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Disjunct eastern hemlock (*Tsuga canadensis*) stands at its southern range boundary[1]

Justin L. Hart[2,3] and David Shankman

Department of Geography, University of Alabama, Box 870322, Tuscaloosa, AL 35487

HART, J. L. AND D. SHANKMAN (Department of Geography, University of Alabama, Box 870322, Tuscaloosa, AL 35487). Disjunct eastern hemlock (*Tsuga canadensis*) stands at its southern range boundary. J. Torrey Bot. Soc. 132: 602–612. 2005.—Eastern hemlock (*Tsuga canadensis*) occurs throughout much of the Appalachian Mountains, extending from southern Quebec and Ontario southward to Georgia and along the Appalachian Plateau to Alabama. Eastern hemlock is one of the most dominant trees in Appalachian forests. Near its southern boundary in central Alabama, eastern hemlock occurs in small, isolated populations restricted to cool, moist slopes with north to east aspects and low and middle slope positions. Ten stands of eastern hemlock, believed to be the southernmost populations, were studied in order to determine reproductive viability and habitat characteristics. In each of the stands, eastern hemlock dominates the canopy and is present in a wide range of size and age classes. Eastern hemlock is most abundant in seedling size classes and the number of individuals generally decreases with increasing size. Population size, age, and vertical structure indicate that eastern hemlock stands at the species' southernmost boundary contain viable populations that are regenerating, even if highly localized. During the late Pleistocene and early Holocene, eastern hemlock likely had a broader distribution in the southern Appalachian Mountains. The remnants of this larger distribution are now restricted to steep slopes where a combination of sandstone outcrops, seepage, and springs maintain adequate microclimatic conditions needed for regeneration of the species.

Key words: Alabama, Appalachian Mountains, forest regeneration, Pinaceae, population structure, *Tsuga canadensis*.

Eastern hemlock (*Tsuga canadensis* (L.) Carr.) is among the most dominant tree species in the Appalachian Mountains in eastern North America. Its range extends from southern Quebec and Ontario southward to Georgia and along the Appalachian Plateau to Alabama (Fig. 1) (Kessell 1979, Godman and Lancaster 1990). It is among the longest lived trees in eastern North America. Individuals may live for over 800 yrs and can grow to 40 m of height and greater than 2 m in diameter (Godman and Lancaster 1990). Eastern hemlock is among the most shade tolerant tree species in this region and sometimes occurs in almost pure stands on lower slopes and stream valleys. Large tracts of old-growth eastern hemlock can still be found in northern Ontario and Quebec, in Michigan and Minnesota, and in the Great Smoky Mountains National Park.

During the late Pleistocene, southeastern US forests were composed of many species which now occur only at higher latitudes (Davis 1981, Delcourt et al. 1983). However, eastern hemlock was absent from the pollen record through much of the southeastern US during the late Wisconsin glaciation. Davis (1981) suggests the refugium for eastern hemlock during the glacial maximum was in the Appalachian Mountains, Atlantic Coastal Plain, or on the continental shelf exposed during the lower sea level of that time. Eastern hemlock likely spread from its refugium during the late Pleistocene and early Holocene, and was abundant in central Alabama throughout the southernmost sections of the Appalachian Plateau 10,000 YBP. However, eastern hemlock probably did not spread southward onto the Gulf Coastal Plain during this period of expansion (Segars et al. 1951).

Climatic warming during the early Holocene resulted in southern range contraction for many species (Oosting and Hess 1956), with taxa, such as eastern hemlock, becoming restricted to sites with favorable microhabitats (Delcourt et al. 1983). Outlying populations of eastern hemlock, which now occur at the species' southern range boundary, likely represent remnants of the once widespread distribution of the late Pleis-

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[3] Author for correspondence and current address: Laboratory of Tree-Ring Science, Department of Geography, University of Tennessee, Knoxville, TN 37996. E-mail: jhart13@utk.edu

