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Soil and Stocking Effects on Caliciopsis Canker of *Pinus strobus* L.

Isabel A Munck [1,*], Thomas Luther [1], Stephen Wyka [1], Donald Keirstead [2], Kimberly McCracken [2], William Ostrofsky [3], Wayne Searles [3], Kyle Lombard [4], Jennifer Weimer [4] and Bruce Allen [4]

1. Northeastern Area State & Private Forestry, U.S. Department of Agriculture (USDA) Forest Service (USFS), Durham, NH 03861, USA; imunck@fs.fed.us (T.L.); stephenwyka@gmail.com (S.W.)
2. USDA Natural Resources Conservation Service (NRCS), Dover, NH 03861, USA; donald.keirstead@nh.usda.gov (D.K.); kimberly.mccracken@nh.usda.gov (K.M.)
3. Maine Forest Service, Maine Department of Agriculture, Conservation and Forestry, Augusta, MA 04692, USA; bill.ostrofsky@maine.gov (W.O.); Wayne.Searles@maine.gov (W.S.)
4. New Hampshire Department of Resources and Economic Development, New Hampshire Division of Forests and Lands, Concord, NH 03861, USA; kyle.lombard@dred.state.nh.us (K.L.); Jennifer.Weimer@dred.nh.gov (J.W.); Bruce.Allen@dred.nh.gov (B.A.)

* Correspondence: imunck@fs.fed.us; Tel.: +1-603-868-7636

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Abstract: Soil and stand density were found to be promising predictive variables associated with damage by the emerging disease of eastern white pine, Caliciopsis canker, in a 2014 survey with randomly selected eastern white pine (*Pinus strobus* L.) stands. The objective of this study was to further investigate the relationship between soil and stocking in eastern white pine forests of New England by stratifying sampling across soils and measuring stand density more systematically. A total of 62 eastern white pine stands were sampled during 2015–2016. Stands were stratified across soil groups and several prism plots were established at each site to measure stand density and determine stocking. Caliciopsis canker incidence in mature trees was greater in sites with drier or shallow soils compared to sites with loamy soils and in adequately stocked stands compared to understocked stands ($p < 0.0001$). Caliciopsis canker signs and symptoms were observed in all size classes. Live crown ratio, a measure of forest health, decreased with increasing Caliciopsis canker symptom severity. The fungal pathogen, *Caliciopsis pinea* Peck, was successfully isolated from cankers on trees growing in each soil group. Forest managers will need to consider damage caused by Caliciopsis canker related to stand factors such as soil and stocking when regenerating white pine stands.

Keywords: forest health monitoring; eastern white pine; tree density; tree disease

1. Introduction

In New England and New York, where the forest cover surpasses 60% of the land area and the annual value of forest products industry exceeds $18.8 billion, forests are vital to the region's economy [1]. Eastern white pine (*Pinus strobus* L.) is an important component of the region's forests. For example, in Massachusetts white pine forest types comprise 25% of the forest [2]. White pine often grows in pure stands, but it can also grow well in association with other conifers and hardwoods. The geographic range of eastern white pine extends from Canada to South Carolina and west to Iowa. Eastern white pine grows in all the soils throughout this range, but does best in sandy, well-drained soils where it is not outcompeted by hardwoods [3,4].

