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Assessment of abiotic and biotic factors associated with eastern white pine (*Pinus strobus* L.) dieback in the Southern Appalachian Mountains☆

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ABSTRACT

A novel and emerging eastern white pine (*Pinus strobus* L.) dieback phenomenon is occurring in the Southern Appalachian Mountains in the eastern United States. Symptomatic eastern white pine trees exhibit canopy thinning, branch dieback, and cankers on the branches and bole. These symptoms are often associated with the presence of a scale insect, *Matsucoccus macrocicatrices* Richards (Hemiptera: Matsucoccidae), and a fungal pathogen, *Caliciopsis pinea* Peck (Coryneliales: Coryneliaceae). We determined the extent, range, and severity of dieback of 2,061 eastern white pine trees from 40 sites in Georgia, North Carolina, South Carolina, Tennessee, Virginia, and West Virginia. We also evaluated associations between eastern white pine health and abiotic (aspect, elevation, latitude, precipitation, slope, and temperature) and biotic (eastern white pine basal area and density, relative stand density, and presence of *C. pinea* and *M. macrocicatrices*) factors. Our results indicate that trees ≥ 2.54 cm DBH had an average health rating of 3.57 (1 = healthy tree, 5 = dead tree), with 57% being in the 4–5 health rating groups. Eastern white pine dieback was positively associated with presence of *C. pinea*, and negatively associated with mean annual temperature and tree size. Sawtimber (≥ 22.86 cm) were healthier than poletimber (12.70–22.61 cm) and sapling sized trees (2.54–12.45 cm). Further, *C. pinea* incidence was positively correlated with eastern white pine density and *M. macrocicatrices*. The insect-pathogen complex was present in all six states and 80% of the sites. If eastern white pine dieback continues, effective management practices will be needed to conserve and maintain this economically and ecologically important pine species in the eastern United States.

1. Introduction

Eastern white pine (*Pinus strobus* L.), the most widely distributed pine species in eastern North America, is a component of more than 28 Society of American Foresters coniferous and deciduous forest types, and serves many important functions (Barrett, 1995; Wendel and Smith, 1990). It tends to dominate the dominant and codominant canopy classes, thereby providing crucial habitat for many notable wildlife species including bald eagles (*Haliaeetus leucocephalus* L.), black bears (*Ursus americanus* Pallas), and osprey (*Pandion haliaetus* L.) (Abbott and Quink, 1970; Abrams et al., 1995; Rogers and Lindquist, 1992; Wendel and Smith, 1990). Its ecological importance as a canopy tree species has become even more critical because another dominant conifer characteristic of the eastern montane forests, eastern hemlock [*Tsuga canadensis* (L.) Carr.], has experienced a broad-scale decline due to the invasion of the non-native hemlock woolly adelgid (*Adelges tsugae* Annand) (Lovett et al., 2006).

The economic importance of eastern white pine cannot be understated, as it is one of the most widely planted commercial pine species in eastern North America, and has increased in numbers in urban and suburban areas, especially outside of its original range (Czapowskyj and McQuilkin, 1966; Wendel and Smith, 1990). The bark, wood, resin, seeds, and needles of eastern white pine have many uses, from construction material to terpene extracts and medicinal products (Betts, 1954; Krochmal et al., 1969; Wendel and Smith, 1990). It is worth over $18 billion to the local, regional, and national economies, and accounts for more than 20% timber stock value in Massachusetts and New Hampshire alone (Morin and

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Woodall, 2012; Widmann and McWilliams, 2003). In the southeastern United States, the eastern white pine portion of the Christmas tree industry contributes millions of dollars to local and state economies annually (Johnson et al., 2005). In Canada, approximately 14 million m^3 of eastern white pine was harvested in Ontario alone in 2014, which provided domestic revenue of over $11 billion from manufactured goods (Natural Resources Canada, 2016).

Several anthropogenic, abiotic, and biotic factors have historically threatened the existence of eastern white pine as a dominant tree species in eastern North America. Past extensive logging of eastern white pine forests nearly eliminated the species from much of its native area (Ostry et al., 2010). Biotic threats to eastern white pine include non-native insects, such as the introduced pine sawfly (*Diprion similis* Hartig), and native insects, such as the white pine weevil (*Pissodes strobi* Peck) (Drooz, 1985; Wendel and Smith, 1990). Eastern white pine is also susceptible to fungal pathogens, such as the non-native white pine blister rust (*Cronartium ribicola* Fisch.), native *Heterobasidion irregulare* (Underw.) Garbel, various foliar diseases, and a needle damage fungal complex (Broders et al., 2015). Eastern white pine has been noted to frequently colonize and develop pure stands on old fields (Spurr, 1956). This high abundance may make it more susceptible to biotic damaging agents. Extensive logging and threats from biotic agents have significantly influenced the prevalence and survival of eastern white pine over time (Ostry et al., 2010).

In the early 1930s, eastern white pine's desirable characteristics, such as its tall stature, high quality wood, and fast growth rates, drew the attention of many entities, including the Civilian Conservation Corps (CCC) that used eastern white pine for reforestation projects (Vimmerstedt, 1962). Although eastern white pine was replanted through much of the eastern United States, mass production of eastern white pine lumber dwindled except in the northeastern region, leaving trees to grow primarily for biodiversity and aesthetics (Ostry et al., 2010). Without harvest or regular management, eastern white pine has become dominant in eastern hemlock and mixed-hardwood stands in the southeastern United States.

Over the last 10–15 years, forest resource managers and health specialists have documented health issues for eastern white pine trees in the Southern Appalachian Mountains, specifically in Georgia and Virginia (Asaro, 2011; Asaro et al., 2018; Mech et al., 2013). Symptomatic eastern white pine trees had cankerous growths, significant resinosis, crown thinning, branch flagging, and decreased crown density of all age classes and over many site conditions (Fig. 1) (Asaro, 2011; Mech et al., 2013; Rose, 2011; Rosenholm, 2012). A closer inspection of the branches and stems on dying pines revealed a novel insect-fungal complex involving a scale insect, *Matsucoccus macrocicatrices* Richards, found embedded under lichen, or in branch crotches or cankers (Mech et al., 2013). Many trees also had discernable cankers from the pathogen *Caliciopsis pinea* Peck (Cram et al., 2009; Mech et al., 2013). *Caliciopsis pinea* is a common pathogen of eastern white pine (Overholts, 1930; Ray, 1936). Cankers without *C. pinea* fruiting structures have been noted to occur, but with less apparent frequency (Cram et al., 2009). Until recently (e.g., Mech et al., 2013; Munck et al., 2015; Rose, 2011; Rosenholm, 2012), significant damage to eastern white pine from both *C. pinea* and *M. macrocicatrices* has not been reported. It has been hypothesized that *M. macrocicatrices* scale insects may be associated with opportunistic fungi (Mech et al., 2013; Schulz et al., this issue).

