CASTANEA 75(1): 1–18. MARCH 2010

Terrain and Landform Influence on *Tsuga canadensis* (L.) Carrière (Eastern Hemlock) Distribution in the Southern Appalachian Mountains

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ABSTRACT We examined the relationships between hemlock distribution and abundance and terrain attributes for the Coweeta Basin in the southern Appalachian Mountains. Field measurements were combined with GIS mapping methods to develop predictive models of abundance and distribution of *Tsuga canadensis* (L.) Carrière (eastern hemlock) and evaluate the co-occurrence of *Rhododendron maximum* L. (rosebay) and *Kalmia latifolia* L. (mountain laurel). Terrain variables were derived from USGS DEM 30-meter digital maps. Elevation, slope, aspect, terrain shape index, landform, and distance from stream were calculated from field measurements and the digital data. Terrain attributes such as elevation ($r^2 = 0.97$, $p < 0.0001$), distance to stream ($r^2 = 0.94$, $p < 0.0001$), and terrain shape index ($r^2 = 0.61$, $p = 0.0015$) were good predictors of *T. canadensis* abundance. Terrain shape index explained 56% of the variation in *R. maximum* percent aerial cover ($r^2 = 0.56$, $p = 0.005$). In the Coweeta Basin, *T. canadensis* was distributed as few, large trees mostly concentrated in near-stream locations, and it was closely associated with *R. maximum*. *Tsuga canadensis* mortality due to *Adelges tsugae* Annand (hemlock wooly adelgid) will result in a minor decrease in basin-wide basal area, but will substantially reduce near-stream basal area, and will also remove the largest trees in near-stream environments. In similar landscapes across the southern Appalachians, where *T. canadensis* co-occurs with *R. maximum*, riparian shading will likely remain unchanged.

INTRODUCTION Forest vegetation patterns in the southern Appalachians are related to complex environmental gradients associated with climate, soils, and topography, as well as disturbance history, from natural events and direct and indirect human actions (Harmon et al. 1983). *Tsuga canadensis* (L.) Carrière (eastern hemlock) responds strongly to this environmental gradient (Elliott et al. 1999). *Tsuga canadensis*, a long-lived, shade tolerant conifer, can persist for decades in the forest understory, live 250 to 300 yr, with the oldest examples surviving up to 400 yr (Godman and Lancaster 1990, Orwig and Foster 1998, Bonneau et al. 1999, Young et al. 2002). *Tsuga canadensis* grows in a wide range of topograhic positions including steep slopes, deep gorges, and riparian borders. *Tsuga canadensis* ranges from western Nova Scotia to southern Ontario and northeastern Minnesota, extending south throughout New England and along the Appalachian Mountains into northern Georgia and Alabama (Elias 1987). In general, *T. canadensis* is more abundant and evenly distributed in the northeast than in the southern and western portions of its range (Evans 1995, Williams and Schmidt 2000), where it reaches greatest abundance in cool, moist microclimates (Goodman and Lancaster 1990). In the southern Appalachians, *T. canadensis* distribution varies from isolated individual trees to scattered clusters, pure small stands (defined as at least five trees with adjacent canopies), or mixed stands.

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Received October 15, 2008; Accepted June 3, 2009.

However, *T. canadensis* distribution and abundance are currently changing due to infestation by *Adelges tsugae* Annand (hemlock wooly adelgid [HWA]). HWA is an introduced insect species from Asia that has caused extensive mortality of *T. canadensis* in the northeastern United States since it arrived in Virginia in the 1950's. It has been spreading at an average rate of approximately 30 km per year through dispersal by wind, mammals, and birds (McClure 1990, Benzinger 1994). Concerns about the long-term effects of HWA on *T. canadensis* forest ecosystems have increased in recent years, as the rate of spread has accelerated through the southern Appalachians, causing nearly complete infestation of the host species in some areas (Elliott unpubl. data). The loss of *T. canadensis* may substantially alter canopy composition, diversity, ecosystem structure, and ecosystem function in the southern Appalachians (Jenkins et al. 1999, Yorks et al. 2000, Eschtruth et al. 2006). Since HWA attacks hemlock trees of all ages and sizes, and infested trees seldom recover (Foster and Zebryk 1993, Orwig and Foster 1998, Kizlindki et al. 2002), it has the potential to remove *T. canadensis* from southern forests. Several studies of *T. canadensis* have focused on detecting change in declining stands (Royle and Lathrop 1997, 2002; Bonneau et al. 1999; Jenkins et al. 1999; Young et al. 2002; Stadler et al. 2006; Ford and Vose 2007; Orwig et al. 2008). For example, a recent study (Nuckolls et al. in press) concluded that hemlock is declining more rapidly from HWA infestation in the Southeast than in the Northeast, and that hemlock decline has a surprisingly rapid effect on carbon cycling. Post HWA successional patterns are likely to be influenced by co-occurring ericaceous shrubs (*Rhododendron maximum* and *Kalmia latifolia*), which impact tree seedling recruitment and survival (Beckage et al. 2000, Ford and Vose 2007). Hence, understanding the controls on the spatial distribution of *T. canadensis* and ericaceous shrubs is critical for predicting areas of HWA impact and developing post HWA restoration strategies.

While numerous studies have identified relationships between vegetation distribution and environment or terrain variables (Trimble and Weitzman 1956, Whittaker 1956, McNab 1989, McNab 1993, Moore, I.D. et al. 1991, Moore, D.M. et al. 1991, Brzeziecki et al. 1993, Franklin 1998, Elliott et al. 1999, Bolstad et al. 2001, Miller and Franklin 2002, Zomer et al. 2002, Pfeffer et al. 2003, Bolstad 2005), species-specific predictive relationships have only been developed for a few single species and in a few areas. Mean climatic conditions often adjust predictably in space. For example, mean annual and seasonal temperatures decrease and mean precipitation increases with elevation. Terrain affects the distribution and abundance of precipitation (Swift 1968) and soil moisture (Yeakley et al. 1998) across the landscape. These factors in turn affect the distribution, composition, and abundance of vegetation, and over the long term, the development of soil properties. If terrain characteristics are known or can be mapped across the landscape, then vegetation composition, condition, or structure may be predicted based on these species-terrain relationships.

Previous work has compared various methods for estimating species abundance or importance based on species-environment relationships (Brzeziecki et al. 1993, Franklin 1995, Pinder et al. 1997, Bolstad et al. 1998, Lookingbill and Urban 2005). A number of approaches have been tested, including those based on vegetation sampling and measured climatic variables (Franklin 1998, Horsch 2003) with the addition of disturbance and other factors (Brown 1984). These relationships can be used to estimate distribution, abundance, composition, and potential for restoration by using approaches such as cluster analysis, linear or logistic regression, and geostatistical estimation (Moore et al. 1991b, Michaelson et al. 1994, Franklin 1995, Bolstad et al. 1998, Florinsky 1998, Austin 2007). For example, in the southern Appalachians, Bolstad et al. (1998) compared four different models (mosaic diagram, linear regression, kriging and co-kriging) for predicting forest composition using field measurements of tree density and diameter to calculate basal area. They concluded that mosaic diagram and linear regression models showed higher accuracy than kriging or co-kriging and generally improved vegetation mapping when using spatial data on terrain (Bolstad et al. 1998).

In this paper, we integrated field measurements and spatial modeling to build a predictive model of *T. canadensis* abundance and distribution across a mountainous landscape in the southern Appalachians. Field measurements were coupled with a digital elevation model (DEM) that derived terrain variables to develop the relationships. Our objectives were: (1) to quantify the relationships among *T. canadensis* distribution and abundance and terrain variables, (2) to build a predictive model for *T. canadensis* occurrence across mountainous landscapes, and (3) to identify the co-occurrence of *Rhododendron maximum* and *Kalmia latifolia* with *T. canadensis* abundance. We focused on the distribution of *T. canadensis*, but we recognize that there is a small contribution of *Tsuga caroliniana* Engelm. (Carolina hemlock) on drier ridges and more exposed habitats within the region.

MATERIALS AND METHODS

Study Site Description

All measurements occurred at the Coweeta Hydrological Laboratory, a research station located in the southern Appalachian Mountains of western North Carolina (Latitude 35°03′N, Longitude 83°25′W). Coweeta Hydrological Laboratory is a 2,185 hectare experimental forest of the United States Department of Agriculture, Forest Service, Southern Research Station (Figure 1), and it is primarily used for watershed experimentation (Swank and Crossley 1988). It is also a Long Term Ecological Research site funded by the National Science Foundation (DEB 0218001).