Caliciopsis pinea Peck is a fungal pathogen that causes cankers to pine and other conifer hosts in North America and Europe [5]. In eastern North America, *C. pinea* frequently causes damage to eastern white pine [6,7]. Reports of Caliciopsis canker were frequent during the 1930s [8,9], but since then, the disease has been mostly overlooked until more recent reports of unexpected damage by this disease [7,10,11]. Concern over loss of value to eastern white pine led to a 2014 survey of randomly selected sites throughout Maine, Massachusetts, and New Hampshire—states with the greatest concentration of white pine in New England [2,6]. Results from that initial survey indicated that soil group and stand density were promising, predictive factors of the probability of a site having symptoms associated with Caliciopsis canker [12]. In that study, Caliciopsis canker symptoms were more frequently observed on trees growing in excessively drained (86%) or poorly drained soils (78%) than in well drained more fertile soils (59%) ($p = 0.1$). Stand density was greater for stands with Caliciopsis than for stands without Caliciopsis ($p = 0.1$). The relationship between presence of Caliciopsis canker symptoms and soil or stand density, however, was not statistically significant at $p = 0.05$. In addition, stand density measurements in that study were limited. The objective of this study, therefore, was to further explore the relationship between Caliciopsis canker symptoms and soil or tree density in eastern white pine stands. We hypothesize that eastern white pine growing in more productive soils with adequate soil moisture are less likely to have Caliciopsis canker symptoms than trees growing in nutrient poor, excessively drained, and poorly drained soils. We also hypothesize that incidence of Caliciopsis canker symptoms will increase with increasing stand density.

2. Materials and Methods

2.1. Site Selection

A modified version of the New Hampshire Important Forest Soil groups was developed specifically for conditions potentially related to white pine growth and productivity [13]. Soils from Belknap, Merrimack, and Hillsborough counties in New Hampshire (NH) and Oxford, Androscoggin, Sagadahoc, and York counties in Maine (ME), where eastern white pine is abundant, were classified into four soil groups (Table 1). Layers of these modified soil groups for use in Geographic Information System (GIS) were generated for New Hampshire and Maine counties with the greatest concentration of eastern white pine basal area. Modified methods from Munck et al. (2015) were used to sample eastern white pine sites within each soil group during two consecutive years. In 2015, at least 12 sites per soil group with more than 2 contiguous hectares with more than 75% basal area of eastern white pine as predicted by the National Insect and Disease Risk Map (NIDRM) eastern white pine host layer for use in GIS were randomly selected for sampling [14]. The sites visited during 2015 were sawtimber (mean stand diameter at breast height, 1.3 m from the ground: DBH > 23 cm) stands because most of the eastern white pine resource in New England is mature and these site were randomly selected. Previously, Caliciopsis canker symptoms were more frequently observed on pole-size trees (DBH = 11.5–22.9 cm) [6]. In addition, during 2015, Caliciopsis cankers and fruiting bodies were frequently observed on white pine regeneration (Figure 1). In 2016, therefore, poletimber stands and eastern white pine regeneration within these were surveyed to better quantify probability of Caliciopsis canker symptoms in these stands at greater risk of damage by *C. pinea*. Inventories of New Hampshire State Lands were used to locate three sites with poletimber (mean stand DBH = 11.5 to 23 cm) white pine stands within each soil group. Latitude and longitude coordinates for the center point of each stand were generated and imported into a Global Positioning System (GPS) receiver (GPSmap 64, Garmin International Inc., Olathe, KS, USA).

Table 1. New Hampshire important forest soil groups (NHFSG) modified for Belknap, Merrimack, and Hillsborough counties in New Hampshire (NH) and Oxford, Androscoggin, Sagadahoc, and York counties in Maine (ME). Groups are generally rated from 1–4 along a continuum of water holding capacity, drainage class, and depth. Soils in Group 1 are very dry (low water holding capacity and excessively drained) to Groups 4 where water is more plentiful due to finer soil texture, landscape position, or root restrictive layers.