To better understand the extent and severity of eastern white pine dieback in the Southern Appalachian Mountains, we examined eastern white pine trees of all size classes in mixed and pure conifer stands in the Southern Appalachian Mountains. Our specific objectives were to assess: (1) the range and severity of eastern white pine dieback; (2) the distribution of *C. pinea* and *M. macrocicatrices* on eastern white pine in the Southern Appalachian Mountains; (3) effects of various abiotic and biotic factors on eastern white pine health; and (4) if eastern white pine health rating varied with diameter at breast height (DBH) and among different growing stock categories (sapling, poletimber, and sawtimber).

2. Materials and methods

2.1. Study sites

Our study sites were located in the eastern temperate forests of the Southern Appalachian Mountains in the eastern United States. The general soil orders (and dominant suborders) found at these sites include Inceptisols (Udepts), Ultisols (Udults), and to a lesser extent, Spodosols (Orthods) [USDA Natural Resources Conservation Service (NRCS), 1998; Wendel and Smith, 1990]. Average annual precipitation and temperature varied from 126.7 cm $year^{-1}$ and 17.4 °C in Georgia, to 109.5 cm $year^{-1}$ and 12.8 °C in Virginia, respectively (NOAA National Climatic Data Center, 2014). Elevation in this region ranges from < 100 m to over 2000 m, but all of the sampled sites were located between 300 and 900 m.

We identified 40 sites from Georgia, North Carolina, South Carolina, Tennessee, Virginia, and West Virginia. To determine the number of sampling sites per state, we retrieved data on eastern white pine basal area for each state from the USDA Forest Service Forest Inventory Data

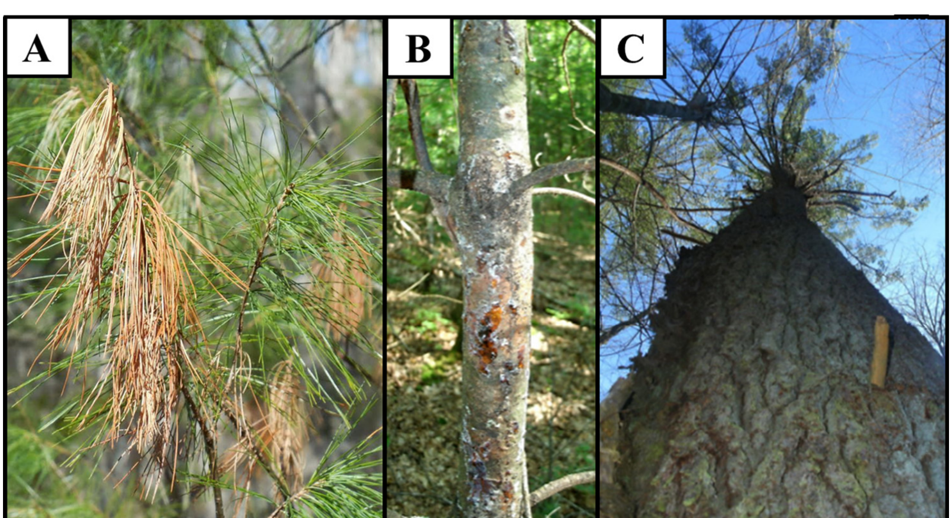

Fig. 1. Symptoms observed on eastern white pine include (A) branch flagging, (B) cankerous growths with resinosis, and (C) crown thinning. Photos by C. Asaro and A.N. Schulz.

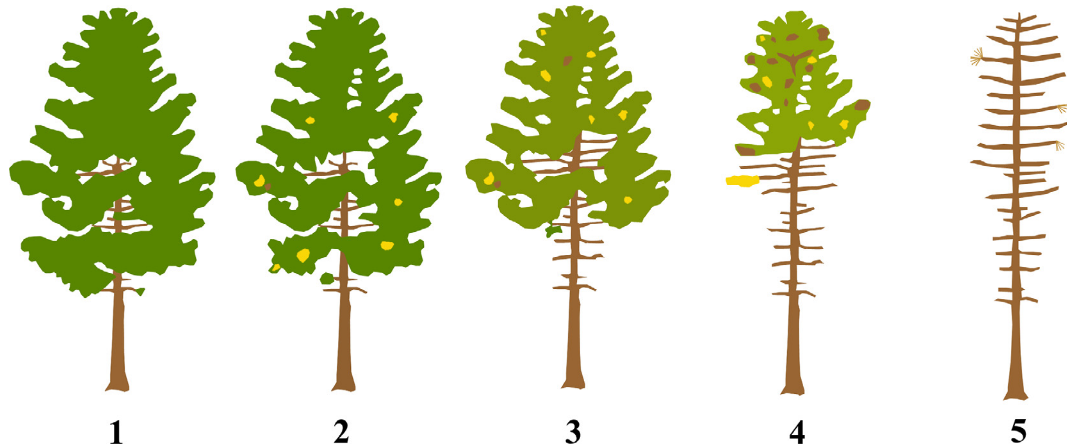

Fig. 2. Eastern white pine health rating scale, where 1 is healthy, 2 – 4 is a gradual thinning of the crown, and 5 is a dead tree (adapted from Schomaker et al., 2007).

Online (available through the Forest Inventory and Analysis National Program) (USDA Forest Service, 2014). We totaled the eastern white pine basal area for these six states, calculated the proportion for each state, and then used this proportion to calculate the number of sites for each state. Based on the proportion of eastern white pine within each state, we assigned sites as follows: Georgia (8), North Carolina (4), South Carolina (2), Tennessee (7), Virginia (13), and West Virginia (6), for a total of 40 sites. To determine where eastern white pine was present within each state, we used USDA Forest Service Forest Inventory Data Online, Google Earth, Arc Geographic Information Systems (ESRI, 2013), USDA Forest Service National Forest maps, and communication with local forestry professionals. As part of the site selection process, sites had to be: (1) accessible by vehicle or on foot; (2) located on USDA Forest Service land (wilderness and private land excluded); (3) available for future sampling and monitoring, and free from active anthropogenic disturbances (silvicultural cutting, prescribed fire, etc.) for the next 5–10 years (determined through communication with local forestry professionals); and (4) > 5 km from other study sites. Extensive consulting with local forestry professionals was required to gain access to sites that met these selective criteria. Given the restrictedness of this criteria, our sample size of 40 sites provides an adequate representation of our area of study.

