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VEGETATION, BROWSING, AND SITE FACTORS AS DETERMINANTS OF CANADA YEW (*TAXUS CANADENSIS*) DISTRIBUTION IN CENTRAL NEW HAMPSHIRE

John J. Stachowicz and Taber D. Allison

ABSTRACT

Taxus canadensis (Canada yew) in Hanover, New Hampshire, was studied to determine the relative importance of site factors, deer browsing, and past land-use in determining its distribution. Data indicate that the species' distribution is strongly linked to habitats with high soil moisture and low solar radiation (e.g., concave and/or north-facing slopes). *Taxus canadensis* is less abundant on slopes and in habitats with southern exposure. Deer browsing is greater on south-facing than on north-facing slopes and higher under deciduous than under coniferous canopies. Species associations do not indicate a restriction of *Taxus canadensis* to sites of particular (canopy) successional status, but land-use data suggest that it may be absent from areas which have been recently logged. *Taxus canadensis* is more abundant in Hanover than in sites in north-central Massachusetts, suggesting that suitable habitat for this species may increase with latitude.

Key Words: *Taxus canadensis,* land-use history, plant-site relationships, deer browsing, New Hampshire, Canada yew

INTRODUCTION

The genus *Taxus* L. comprises eight species worldwide. It is well known for its horticultural importance and has a long economic and mythical association with humans (e.g., Hartzell, 1991). Public awareness of this genus has recently been increased by the discovery that taxol, a chemical constituent of all parts of the yew plant, is an effective anti-tumor agent (National Cancer Institute, 1992). As a result, there was a major increase in the exploitation of yew species, particularly for their bark. Recent development of synthetic sources of taxol (e.g., Wheeler and Hehnen, 1993; Nicolau et al., 1994) has reduced the pressure on wild *Taxus* species, but the threat of harvesting wild populations has highlighted the lack of detailed information on the ecological status of all species in the genus.

Taxus canadensis Marsh. (Canada yew) is a spreading, evergreen shrub of cool, moist forests of the northeastern United States and southeastern Canada. The southern limit of its range in New England extends roughly in a line from Newburyport, Massachusetts, through Providence, Rhode Island, to New Haven, Connecticut. We conducted a survey of the distribution and abundance of this species in Hanover, New Hampshire, in order to determine its ecological status and, specifically, to assess which environmental factors are important in influencing its current distribution.

It has been suggested that logging can have a negative effect on *T. canadensis* distribution (Nichols, 1913; Hosley and Ziebarth, 1935). New England's forests were heavily logged during the 18th and 19th centuries when much of the land was cleared for agriculture, and subsequent reforestation beginning in the mid-19th century has resulted in a mosaic of primary (areas cut but never cleared for agriculture) and secondary woodlands (Foster, 1993). Vegetation surveys performed in the 1930's indicated that *T. canadensis* was associated with primary woodlands in Petersham, Massachusetts, but the species was too rare for this conclusion to have been stated with statistical confidence (Whitney and Foster, 1988; Whitney, 1991). Anecdotal reports also have suggested that winter browsing by white-tailed deer (*Odocoileus virginianus* Zimmermann) and moose (*Alces alces americana* Clinton) can locally extirpate *T. canadensis* populations (Allison, 1990, and references cited therein).

A review of the literature on forest community composition of New England and New York (a list of papers is available from the authors) and preliminary surveys of areas supporting *T. canadensis* populations indicated that most sites supporting this species were located at or near the base of slopes with a northerly or westerly aspect. While such surveys of forest composition can yield information on where *T. canadensis* is present, they are not useful in determining where the species is absent. This is significant, as these surveys are often biased to old-growth stands where *T. canadensis* may be more likely to occur.

We sampled *T. canadensis* in the town of Hanover, New Hampshire, in order to characterize its distribution in relation to specific environmental variables and associated vegetation. Based on the results of our preliminary survey and literature search, we evaluated our data with reference to the hypotheses that *T. canadensis*: (1) is restricted to sites which have experienced low browsing pressure in the past and/or present; (2) is limited by the availability of microhabitats with suitable moisture regimes, growing particularly on north-facing slopes which typically receive low insolation and have high humidity (Geiger, 1965); and (3) has been eliminated by extensive forest clearing and is currently confined to primary woodlands.