Soil Group	Soil Properties and Interpretations	Brief Description
Very dry	NHFSG = 1C Drainage Class = excessively drained Flooding Frequency = none or very rare	Soils are coarse textured and have a significant amount (>35%) of gravel and are somewhat excessively drained or excessively drained. Fertility and soil moisture is limiting for hardwoods but may produce high quality softwoods. Pine should dominate with *Pinus rigida* P. Mill. and *P. resinosa* Aiton.
Dry	NHFSG = 1C Drainage class = somewhat excessively drained (NH and ME), and well-drained (ME only) Flooding frequency = none, very rare, rare	Soils are coarse textured with only a small amount (10%) of gravel and are somewhat excessively drained. Fertility and soil moisture is limiting for hardwoods but may produce high quality softwoods. No apparent water table. Pine should dominate with oak and beech.
Loamy	NHFSG = 1B Drainage class = well drained Flooding frequency = none, rare, occasional	Loamy sand to loamy textures (with or without gravel/cobble). Not moderately well drained or wetter. Productive soils with adequate, but not excessive, soil moisture.
Shallow	NHFSG = 1A, 1B, 1C, or 2B Shallow soils and soils with layer restricting water movement and root growth (ME only)	Wetter soils. Soils are considered poor for most plant growth due to excess moisture or shallow depth. These soils have features (bedrock or dense sub-surface layer) restricting movement of water and root growth—no additional grouping by drainage class or flooding frequency.

Figure 1. Eastern white pine (*Pinus strobus* L.) seedling in Rhode Island, USA, photographed on April of 2013 with Caliciopsis canker symptoms and signs (black, hair-like fruiting structures, 2–3 mm).

2.2. Field Sampling

In the field, a GPS receiver and compass were used to locate the center point of each site generated by the intersection of GIS soil groups and white pine layers. A 10 basal-area-factor prism was used at plot center to select sample trees (DBH > 11.5 cm). Three more prism plots at 120° (0, 120, and 240) and 17 m from the initial plot center were installed for a total of four prism plots per site). Trees per prism plot were converted to trees per hectare by calculating an expansion factor unique to each tree's DBH. In addition, the following data were collected for each eastern white pine: live crown ratio, presence of *C. pinea* fruiting bodies, incidence and severity of Caliciopsis canker symptoms. Caliciopsis canker symptom severity was visually assessed by dividing the bole of the tree into thirds (bottom, middle, and upper stem) and counting the number of resin streaks in each section up to ten streaks per section. This assessment was conducted on two opposing faces of each tree and added for a maximum score of 60 resin streaks per tree. Resinosis associated with white pine blister rust symptoms, insect boring, decayed branch stubs, or mechanical damage was not considered in Caliciopsis canker disease severity assessments. In 2015, the presence of *C. pinea* in understory regeneration was recorded for each prism plot, but not for individual seedlings. In 2016, consequently, the presence of Caliciopsis fruiting bodies from the five closest eastern white pine seedlings (DBH < 2.54 cm, height > 30 cm) to each prism plot center as well as maximum distance to prism plot center were recorded. Caliciopsis fruiting bodies and infected plant tissue were collected from symptomatic eastern white pines trees or seedlings during 2015 for diagnoses.

2.3. Isolation and Identification of Caliciopsis pinea

Modified methods described by Munck et al (2015) were used to isolate and identify *C. pinea* isolates. Briefly, a piece of the bark containing the fruiting structure was placed onto the lid of an inverted petri dish, so that the lid was on the bottom and potato dextrose agar (PDA) media on top, and then sealed with Parafilm to induce sporulation. Small colonies that were formed on the PDA were transferred onto fresh PDA plates after two to three days. Once pure cultures were established, isolates were transferred onto 2% PDA plates overlaid with a cellophane membrane and grown for one to two weeks. Using direct colony polymerase chain reaction (PCR) [15] on 21 of these strains, at least three from each soil group, the internal transcribed spacer (ITS1-5.8s-ITS2) region of the rDNA using the primers ITS1 and ITS4 was amplified and sequenced in the forward direction (GENEWIZ, South Plainfield, NJ, USA).