All 40 sites were within four of the five major Society of American Foresters forest cover types for this region: eastern white pine-northern red oak-red maple (Type 20), eastern white pine (Type 21), eastern white pine-eastern hemlock (Type 22), or eastern white pine-chestnut oak (Type 51). Other species occurring within the 40 sites included: American beech (*Fagus grandifolia* Ehrh.), birch (*Betula* spp.), black gum (*Nyssa sylvatica* Marshall), eastern hemlock, Fraser magnolia (*Magnolia fraseri* Walt), hickory (*Carya* spp.), maple (*Acer* spp.), pitch pine (*Pinus rigida* Mill.), red oak (*Quercus rubra* L.), table mountain pine (*P. pungens* Lamb.), tulip-poplar (*Liriodendron tulipifera* L.), Virginia pine (*P. virginiana* Mill.), and white oak (*Q. alba* L.). Common understory species included bracken fern (*Pteridium aquilinum* L. Kuhn), buckberry (*Vaccinium stamineum* L.), dogwood (*Cornus* spp.), mountain laurel (*Kalmia latifolia* L.), and rhododendron (*Rhododendron maximum* L.) (Wendel and Smith, 1990).

2.2. Sampling of forest attributes

During January – August 2014, we sampled sites using three, 10 m fixed radius circular plots within each of the 40 sites for a total of 120 plots. Plots were selected using a combination of Google Earth maps and on-the-ground scouting. Since the aim of this study was to evaluate eastern white pine, we searched for areas that had both young and mature eastern white pine trees, and were greater than 50 m from our other plots within the site. Once the eastern white pine trees were located, we installed a georeferenced, tagged rebar marker at the randomly selected plot center, and a second tag on the tree nearest to the center, so the plot could be found for future monitoring. For each plot, aspect, elevation, latitude, and slope were recorded in the field using a compass, GPS unit, and clinometer. Temperature and precipitation data from the year 2013 were gathered remotely from Oregon State University's PRISM Climate Group data explorer tool (PRISM Climate Group, 2004). Counts and DBH of all live and dead standing trees ≥ 2.54 cm DBH were measured to calculate basal area ($m^2\,ha^{-1}$) and density (trees ha^{-1}). A health rating ranging from 1 (healthy) to 5 (completely dead) was assigned to eastern white pine trees within each plot (Fig. 2). Health ratings were based on crown coverage, branch flagging, foliar transparency [based on the foliage transparency scale from Schomaker et al. (2007)], and tree size. We included tree size in the health rating since saplings naturally have a higher crown transparency, and are not comparable to more mature trees. All health ratings were completed by the same person to limit potential observer bias.

To assess eastern white pine regeneration, we counted the number of eastern white pine seedlings that were < 2.54 cm DBH, but ≥ 61 cm tall within each plot (hereafter called "large seedlings"). Each large seedling was counted as unhealthy/dead if it had ≤25% crown coverage and healthy (i.e., vigorous enough to survive) if it had > 25% crown coverage. The number of eastern white pine seedlings that were < 2.54 cm DBH and < 61 cm tall were also documented within each plot (hereafter called "small seedlings"). Due to the abundance of small seedlings, subsampling was conducted in which we counted the total number unhealthy/dead and healthy small seedlings that were present within a 1 m wide transect along each cardinal direction within the plot. Using the seedling data collected at each plot, we calculated percent mortality for large and small seedlings at each site.

2.3. Sampling of *Caliciopsis pinea* and *Matsucoccus macrocicatrices*

We collected two large eastern white pine seedlings from outside of each plot for a total of six large seedlings per site to look for the presence of *C. pinea* and *M. macrocicatrices*. All seedlings were stored in a refrigerator at 4.4 °C to prevent mold and to preserve fungal cankers and *M. macrocicatrices*. On each seedling, we documented the life stage of *M. macrocicatrices*, including eggs, crawlers (first instar, mobile nymphs), cysts (heavily sclerotized, legless stage between legged crawler and adult), shells (shed skin from adult emergence), and adults (Richards, 1960; Schulz et al., this issue). Only cysts and shells were found on the seedlings. The lack of crawlers and adults could be due to the phenology of the insect and the time of sampling (i.e., they were not hatching or emerging at the time when we cut the seedlings), or perhaps due to the short period of time in which they are in these mobile stages in relation to the time they are within the immobile cyst stage. To determine the presence/absence of *C. pinea*, we examined the seedlings for reddish-brown depressions in the bark with black, hair-like ascocarps (sexual stage), or small, black-conical lobes (spermagonia stage), both usually form in clusters (Funk, 1963; Ray, 1936). If at least one *M. macrocicatrices* insect was present on one of the six seedlings collected per site, it was determined that *M. macrocicatrices* was present at that site. Similarly, if at least one *C. pinea* canker was present on one of the six seedlings collected per site, or if *C. pinea* was detected and noted in the field, *C. pinea* was considered present at that respective site. Coordinates collected at each of the 40 sites in this study, and the coordinates from Mech et al. (2013) were compiled and entered into ArcGIS 10.2 (ESRI, 2013) to map the presence or absence (i.e., no record in our samples) of *C. pinea* and *M. macrocicatrices* on the range of eastern white pine (Little, 1971; USGS, 2013) within our sites in Georgia, North Carolina, South Carolina, Tennessee, Virginia, and West Virginia.

2.4. Statistical analyses

Aspect, elevation, latitude, mean annual precipitation, slope, and maximum, minimum, and mean annual temperatures for each site were included as abiotic variables. Aspect data were converted using the Beers transformation (Beers et al., 1966), which rescaled the 360° aspect to reflect site productivity by assigning a value of 2 to northeast facing slopes which receive less sunlight and are more mesic, and a value of 0 to southwest facing slopes, which receive more sunlight and are more xeric (Graham and McCarthy, 2006; Iverson et al., 1997). Eastern white pine health rating was calculated by averaging the health rating of all trees within each site, which was the unit of replication. Eastern white pine DBH and count measurements were used to calculate basal area ($m^2\ ha^{-1}$) and density (trees ha^{-1}) for eastern white pine at each site. Basal area and density measurements for all of the trees ≥2.54 cm measured at each site were used to calculate the relative stand density (RSD) (Curtis, 1982):

$$\text{RSD} = \frac{\text{Basal area}(m^2 ha^{-1})}{\sqrt{\text{Quadratic Mean Diameter}}} \tag{1}$$

Caliciopsis pinea and *M. macrocicatrices* presence were also included as indicator variables based on the presence (1) or absence (0) of *C. pinea* and *M. macrocicatrices*.