Two streams, Ball Creek and Shope Fork, drain the Coweeta Basin and join to form Coweeta Creek. Coweeta Creek flows east approximately seven kilometers to connect with the Little Tennessee River (Swank and Crossley 1988). Elevation ranges from 677 m near the junction of Ball Creek and Shope Fork to 1592 m at Albert Mountain, the highest point in the Coweeta Basin. Slopes range from 0 percent to 126 percent and aspect for the basin is east-facing with major north- and south-facing side slopes. Soils are deep sandy loams and are underlain by folded schist and gneiss (Hatcher 1974). Two soil orders are found within Coweeta, immature Inceptisols and older developed Ultisols (Thomas 1996). Streams flow throughout the year, fed by approximately 2,000 mm of precipitation per year, most of which is rain. Mean annual temperature is 12.6°C and ranges from an average of 11.7°C in winter to 21.6°C in summer (Swift et al. 1988).

Field Measurements

Field measurements were conducted during the winters of 2005 and 2006 and the summer of 2006. Sampled plots were located in a stratified random manner on the Shope Fork and Ball Creek watersheds, and randomly within four unmanaged sub-watersheds within the Coweeta Basin. A total of 201, 0.2-hectare circular plots were installed across the basin. Approximately half the plots were within 200 m of the main branches of Shope Fork and Ball Creek, and approximately half the plots were within the four sub-watersheds that comprise about 20% of the Coweeta Basin (Figure 2). Plot centers were established using a Global Positioning System (GPS) receiver (Trimble GeoXT, Sunnyvale, California) and positions were differential corrected (DGPS). ArcPad 6.0 (Environmental Systems Research Institute [ESRI], Redlands, California) was used for data collection. Position Dilution of Precision (PDOP) value of 10 and Signal to Noise Ratio (SNR) setting of 2.5 were used to ensure accurate location collection. GPS Pathfinder Office 2.90 was used for DGPS. Base station files from Conover and Franklin, North Carolina were used for DGPS. Preliminary tests over known locations verified positional errors of less than two meters after differential correction.

Plot centers were marked with a stake and all *Tsuga canadensis* trees taller than 1.3 m and within a 25 m horizontal radius of plot center were tallied. Slope distance was converted to horizontal distance by adjusting for slope angle (Avery and Burkhart 1994) as measured with a Sunto clinometer. Diameter of all *T. canadensis* $\geq$20 cm DBH was measured to the nearest 0.1 cm. On each plot, aerial coverage of understory *Kalmia latifolia* and *Rhododendron maximum* was calculated by field sketching the canopies of the two species on graph paper and then overlaying a transparent dot grid sheet on the sketch to calculate percent aerial coverage.

Analytical and Statistical Methods

Spatial data were developed and processed with a combination of Trimble Pathfinder

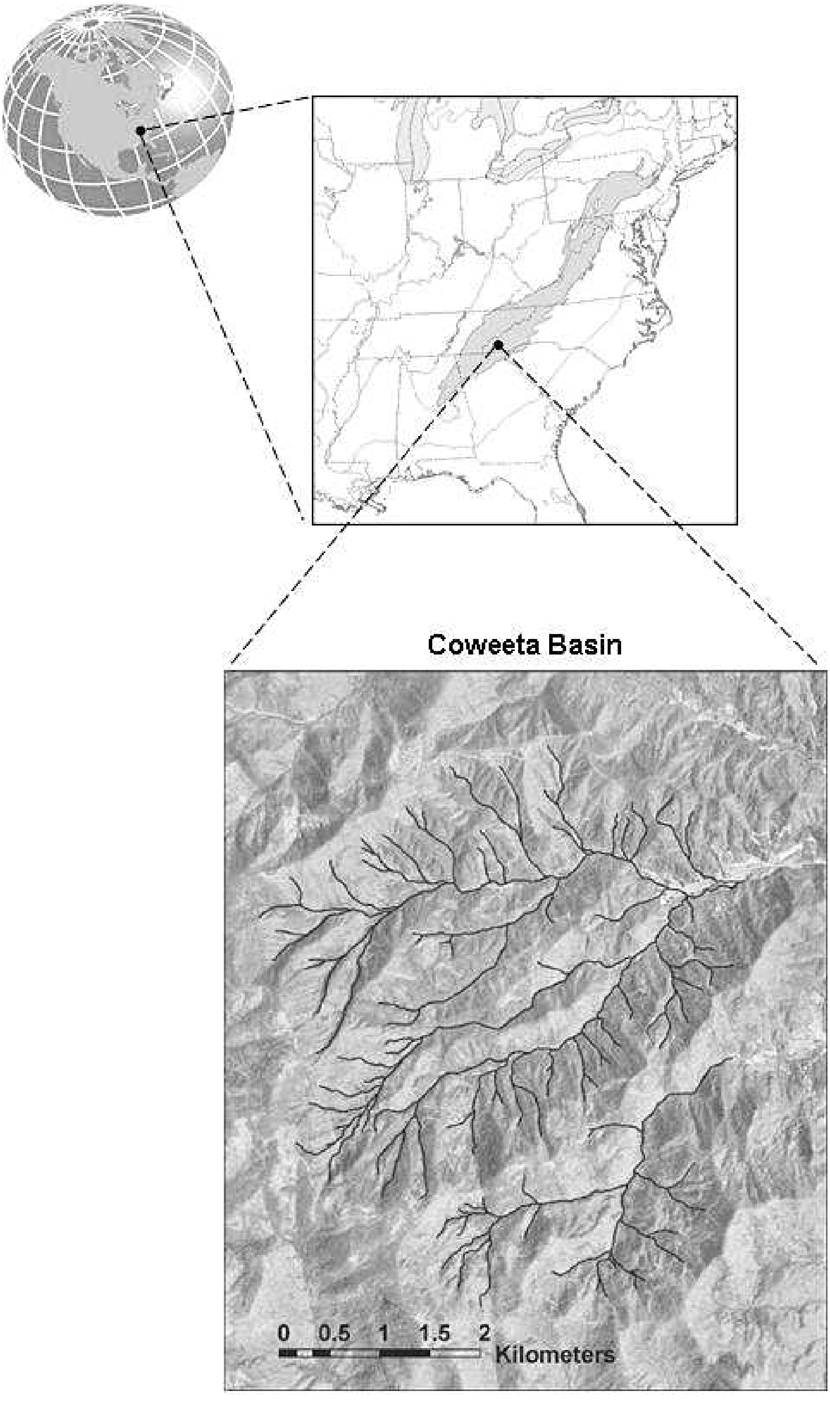

Figure 1. Geographical location of the Coweeta Basin, western North Carolina.