2.4. Statistical Analyses

To explore the effect of soil and stocking on the incidence of eastern white pine with symptoms associated with Caliciopsis canker, single binary regressions were executed with the GLIMMIX procedure (Statistical Analyses Software v. 9.2, SAS Institute Inc., Cary, NC, USA) in SAS by specifying binomial distribution and the logit link function for the response variables "presence or incidence of Caliciopsis canker symptoms". Before data analysis, the mean counts of trees or seedlings with Caliciopsis damage per site (y) were calculated by averaging prism plot counts for each site and transformed (y + 0.0001). Stocking guides developed for eastern white pine which took into account tree density and basal area were used to determine stocking at each site [16]. Sites with stocking levels below the "unmanaged B-line" were considered to be under-stocked whereas sites with stocking levels between the "unmanaged B-line" and the "A-line" were considered to be adequately stocked. One-way analyses of variances (ANOVA) were performed using the GLIMMIX procedure to explore the main effects of soil group on tree density. The response variable was either "basal area per hectare" of "trees per hectare". Similarly, to determine the main effect of soil group on seedling density linear mixed model (PROC GLIMMIX) was used with "soil group" as a fixed effect, "site" was a random factor, and the response variable was "seedlings per hectare". To quantify the relationship between symptoms on the main stem and tree crown health, one-way analyses of variances (ANOVA) were performed using the GLIMMIX procedure to investigate main effects of Caliciopsis canker severity on live crown ratios. Caliciopsis canker disease severity categories were defined as: "None" = Caliciopsis canker symptoms absent; "Low" = 1 to 4 resin streaks per tree, "Medium" = 5 to 19 resin streaks per tree, and "High" = 20 to 60 resin streaks per tree. The response variable was the live crown ratio of eastern white pine. For all analyses, when the main effects were significant ($\alpha = 0.05$), a Tukey–Kramer test was used to identify differences between categories.

3. Results

A total of 62 white pine stands or sites were sampled in Maine and New Hampshire during 2015–2016 (Figure 2). Fifty of these (81%) had symptoms associated with Caliciopsis canker. During 2015, 50 sawtimber stands, at least 11 in each soil group (Table 1) were sampled in New Hampshire and Maine, 13 of which were privately owned. For 2015, mean stand diameter was 34 cm, mean tree density per stand was 336 trees per hectare, on average eastern white pine comprised 80% of the stand basal area, and 20% of eastern white pines exhibited symptoms associated with Caliciopsis canker. During 2016, 12 poletimber stands, at least three in each soil group were sampled in New Hampshire all on lands owned and managed by the State. For 2016, mean stand diameter was 23 cm, mean tree density per stand was 459 trees per hectare, on average eastern white pine comprised 86% of the stand basal area, and 66% of eastern white pines exhibited symptoms associated with Caliciopsis canker.

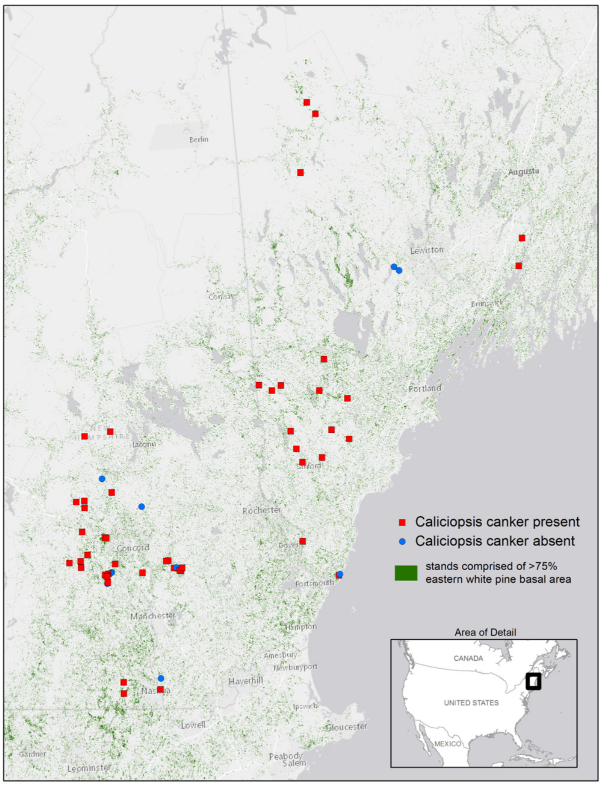

Figure 2. Location of 62 *Pinus strobus* stands in Maine and New Hampshire sampled during 2015 and 2016 and the presence of symptoms associated with Caliciopsis canker in those sites.

