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RESEARCH NOTE

Spatial Dynamics of Canopy Trees in an Old Growth Eastern Hemlock Forest in the Central Appalachian Highlands

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ABSTRACT: Understanding the shifting spatial distribution of trees is central to our knowledge of forest dynamics. We studied the spatial distribution of *Tsuga canadensis* L. Carr (Eastern Hemlock) as a function of age and size of canopy trees (greater than 75 cm dbh) and proximity to a stream in a remnant old growth forest fragment that has no record of human clearing or logging (Cathedral State Park, West Virginia). There appeared to be relatively continuous regeneration; however, cohort peaks indicated some disturbance history. We found spatially distinct age structures, with trees up to 315 years old. Trees greater than 102 cm dbh, or greater than 241 years old, were, on average, significantly closer to the stream. We suspect that the oldest individuals are concentrated near the stream because they are sheltered from wind disturbance. This knowledge can help us prioritize sites that are most important to protect from the woolly adelgid (*Adelges tsugae* Annand) when treating individual trees.

Index terms: dendrochronology, eastern hemlock, Geographic Information Systems (GIS), spatial distribution, succession

INTRODUCTION

The spatial distribution of trees is central to our understanding of the dynamics of forest communities (Dale 1999; Condit et. al. 2000). Usually, the spatial distribution of plant species is not random and is a consequence of environmental factors, human impacts and competitive interactions (Moeur 1997; Dale 1999). The same species often shows one pattern at the seedling stage and another pattern at the canopy stage (Kanzaki 1984; Duncan and Stewart 1991; Oliver and Larson 1996; Moeur 1997; Busing 1998; Hart and Shankman 2005; Rozas 2006; Kincaid and Parker 2008). While many studies have compared the spatial distribution of juvenile versus canopy tree size, no study has compared spatial distribution patterns among canopy trees stratified by age and size classes. This is an important distinction because silvicultural characterization of tree species has been mostly based on relatively young stands less than 100 years old, with an implied assumption that spatial patterns do not change much once trees reach the mature canopy size and age classes. Looking at canopy species within old growth forests may yield a different characterization of forest stand dynamics, which may, in turn, have implications for the way we manage long-lived species. Disturbances, land-use history, and other spatially distributed environmental factors may affect mortality and growth rate of trees, resulting in differing spatial distributions with respect to age and size in canopy trees.

Our model species for this study was eastern hemlock (*Tsuga candadensis* L. Carr) because it is one of the longest-lived species in the eastern United States, thus offering a substantial range of age and size classes within the category of "canopy" trees. Adult and juvenile eastern hemlocks have been found to be both random and aggregated (Brown et al. 1982; Busing 1998; Hart and Shankman 2005). The random spatial arrangement of eastern hemlock adults has been explained by a tolerance for competition and ability to fill canopy openings (Brown et al. 1982), while the aggregated pattern of seedlings and understory eastern hemlocks has been attributed to preference for particular environmental conditions (Hart and Shankman 2005) and positive associations between juveniles and adults (Busing 1998). The question framing this study was whether spatial patterns change among canopy age (100+) or size classes (> 75 cm dbh) after trees have reached mature canopy status.

The threat of hemlock mortality due to the exotic, invasive woolly adelgid (*Adelges tsugae* Annand) (HWA) increases the urgency of research on the few relic old growth hemlock forests that remain. Old growth stands of eastern hemlock can still be found throughout its native range, although they are rare (Frelich and Lorimer 1991; Abrams et al. 2000; Ziegler 2002). Those fragments that do persist are generally small (1 – 8 ha) (Rogers 1978; Abrams and Orwig 1996; Black and Abrams 2005). The few relatively large tracks of hemlock forest that remain, such as in Cathedral State Park in West Virginia (53 ha), are critical resources for research.

In the future, we may have the opportunity to reintroduce hemlocks where they have previously died off from HWA. Species reintroductions have a greater chance of success if they are designed with an understanding of long-term forest successional dynamics demonstrated by late-successional forests of the region.