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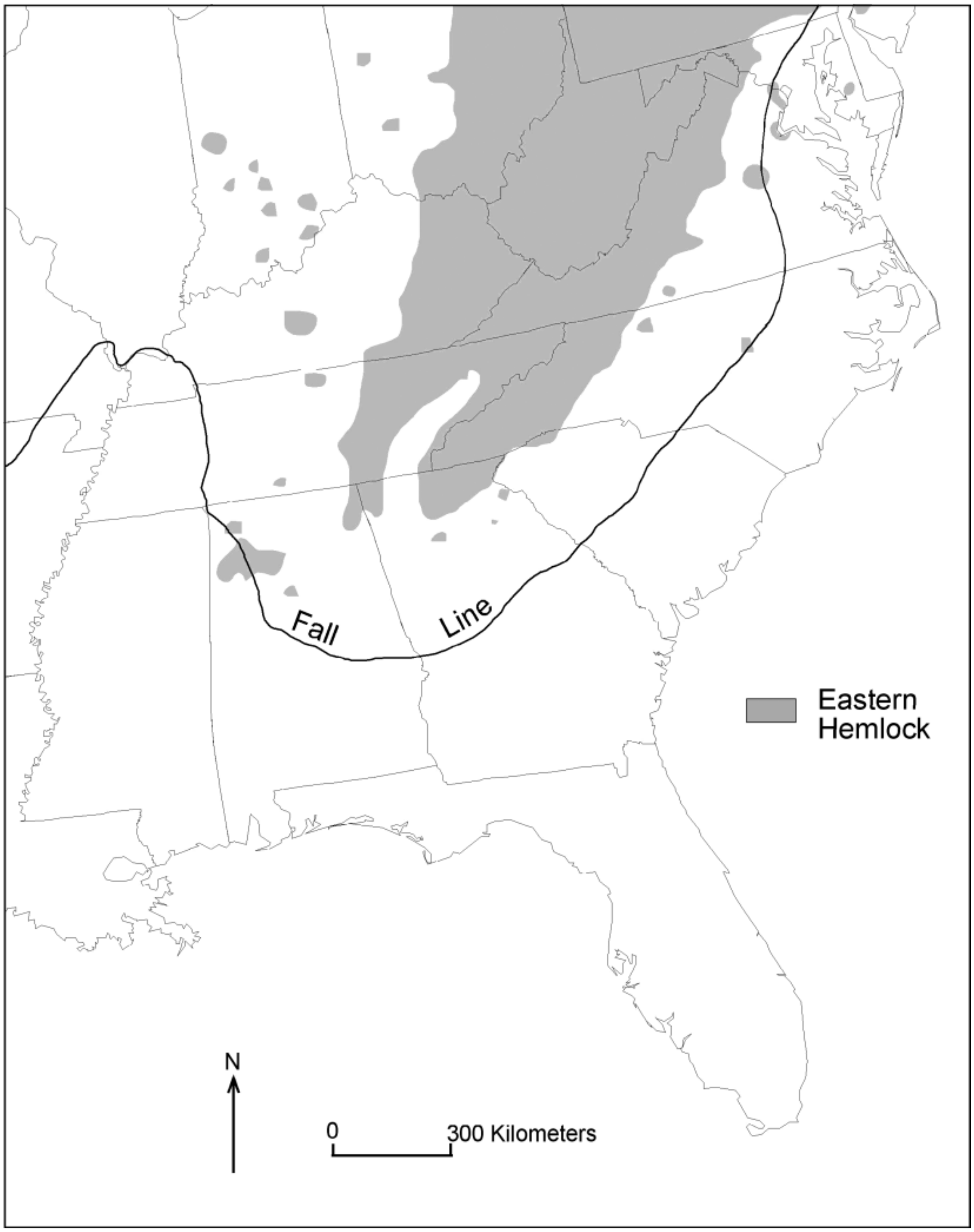

FIG. 1. Map showing the central and southern range of eastern hemlock (from Little 1971).

tocene and early Holocene. The purpose of this research is to document previously undescribed populations of eastern hemlock at its southern range limit in central Alabama. Specifically, we examine both the viability of these stands and the preferred habitat of the species at its southernmost extent. Also, we discuss evidence of a historically larger distribution of eastern hemlock in the southern Appalachian Highlands, including the expansion and contraction of the southern range boundary.

EASTERN HEMLOCK REGENERATION ECOLOGY. Regeneration of eastern hemlock is generally intermittent (Kavanagh and Kellman 1986), occurring when good seed crops coincide with adequate moisture conditions (Bormann and Platt 1958). Eastern hemlock typically produce large seed crops every two to three years (Hett and Loucks 1976, Rooney and Waller 1998), although seed viability is low (Godman and Lancaster 1990). A favorable seedbed is important for successful reproduction of eastern hemlock (Friesner and Potzger 1944, Bormann and Platt 1958). Germination is facilitated by decomposing woody debris such as rotten logs, stumps, windthrow mounds, and other substrates such as mosses (Friesner and Potzger 1944, Bormann and Platt 1958, Brown et al. 1982, Mladenoff and Stearns 1993, Rooney and Waller 1998), especially in areas of little or no understory (Godman and Lancaster 1990). Eastern hemlock seedlings are typically shallow rooted and are susceptible to high temperatures and soil drying (Godman and Lancaster 1990, Mladenoff and Stearns 1993).

When eastern hemlock dominates stands it influences both microclimatic and pedologic conditions (Rogers 1978). The dense canopy of overstory eastern hemlock restricts the amount of light reaching the forest floor (Hadley 2000, Rankin and Tramer 2002), thus modifying the microclimate of the understory. Eastern hemlock also modifies the soil of inhabited sites (Rogers 1978, Finzi el al. 1998) by creating thick acidic humus. The combination of low light and acidic soils under a mature eastern hemlock canopy may inhibit the establishment of competing species, while facilitating the success of eastern hemlock regeneration (Rogers 1978, Maguire and Forman 1983, Elliott et al. 1990, Hadley 2000, Rankin and Tramer 2002). Eastern hemlock are extremely shade tolerant and can withstand long periods of suppression in the understory. Under these conditions growth is slow, but individuals may quickly fill canopy gaps when they are created (Friesner and Potzger 1944, Kelty 1986, Foster and Zebryk 1993, Davis et al. 1996).