All statistical analyses were performed using R v. 3.4.0 (R Core Team, 2017) at a significance level of α = 0.05. We built a correlation matrix using Spearman's rank correlations between each individual abiotic (aspect, elevation, latitude, mean annual precipitation, slope, maximum annual temperature, mean annual temperature, and minimum annual temperature) and biotic (eastern white pine basal area, eastern white pine density, relative stand density, and presence of *C. pinea* and *M. macrocicatrices*) independent variable. We used the correlation matrix to determine which variables were associated, and thus should be excluded from our regression to examine associations between eastern white pine dieback and measured abiotic and biotic variables. Elevation, latitude, and mean annual precipitation were correlated with all three temperature variables. Mean annual temperature was selected from the group of correlated variables, since it varies consistently across both elevation and latitude. Eastern white pine basal area and presence of *M. macrocicatrices* were both correlated with relative stand density, so we selected relative stand density because it includes the basal area of eastern white pine and all other tree species present at the site, thus representing the overall competition within the stand. Lastly, eastern white pine density and presence of *C. pinea* were correlated, so we selected the presence of *C. pinea* because, recently, *C. pinea* has been noted widely throughout the northeastern United States as an important damaging agent of eastern white pine (Munck et al., 2015). We used an ordinal logistic regression using the *polr* function in the MASS package in R (Agresti, 2002; Venables and Ripley, 2002) to regress the average site eastern white pine health rating (1–5) on the following uncorrelated predictors: aspect, mean annual temperature, presence of *C. pinea*, relative stand density, and slope.

To assess whether the health rating of an individual eastern white pine tree varied with its DBH, we used an ordinal logistic regression (*polr* function of MASS package) to model the probability distribution of each eastern white pine health rating along with a series of DBH values ranging from 2.54 cm to 100 cm using the values produced from the regression. To evaluate eastern white pine health across different growing stock categories, we grouped each of the trees as: saplings (2.54–12.45 cm), poletimber (12.70–22.61 cm), and sawtimber (≥22.86 cm) (USDA Forest Service Northeastern FIA Program, 2013). A Shapiro-Wilk normality test and residual plot was used to check the data for normality and homoscedasticity. Since data were not normal, we used a non-parametric, Kruskal-Wallis Rank Sum test and post-hoc Pairwise Wilcoxon Rank Sum test to determine if there were significant differences in mean eastern white pine health rating among the three growing stock categories.

3. Results

We sampled 2,061 eastern white pine trees ≥2.54 cm DBH across the 40 sampled sites. On a health rating scale where 1 is healthy and 5 is a dead tree (Fig. 2), approximately 4% of the assessed trees were assigned a health rating of 1 (healthy or no symptoms), 12% as 2 (some branch flagging and minor symptoms), 27% as 3 (intermediate symptoms), 35% as 4 (severe symptoms and dieback, but not dead), and 22% as 5 (dead). Eastern white pine health rating ranged from 2.42 to 4.21 with a mean (±SE) of 3.57 ± 0.08 (Table 1). Mean (±SE) percent mortality of larger eastern white pine seedlings was 12.5 ± 2.5%, while mean dieback of smaller eastern white pine seedlings was 4.39 ± 2.5%.

Matsucoccus macrocicatrices was present in 34 (85%) of the 40 study sites sampled in 2014 (Fig. 3). Some sites with no record of *M. macrocicatrices* were < 20 km from sites with a positive record of *M. macrocicatrices*. *Caliciopsis pinea* was found in 88% of the 40 sites sampled in 2014 (Fig. 3). In total, 80% of sites had both *C. pinea* and *M. macrocicatrices*, 8% had only *C. pinea*, 5% had only *M. macrocicatrices*, and 8% had neither of the species.

The values for the non-indicator, abiotic variables (aspect,

Table 1
The range and mean (±SE) of abiotic and biotic factors in the 40 study sites in the Southern Appalachian Mountains.

Variable	Minimum	Maximum	Mean (±SE)
Abiotic variables			
Aspect	0.12	1.78	1.01 ± 0.06
Elevation (m)	325.2	871.5	633.6 ± 25.4
Latitude (°)	34.698	38.868	36.420 ± 0.22
Mean annual precipitation (cm)	106.4	268.2	167.8 ± 7.8
Maximum annual temperature (°C)	14.3	20.1	17.3 ± 0.3
Mean annual temperature (°C)	8.5	14.3	11.6 ± 0.3
Minimum annual temperature (°C)	2.6	9.2	5.9 ± 0.3
Slope (%)	5	36	15.9 ± 1.3
Biotic variables[a]			
Eastern white pine basal area ($m^2\ ha^{-1}$)	5.63	52.74	25.87 ± 2.02
Eastern white pine density (trees ha^{-1})	95.00	1,316.00	547.00 ± 52.00
Eastern white pine health rating[b]	2.42	4.21	3.57 ± 0.08
Relative stand density	6.92	17.14	11.45 ± 0.36

[a] Indicator variables not shown: presence of *Caliciopsis pinea* and presence of *Matsucoccus macrocicatrices*.
[b] Health rating, where 1 = live tree, 2–4 = gradual thinning of the crown, and 5 = dead tree.