METHODS

Site Description

Cathedral State Park, an old growth eastern hemlock forest in Northeastern West Virginia, is located at 39° 19.5'N, 79° 32.5'W in the Alleghany Mountains surrounded by high-plateau farmland (Figure 1). The elevation ranges from 750 to 800 m (2537 – 2578 feet). Annual rainfall averages 1420 mm. The park lies in the coldest part of the state where annual average temperature is 10 °C (Maguire and Forman 1983). The forest has been protected from anthropogenic disturbance for hundreds of years first under private landowner protection and later by state protection when it became a park. Large woody debris, characteristic of old growth, covers the ground. Two streams run through the forest. Over 170 species of plants have been inventoried within the 53 hectares of park. The hemlocks in this park are not associated with steep slopes or wetlands. However, the site could be classified as mesophytic with potentially high radial growth rates. Eastern hemlock represented 59% of the basal area, followed by red maple (*Acer rubrum*) (11%), black cherry (*Prunus serotina*) (9%), and white oak (*Quercus alba* L.) (6%) (Beane et al. 2010). HWA has infected trees within the park, but the majority of trees are currently being treated with the systemic insecticide imidacloprid, either by stem or soil injection.

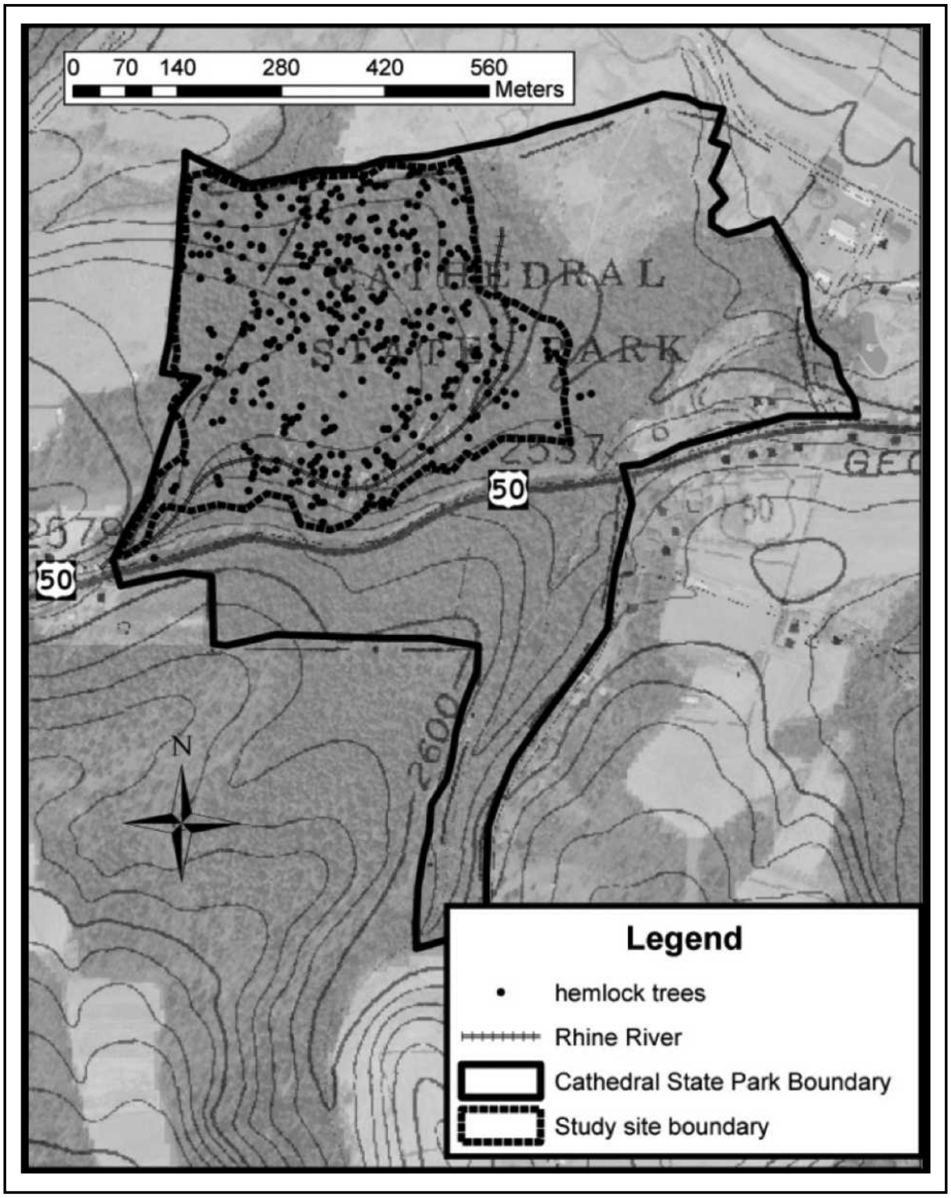

Figure 1. Cathedral State Park, West Virginia. Black points indicate core samples collected. The USGS topographic layer is a 1:24,000-scale digital raster graphic (DRG) from West VA GIS Technical Center.

Field Data Collection

We cored all trees greater than 75 cm dbh in a 20 ha portion of the park (representing over 40% of the total park area), for a total of 314 trees to create a spatial distribution map of the canopy trees. This twenty hectare section was located within the interior of the park to avoid edge affects (proximity to roads) and to include a maximum range of topoedaphics within the park. To establish whether there was a correlation between age and dbh for all age and size classes, we measured and cored all hemlock trees greater than 10 cm dbh in four randomly selected circular plots (60 m in diameter) within the interior of the park.

We recorded the locations of canopy trees in our 20 ha plot with a Garmin® Oregon GPS unit (using the averaging function until greater than or equal to a 5 meter error). Cores were stored in plastic straws and later mounted on wooden boards. The core surfaces were sanded and age was determined using a dissecting microscope. We verified age for a subsample of cores using a Velmex measuring stage.

Spatial Analyses