Methods. STUDY SITES. We surveyed and described all stands of eastern hemlock known to exist on the southernmost part of the Appalachian Plateau (Fig. 2). To ensure we sampled all eastern hemlock outliers we used topographic maps, published botanical surveys, and conducted interviews with landowners and those knowledgeable about forest vegetation in this region. Sections of the Sipsey River and Blackwater Creek were also surveyed by canoe to search for other outlying populations. Data are reported from ten eastern hemlock stands located in central Alabama. The outlying populations reported in this paper further extend the known range of eastern hemlock in Alabama south and southwest. Together these stands represent the southern boundary of the species. Stands 8, 9, and 10, in Jefferson County, were noted but not described by Segars et al. (1951). Clark (1971) documented eastern hemlock in Walker and Jefferson Counties, but the stands were never described and the locations of the stands were never reported. Harper (1919) documented other stands in Jefferson County but those populations have since been extirpated.

In this area, all of the remaining stands are located along permanent watercourses upstream of the Coastal Plain on north to east-facing river banks and bluffs (Table 1). Due to remote stand locations, rugged terrain, and private land holdings three stands are accessible only by canoe. Most eastern hemlock individuals occur within 20 m of stream channels or along incised tributary streams. The stands vary in length along the watercourses from 26 to 130 m. With the exception of stand 9, all of the stands are found on slopes with steep gradients. The elevations of the stands range from about 110 to 125 m and all have shallow soils overlying sandstone. Much of the sandstone along the river bluffs is exposed and covered with lichens, and cracks in the rocks often support vegetation, including eastern hemlock. Sandstone outcrops contribute to the moist conditions at the study sites (Lacefield 2000). During the dry summer months, water is available at the surface through seepage and springs. The seepage is attributed to permeable layers of sandstone overlying impermeable rock strata.

Eastern hemlock dominates the canopy of each stand. Other overstory tree species occurring in these stands include, American beech (*Fagus grandifolia* Ehrh.), white oak (*Quercus alba* L.), chestnut oak (*Q. prinus* L.), red maple (*Acer rubrum* L.) and tulip-poplar (*Liriodendron tulipifera* L.). Primary understory species include American holly (*Ilex opaca* Ait.), mountain laurel (*Kalmia latifolia* L.), eastern redcedar