The proportion of trees (DBH > 11.5 cm) or seedlings (DBH < 2.54 cm, height > 30 cm) with symptoms associated with Caliciopsis canker differed significantly across soil groups ($p < 0.0001$) and stocking categories (Table 2, Figure 3). Trees in poletimber stands were more likely to have Caliciopsis canker symptoms than trees in sawtimber stands. For example, the probability (ranging from 0 to 1) of having Caliciopsis canker symptoms was 0.7 for trees in poletimber stands in the dry soil group compared to 0.3 for trees in poletimber stands in the dry soil group.

Table 2. Type III test for fixed-effect model results for the probability of symptoms associated with Caliciopsis canker.

Sample	Parameter	*F*-test (Degrees of Freedom = *df*)	*p*-Value
Live trees (>11.5 cm DBH) in sawtimber (>23 cm mean stand diameter) stands sampled in 2015	Soil	48.81 (3, 46)	<0.0001
	Stocking	59.56 (1, 48)	<0.0001
Live trees in poletimber (11.5 to 23 cm mean stand diameter) stands sampled in 2016	Soil	42.79 (3, 7)	<0.0001
	Stocking	45.79 (1, 9)	<0.0001
Seedlings (>30.5 cm height, and <2.54 cm DBH) in poletimber stands sampled in 2016	Soil	859.01 (3, 3)	<0.0001
	Stocking	14,248.3 (1, 5)	<0.0001