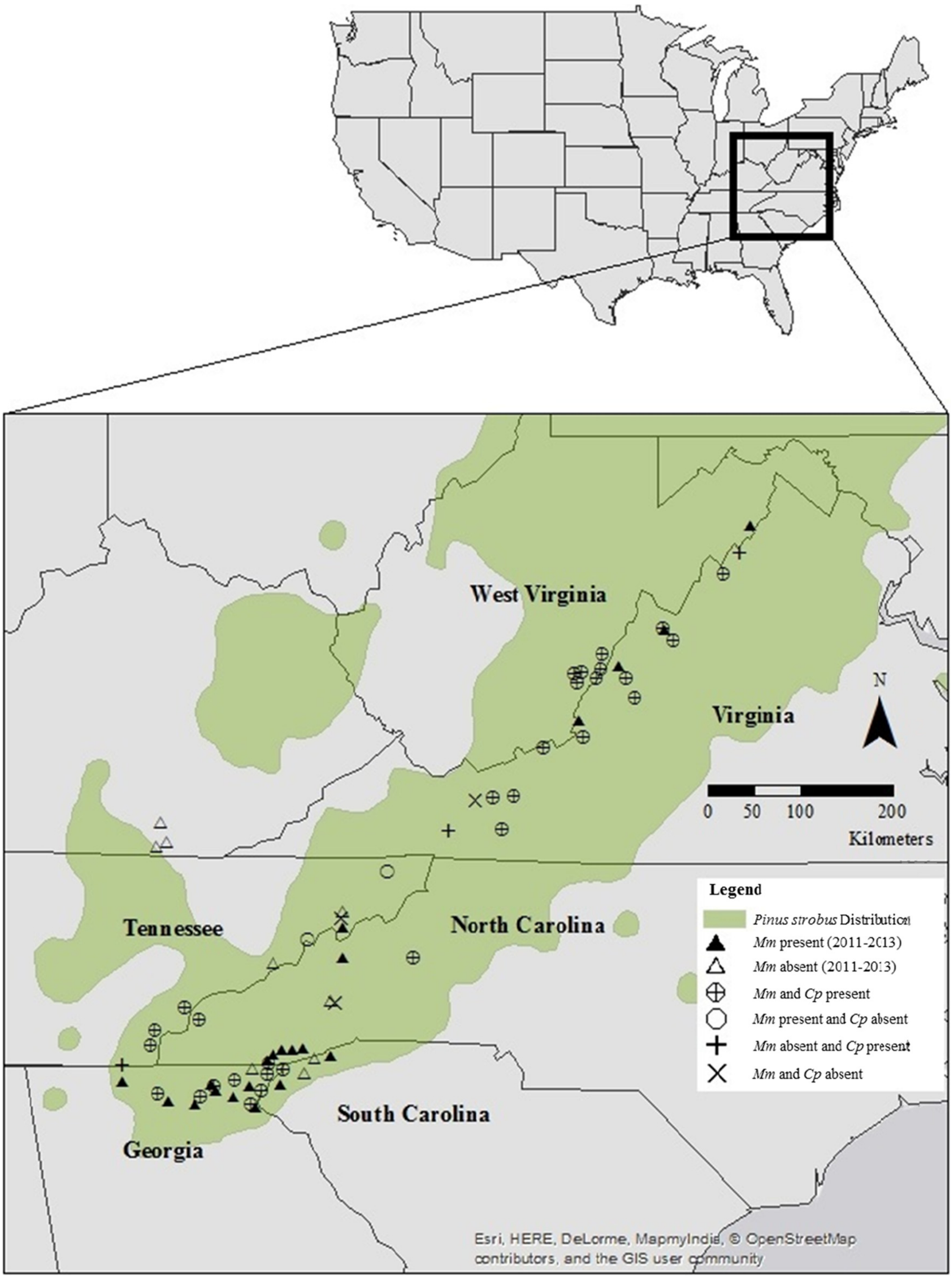

Fig. 3. Occurrence of *Matsucoccus macrocicatrices* (*Mm*) from 2011 to 2014, and *Caliciopsis pinea* (*Cp*) in 2014 in the Southern Appalachian Mountains, United States. Data from 2011 to 2013 were collected by Mech et al. (2013). Approximately 77% of the sites sampled from 2011 to 2014 had *M. macrocicatrices*.

elevation, latitude, slope, maximum annual temperature, mean annual temperature, and minimum annual temperature), and biotic variables (eastern white pine basal area, eastern white pine density, and relative stand density) varied in range (Table 1). Correlation tests between abiotic and biotic variables, including the presence of *C. pinea* and *M. macrocicatrices*, determined the presence of *C. pinea* was positively associated with eastern white pine density ($P < 0.01$, $r_s = 0.43$, Fig. 4A) and presence of *M. macrocicatrices* ($P < 0.01$, $r_s = 0.48$, Fig. 4B). Additionally, the presence of *M. macrocicatrices* was positively associated with aspect ($P < 0.01$, $r_s = 0.45$, Fig. 4C), in which the scale insect is

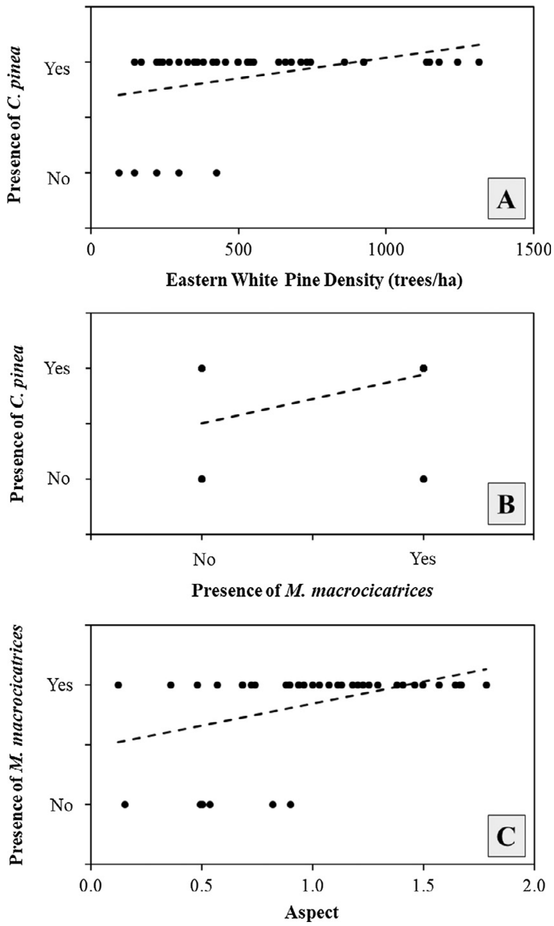

Fig. 4. Significant, positive correlations between (A) presence of *Caliciopsis pinea* and eastern white pine density (trees ha^{-1}), (B) presence of *C. pinea* and presence of *Matsucoccus macrocicatrices*, and (C) presence of *M. macrocicatrices* and aspect.

found more often on mesic, northeastern-facing slopes than xeric, southwestern-facing slopes.

Of the five uncorrelated variables (aspect, mean annual temperature, presence of *C. pinea*, relative stand density, and slope) that were regressed against eastern white pine health rating, two were significant (Table 2). The only significant abiotic variable was mean annual temperature ($t = -2.92$, $P < 0.001$). This indicates that, for a 1 °C increase in mean annual temperature, we would expect a 0.61 ± 0.21 decrease in the expected value of eastern white pine health rating on the log odds scale (Table 2; Fig. 5A). The significant biotic variable was the presence of *C. pinea* ($t = 1.96$, $P < 0.001$). These results indicate that, for an one-unit increase in presence of *C. pinea* (i.e., going from absent to present), we expect a 1.79 ± 0.92 increase in the expected value of eastern white pine health rating on the log odds scale given that all other variables were held constant (Table 2; Fig. 5B).