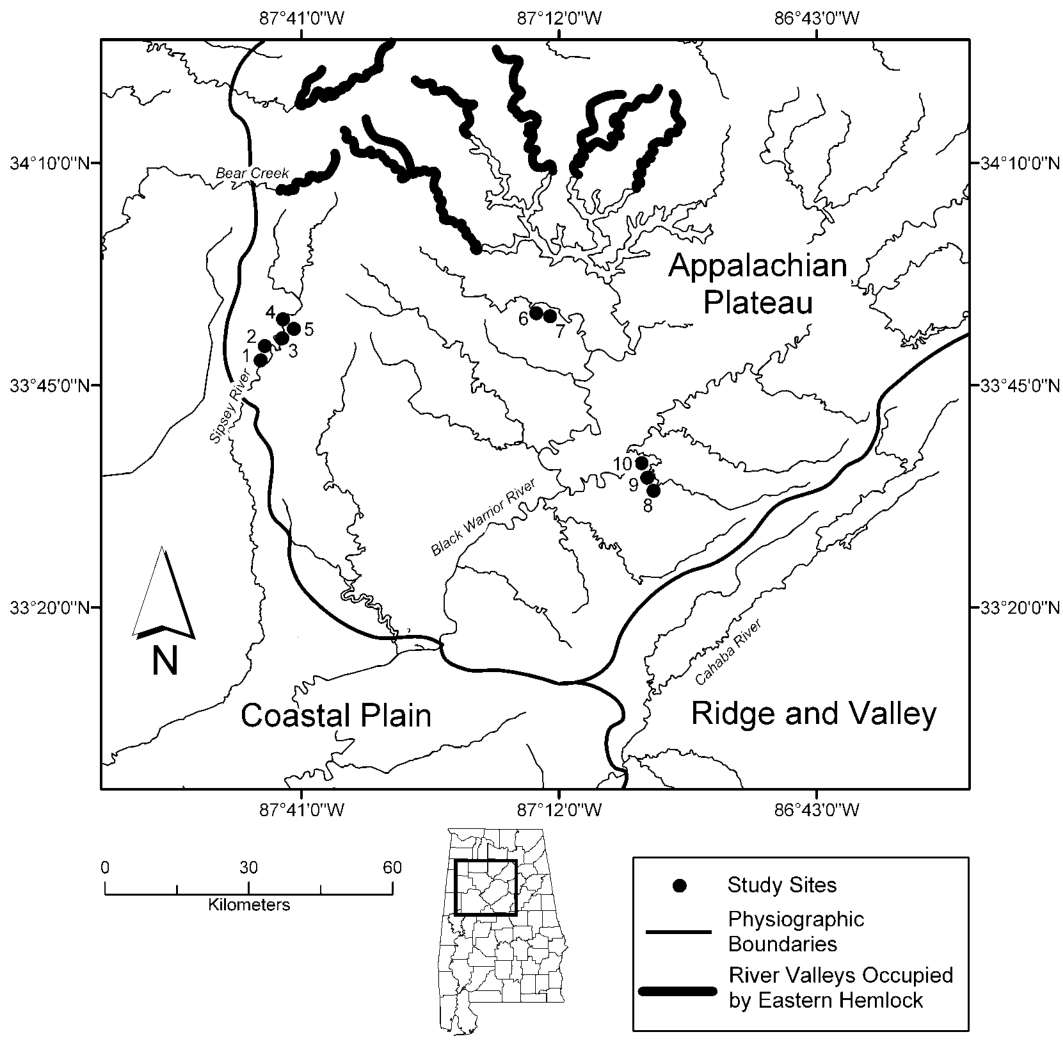

FIG. 2. Map showing study sites, (stands 1–5 are along the Sipsey River in Fayette County, stands 6–7 are along Blackwater Creek in Walker County, stands 8–10 are along Village Creek in Jefferson County, Alabama), documented eastern hemlock locations along streams, and physiographic regions in central Alabama.

(*Juniperus virginiana* L.), and bigleaf magnolia (*Magnolia macrophylla* Michx.). There is little woody vegetation present underneath the closed forest canopy of these stands, which is common for understory conditions of eastern hemlock forests throughout its range (Hadley 2000).

FIELD DATA COLLECTION AND ANALYSIS. At each study site we recorded topographic position, slope aspect, slope gradient, and elevation. Attempts were made to measure the diameters of all eastern hemlock $\geq$ 4 cm dbh (at approximately 1.4 m). However, because of nearly vertical bluffs at most study sites, some individuals were not accessible. Thus, eastern hemlock were placed into one of four vertical forest layer categories. All stems shorter than 1.5 m were listed as seedlings. Stems equal to and taller than 1.5 m but not in canopy positions were listed as understory individuals. Eastern hemlock at canopy level, with the crown not restricted from above, but crowded on the sides were listed as canopy co-dominants and individuals with dominant positions in the forest canopy were listed as canopy trees (Oliver and Larson 1996). Canopy composition and canopy dominance were visually estimated. Observations were made in the field to determine if eastern hemlock seedling abundance in the stands is influenced by substrate.

In all but one of the stands eastern hemlock were cored at breast height using an increment

Table 1. Site characteristics for the ten eastern hemlock stands sampled on the southern Appalachian Plateau in central Alabama.

Stand	Number of eastern hemlock stems	Elevation (m)	Slope aspect[a]	Slope position	Canopy dominance
1	106	110	E	Low-mid-high	Eastern hemlock - American beech - red maple
2	134	116	NNE	Low-mid-high	Eastern hemlock - mixed oaks - American beech
3	40	116	NW	Mid-high	Eastern hemlock - mixed oaks
4	213	116	ENE	Low-mid-high	Eastern hemlock - American beech - red maple
5	127	122	N	Low-mid	Eastern hemlock - mixed oaks
6	228	115	N	Low-mid	Eastern hemlock - mixed oaks
7	218	115	N	Low-mid	Eastern hemlock - mixed oaks
8	325	125	N	Low-mid-high	Eastern hemlock - mixed oaks - American beech
9	68	121	E	Mid	Eastern hemlock - mixed oaks - American beech
10	28	125	E	Mid-high	Eastern hemlock - mixed oaks - American beech

[a] All stands are located on bluffs above streams. Less than 30 m separates low from high slope positions. Eastern hemlock dominates the canopy of each stand.

borer. Cored trees were selected based primarily on their accessibility and to represent a wide assortment of diameter classes. Most eastern hemlock individuals occur on steep, in some cases vertical slopes that were not easily accessible. Age sampling was also limited because many of the large eastern hemlocks had rotten centers. A total of 78 trees were cored. At stand 3 no trees were cored per request of the landowner and at stand 10 only three eastern hemlocks were cored because the few present were difficult to access on the steep river bluffs. The cores were taken to the laboratory and annual rings were counted to determine tree age. Spearman's rank correlation was employed to examine diameter-age relationships.

Results and Discussion. VERTICAL AND HORIZONTAL STRUCTURE. The number of eastern hemlock individuals in each stand range from 28 to 325. Eastern hemlock stem density ranges from about 28 to 60 individuals per 0.1 ha. Eastern hemlock in all stands occupies multiple vertical layers of the forest (Fig. 3). Eastern hemlock seedling and understory individuals are common in all stands. Stems classified as understory are $\geq$ 1.5 m of height and may be considered successfully established (Godman and Lancaster 1990). These individuals may remain suppressed in the understory for long periods of time until the formation of canopy gaps (Friesner and Potzger 1944, Kessell 1979, Godman and Lancaster 1990, Hadley 2000).

The stands show distinct clustering of eastern hemlock seedlings and understory individuals indicating favorable microhabitats within each stand. We observed seedlings are concentrated underneath mature eastern hemlock individuals, and are most common growing on a moss substrate. Seeds may get lodged in moss preventing them from sliding down the steep slopes (Friesner and Potzger 1944). Moss also provides moist sites for seed germination (Brown et al. 1982, Godman and Lancaster 1990, Rooney and Waller 1998). Seedlings also occur on coarse woody debris including stumps, fallen logs, and mounds resulting from forest blowdown in the stands. Such findings are consistent with previous research concerning the spatial distribution of eastern hemlock seedlings (Graham 1941, Friesner and Potzger 1944, Brown et al. 1982). The larger understory individuals are also clustered, which is common in eastern hemlock forests (Graham 1941, Brown et al. 1982).