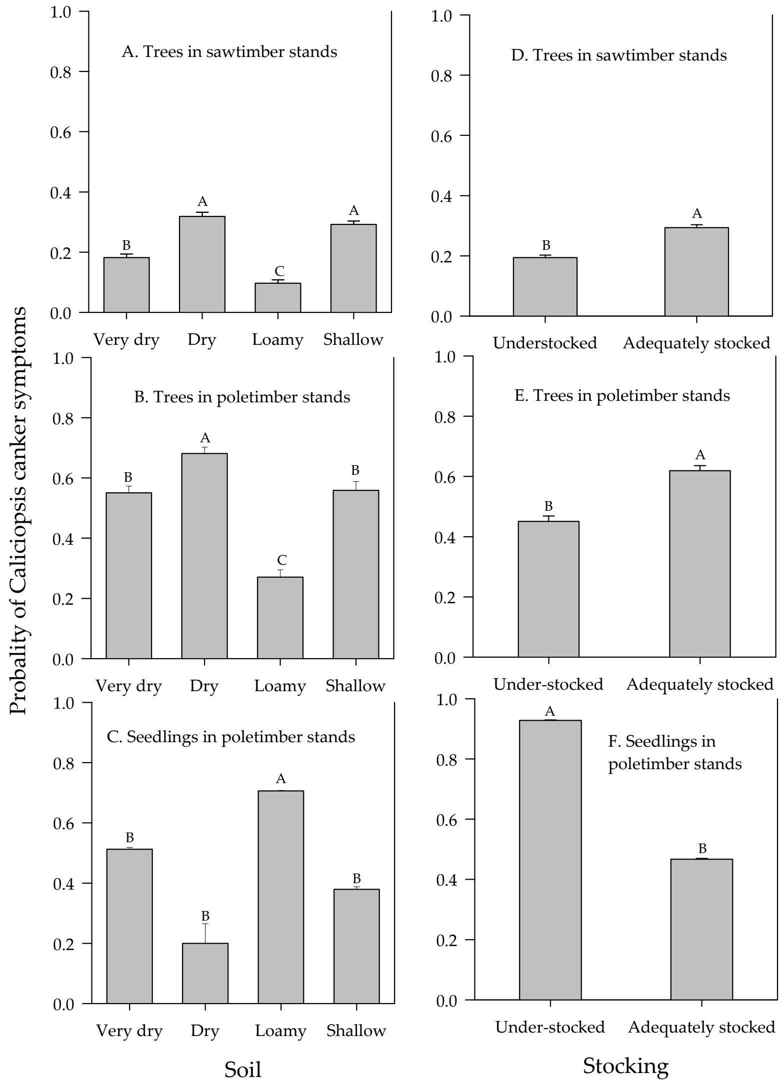

Figure 3. Incidence of symptoms associated with Caliciopsis canker in relation to soil groups for (**A** and **D**) *Pinus strobus* trees (DBH > 11.5 cm) in sawtimber stands (mean stand DBH > 23 cm) sampled in New Hampshire and Maine during 2015; (**B** and **E**) *P. strobus* trees in poletimber (mean stand DBH = 11.5 to 23 cm) stands sampled in New Hampshire during 2016; and (**C** and **F**) *P. strobus* seedlings (height > 30.5 cm and DBH < 2.54 cm) sampled in New Hampshire during 2016. Values with the same letter within each graph are not statistically different ($\alpha = 0.05$).

Trees in loamy soils and understocked stands were less likely to be damaged by Caliciopsis canker than trees in other soil groups or adequately stocked stands. The proportion of live trees with symptoms associated with Caliciopsis canker was less for loamy soils than any other soil group, and greatest for dry soils (Figure 3A,B). The proportion of live trees with symptoms associated with Caliciopsis canker was less in understocked stands than in adequately stocked stands (Figure 3D,E). Pinus strobus seedlings in poletimber stads were more likely to be damaged by *C. pinea* in sites with loamy soils (Figure 3C) and understocked over story (Figure 3F). Stand density was not related to soil groups (for basal area per hectare: $p = 0.47$, F-value = 0.86, $df = 3, 58$; or for trees per hectare: $p = 0.9$, F-value = 2.3, $df = 3, 58$) (Figure 4A,B).

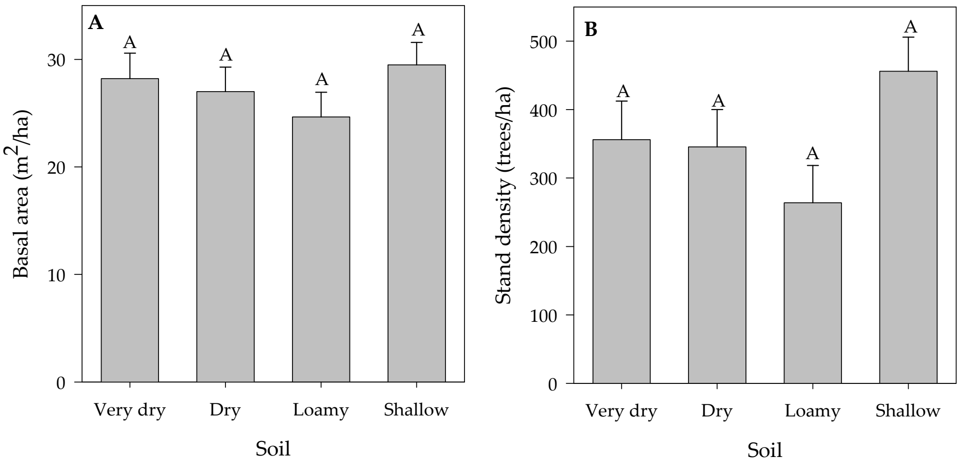

Figure 4. Relationship between soil group and stand density expressed as: (**A**) basal area per hectare; or (**B**) trees per hectare, for *P. strobus* trees sampled in New Hampshire and Maine during 2015–2016. Values with the same letter within each graph are not statistically different ($\alpha = 0.05$).