Eastern white pine health rating for individual trees was found to vary with tree DBH ($t = -17.12$, $P < 0.001$). Overall, for a 1 cm increase in DBH, we would expect a 0.04 ± 0.003 decrease in the expected value of eastern white pine health rating on the log odds scale (Fig. 6). Eastern white pine health also varied among the growing stock categories ($\chi^2 = 306.10$, $P < 0.001$), as there were differences between saplings and poletimber ($P = 0.01$), saplings and sawtimber ($P < 0.001$), and poletimber and sawtimber ($P < 0.001$). Mean

Table 2
Summary for an ordinal logistic regression model examining abiotic and biotic parameters on the average eastern white pine health rating at the site level (N = 40) in the Southern Appalachian Mountains.

Variable	Value	SE	t-value	P*
Aspect	−0.41	0.64	−0.65	0.52
Slope	−0.02	0.04	−0.59	0.56
Mean annual temperature	−0.61	0.21	−2.92	**0.004**
Relative stand density	0.10	0.14	0.76	0.45
Presence of *C. pinea*	1.79	0.92	1.96	**0.05**

P-values in bold are significant at the alpha = 0.05 level.
* Significant at α = 0.05.

(± SE) eastern white pine health rating ranged from 3.8 ± 0.03 for saplings, to 4.0 ± 0.05 for poletimber, and 2.9 ± 0.04 for sawtimber trees (Fig. 7).

4. Discussion

We assessed the range and severity of eastern white pine dieback, updated the distribution of *C. pinea* and *M. macrocicatrices* in the Southern Appalachian Mountains, and evaluated which abiotic and biotic factors were associated with eastern white pine dieback. Dieback of trees ≥ 2.54 cm, which includes advanced regeneration, appeared to be considerable, as 84% of the trees had a health rating of ≥3 and 22% were dead, indicating that many of the eastern white pine trees throughout the southern extent of the range were already in moderate stages of dieback. This range and severity of eastern white pine dieback is similar to the patterns of dieback that have been reported since 2001 in Maine, New Hampshire, and Vermont (Lombard, 2003; Rosenholm, 2012; Vermont Department of Forests, Parks, and Recreation, 2001). Forest resource managers and health specialists have noted the presence of characteristic black fruiting bodies of *C. pinea* on cankers with abundant resin flow on trees of all size and age classes (Lombard, 2003; Rosenholm, 2012; Vermont Department of Forests, Parks, and Recreation, 2001). In addition to *C. pinea*, eastern white pine seedlings from New Hampshire, Massachusetts, and Maine had *M. macrocicatrices* (Schulz et al., this issue; personal observations). Branch dieback and cankers on poletimber-sized eastern white pine trees became prevalent in Virginia and West Virginia around 2006 and 2007 (Asaro, 2011; Asaro et al., 2018). In Ontario, Canada, symptomatic eastern white pine trees have become prevalent, though no pathogens or insects have yet been isolated from the cankers (Llewellyn, 2013). Reports of symptomatic eastern white pine have increased over the last decade, indicating that eastern white pine dieback may be an important factor to consider when managing eastern white pine in the eastern United States.

The range of *M. macrocicatrices* was documented to extend from Georgia to West Virginia in the Southern Appalachian Mountains, and dieback is being observed across the entire range of eastern white pine. These trends are similar to those of other invasive species such as the emerald ash borer (*Agrilus planipennis* Fairmaire) and beech bark scale (*Cryptococcus fagisuga* Lind.) (Houston, 1994; Smith et al., 2015), in which a lag phase occurs before symptoms appear at the landscape-level. During this lag phase, populations of the organisms establish, grow, and expand their range before tree dieback is evident (Crooks, 2005). We currently do not know whether *M. macrocicatrices* is native to the southeastern United States, as it has only previously been documented in the northeastern United States and Canada (Watson et al., 1960). Genetic analyses of *M. macrocicatrices* throughout North America are underway to evaluate if the scale insects found in the

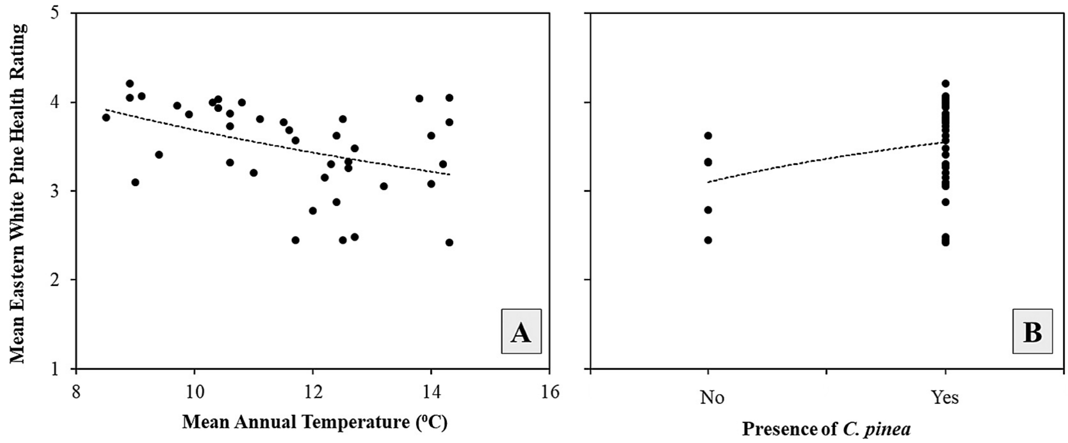

Fig. 5. Eastern white pine health rating as a function of (A) mean annual temperature (°C) and (B) the presence of *Caliciopsis pinea* at the site level (N = 40).

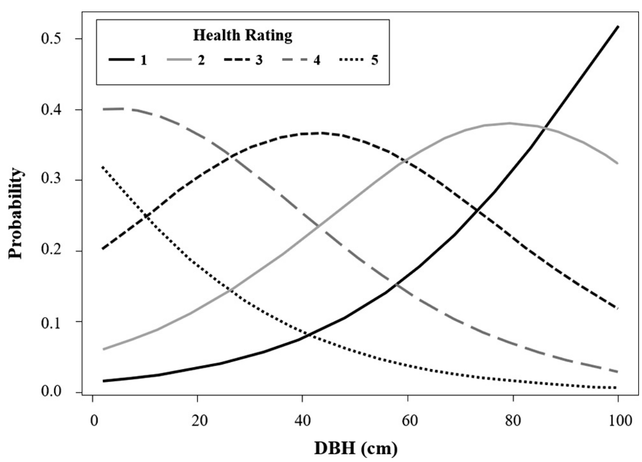

Fig. 6. Probability of each eastern white pine health rating category as a function of eastern white pine diameter at breast height (DBH).