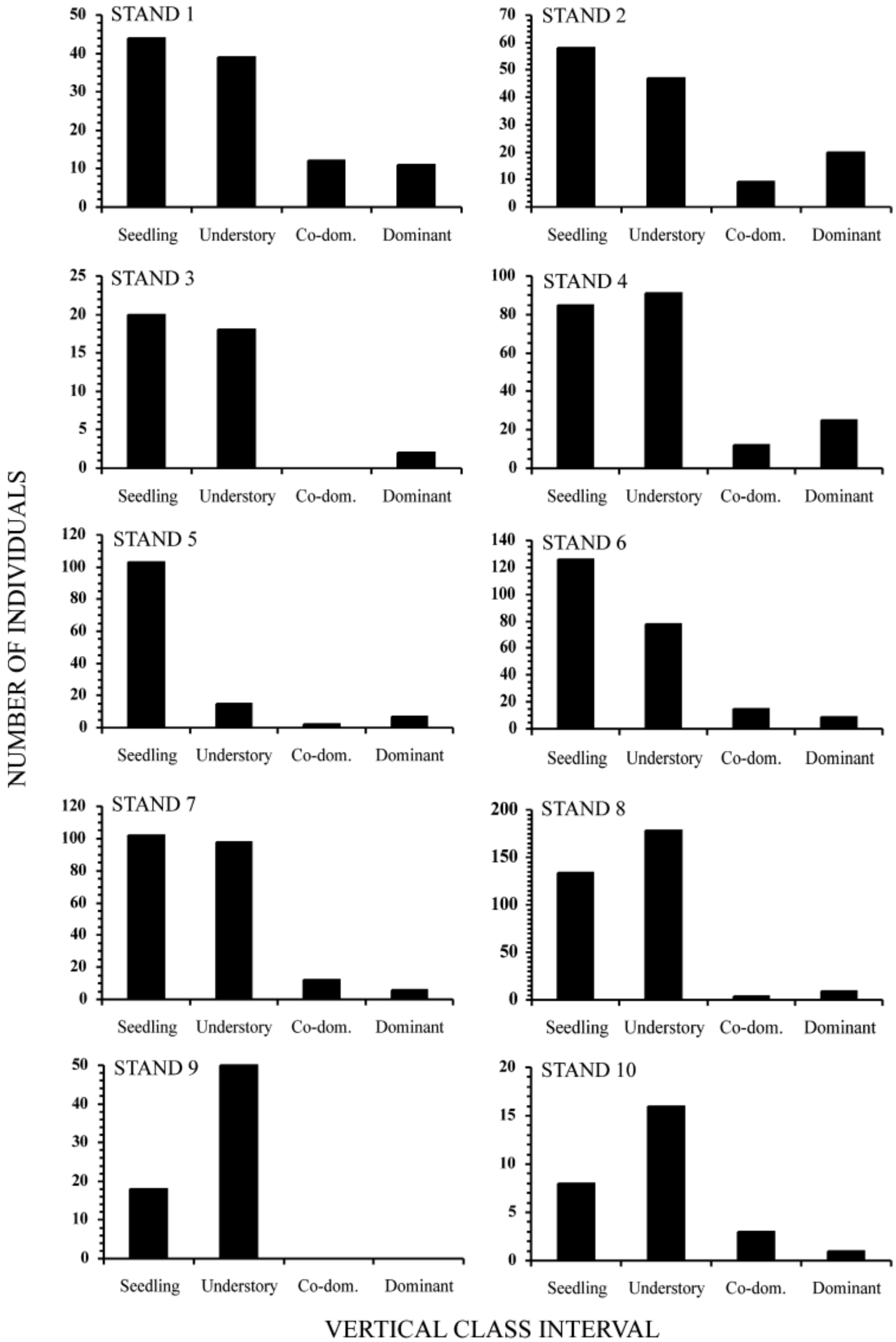

FIG. 3. Vertical class distributions for eastern hemlock in each study plot. Number of eastern hemlock individuals are shown for each classification, seedling: < 1.5 m height, understory: ≥ 1.5 m height, co-dominant (co-dom.): individuals at canopy level, with crowns not restricted from above, but crowded on the sides, dominant: dominant positions in the forest canopy (y-scale varies among stands).

DIAMETER-AGE RELATIONSHIPS. Diameter and age are positively associated in all sampled stands (Fig. 4). The Spearman's rank correlation values range from 0.77 to 0.94. On all but stands 5 and 8, diameter-age relationships are statistically significant ($P = 0.01$). Diameter and age are positively associated on stands 5 and 8, but few large trees were successfully aged because of rotten centers precluding a statistically significant association. Strong diameter-age relationships show size is a reliable predictor of age. In the northern portion of its range studies have found diameter and age to be weakly associated (Seymour and Kenefic 1998, Kenefic and Seymour 2000). However, our diameter-age results are consistent with other studies in the southern Appalachian Mountains (Lorimer 1980). These are uneven-aged stands, with individuals in a wide range of age classes indicating the trees are successfully regenerating through time. The oldest individual successfully aged was 211 years old. However, there are many other large trees that may be at least this old, but could not be aged because of rotten centers.