All analyses of spatial distribution were performed using GIS Arc Info (ESRI). We assessed the spatial distribution of all hemlocks over 75cm dbh using Average Nearest Neighbor analysis. Values close to one indicate a random distribution, values less than one indicate clustering, and values greater than one indicate dispersion. We further characterized the spatial distribution of hemlocks in Cathedral State Park with respect to distance from the stream that runs through the southern portion of the park (Figure 1). We divided trees into three classes of equal interval by age: class 1 (trees aged 90 – 165 years); class 2 (trees aged 166 – 240 years); and class 3 (trees aged 241 – 315 years). Mean distances to the stream for the three age classes were then compared using the Mann-Whitney U test. We repeated this procedure for dbh: class 1 (trees 75 – 102 cm dbh); class 2 (trees 102 – 130 cm dbh); and class 3 (trees 130 – 157 cm dbh).

RESULTS

Structure of the hemlock forest

The oldest hemlock tree in our study area of canopy trees was 315 years old with a dbh of 120.5 cm. The youngest hemlock canopy tree > 75 dbh was 90 years old (77.5 cm dbh). Age and dbh of trees greater than 10 cm but less than 75 cm dbh (from the circular subplots) were significantly correlated with an r^2 value of 0.541 ($p < .0001$) (Figure 2). In contrast, canopy trees (> 75 cm in diameter) showed no correlation between age and dbh (r^2 = 0.092l; $p > 0.1$). Trees greater than 10 cm in diameter followed the typical J shaped curve in terms of their abundance by size class, with trees of 10 – 19 cm dbh having three times as many trees as the other size classes (Figure 3). The age pattern was different with a peak not in the youngest category but in the 40 – 59 year old cohort (Figure 4a). We also found two cohorts, identified as two peaks in the histogram at 140 – 179 and 220 – 239 years of age (Figure 4b).

Spatial distribution of the hemlock forest

Overall, canopy trees greater than 75 cm dbh were randomly distributed (Average Nearest Neighbor analysis, Z = -1.4, $p > 0.10$). However, when canopy trees were sub-divided into age and size classes, spatial patterns emerged (Figure 5). We divided trees into three equal interval age groups. The Average Nearest Neighbor index showed significant spatial clustering ($p = 0.01$) within each age class group. On average, trees greater than 240 years in age and 102 cm in dbh were significantly closer to the stream than younger and smaller trees ($p < 0.001$) (Figure 5). Trees in age class 3 (241 – 315 years) had a mean distance of 74 (+/- 73) m from the stream, whereas trees in the younger age classes (classes 1 and 2) had a mean stream distance of 135 (+/- 95) m and 151 (+/- 92) m, respectively.