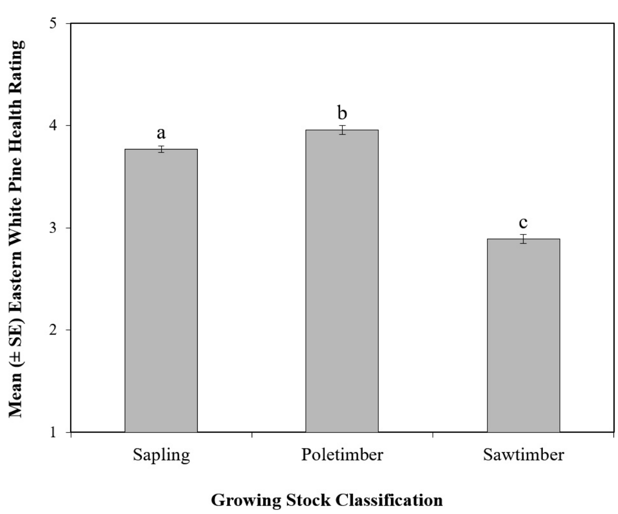

Fig. 7. Mean (± SE) eastern white pine health rating for three growing stock classifications: saplings (2.54–12.45 cm), poletimber (12.7–22.61 cm), and sawtimber (≥22.86 cm). Bars with different letters are statistically significantly different from one another.

Southern Appalachian Mountains are the result of a recent dispersal event or population expansion of a relict species in the southern United States (Whitney et al., 2017). Although *M. macrocicatrices* has not historically been reported to cause damage to eastern white pine, it is in the pine bast scale insect group, which includes significant pests of pine forests, including the red pine scale (*Matsucoccus resinosae* Bean & Godwin; *Matsucoccus matsumurae* Kuwana) and maritime pine bast scale (*Matsucoccus feytaudi* Ducasse) (Foldi, 2004; Jactel et al., 1998). More basic research on the biology and phenology of *M. macrocicatrices* will be necessary to better determine whether this particular phenomenon is an invasion or not.

Caliciopsis pinea was positively associated with *M. macrocicatrices* since they both occurred in over 80% of our sampled sites, meaning that the insect-pathogen complex has a widespread distribution in the southern portion of the Appalachian Mountains. We hypothesize that *M. macrocicatrices* scale insects are creating feeding wounds that are subsequently infected by opportunistic fungi, such as *C. pinea,* which may create cankers that contribute to girdling and tree mortality (Schulz et al., this issue). This is supported by our results that indicate eastern white pine trees experienced significantly more dieback when *C. pinea* was present. Most of the dieback was in smaller, poletimber- and sapling-sized trees than larger, sawtimber-sized trees. Similar results were also observed by Asaro et al. (2018) and Whitney et al. (2018). To girdle the stem of a large diameter tree, more time and/or greater density of pests and larger cankers are needed to affect the length of a tracheid and prevent xylem redistribution of water horizontally through the pits (MacKay and Weatherley, 1973). For smaller trees and branches of larger trees, it takes less time and/or smaller cankers to effectively girdle the tree. If there are multiple infections on the trees, the developing cankers may coalesce to girdle the stem, causing stem and branch death (Tainter and Baker, 1996). Small diameter trees also have thin, smooth bark, whereas larger trees have thicker, deeply grooved bark. Those with thinner bark may be more susceptible to insect feeding damage and canker-forming fungi that exploit wounds, since they have fewer layers of protection between them and the damaging agent (Munck et al., 2016; Whitney et al., 2018). However, thin, smooth bark has also been argued to be advantageous to smaller saplings, since smooth bark can act as an anatomical defense against insects by reducing their ability to grip the surface (Ferrenberg and Mitton, 2014). *Matsucoccus macrocicatrices* may overcome this by nestling into branch crotches, margins of existing cankers, and under lichen and moss, all of which allow the scale insect to remain secured to the tree.

We also found the presence of *C. pinea* was positively correlated to eastern white pine density, an indicator of host availability within a site. These results are consistent with Munck et al. (2015), which reported a greater incidence of *C. pinea* cankers at sites with greater eastern white pine density. Sites with a higher density of trees may contain more small trees with thinner bark, which makes them more susceptible to damage and canker-forming fungi (Munck et al., 2016). Eastern white pine trees in denser sites may also face increased intraspecific and interspecific competition for resources such as sunlight, water, nutrients, and root or stem space, which may cause trees to lose vigor, become stressed, and/or have fewer resources to allocate to defense against pests and pathogens (Munck et al., 2016; Root, 1973; Smith et al., 1997; Tilman, 1982). Water availability is an especially important component for pine defense. Competition for water in dense stands may lead to water stress that concentrates nutrients in the sapwood and reduces oleoresin exudation pressure, which may benefit colonizing insects and fungi (Mattson and Haack, 1987; Parker, 1961; Vitè, 1961). Sites with higher eastern white pine density may also have less space between individual trees and/or less species diversity to act as buffer, which promotes the dispersal of pests and pathogens (Munck et al., 2016). Ascospores of *C. pinea* likely disperse via wind, rain, and/or insects (Funk, 1963; Ray, 1936). Mechanisms for dispersal for adult and crawler stages of *M. macrocicatrices* are unknown, but they may use passive strategies such as wind and animals, similar to hemlock woolly adelgid and red pine scale (McClure, 1989).

In addition to the presence of *C. pinea*, eastern white pine dieback decreased with increasing mean annual temperature. Hence, trees were healthier in sites with a higher annual temperature (i.e., those in the southernmost part of the Southern Appalachian Mountains and/or in low elevation areas). Temperature may influence the life cycle, distribution, and/or abundance of all three organisms (McClure, 1989; Munck et al., 2016; Wendel and Smith, 1990). For example, eastern white pine generally grows best in areas that are cool and humid (Wendel and Smith, 1990), so it may be less abundant in warmer sites. Limited density may limit the spread of pathogens and pests, which would mean less dieback due to biotic factors. Species of *Matsucoccus*, especially in an advanced nymphal stage, have been documented to have high tolerance to cold except when their densities are high (McClure, 1983). Thus, if *M. macrocicatrices* populations develop in higher densities in the warmer parts of the range, they may face more overwinter mortality than populations in the cooler parts of the range, making them less impactful, overall, to eastern white pine trees. Little is known about how temperature affects growth and reproduction of *C. pinea*, although it has been suggested that increased sunlight and temperature may help reduce *C. pinea* spore production and dissemination (Lombard, 2003; Munck et al., 2016). Finally, this pattern of dieback may also reflect the historical incidence of the insect-pathogen complex, since *M. macrocicatrices* has only previously been recorded from the northeastern United States and Canada (Mech et al., 2013; Watson et al., 1960). It is possible that eastern white pine dieback is progressing southward, so dieback in the warmer, southeastern part is not as severe as the cooler, more northern part of the Southern Appalachian Mountain range. Long-term monitoring of these sites in the Southern Appalachian Mountains will be necessary to track changes in patterns of eastern white pine dieback.

