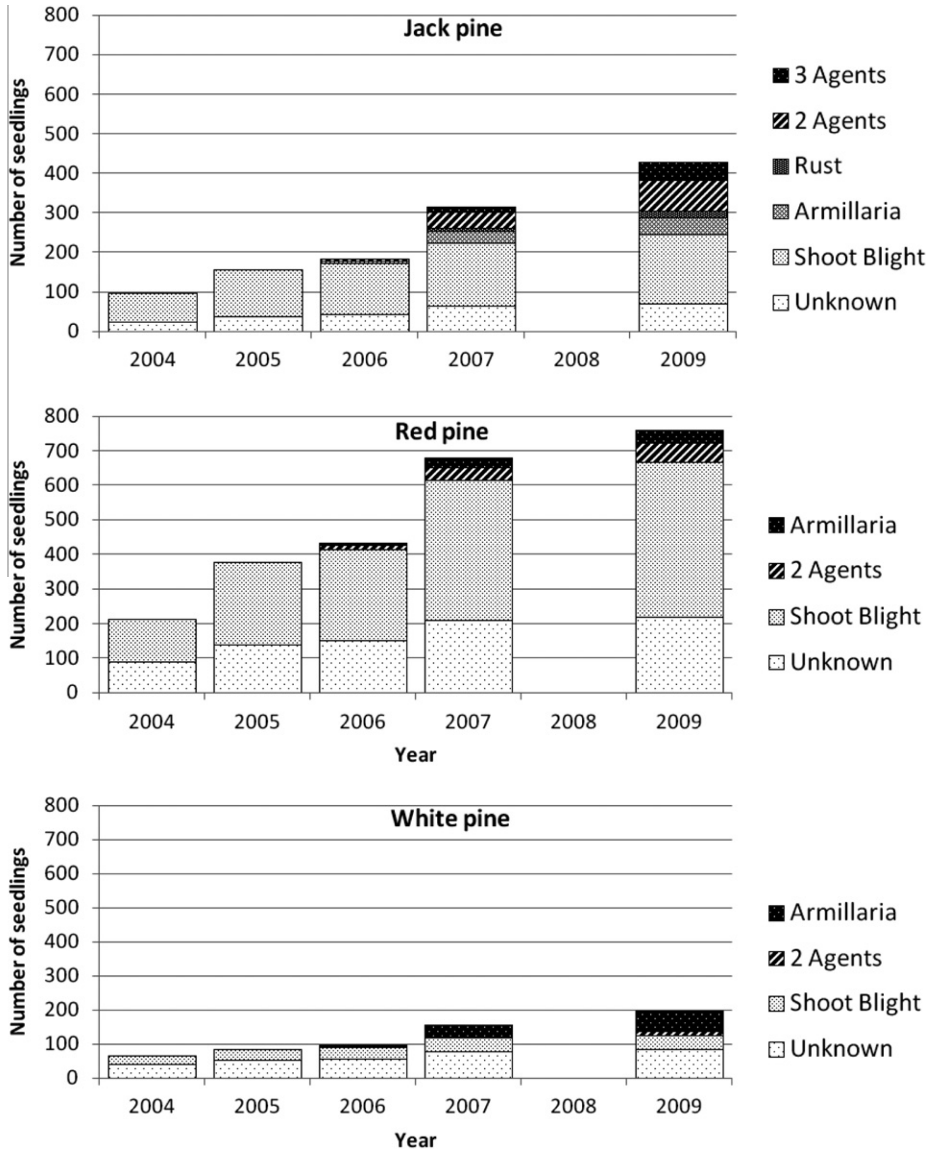

Fig. 5. Cumulative dead seedlings by damage agent in 2004–2007 and 2009. No data were collected in 2008.

1948) and there are extant examples of old-growth stands having two and three cohorts (Fraver and Palik, 2011). Today, one option to diversify red pine stands known to be affected by shoot blights is to either plant or provide conditions for recruitment of white pine into these stands since white pine is resistant to serious damage by shoot blight diseases. With such an approach, after an initial retention harvest, emphasis could be placed on regenerating primarily eastern white and jack pines. Then as this younger cohort matures, primarily mature white and potentially some jack pine can be retained during a second regeneration harvest, with emphasis on establishing a new cohort of red pine. In this way, overstory and understory red pine are disassociated in time and space, potentially lowering the incidence of shoot blight infection.

However, eastern white pine was highly susceptible to *A. solidipes* and the presence of this pathogen in the stands presents a risk to the survival of white pine seedlings in root rot centers. Thus, the incidence and interaction of shoot blight diseases, affecting mostly red pine, and *A. solidipes*, affecting mostly eastern white pine and jack pine, may call into question the alternation of pine dominance approach suggested above.

Jack pine gall rust incidence was higher than expected. This was most likely a consequence of the extensive red oak regeneration (the alternate host for *C. quercuum* f. sp. *banksianae*), predominantly in the canopy gaps that were often the result of mortality of overstory pines caused by *A. solidipes*. However, the pine–pine gall rust may also be present as it has been found near the study areas (Anderson, 1965; Dietrich et al., 1985). The numerous potentially lethal main stem galls on trees may severely limit recruitment of jack pine in the future stand as mortality of affected trees is expected to increase.

Diversifying red pine stands may be possible if forest managers consider existing disease conditions within the current stands as well as the potential risk for development of diseases in the future when selecting stands, thinning treatments, and species to artificially or naturally regenerate. Greater emphasis should be placed on assessing the current level of shoot blight and root rot during stand examinations. A high incidence of shoot blight in a stand will necessarily influence the choice of pine species to regenerate to avoid damage. Perhaps the use of fire can return red pine stands to conditions less conducive to diseases (Dickmann, 1993) by removing existing pathogen inoculum within lower crowns and on cones and debris on the ground within treated stands. In the absence of fire, careful selection of stand treatments to diversify current red pine stands will help minimize future problems.

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