DISCUSSION

We found little correlation between size and age for individuals greater than 75 cm dbh, when trees reached 100 years or more (r^2 = 0.09). This was similar to findings in the northern part of hemlock's range where only a weak relationship across the entire age-size range was found (Rogers 1978; Seymour and Kenefic 1998; Kenefic and Seymour 2000). These studies suggested that the lack of a relationship was due to small size classes representing very old individuals. However, we found a stronger relationship between size and age in the smaller size classes that disappeared as trees became progressively larger and older.

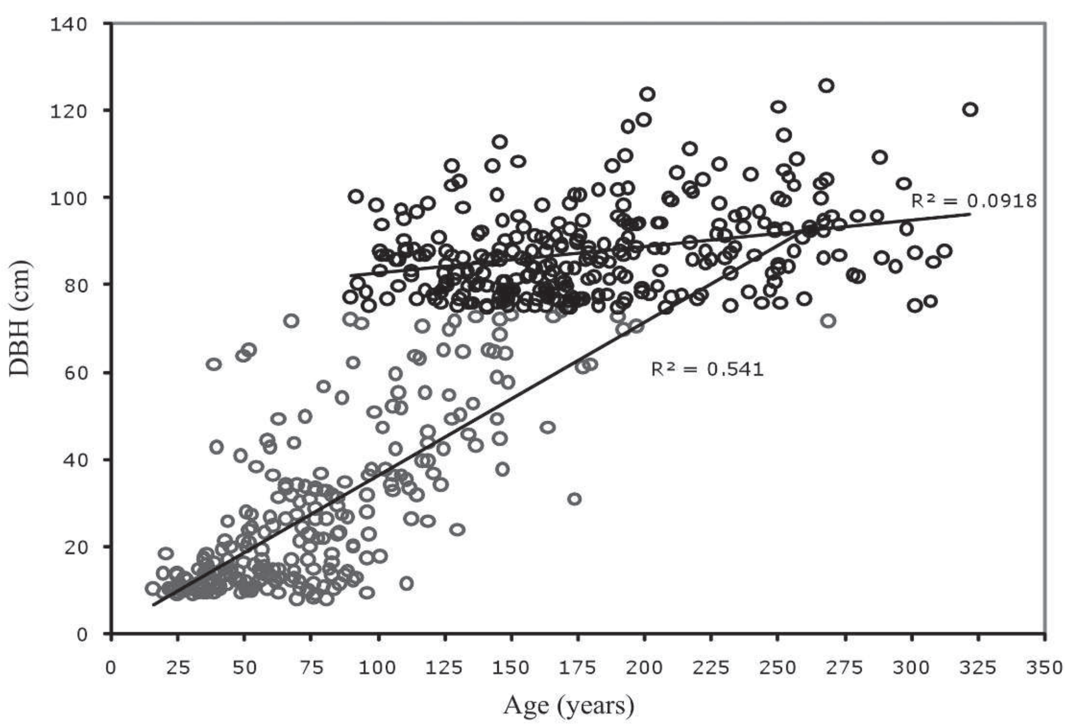

Figure 2. Age versus diameter at breast height (dbh) for eastern hemlock trees in Cathedral State Park, West Virginia. Two sampling methods were employed for trees greater than or equal to 10 cm in diameter (circular subplots) and for trees greater than or equal to 75 cm in diameter (20 ha area). A logarithmic regression line was used, giving an r^2 value of 0.09 for trees greater than 75 cm dbh and 0.54 for trees greater than 10 cm dbh.