DIAMETER CLASS DISTRIBUTIONS. Diameter class distributions were constructed for each stand (Fig. 5). With the exceptions of stands 3 and 9 individuals are present in all size classes. In all cases, the majority of eastern hemlock stems are $<$ 4 cm dbh, and the number of individuals generally decreases with increasing size. Diameter structure analyses reveal a reverse J-shaped curve at all but stand 9. The reverse J-shaped curve indicates continuous or intermittent regeneration and recruitment into larger size classes. Eastern hemlock regeneration and recruitment is generally not considered continuous (Kavanagh and Kellman 1986) but intermittent. The size structure of stand 9 does not reveal the reverse J-shaped curve. However, there are a large number of understory individuals as well as a number of eastern hemlock seedlings suggesting this is a reproductively viable population.

The strong diameter-age relationships of the sampled stands combined with the reverse J-shaped diameter class distributions, indicate these are self-perpetuating, stable populations. This is true even for stand 9, which lacks the classical uneven-aged distribution. Conditions at these sites have been suitable for successful establishment and recruitment for a long period of time. Eastern hemlock is germinating under a well developed canopy and individuals are being recruited to dominant canopy positions in the absence of large-scale disturbance events.

HABITAT REQUIREMENTS. Each of the ten stands have discrete boundaries with a high density of eastern hemlock individuals within the stands and no isolated individuals outside of the stands. The abrupt boundaries of eastern hemlock in these stands indicate eastern hemlock regeneration requires specific environmental conditions and that stand size is not limited by seed dispersal. With the exception of stand 9, all stands have similar physical characteristics that include steep sandstone bluffs bordering permanent streams. Stand 9 has a relatively gentle slope, but is probably located on shallow soil underlain by sandstone. Many of the individuals exhibit J-shaped boles, attributable to downslope creep and phototropism. Many of these have organic rich soil on the upslope side of the bole with exposed sandstone on the downslope side. Many of the larger individuals have fallen over, because of the steep slopes. Also, there are several downed trees in most stands as a result of windthrow, which is probably influenced by the steep topography.

As previously mentioned these eastern hemlock stands occur on north to east-facing river bluffs. None occur on south-facing slopes because of high intensity solar radiation and lower soil moisture, or west-facing slopes that are generally drier because of the prevailing westerly winds. Eastern hemlock individuals are present in low, middle, and high slope positions. However, the majority of large individuals occur in middle slope positions because of sandstone outcrops and seepage that occurs there. Seepage was noted in the fall months, which are the driest in the region, suggesting that it aids in maintaining moist conditions. Previous studies concerning outlying eastern hemlock populations have also noted seepage and found it to be important in maintaining cool, moist site conditions (Harper 1937, Bormann and Platt 1958). Only a few eastern hemlock individuals were located at high slope positions in our study plots probably because of intense solar radiation and less available soil moisture.

Windthrow appears to be the most common disturbance mechanism in these stands as evidenced by the number of downed trees. The removal of overstory vegetation creates canopy gaps and allows for the recruitment of individuals into larger size classes. Other disturbance mechanisms such as fire, snow and ice accu-