In contrast to results from the tree density analyses, seedling density of seedling in poletimber stands was related to soil type ($p = 0.0239$, F-value = 3.49, $df = 3, 42$). Seedling density was greater in poletimber stands on loamy soils than those on shallow soils (Figure 5).

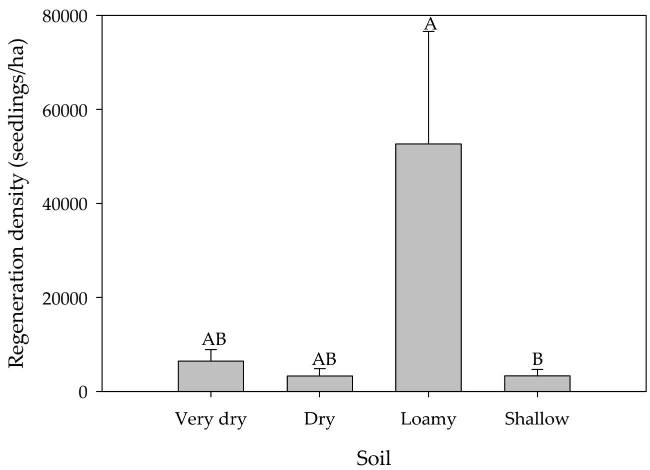

Figure 5. Relationship between soil group and *P. strobus* seedling density in poletimber stands sampled in New Hampshire during 2016. Values with the same letter are not statistically different ($\alpha = 0.05$).

Live crown ratio of eastern white pines decreased with increasing Caliciopsis canker symptom severity (Figure 6), ranging from 28% for trees without symptoms to 20% for trees with high disease severity ($p = 0.002$). BLASTn analyses of ITS locus of *C. pinea* isolates displayed 100% homology to the ITS locus of *C. pinea* in the GenBank CBS 139.64 (Accession # KP881691.1).

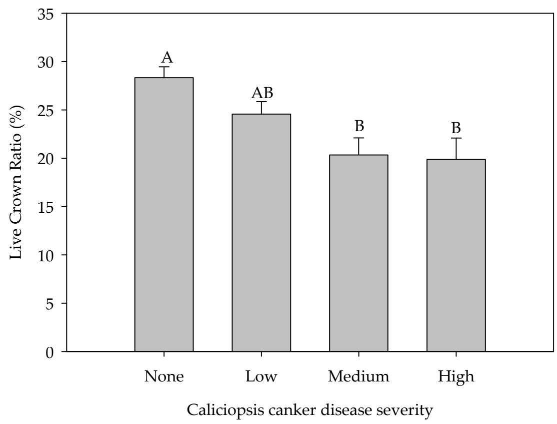

Figure 6. Live crown ratio of eastern white pines in relation to Caliciopsis canker symptom severity for trees sampled in Maine and New Hampshire in 2015–2016. Values with the same letter are not statistically different (α = 0.05).

4. Discussion

In New England and New York, *Pinus strobus* grows from sea level to 460 m [3] and competes better on drier soils with low to medium site quality that do not favor growth of hardwood species. In this study, we sampled 62 eastern white pine stands across a variety of soils. We did not have prior knowledge of Caliciopsis canker incidence in these sites prior to sampling. The 62 sites had an average slope of 3.4% ranging from 0% to 25%, therefore, soil was the most salient topographic feature differing among sites. Incidence of symptoms associated with Caliciopsis canker in mature white pines was greater in drier and shallow soils compared to loamy soils. Conceivably, white pine trees growing in soils with more nutrients, and adequate but not excessive water-holding capacity, likely have more resources to grow and allocate towards defense than trees growing in more nutrient poor and excessively or poorly drained sites. Plants have to grow to compete for resources such as light and water and also to synthesize plant defense compounds, thus facing a continuous tradeoff between growth and defense [17].