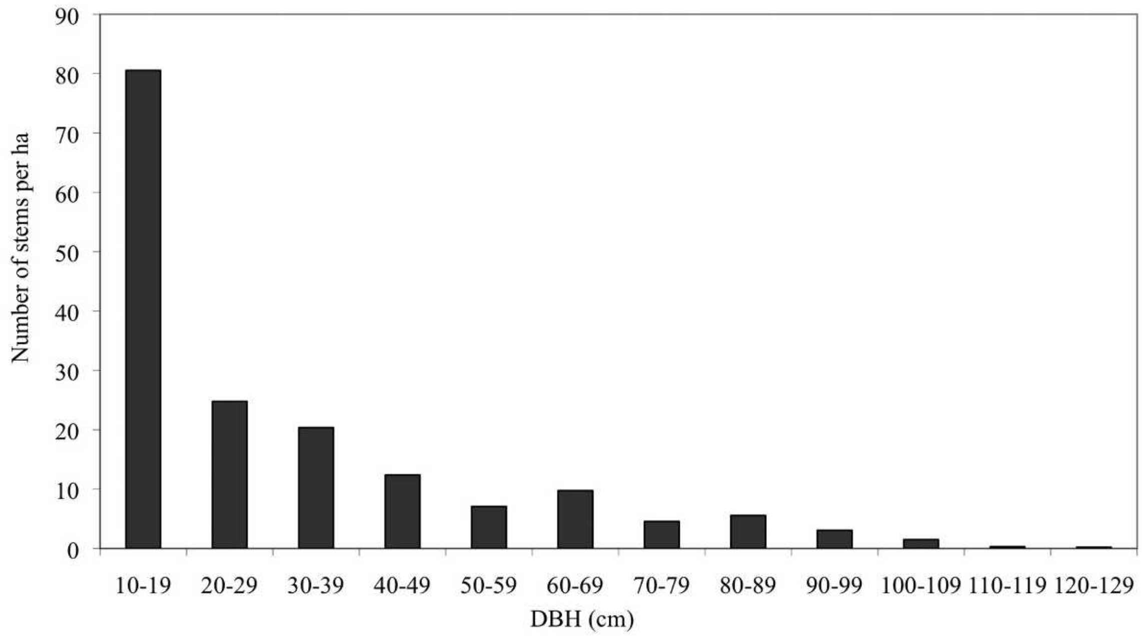

Figure 3. Diameter distribution of eastern hemlock trees greater than 10 cm dbh per ha in Cathedral State Park, West Virginia (within circular subplots).

We initially found that canopy hemlocks were randomly distributed in this forest fragment, similar to Brown et al's (1982) finding for overstory hemlocks in Rhode Island. The random spatial pattern of hemlocks has been explained by the lack of major disturbances (Brown et al. 1982). Absence of catastrophic disturbances over the past 300 years was confirmed in our study by the reverse J-shaped dbh histogram (Figure 3) and relatively smooth age histogram (Figure 4a). This data indicates continuous rather than pulsed regeneration, suggesting a self-perpetuating, stable population with long-standing conditions suitable for successful establishment. However, we did find peaks in the age histogram (Figure 4a,b) at 40 – 59 and at 140 – 179 and 220 – 240 years of age. The lower numbers in the 20 – 39 age category and 100 – 139 is most likely a function of not measuring trees less than 10 cm (Figure 4a) or less than 75 cm (Figure 4b) (e.g., smaller trees would add to total number in these age cohorts). However, the noticeable drop in density in the age range of 180 – 219 indicates partial disturbance events.

The spatial pattern of age structure was not uniform when canopy trees were subdivided into age and size classes. Ecological patterns can be missed when trees are grouped into two (juvenile, adult) or four age classes (seedlings, saplings, understory, canopy). Other studies have found aggregated patterns of hemlock seedlings and understory (attributed to geological/hydrological conditions and positive associations between juveniles and adults) but did not comment on specific patterns within the canopy (Willis and Coffman 1975; Busing 1998; Hart and Shankman 2005). We found that spatial patterns varied substantially when we looked at three different age and size classes within the canopy trees (> 75 cm dbh).