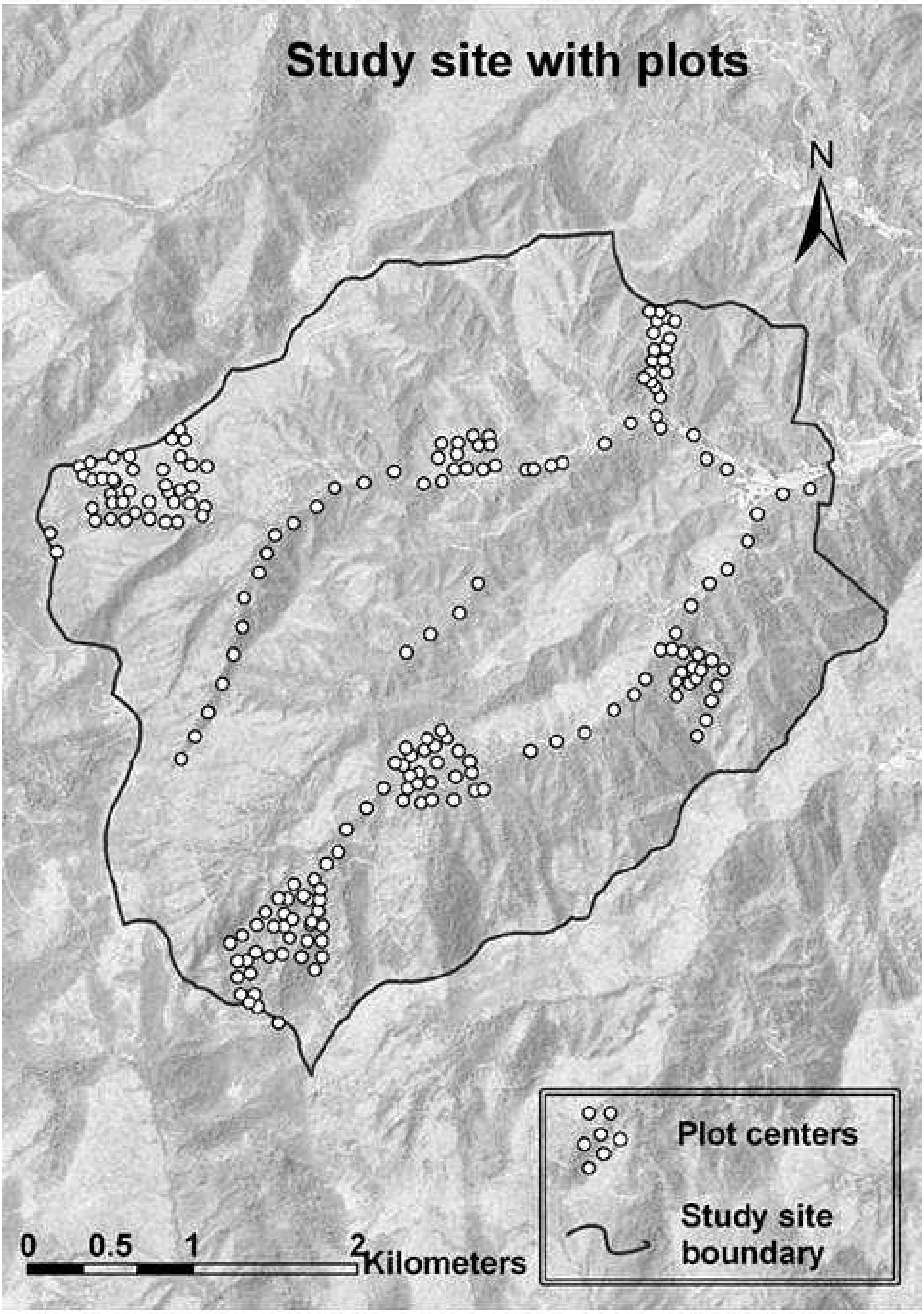

Figure 2. Map of Coweeta Basin with the sample plot locations.

Office (V3.1) and ESRI ArcGIS (V9.2) software (ESRI 2005). Terrain variables were derived from USGS (United States Geological Survey) DEM 30-meter resolution data. A 30-m USGS DEM for the Prentiss, North Carolina quadrangle was downloaded and projected to a Universal Transverse Mercator, NAD83 Datum, Zone 17 coordinate system. Slope,

Table 1. Mean basal area and density of *Tsuga canadensis* (eastern hemlock), and percent aerial cover of *Rhododendron maximum* and *Kalmia latifolia* in the Coweeta Basin, western North Carolina

Variables	Mean	Range
Hemlock basal area (m^2 ha^{-1})	2.0 (0.26)	0–16.7
Hemlock density (stems ha^{-1})	12.2 (1.51)	0–112.0
Rhododendron maximum aerial cover (%)	46.7 (2.42)	0–87.5
Kalmia latifolia aerial cover (%)	11.0 (1.81)	0–87.5

aspect, terrain shape, landform, and other terrain indices were calculated from the digital data (Moore et al. 1991b). Field-measured plot centers were combined to create a layer of plots as points, and this point layer was intersected with the derived terrain data. For comparison, digital terrain values were extracted and combined with the field measured terrain values for each sample plot. Stream locations were determined from USGS 1:100,000 scale hydrography data. These data were combined with the field-measured plot locations to calculate distance to the nearest stream.

Field and spatial variables were summarized and combined into one data set and statistical analyzes were performed using JMP 6.0 software (SAS Institute 2005). Aspect raw values were sine-transformed and rescaled into north-south and east-west components. Rescaled aspect sine values ranged from -2 at due south to 2 at due north. Terrain Shape Index (TSI) was calculated using McNab's (1989) procedure with a modified aml programming language script. Distance to stream was calculated using a Euclidian distance function.

Univariate linear regression was used to develop models of *T. canadensis* abundance versus terrain variables (SAS Institute 2005). Parameters were estimated using standard least squares with a probability value of $\alpha = 0.05$ for statistical significance. The independent terrain variables (elevation, slope, aspect, terrain shape index, and distance to stream) were individually fit to models with the dependent variables of *T. canadensis* basal area and density, and sine-transformed *K. latifolia* and *R. maximum* percent aerial cover.

Terrain variables, elevation, slope, terrain shape index, and distance to stream were binned to remove un-sampled and small-sampled intervals in subsequent estimates of univariate regression parameters (Sokal and Rolf 1981). Elevation was binned in 150 m increments (over the 710 to 1,450 m range), slope was binned into twenty percent increments (from 0 to 120 percent), terrain shape index (TSI) was binned along 0.1 increments, and distance to stream was binned into 10 m increments. Because the relationship between distance to stream and *T. canadensis* basal area was non-linear, distance to stream was square root transformed prior to model fits with *T. canadensis* basal area and density.

RESULTS Of the 201 plots sampled, *Tsuga canadensis* was found in 85% of the plots; 15% of the plots had 0 stems ha^{-1} and 37% of the plots had low density ($\leq$10 stem ha^{-1}). Where *T. canadensis* was present, density varied substantially from 5.1 to 112.0 stems ha^{-1} (Table 1). *T. canadensis* basal area averaged 2.0 m^2 ha^{-1}, which is about 6–10% of the expected total basal area for a mature, mixed hardwood southern Appalachian forest (Elliott et al. 1999, Bolstad et al. 2001). We found a maximum basal area of 16.7 m^2 ha^{-1} (Table 1).

Tsuga canadensis was more abundant near streams, on flat to gently sloping terrain, and at lower elevations. We found significant linear relationships between *T. canadensis* abundance and terrain variables that reflected these trends (Figures 3–6). *T. canadensis* basal area and density were significantly related to elevation (Figure 3A, B), with its abundance decreasing as elevation increased. *T. canadensis* was absent on all plots above 1,250 m. It was most abundant at elevations between 650–750 m with an average of 20 stems ha^{-1}, and had intermediate density at elevations between 750–1,250 m with an average of 6 stems ha^{-1}.

Tsuga canadensis density and basal area were significantly related to slope, and its abundance decreased as slope increased (Figures 4A, B). *T. canadensis* density averaged almost 25 stems ha^{-1} on gentle slopes

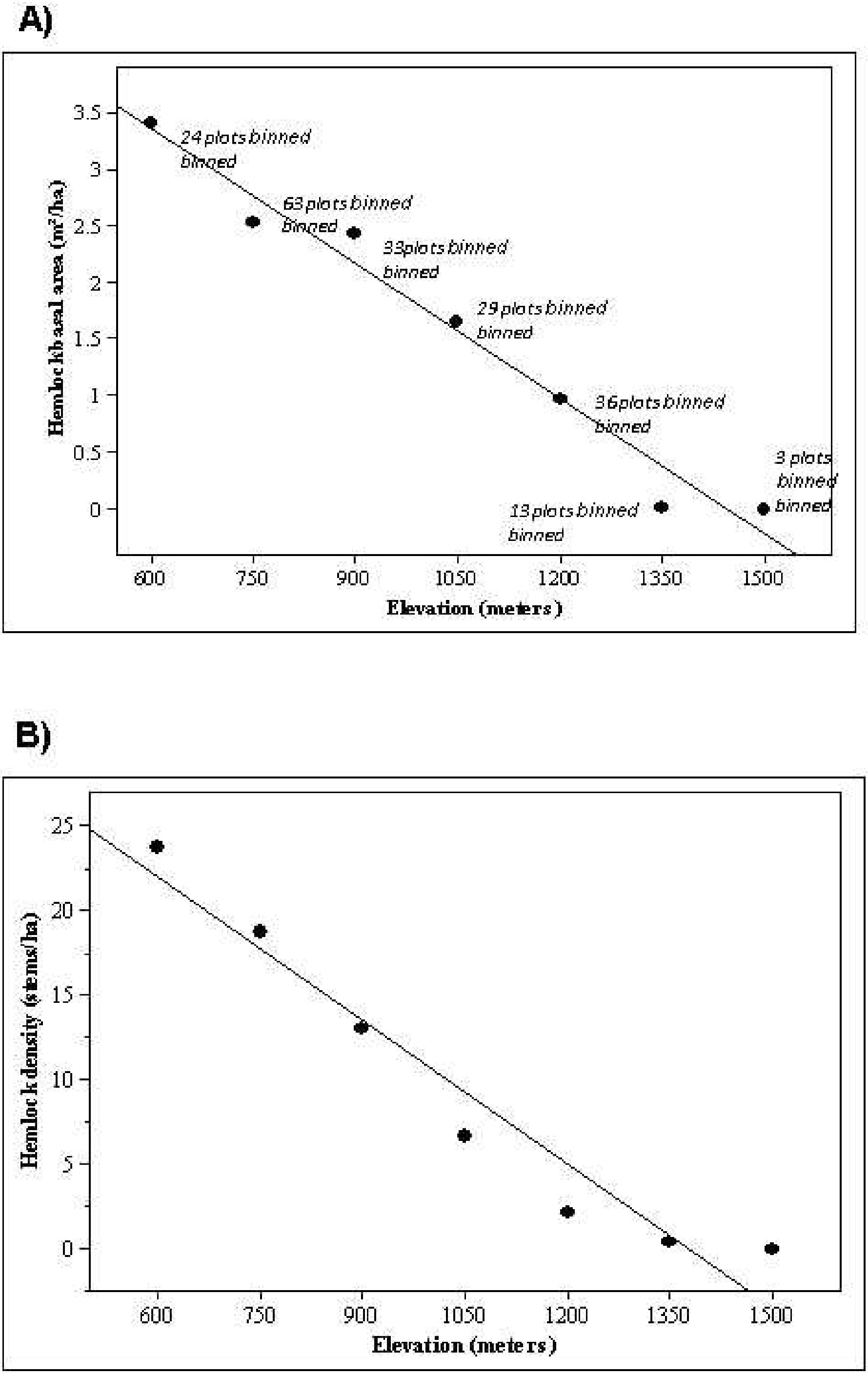

Figure 3. Relationships between *Tsuga canadensis* (eastern hemlock): **A)** basal area (m^2/ha) and elevation, $r^2 = 0.97$, $p < 0.0001$, basal area = 5.7385951 − 0.0039669 * (elevation); and **B)** stem density (stems/ha) and elevation, $r^2 = 0.94$, $p = 0.0003$, stem density = 38.941512 − 0.028294 * (elevation).