The water holding capacity of soils affects the amount of water available for tree growth. Other studies have associated canker diseases of pine, such as Diplodia canker of red pine (*Pinus resinosa* Aiton), to soil type [18]. Drier soils are more conducive to drought stress which might render trees more susceptible to damage by Caliciopsis canker because these trees might have less water to allocate towards growth and defense. Many published studies have found a positive association between drought and canker diseases [18]. For example, red pines suffering from drought stress exhibited greater symptom severity when inoculated with *Diplodia sapinea* (Fr.) [19]. Pathogens and drought can interact and effect the carbon economy of trees resulting in tree death [20].

In contrast to mature trees, white pine regeneration in loamy soils exhibited greater incidence of Caliciopsis canker symptoms than seedlings growing in other soil groups. Seedling density was also greater in loamy soils compared to other soils. Stem density increases the probability of damage by Caliciopsis canker. For example, mature trees in stands that were adequately or fully stocked were more likely to have Caliciopsis canker symptoms than trees in understocked stands.

Stem density could affect disease development because trees in denser stands or seedlings growing at high densities have less resources to allocate towards defense due to competition. Stem density could also influence disease development by creating an environment more favorable to pathogen reproduction and dissemination. Thickets of white pine regeneration are probably more likely to retain moisture and create high humidity conditions that could favor reproduction and dissemination of *C. pinea*. Furthermore, stem density could also affect tree physiology. Trees growing in denser stands typically have thinner bark, which is associated with greater Caliciopsis canker severity, allegedly because the pathogen is better able to penetrate thinner bark. Currently, all these hypotheses are highly speculative because the epidemiology of *C. pinea* has not been investigated. For example, we do not know what temperature and humidity favor growth and reproduction of *C. pinea*. The time of the year at which inoculum is most abundant and how inoculum is disseminated are both also unknown.

Caliciopsis pinea appears to be the primary pathogen associated with white pine damage in the Northeast, however, other insects (*Matsucoccus macrocicatrices* Richards) and pathogens (*Diplodia scrobiculata* J. de Wet, Slippers & M.J. Wingf.) have been associated with white pine cankers [6,7]. The pathogenicity of *C. pinea* to eastern white pine was demonstrated by Ray in 1936 [8]. In this study, isolates of *C. pinea* were obtained from fruiting bodies protruding from cankers, mostly of seedlings. Caliciopsis canker has been successfully isolated from wood in the cankers of mature trees and inoculation trials are underway to clarify pathogenicity of *C. pinea* and other opportunistic fungi [21].

Forest health management of white pine in past decades has focused on reducing damage by white pine blister rust (*Cronartium ribicola* J. C. Fisch.) and white pine weevil (*Pissoides strobi* Peck) [22]. In this study, trees of all size classes were affected by *Caliciopsis pinea*, did not have white pine blister rust symptoms, and were rarely damaged by the white pine weevil. Management recommendations to reduce damage from white pine blister rust, such as promoting high density of young trees to promote pruning of branches that are susceptible to white pine blister rust, may have improved conditions for the development of *C. pinea*. It is difficult to test this hypotheses due to lack of past baseline data. Most of the eastern white pine resource is mature, and thus, white pine regeneration is important to the future of the resource [2].

5. Conclusions

The objective of this study was to further investigate the relationship between soil and stocking in eastern white pine forests of New England. Eastern white pines growing in excessively drained, poorly drained, and nutrient poor soils are at greater risk of being damaged by Caliciopsis canker. Stem density was also positive correlated with Caliciopsis canker damage for mature trees and regeneration. Poor soils and high stem density could predispose trees to Caliciopsis canker or could affect environmental conditions that favor disease development. The epidemiology of Caliciopsis canker is not understood at this time. Given the prevalence of Caliciopsis canker in important white pine growing regions, this topic deserves further investigation. Foresters will have to take *C. pinea* into account in eastern white pine management.

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Conflicts of Interest: The authors declare no conflict of interest.

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