We found increasing spatial clustering for the largest size classes. The spatial distribution of canopy tree size and age classes differed with respect to stream proximity. Hemlocks shifted from avoiding riparia for old trees (> 75 and < 240 years old) to clustering near riparia for very old trees (> 240 to 315 years old). We suspect that the oldest individuals in our study site are concentrated near the topographically lower stream because they are more sheltered from wind disturbance as well as snow and ice accumulation due to lower topographic position. If large-scale disturbances, such as fire, were part of the disturbance regime, a different pattern with canopy trees might have emerged but we found no evidence of fire scars in the 314 tree cores, or of charcoal in the soil horizon.

One remaining question is what limits the lifespan of hemlocks at this study site to approximately 300 years old? On favorable sites, hemlocks can live to over 800 years of age (Godman and Lancaster 1990). One possible explanation is that older trees (greater than 350 years) do not yield complete cores, as hemlocks are notorious for having rotten centers. However, of our 350 tree samples, only 14% of the cores were rotten. The maximum life span of trees is most likely related to the dominant disturbance regime. Windthrow has been found to be a common disturbance in hemlock stands (Lorimer 1980; Brown et al. 1982; Mladenoff and Stearns 1993; Hart and Shankman 2005). Hemlocks have shallow roots and larger individuals may be more susceptible to windthrow on slopes. We also observed significant damage to mature hemlock trees in the park from heavy snow and wind caused by Hurricane Sandy in October 2012. We encourage a study following this event to assess hurricane damage as a function of geography. Rare events, such as Hurricane Sandy, may