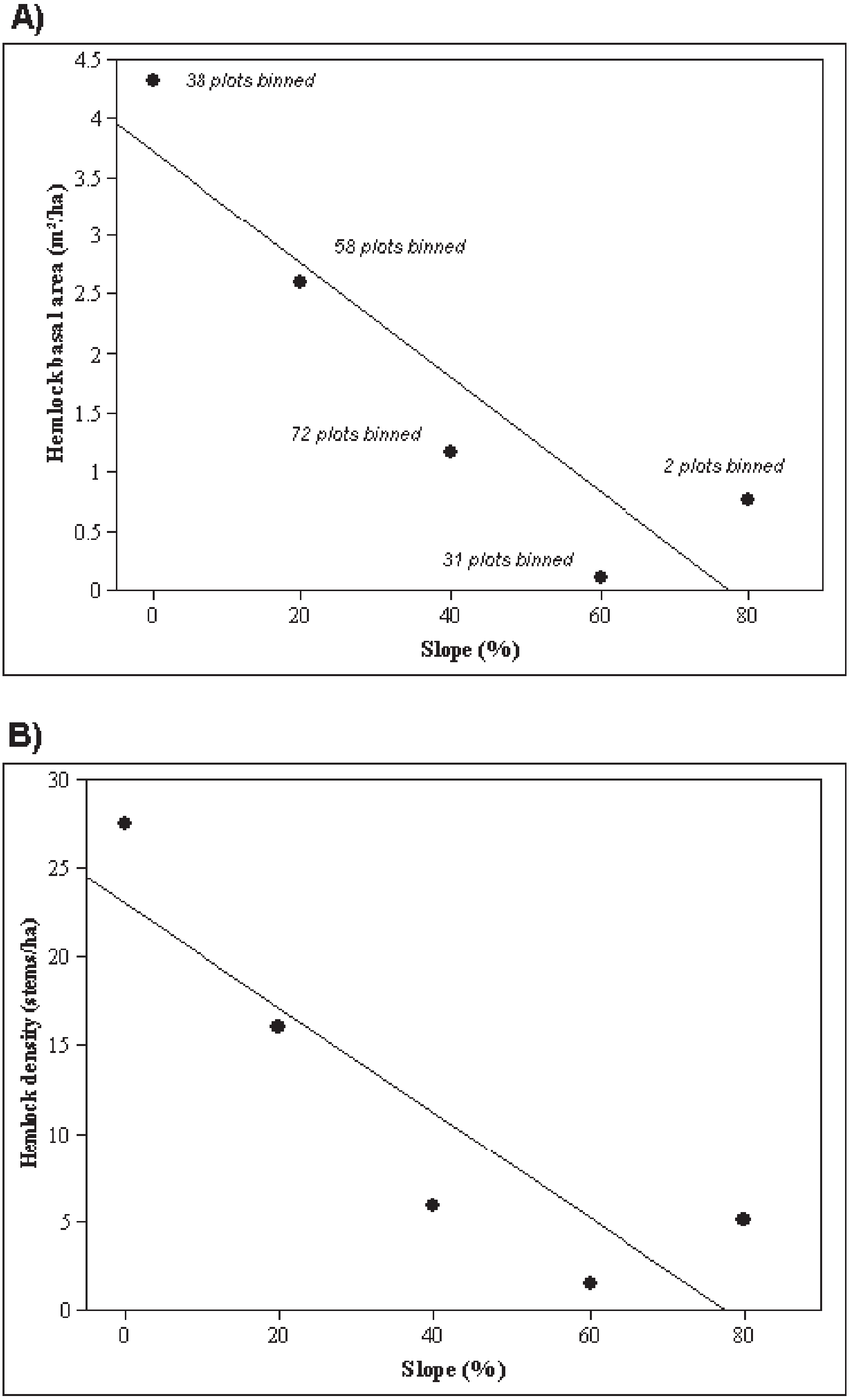

Figure 4. Relationships between *Tsuga canadensis* (hemlock): **A)** basal area (m^2/ha) and slope, $r^2 = 0.81$, $p = 0.0362$, basal area = 3.7157787 − 0.048043 * (slope); and **B)** stem density (stems/ha) and slope; $r^2 = 0.78$, $p = 0.0456$, stem density = 23.035538 − 0.2963826 * (slope).

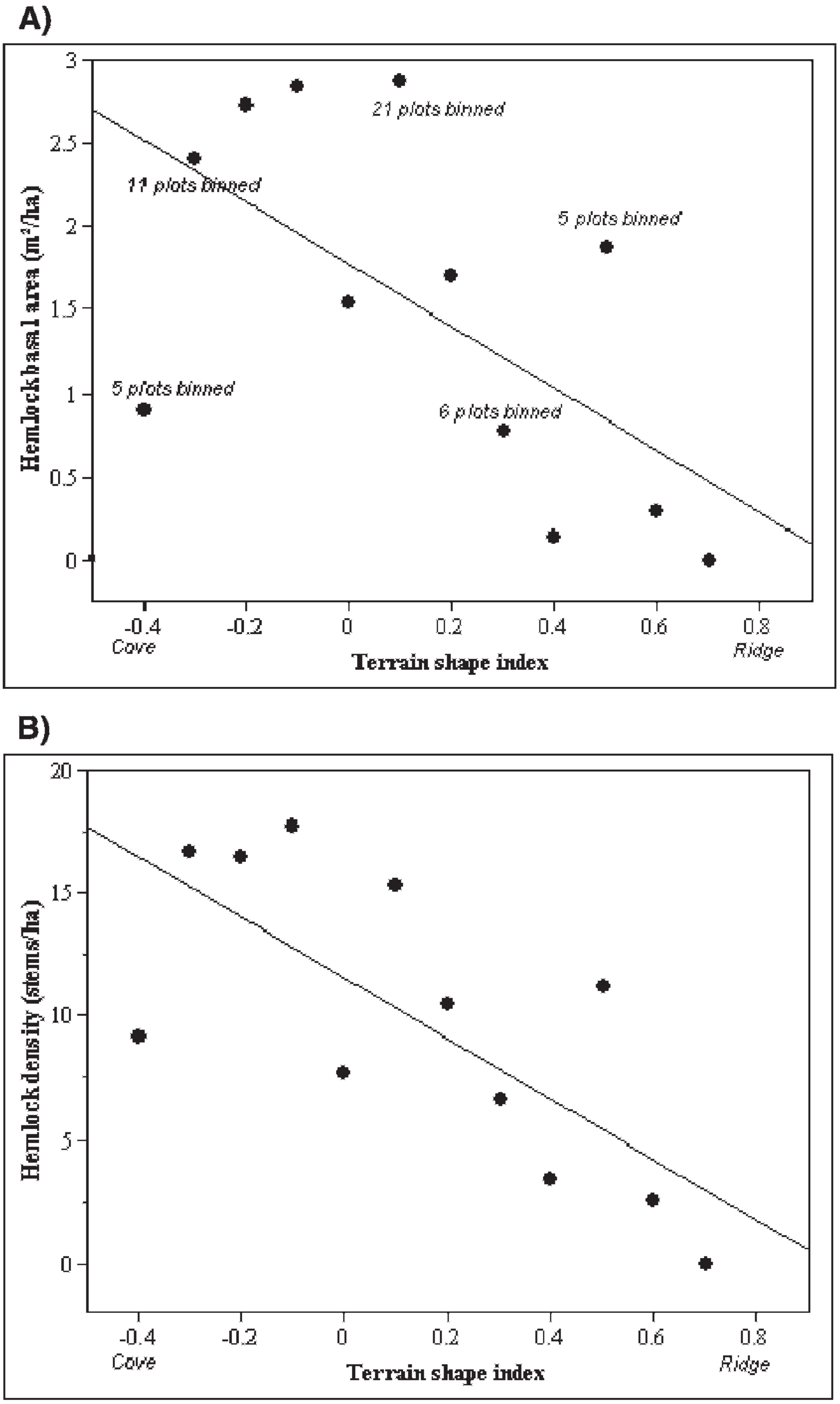

Figure 5. Relationships between *Tsuga canadensis* (hemlock): **A)** basal area (m^2/ha) and terrain shape index (TSI), $r^2 = 0.26$, $p = 0.0634$, basal area = 1.5294995 − 1.2343133 * (TSI); and **B)** stem density (stems/ha) and terrain shape index (TSI); $r^2 = 0.61$, $p = 0.0015$, density (stems/ha) = 11.588618 − 12.320068 * (TSI).