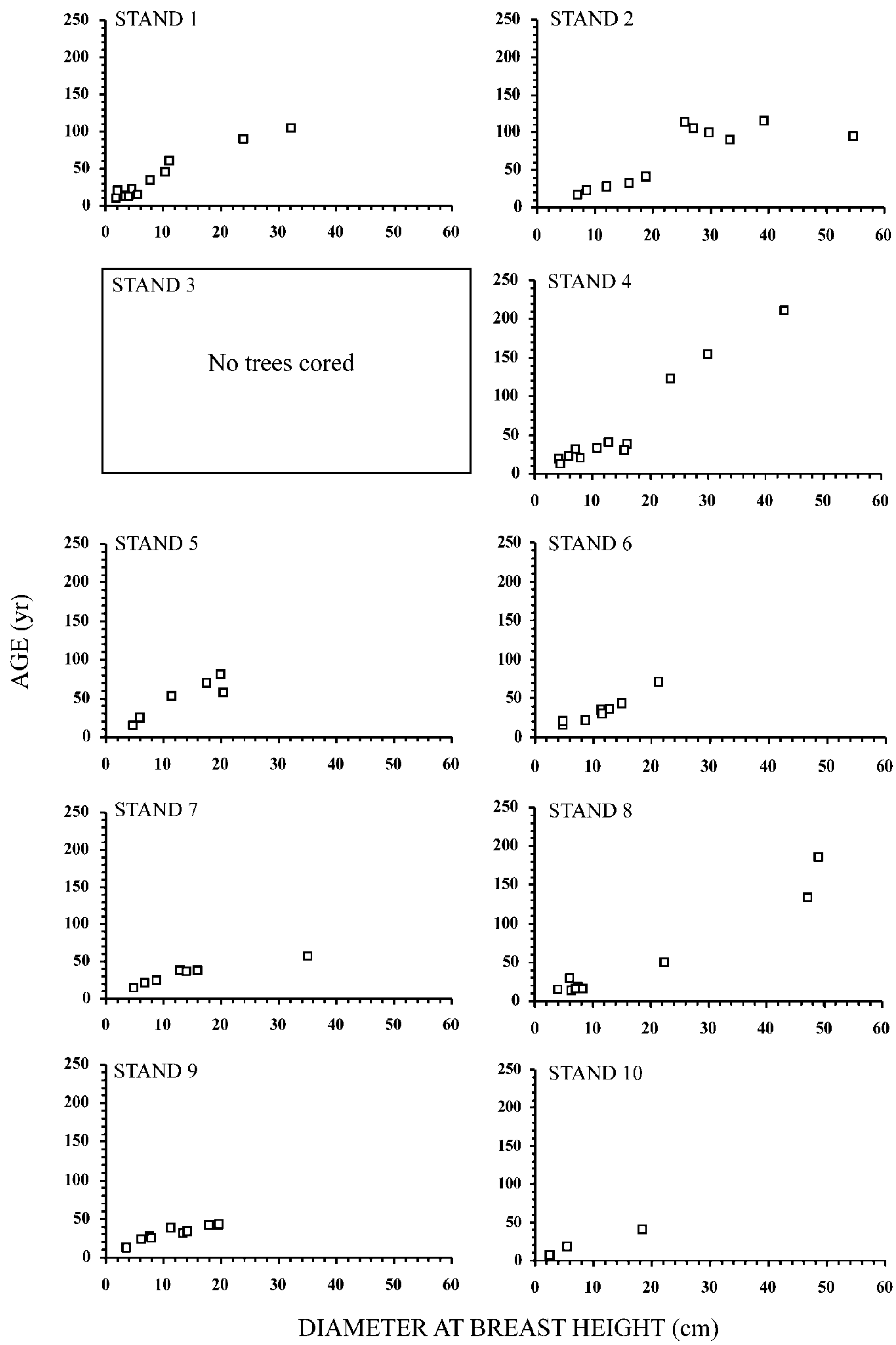

FIG. 4. Diameter-age relationships of eastern hemlock in each study plot.