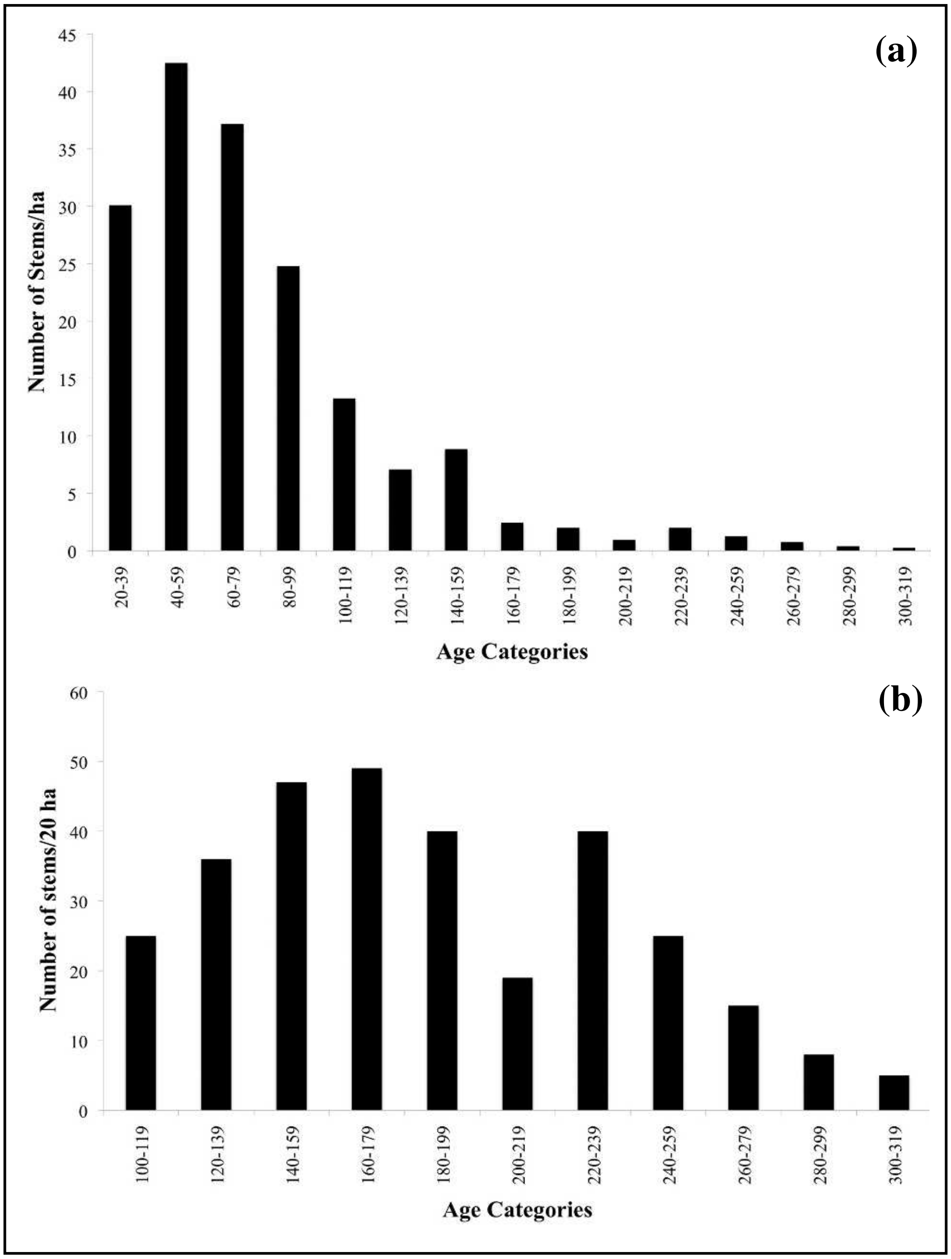

Figure 4. (a) Age distribution of eastern hemlock trees per ha sampled in circular subplots, and (b) age distribution of trees > 75 cm dbh within 20 ha in Cathedral State Park, West Virginia.

explain the age limit in Cathedral State Park. If HWA resistant hemlock seedlings become available in the future, we suggest prioritizing replanting along streams and in coves where they are likely to achieve the greatest size and age due to greater protection from disturbance.

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Leigh Siderhurst received her master's degree in Forest Ecology from James Madison University.

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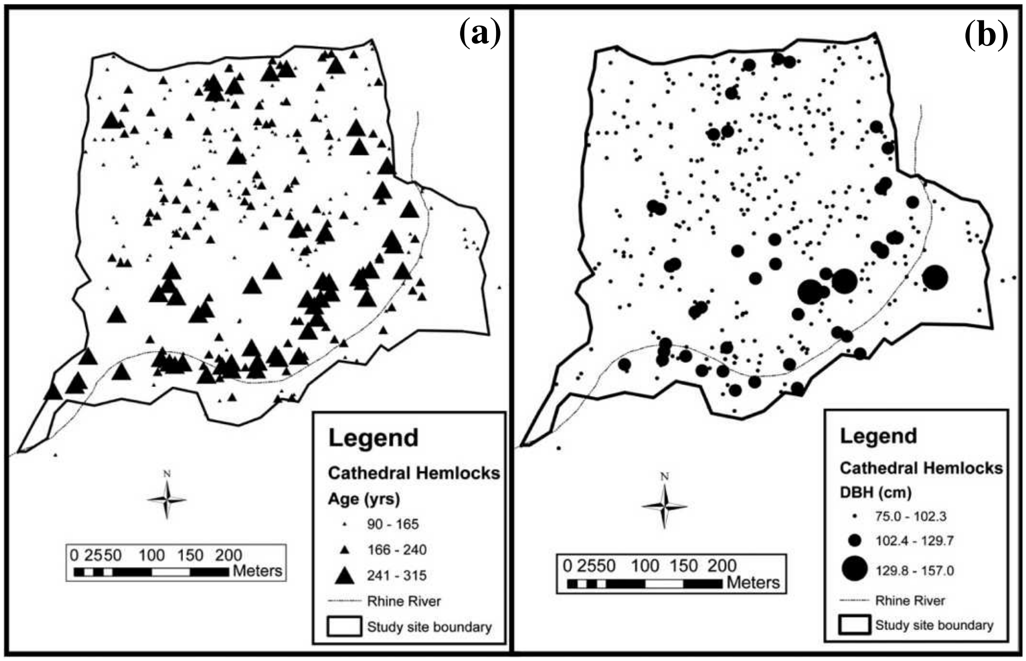

Figure 5. (a) Age of eastern hemlocks in Cathedral State Park. Trees > 240 years old were on average significantly closer to the stream than younger trees; (b) dbh (cm) of eastern hemlocks. Trees > 102 cm dbh were on average significantly closer to the stream than smaller trees.

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