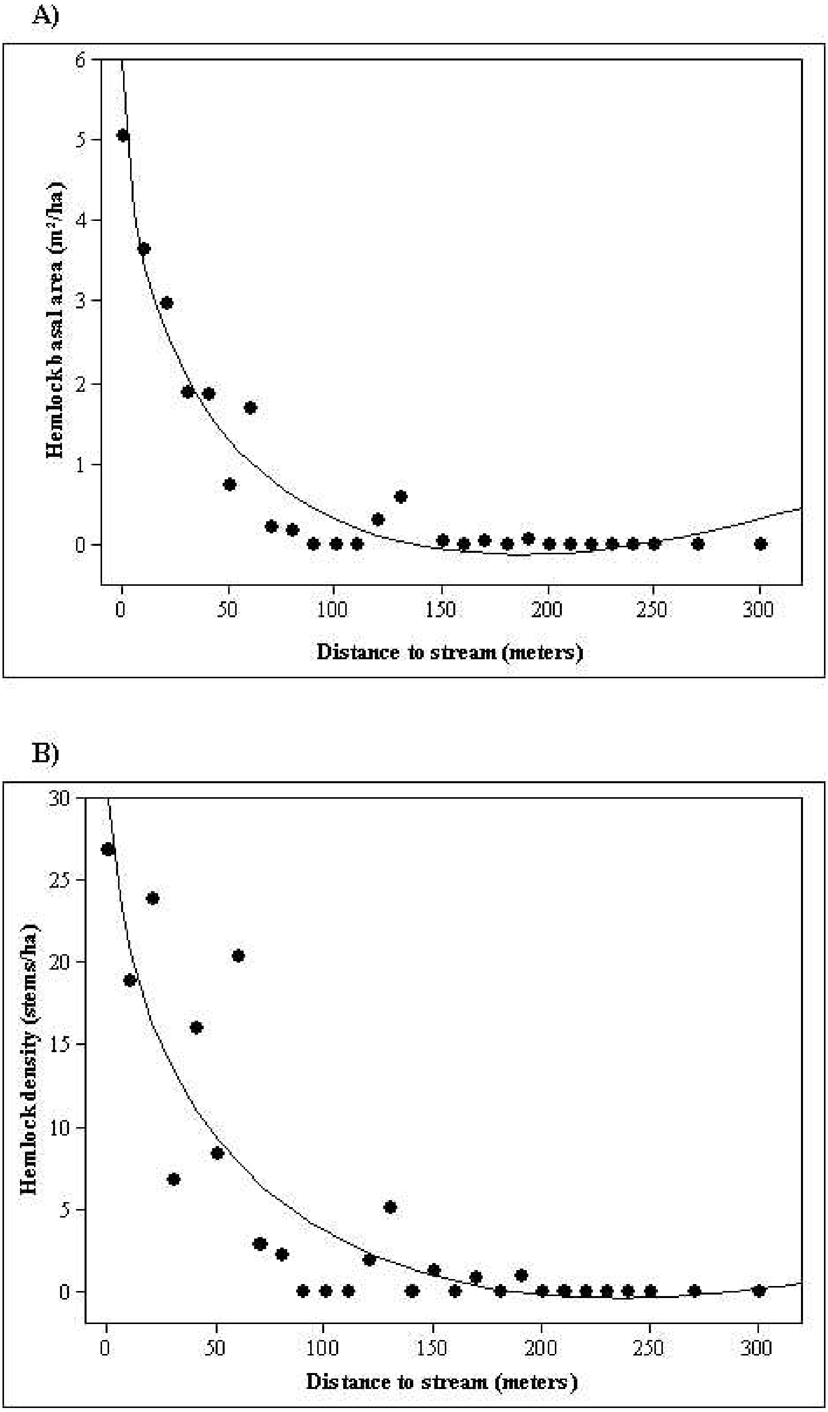

Figure 6. Relationships between *Tsuga canadensis* (hemlock): **A)** basal area (m^2/ha) and distance to stream, $r^2 = 0.94$, $p < 0.0001$, basal area $= 6.0247216 - 0.8993364 * SD^{0.5} + 0.0328904 * SD^2$; and **B)** stem density (stems/ha) and distance to stream, $r^2 = 0.79$, $p < 0.0001$, stem density $= 33.399771 - 4.3971877 * SD^{0.5} + 0.1431821 * SD^2$.

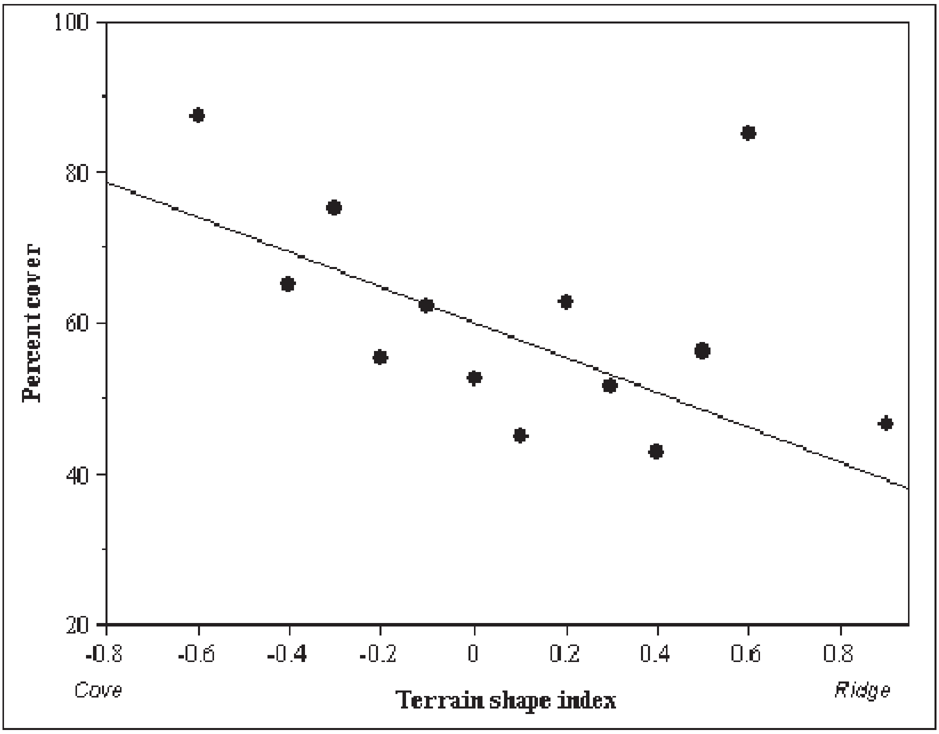

Figure 7. Relationship between *Rhododendron maximum* percent aerial cover and terrain shape index (TSI); $r^2 = 0.56$, $p = 0.0048$, percent cover = 60.146942 − 23.08143 (TSI).

(<20%), reaching nearly zero on steep slopes. The transformed aspect value showed no significant relationship with *T. canadensis* basal area or density, indicating there was no preferred aspect for *T. canadensis*, at least within the range of aspects we sampled (Figure 2).

Tsuga canadensis basal area decreased from cove to ridge locations and had a significant relationship with TSI (Figure 5A). *T. canadensis* density generally decreased from cove to ridge (Figure 5B), and there was greater variation in density among cove plots compared to ridge plots, largely because ridge plots (TSI $\geq$ 0.6) were zero or very low densities, while there was a range of densities from low to high at cove locations (TSI ≤ -0.2). *T. canadensis* density and basal area significantly decreased in a nonlinear manner with distance from stream (Figure 6A, B). *T. canadensis* basal area decreased rapidly up to locations ~50 m from the stream, and then decreased more gradually beyond 50 m (Figure 6A). *T. canadensis* density was highest near the stream and decreased as distance from the stream increased, approaching zero at distances greater than 75 m (Figure 6B).

The multiple linear regression model revealed a significant relationship between *T. canadensis* basal area and three independent variables, based on unbinned data: elevation, distance to stream, and terrain shape index ($r^2 = 0.30$, $p \leq 0.0001$). The model equation was *Tsuga canadensis basal area* = 2.7329556 + [*Distance to stream-weighted*] * −2.436 + [*Elevation*] * −0.001338 + [*Terrain shape index*] * −1.053077.