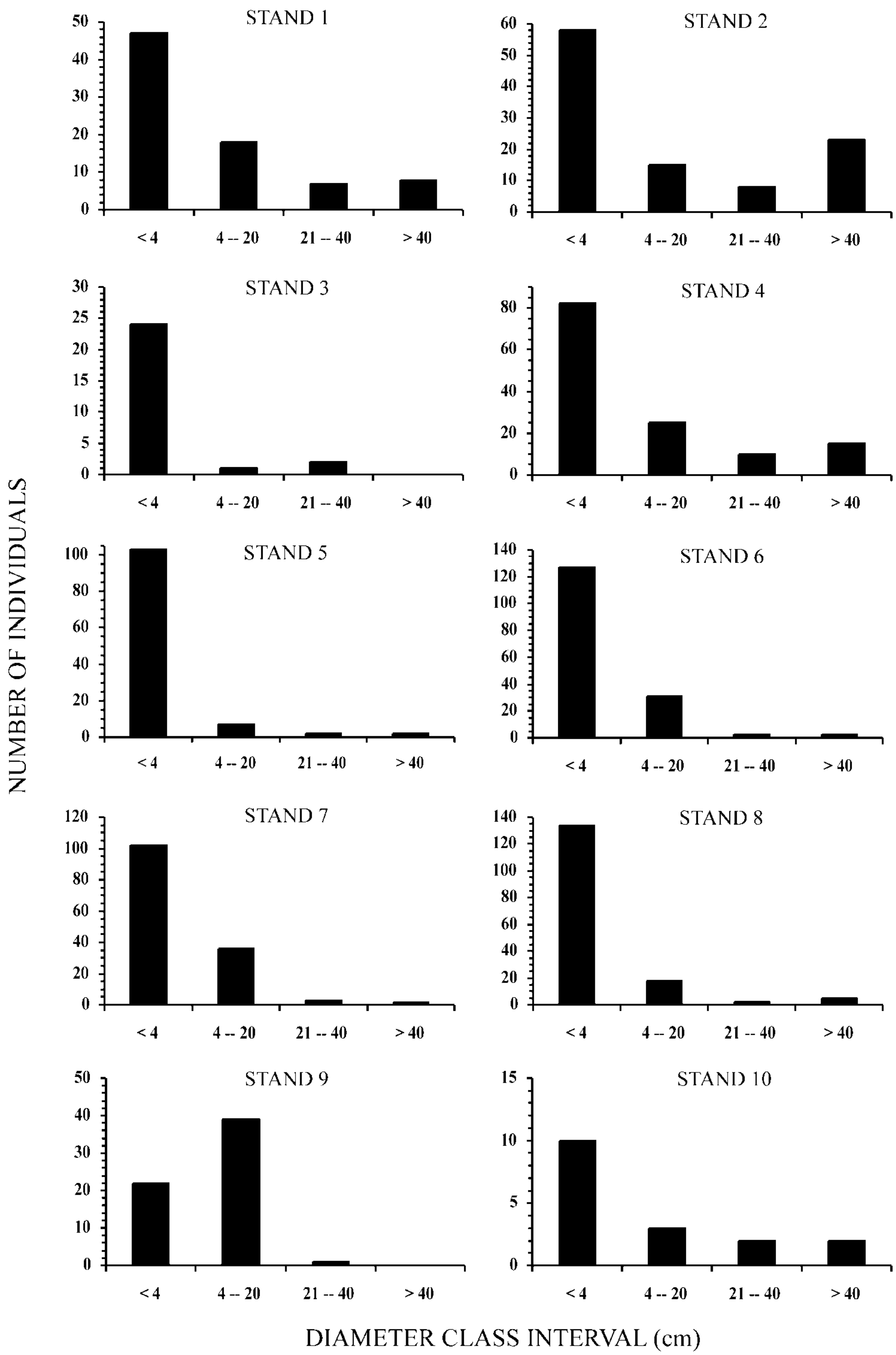

FIG. 5. Diameter class distributions for eastern hemlock in each stand (y-scale varies among stands).

mulation, and herbivory seem unlikely in influencing the dynamics of these communities. The stands are located in moist, riparian areas on exposed bedrock bluffs. We found no fire scarred trees and believe it is doubtful fire is a mechanism influencing these communities. It is also doubtful snow and ice accumulation are downing large trees or inhibiting the establishment of eastern hemlock individuals. Unlike other areas in the eastern hemlock range, this region receives little if any snow or ice accumulation most years. Herbivory by white-tail deer (*Odocoileus virginianus* Zimmerman) has been noted as inhibiting eastern hemlock regeneration in parts of its range (Anderson and Loucks 1979). We saw no deer, deer scat, rubs, or partially eaten eastern hemlock stems to suggest heavy white-tail deer populations in the area. The steep topography of these stands is not conducive to deer movement. The wildlife trails that exist are located at high slope positions. It is unlikely that herbivory is limiting eastern hemlock regeneration or significantly influencing stand dynamics.

Conclusions. Population size, age, and vertical structure indicate that eastern hemlock stands at the species' southernmost boundary contain viable populations that are regenerating, even if highly localized. Eastern hemlock is germinating under a well-developed canopy and individuals are being recruited to dominant canopy positions in the apparent absence of large-scale disturbance events. These are uneven-aged stands with individuals occurring in a wide range of ages and sizes, which is indicative of shade tolerant species.

Eastern hemlock has likely occupied these sites throughout much of the Holocene. The oldest individual successfully aged was 211 years old, which is relatively young for the species. Eastern hemlock may live for several centuries on favorable sites, and individuals have been documented over 800 years of age (Godman and Lancaster 1990). The absence of even older trees may be attributable to several different mechanisms. Environmental conditions at the species' range limits may be less than optimal, increasing physiological stress. Also, much of the area surrounding these stands has been logged. The largest eastern hemlock individuals may have been cut. However, no old stumps are present that would indicate recent logging at these sites. The steep topography and difficult access may have prevented logging of these stands. It is also probable that slope gradient and exposed bedrock limit the size of an individual that may be supported. With the exception of stand 9, all of the stands are located on steep slopes and all stands are underlain by shallow soils. Eastern hemlock have shallow root structures and progressively larger individuals are less able to support themselves on the steep slopes. Many eastern hemlock in these stands have fallen over into the streams. In nine of the ten stands large trees have fallen downslope. Windthrow related to topographic influences is likely a common disturbance mechanism in these stands. Previous studies concerning eastern hemlock stand dynamics have noted windthrow as a common disturbance event for some stands (Lorimer 1980, Brown et al. 1982, Mladenoff and Stearns 1993).

During late Wisconsin glaciation eastern hemlock occurred over a very small range in eastern North America (Davis 1981). As the climate warmed beginning about 14,000 years BP, eastern hemlock spread throughout the southern Appalachian Mountains. During the early Holocene eastern hemlock likely reached its maximum distributional range. Continued climatic warming resulted in eventual contraction of its southern range boundary. The stands investigated in this study likely represent the remnants of a wider distribution on the southernmost part of the Appalachian Plateau. Eastern hemlock was extremely limited on the Coastal Plain. The Coastal Plain is characterized by broad alluvial valleys with relatively little relief and lacks deeply incised channels and steep sided valleys where eastern hemlock normally occurs in the central and southern Appalachian Mountains. Harper (1919, 1943) documented an exception, describing eastern hemlock stands in Marion County, Alabama in the Fall Line Hills physiographic region, which is a transitional zone from the Appalachian Highlands to the Coastal Plain.

Based on its size, longevity, and dominance over large areas of the Appalachian Mountain region, eastern hemlock is widely regarded as among the grandest trees in eastern North America. Unfortunately, vast stands of eastern hemlock in the central portion of its range have been devastated by the defoliating hemlock woolly adelgid (*Adelges tsugae* Annand.) (HWA) (Orwig and Foster 1998). The HWA is an aphid-like insect native to Asia and it is currently advancing toward the southern range of eastern hemlock. It is not yet known if outlying stands have better chances of avoiding the HWA because of their isolated locations.

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