Other unmeasured factors such as soil type may also have an influence on eastern white pine health. For example, Munck et al. (2015) demonstrated that the severity of *C. pinea* symptoms was greater for excessively drained, nutrient poor soils than for well-drained, more fertile soils in the northeastern United States. A study on beech bark disease indicated that nitrogen and phosphorous levels in the soil, and bark chemistry could impact tree defenses and affect the pathogenicity of fungal pathogens (Cale et al., 2015). Future research may aim to identify other factors that may have a role in eastern white pine dieback, including other abiotic and biotic factors that may be associated with the insect-pathogen complex.

5. Conclusions

Eastern white pine is a vital component in some forests of eastern North America, and has historically been significantly impacted by major anthropogenic factors, as well as native and non-native pests (Costanza et al., 2018). Results from this and other studies indicate that most of the healthy eastern white pine trees are large and mature (Asaro et al., 2018; Whitney et al., 2018), thus it will be essential to promote the health and survival of eastern white pine regeneration. If eastern white pine fails to regenerate and survive in pure and mixed forest ecosystems, many common hardwood species such as tulip-poplar, maples, and oaks may become the dominant canopy species (Ellison et al., 2005; Ford et al., 2012; Orwig et al., 2002), further shifting composition from conifer- to hardwood-dominated stands in eastern North American forests. These shifts in composition may alter nutrient cycling and stream health in riparian areas, especially in stands that have already experienced severe senescence of eastern hemlock (Stadler et al., 2005). The results from this study indicate eastern white pine stands may benefit from management strategies that would reduce density and increase sunlight, thus increasing temperature near the forest floor. This change in site conditions could decrease competition among trees, create conditions that are not ideal for *M. macrocicatrices*, and reduce *C. pinea* spore production and dissemination (Lombard, 2003; Munck et al., 2016). Further research will be necessary to better understand: (1) the biology of *C. pinea* and *M. macrocicatrices* throughout the range of eastern white pine; (2) other ecological drivers that may be involved in eastern white pine dieback; (3) long-term impacts of eastern white pine mortality on forest ecosystems; and (4) viable management options to protect and maintain one of the most important pine species in eastern North America.

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Appendix A

A1. Eastern white pine sampling and collection locations (sites) in the Southern Appalachian Mountains.

State	County	National forest	Latitude and longitude	Collection date
Georgia	Habersham	Chattahoochee	N 34.69767°, W 83.41489°	1/31/2014
	Rabun	Chattahoochee	N 34.92200°, W 83.25822°	2/5/2014
	Rabun	Chattahoochee	N 34.88304°, W 83.56023°	2/21/2014
	Towns	Chattahoochee	N 34.83934°, W 83.76933°	2/25/2014
	Union	Chattahoochee	N 34.75518°, W 83.89426°	2/26/2014
	Murray	Chattahoochee	N 34.87796°, W 84.70926°	3/9/2014
	Gilmer	Chattahoochee	N 34.77939°, W 84.32744°	3/9/2014
	Fannin	Chattahoochee	N 34.79816°, W 84.18977°	3/11/2014
North Carolina	Buncombe	Pisgah	N 35.48113°, W 82.59150°	6/16/2014
	Burke	Pisgah	N 35.82455°, W 81.84663°	6/16/2014
	Graham	Nantahala	N 35.35266°, W 83.90728°	6/17/2014
	Macon	Nantahala	N 35.00928°, W 83.24178°	6/17/2014
South Carolina	Oconee	Sumter	N 34.96559°, W 83.09306°	3/19/2014
	Oconee	Sumter	N 34.79885°, W 83.31249°	5/21/2014
Tennessee	Monroe	Cherokee	N 35.26812°, W 84.33806°	3/30/2014
	Polk	Cherokee	N 35.15207°, W 84.37422°	3/30/2014
	Sullivan	Cherokee	N 36.48812°, W 82.08171°	4/22/2014
	Unicoi	Cherokee	N 36.12572°, W 82.53853°	4/22/2014
	Greene	Cherokee	N 35.97279°, W 82.85342°	4/23/2014
	Monroe	Cherokee	N 35.43005°, W 84.06290°	4/23/2014
	Polk	Cherokee	N 34.99749°, W 84.63921°	5/30/2014
Virginia	Smyth	Jefferson	N 36.79331°, W 81.49586°	7/7/2014
	Carroll	Jefferson	N 36.79961°, W 80.98392°	7/7/2014
	Wythe	Jefferson	N 37.01903°, W 81.23375°	7/8/2014
	Bland	Jefferson	N 37.05272°, W 81.06964°	7/8/2014
	Pulaski	Jefferson	N 37.05269°, W 80.87303°	7/8/2014
	Giles	Jefferson	N 37.41422°, W 80.59153°	7/9/2014
	Craig	Jefferson	N 37.49433°, W 80.19567°	7/9/2014
	Alleghany	Jefferson	N 37.78928°, W 79.70103°	7/9/2014
	Bath	George Washington	N 37.92225°, W 79.79086°	7/10/2014
	Highland	George Washington	N 38.30536°, W 79.43025°	7/10/2014
	Augusta	George Washington	N 38.22136°, W 79.32392°	7/10/2014
	Rockingham	George Washington	N 38.71194°, W 78.84325°	7/11/2014
	Shenandoah	George Washington	N 38.86669°, W 78.68550°	7/11/2014
West Virginia	Greenbrier	Monongahela	N 37.98781°, W 80.21772°	8/14/2014
	Greenbrier	Monongahela	N 37.97897°, W 80.28106°	8/14/2014
	Greenbrier	Monongahela	N 37.90417°, W 80.25161°	8/14/2014
	Greenbrier	Monongahela	N 38.00278°, W 80.02261°	8/14/2014
	Pocahontas	Monongahela	N 38.11914°, W 80.01197°	8/15/2014
	Greenbrier	Monongahela	N 37.94239°, W 80.07422°	8/15/2014

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