Rhododendron maximum was present on most plots, its percent aerial cover was quite high, averaging nearly half the plot area (Table 1), and its cover was linearly related to TSI (Figure 7). We found that distance from stream and aspect were significant variables in the multiple regression model for *R. maximum* (Table 2). In contrast, *Kalmia latifolia* was less abundant, with an average aerial cover of 11% (Table 1). Elevation was the only significant variable in the multiple regression model for *K. latifolia* (Table 3).

Table 2. Multiple regression model for *Rhododendron maximum* percent aerial cover in the Coweeta Basin, western North Carolina

	Parameter Estimates			
	Estimate	SE	t Ratio	Prob > |t|
Intercept	69.92	12.23	5.72	<.0001
Terrain shape index	−11.25	10.05	−1.12	0.2648
Elevation	0.0112	0.0144	0.78	0.4366
Slope	−0.2418	0.1505	−1.61	0.1102
Aspect (sine transformed)	−10.582	3.188	−3.32	0.0011
Distance to stream	−0.1029	0.0422	−2.44	0.0159

DISCUSSION

The concept of species-environment relationships underpins many descriptions of spatial variation in plant abundance, with expected abundance relying on species-specific affinities to certain environmental conditions (Whitaker 1956, Whitaker 1965, Day and Monk 1974, Clarke 1993). In the Coweeta Basin, we found *T. canadensis* to be largely restricted to topographically concave, low-slope, near-stream environments with a strong, nonlinear relationship (negative exponential) with distance to stream. The relative importance of slope, topographic terrain shape, and stream distance are difficult to disentangle because they are interrelated. Near stream areas are generally flatter and have concave topograpy, so it is not surprising that *T. canadensis* distribution relies on all of these conditions given the correlation among these significant variables. In addition, the combination of these variables suggests that soil moisture is a primary driving factor for *T. canadensis* distribution and abundance in the southern Appalachians; i.e., *T. canadensis* favors sites with high soil moisture.

Partial shading and several years of adequate soil moisture are necessary for *T. canadensis* reproduction (Goerlich and Nyland 2000, Rooney et al. 2000), and both conditions are more likely in near-stream locations. *Tsuga canadensis* has shown notable tolerance to wet soils, often growing at the margins of lakes and interspersed on local high points in swampy areas, and often developing shallow root systems in response to persistently high water tables (Anderson and Gordon 1994). Continuous soil moisture is particularly important, given slow early growth rates, shallow roots, and substantial drought-induced mortality up to several years after seedling establishment (Kotar 1996).

In the southern Appalachians, others have shown strong topographic gradients in surface soil moisture, particularly during periodic drought events (Helvey et al. 1972, Yeakley et al. 1998). Helvey et al. (1972) recorded significant decreases in soil moisture that were most pronounced within the first 25 m from a stream, and substantially more pronounced during periods of low rainfall. Yeakley et al. (1998) measured similar trends along a broader, south-facing cove to ridge gradient, where soil moisture declined significantly as distance from stream increased. This gradient was most significant in the top 30 cm of soil and during drought, but still present after extended periods of normal rain. Soil

Table 3. Multiple regression model for *Kalmia latifolia* percent aerial cover in the Coweeta Basin, western North Carolina

	Parameter Estimates			
	Estimate	SE	t Ratio	Prob > |t|
Intercept	143.89	26.48	5.43	<.0001
Terrain shape index	−15.84	21.45	−0.74	0.4641
Elevation	−0.1041	0.0264	−3.95	0.0003
Slope	0.2498	0.4742	0.53	0.6011
Aspect (sine transformed)	−16.98	9.31	−1.82	0.0750
Distance to streams	0.1363	0.0821	1.66	0.1041

moisture and soil drying were closely related to a topographic index incorporating uphill contributing area and slope (Yeakley et al. 1998).

Our results are consistent with the hypothesis that soil moisture conditions may be a primary factor contributing to reduced abundance of *T. canadensis* away from high moisture, streamside areas. Significant droughts have occurred several times since record keeping began in the Coweeta Basin in 1934 (Kloeppel et al. 2003). Given *T. canadensis*'s characteristic long persistence in the understory and shallow rooting during this period (Goodman and Lancaster 1990), it may be particularly susceptible to periodic drought.

Tsuga canadensis basal area and density were not related to transformed aspect, indicating exposure-related features were less important. Previous work in the northern Hemisphere has shown consistent, although complex relationships between aspect and a number of environmental factors because north-facing slopes receive less solar radiation than south-facing slopes. These variables include integrated and maximum solar radiation, mean and maximum air and soil temperatures, and atmospheric humidity (Barry 1992, Bolstad et al. 1998, Chen et al. 1999, Lookingbill and Urban 2005). In addition, both indices of transformed aspect and related climatic variables have been shown to directly affect the distribution of southern Appalachian species (Bolstad et al. 1998, Desta et al. 2004). Similar to our results, Elliott and Swank (2008) found that aspect was not as important in describing vegetation distribution as other significant variables such as elevation, terrain shape, and soil organic matter content. The contrasting results between our study and those of Bolstad et al. (1998) and Desta et al. (2004) are most likely because our plots did not fall on the upper, side slopes with the most extreme exposures (i.e., midslopes away from ridges and drainages at S-SW aspects) such as those described by Desta et al. (2004).

Tsuga canadensis density and basal area also showed strong relationships with elevation, declining in abundance with increasing elevation, and absent from plots higher than approximately 1250 m. This strong relationship suggests that *T. canadensis* distribution is limited by more than soil moisture alone, because soil moisture increases with elevation, given otherwise similar terrain positions. Temperature decreases, precipitation increases, and the net water balance increases with elevation for similar topographic positions, leading to higher soil moistures.

In our study, *K. latifolia* was located at lower elevation and distributed across upper slopes and ridges (i.e., high terrain shape idex) with a tendency to be absent from concave and near-stream locations. In contrast, *R. maximum* had high percent cover overall, and showed significance relationships to terrain-related variables. *Rhododendron maximum* averaged more than 40% coverage across the range of TSI and increased to nearly 80% cover in near-stream locations. Its proportion was maintained across the ranges of elevations, with a propensity for cove locations. These evergreen species distributions are consistent with findings by others (Monk et al. 1985, Day et al. 1988, Dobbs and Parker 2004).

In this paper, we have identified the spatial distribution of *T. canadensis* relative to easily measured terrain conditions, similar to previous work that has used the concept of plant-environment relationships to identify the distribution of species along environmental gradients, and characterize community structure, patterns, and variation (Austin 1985, Ter Braak 1987, McCune and Grace 2002). These species distribution models do not necessarily identify the direct mechanisms controlling plant distribution and abundance, but may indirectly reflect the relationships with resource limitations, physiological function, disturbance and mortality, dispersal, or other important mechanisms that affect plant abundance through life histories. However, the models do identify potential functional relationships between measurable environmental conditions and species abundance, even when the controlling processes and specific thresholds are poorly identified or understood. These species distribution models may be used in a number of ways, including quantifying the environmental niche, assessing the impact of climate or land use change

(Turner et al. 2003), supporting appropriate sampling and management, or planning for re-introduction (Guisan and Thuiller 2005).

Tsuga canadensis has long been described as having affinities to cool, moist locations, sheltered from drought or wind (Curtis 1959, McNaughton and Wolf 1970, Elias 1987, Goodman and Lancaster 1990, Boyce 2000), with *T. canadensis* generally comprising less of the canopy and restricted to fewer locations in the southern Appalachians (Johnson et al. 2000) than in northern forests (Boyce 2000). However, these relationships have rarely been quantified, in part because of the inherent variability in *T. canadensis* abundance even at suitable sites. Its occurrence is contingent on many factors, only one of which is site suitability. *T. canadensis* may be absent from even the most suitable sites due to its current distribution and local dispersal limitations (Clark 1998). These in turn depend on complex and at times chaotic interactions of past climate regimes, disturbance history, distribution of competing taxa, and past or present human intervention. In addition, these factors may change through time, so future conditions will likely be different from the present or recent past. Regardless of the complexity, an analysis of current *T. canadensis* distribution relative to specific, measureable environmental conditions is helpful, both in uncovering mechanisms that drive its distribution, and to set targets for population management, maintenance, or re-introduction.

We found that *T. canadensis* was most abundant within 50 m of streams. Thus, loss of *T. canadensis* canopy cover due to HWA could substantially affect stream environments (Ross et al. 2003, Ford and Vose 2007). In Coweeta Basin, *T. canadensis* co-occurs with deciduous broadleaved species, so a reduction in canopy cover may increase winter insolation reaching streams. *T. canadensis* loss may alter stream temperature, algal or aquatic plant production, and aquatic food chains (Ross et al. 2003). The evergreen habit leads to greater early and late-season transpiration, thereby affecting water yields and timing (Ford and Vose 2007). However, potential impacts in near-stream areas might be attenuated by the co-occurrence of *R. maximum*, which is also abundant in these near stream areas. Therefore, the ecological impacts of *T. canadensis* loss will be most pronounced in the riparian zones where *R. maximum* is less abundant or absent, and efforts at preservation and restoration should perhaps be concentrated in these riparian areas. Our research on current distribution and abundance of both *T. canadensis* and co-occurring ericaceous shrubs may be helpful in guiding restoration efforts, particularly given the costs and limited means for managing HWA infestations, the impending loss of much of the *T. canadensis* resource, and the need to focus efforts on restoration if effective HWA control strategies are not found.

ACKNOWLEDGMENTS We would like to thank the Coweeta Hydrologic Lab, Southern Research Station, United States Department of Agriculture, Forest Service, and the Long Term Ecological Research Program. (University of Georgia) of the National Science Foundation DEB 0218001. This research work was supported with funding from the USDA Forest Service. We would also like to thank the staff members at the Department of Forest Resources and the MGIS program at the University of Minnesota.

LITERATURE CITED

Anderson, H.W. and A.G. Gordon. 1994. The tolerant conifers: eastern hemlock and red spruce, their ecology and management. Ontario ministry of Natural Resources, Ontario Forest Research Institute, Ontario, Canada.

Austin, M.P. 1985. Continuum concept, ordination methods, and niche theory. Ann. Rev. Ecol. Syst. 16:39–61.

Austin, M.P. 2007. Species distribution models and ecological theory: a critical assessment and some possible new approaches. Ecol. Model. 200:1–19.

Avery, T.E. and H.E. Burkhart. 1994. Forest measurements. McGraw Hill, Inc., New York, New York.

Barry, R.G. 1992. Mountain weather and climate. Routledge, London, United Kingdom.

Beckage, B., J.S. Clark, B.D. Clinton, and B.L. Haines. 2000. A long-term study of tree seedling recruitment in southern Appalachian forests: the effects of canopy gaps and shrub understories. Can. J. For. Res. 30:1617–1631.

Benzinger, J. 1994. Hemlock decline and breeding birds I. Hemlock Ecology. Records of New Jersey Birds 20:2–12.

Bolstad, P.V. 2005. GIS Fundamentals: a first text on Geographical Information Systems. Eider Press, Minneapolis, Minnesota.

Bolstad, P.V., J.M. Vose, and S.G. McNulty. 2001. Forest productivity, leaf area, and terrain in southern Appalachian deciduous forests. For. Sci. 47:419–427.

Bolstad, P.V., W.T. Swank, and J.M. Vose. 1998. Predicting southern Appalachian overstory vegetation with digital terrain data. Landscape Ecol. 13:272–283.

Bonneau, L.R., K.S. Shields, and D.L. Civco. 1999. Using satellite images to classify and analyze the health of hemlock forests infested by the hemlock wooly adelgid. Biol. Invasions 1:255–267.

Boyce, R.L. 2000. Relationship between environmental factors and hemlock distribution in Mt. Ascutney, Vermont. p. 113–121. *In:* McManus, K.A., K.S. Shields, and D.R. Souto (eds.). Proceedings: symposium on sustainable management of hemlock ecosystems in eastern North America. Gen. Tech. Rep. NE-267, United States Department of Agriculture, Forest Service, Northeastern Experiment Station, Newtown Square, Pennsylvania.

Brown, J.H. 1984. On the relationship between abundance and distribution of species. Amer. Naturalist 124:255–279.

Brzeziecki, B., F. Kienast, and O. Wildi. 1993. A simulated map of the potential natural forest vegetation of Switzerland. J. Veg. Sci. 4:499–503.

Chen, J., S.C. Saunders, T.R. Crow, R.J. Naiman, K.D. Brosofske, G.D. Mroz, B.L. Brookshire, and J.F. Franklin. 1999. Microclimate in forest ecosystem and landscape ecology. Bioscience 49:288–297.

Clark, J.S. 1998. Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. Amer. Naturalist 152:204–224.

Clarke, K.R. 1993. Non-parametric multivariate analyzes of changes in community structure. Austral. J. Ecol. 18:117–143.

Curtis, J.T. 1959. Vegetation of Wisconsin. University of Wisconsin Press, Madison, Wisconsin.

Day, F.P. and C.D. Monk. 1974. Vegetation patterns on a southern Appalachian watershed. Ecology 34:329–346.

Day, F.P., D.L. Phillips, and C.D. Monk. 1988. Forest communities and patterns. p. 141–149. *In:* Swank, W.T. and D.A. Crossley (eds.). Forest hydrology and ecology at Coweeta. Ecological Studies. Volume 66. Springer-Verlag, New York, New York.

Desta, F., J.J. Colbert, J.S. Rentch, and K.W. Gottschalk. 2004. Aspect induces differences in vegetation, soil, and microclimatic characteristics of an Appalachian watershed. Castanea 69:92–108.

Dobbs, M.M. and A.J. Parker. 2004. Evergreen understory dynamics in Coweeta forest, North Carolina. Phys. Geogr. 25:481–498.

Elias, T.S. 1987. The complete trees of North America. Gramercy Publishing Company, New York, New York.

Elliott, K.J. and W.T. Swank. 2008. Long-term changes in forest composition and diversity following early logging (1919–1923) and the decline of American chestnut (*Castanea dentata*). Plant Ecology 197:155–172.

Elliott, K.J., J.M. Vose, W.T. Swank, and P.V. Bolstad. 1999. Long-term patterns of vegetation-site relationships in a southern Appalachian forest. J. Torrey Bot. Soc. 126: 320–344.

Environmental Systems Research Institute (ESRI). 2005. ArcGIS 9.1. Redlands, California.

Eschtruth, A.K., N.L. Cleavitt, J.J. Battles, R.A. Evans, and T.J. Fahey. 2006. Vegetation dynamics in declining eastern hemlock stands: 9 yr of forest response to hemlock wooly adelgid infestation. Can. J. For. Res. 36:1435–1450.

Evans, R.A. 1995. Hemlock ravines at Delaware Water Gap National Recreation Area: highly valued, distinctive, and threatened ecosystems. United States Department of

Interior, National Park Service, Milford, Pennsylvania.

Florinsky, I.V. 1998. Combined analysis of digital terrain models and remotely sensed data in landscape investigations. Progress Phys. Geogr. 22:33–60.

Ford, C.R. and J.M. Vose. 2007. *Tsuga canadensis* (L.) Carr. Mortality will impact hydrologic processes in Southern Appalachian forest ecosystems. Ecol. Appl. 17: 1156–1167.

Foster, D.R. and T.M. Zebryk. 1993. Long-term vegetation dynamics and disturbance history of a *Tsuga*-dominated forest in New England. Ecology 74:982–998.

Franklin, J. 1995. Predictive vegetation mapping: geographic modeling of biospatial patterns in relation to environmental gradients. Progress Phys. Geogr. 19:474–499.

Franklin, J. 1998. Predicting the distribution of shrub species in Southern California from climate and terrain-derived variables. J. Veg. Sci. 9:733–748.

Goerlich, P.L. and R.D. Nyland. 2000. Natural regeneration of eastern hemlock: a review. p. 14–22. *In:* McManus, K.A., K.S. Shields, and D.R. Souto (eds.). Proceedings: symposium on sustainable management of hemlock ecosystems in eastern North America. Gen. Tech. Rep. NE-267, United States Department of Agriculture, Forest Service, Northeastern Experiment Station, Newtown Square, Pennsylvania.

Goodman, R.M. and K. Lancaster. 1990. *Tsuga canadensis* Eastern hemlock. p. 604–612. *In:* Silvics of North America. Volume I. Conifers. Agriculture Handbook 654, United States Department of Agriculture, Forest Service, Washington, D.C.

Guisan, A. and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters 8:993–1009.

Harmon, M.E., S.P. Bratton, and P.S. White. 1983. Disturbance and vegetation response in relation to environmental gradients in the Great Smoky Mountains. Vegetatio 55:129–139.

Hatcher, R.D. 1974. An introduction to the Blue Ridge tectonic history of north-east Georgia, Guidbook 13-A. Georgia Geological Survey, Georgia Department of Natural Resources, Atlanta, Georgia.

Helvey, J.D., J.D. Hwelett, and J.E. Douglass. 1972. Predicting soil moisture in the southern Appalachians. Soil Sci. Soc. Amer. Proc. 36:954–959.

Horsch, B. 2003. Modeling the spatial distribution of montane and subalpine forests in the central Alps using digital elevation models. Ecol. Modeling 168:267–282.

Jenkins, J.C., J.D. Aber, and C.D. Canham. 1999. Hemlock adelgid impacts on community structure and N cycling rates in eastern hemlock forests. Can. J. For. Res. 29:139–143.

Johnson, K.D., F.P. Hain, K.S. Johnson, and F. Hastings. 2000. Hemlock resources at risk in the Great Smokey Mountains National Park. p. 111–112. *In:* McManus, K.A., K.S. Shields, and D.R. Souto (eds.). Proceedings: symposium on sustainable management of hemlock ecosystems in eastern North America. Gen. Tech. Rep. NE-267, United States Department of Agriculture, Forest Service, Northeastern Experiment Station, Newtown Square, Pennsylvania.

Kizlinski, M.L., D.A. Orwig, R.C. Cobb, and D.R. Foster. 2002. Direct and indirect ecosystem consequences of an invasive pest on forests dominated by eastern hemlock. J. Biogeogr. 29:1489–1503.

Kloeppel, B.D., B.D. Clinton, J.M. Vose, and A.R. Cooper. 2003. Drought impacts on tree growth and mortality of southern Appalachian forests. p. 43–55. *In:* Greenland, D., D.G. Goodin, and R.C. Smith (eds.). Climate variability and ecosystem response at long-term ecological research sites. Oxford University Press, New York, New York.

Kotar, J. 1996. Relative importance and regeneration success of hemlock on different habitat types, Iron Mountain, MI. Department of Forestry School of Natural Resources, University of Wisconsin-Madison, 91–97.

Lookingbill, T.R. and D.L. Urban. 2005. Gradient analysis, the next generation: towards more plant relevant explanatory variables. Can. J. For. Res. 35:1744–1753.

McClure, M. 1990. Role of wind, birds, deer, and humans in the dispersal of hemlock wooly adelgid (Homoptera: Adelgidae). Environ. Entomol. 19:36–43.

McCune, B. and J.B. Grace. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon.

McNab, W.H. 1989. Terrain shape index: quantifying effect of minor landforms on tree height. For. Sci. 35:91–104.

McNab, W.H. 1993. A topographic index to quantify the effect of mesoscale landform on site productivity. Can. J. For. Res. 23:1100–1107.

McNaughton, S.J. and L.L. Wolf. 1970. Dominance and niche in ecological systems. Science 167:131–139.

Michaelsen, J., D.S. Schimel, M.A. Friedl, F.W. Davis, and R.C. Dubayah. 1994. Regression tree analysis of satellite and terrain data to guide vegetation sampling and surveys. J. Veg. Sci. 5:673–686.

Miller, J. and J. Franklin. 2002. Predictive vegetation modeling with spatial dependence vegetation Alliances in the Mojave Desert. Ecol. Modeling 157:227–247.

Monk, C.D., D.T. McGinty, and F.P. Day, Jr. 1985. Ecological importance of *Kalmia latifolia* and *Rhododendron maximum* in the deciduous forest of the southern Appalachians. J. Torrey Bot. Club 112:187–193.

Moore, D.M., B.G. Lees, and S.M. Davey. 1991. A new method for predicting vegetation distributions using decision tree analysis in a geographic information system. Environ. Manage. 15:59–71.

Moore, I.D., R.B. Grayson, and A.R. Landson. 1991. Digital terrain modeling: a review of hydrological, geomorphological and biological applications. Hydrol. Proc. 5:3–30.

Nuckolls, A.E., N. Wurzburger, C.R. Ford, R.L. Hendrick, J.M. Vose, and B.D. Kloeppel. 2009. Hemlock declines rapidly with hemlock wooly Adelgid infestation: impacts on the carbon cycle of southern Appalachian forests. Ecosystems 12:179–190.

Orwig, D.A. and D.R. Foster. 1998. Forest response to the introduced hemlock wooly adelgid in southern New England, USA. J. Torrey Bot. Soc. 125:60–73.

Orwig, D.A., R.C. Cobb, A.W. D'Amato, M.L. Kizlinski, and D.R. Foster. 2008. Multi-year ecosystem response to hemlock wooly adelgid infestation in southern New England forests. Can. J. For. Res. 38:834–843.

Pfeffer, K., E.J. Pebesma, and P.A. Burrough. 2003. Mapping alpine vegetation using vegetation observations and topographic attributes. Landscape Ecol. 18:759–776.

Pinder, J.E., G.C. Kroh, J.D. White, and A.M.B. May. 1997. The relationships between vegetation type and topography in Lassen Volcanic National Park. Plant Ecol. 131:17–29.

Rooney, T.P., McCormick, R.J, Solheim, S.L, and Waller, D.M. 2000. Regional variation in recruitment of hemlock seedlings and saplings in the upper great lakes, USA. Ecol. Appl. 10:1119–1132.

Ross, R.M., Bennett, R.M, Snyder, C.D, Young, J.A, Smith, D.R, and Lemarie, D.P. 2003. Influence of eastern hemlock (*Tsuga canadensis* L.) on fish community structure and function in headwater streams of the Delaware River basin. Ecol. Freshwater Fishes 12:60–65.

Royle, D.D. and R.G. Lathrop. 1997. Monitoring hemlock forest health in New Jersey using Landsat TM data and change detection techniques. For. Sci. 43:327–335.

Royle, D.D. and R.G. Lathrop. 2002. Discriminating *Tsuga canadensis* hemlock forest defoliation using remotely sensed change detection. J. Nematology 34:213–221.

SAS Institute. 2005. JMP User Guide, version 6.0. SAS Institute Inc., Cary, North Carolina.

Sokal, R.R. and F.J. Rolf. 1981. Biometry, The principles and practice of statistics in biological research. Freeman and Company, New York, New York.

Stadler, B., T. Müller, and D. Orwig. 2006. The ecology of energy and nutrient fluxes in hemlock forests invaded by hemlock wooly adelgid. Ecology 87:1792–1804.

Swank, W.T. and D.A. Crossley. 1988. Introduction and site description. p. 3–16. *In:* Swank, W.T. and D.A. Crossley (eds.). Forest hydrology and ecology at Coweeta. Ecological Studies. Volume 66. Springer-Verlag, New York, New York.

Swift, L.W., Jr. 1968. Comparison of methods for estimating aerial precipitation totals for a mountain watershed. Amer. Meteorol. Soc. Bull. 49:782–783.

Swift, L.W., Jr., G.B. Cunningham, and J.E. Douglas. 1988. Climatology and Hydrology. p. 35–55. *In:* Swank, W.T. and D.A. Crossley (eds.). Forest hydrology and ecology at Coweeta. Ecological Studies. Volume 66. Springer-Verlag, New York, New York.

Ter Braak, C.J.F. 1987. The analysis of vegetation-environment relationships by canonical correspondence analysis. Plant Ecol. 69:69–77.

Thomas, D.J. 1996. Soil survey for Macon County, North Carolina. United States Department of Agriculture, Natural Resources Conservation Service, Raleigh, North Carolina.

Trimble, G.R. and S. Weitzman. 1956. Site index studies of upland oaks in the northern Appalachians. For. Sci. 2:162–173.

Turner, M.G., S.M. Pearson, P.V. Bolstad, and D.N. Wear. 2003. Effect of land cover change on spatial pattern of forest communities in the Sothern Appalachian Mountains (USA). Landscape Ecol. 18:449–464.

Whittaker, R.H. 1956. Vegetation of the Great Smoky Mountains. Ecol. Monogr. 26:1–80.

Whittaker, R.H. 1965. Dominance and diversity in land plant communities. Science 147:250–259.

Williams, W.H. and T.L. Schmidt. 2000. Composition, structure, and sustainability of hemlock ecosystems in eastern North America. p. 5–10. *In:* McManus, K.A., K.S. Shields, and D.R. Souto (eds.). Proceedings: symposium on sustainable management of hemlock ecosystems in eastern North America. Gen. Tech. Rep. NE-267, United States Department of Agriculture, Forest Service, Northeastern Experiment Station, Newtown Square, Pennsylvania.

Yeakley, J.A., W.T. Swank, L.W. Swift, G.M. Hornberger, and H.H. Shugart. 1998. Soil moisture gradients and controls on a southern Appalachian hillslope from drought through recharge. Hydrol. Earth Syst. Sci. 2:41–49.

Yorks, T.E., J.C. Jenkins, D.J. Leopold, D.J. Raynal, and D.A. Orwig. 2000. Impacts of eastern hemlock mortality on nutrient cycling. p. 126–133. *In:* McManus, K.A., K.S. Shields, and D.R. Souto (eds.). Proceedings: symposium on sustainable management of hemlock ecosystems in eastern North America. Gen. Tech. Rep. NE-267, United States Department of Agriculture, Forest Service, Northeastern Experiment Station, Newtown Square, Pennsylvania.

Young, J.A., C.D. Snider, D.R. Smith, and D.P. Lemarie. 2002. A terrain-based paired-site sampling design to assess biodiversity losses from eastern hemlock decline. Environ. Monitoring Assess. 76:167–183.

Zomer, R., S. Ustin, and J. Ives. 2002. Using satellite remote sensing for DEM extraction in complex mountainous terrain: landscape analysis of the Makalu Barun National Park of eastern Nepal. Intl. J. Remote Sens. 23:125–143.