These hypotheses may be confounded. For example, deer browse *T. canadensis* only in the winter when north-facing slopes may be less accessible to deer due to rugged topography and a more persistent snowpack. North-facing slopes are also less likely to have been cleared for farming and are thus frequently associated with primary woodlands. While complete evaluation of these and additional hypotheses requires experimental approaches beyond the scope of our study, we report here the results of our survey and an initial evaluation of these hypotheses based on the survey data.

METHODS

Study Site

The climate of Hanover, New Hampshire, is characterized by long, cold winters with heavy snowfalls and relatively short, cool summers. Precipitation is distributed evenly throughout the year and the average number of frost free days is 134. Elevation ranges from slightly less than 120 m to 712 m. The land in and around the town was extensively cleared during the agricultural period, with a maximum of 65% of the total land area in farms in 1880; over 40% of this land was actually tilled (United States Census Bureau, 1883). The majority of undeveloped land in the town is now forested although recent agricultural census data suggest that about five percent of the town's area remains in cultivation (United States Census Bureau, 1989), most of which is in the floodplain of the Connecticut River or the level plains of the highlands.

In early successional sites, forested lands are dominated by white pine (*Pinus strobus* L.), gray birch (*Betula populifolia* Marsh.), quaking aspen (*Populus tremuloides* Michx.) and pin cherry (*Prunus pensylvanica* L. f.). Northern red oak (*Quercus rubra* L.), red maple (*Acer rubrum* L.), and white pine dominate mid-successional forests. Late successional lower elevation and stream valley forests are dominated by northern hardwoods species such as yellow birch (*B. lutea* Michx. f.), sugar maple (*A. saccharum* Marsh.), and beech (*Fagus grandifolia* Ehrh.). Hemlock (*Tsuga canadensis* (L.) Carr.) is also important at lower elevations and is replaced by red spruce (*Picea rubens* Sarg.) and balsam fir (*Abies* *balsamea* (L.) Mill.) at higher elevations. Nomenclature follows Gray's Manual of Botany (Fernald, 1950).

Vegetation Survey

Twenty study points were selected randomly using Universal Trans-Mercator (UTM) coordinates from areas zoned for forestry and recreation by the town of Hanover. Wetlands were excluded from the sample. The study was limited to these zones in order to assure forest cover in all randomly selected survey sites and to avoid sampling near residences. According to 1989 Town of Hanover zoning maps, approximately 44% of the town's area, and the majority of its undeveloped land, is included in this designation. At each point a transect was established in a compass direction chosen randomly. We located 10 plots of 10 m radius at randomly selected intervals between 20 and 100 m apart along the transect. Twenty transects (200 plots) were sampled. Vegetation data were limited to recording presence of all species in three strata (canopy, understory, and forest floor).

These measures of community composition may not be the most precise method of determining association; however, simple presence-absence data may be the best indicator of a forest's age (Rackham, 1986; Whitney and Foster, 1988). We sampled in this way in order to survey a large number of sample plots that could be easily compared with other available data, since much of the information on *T. canadensis* occurrence and associated forest composition gathered from the literature was available only in presence/absence form. Environmental parameters were also recorded for each plot including elevation, percent slope, aspect, slope shape (concave, planar, or convex), and slope position (base, lower, middle, upper third, or ridge). Land-use history data were collected from historical documents where available, but for most sites detailed historical records were unavailable, and land-use history was inferred using field observations and local (anecdotal) sources.

Sampling of *Taxus canadensis* Populations

Density, biomass, growth, and browse damage of *T. canadensis* were determined in a separate survey of sites known to support

T. canadensis populations, including sites other than those in our vegetation survey. These sites were selected according to the following criteria: (1) each contained a population of *T. canadensis* which extended over an area of at least 1000 m^2; (2) preliminary data indicated that at least a portion of the site contained plots with a density of 0.25 shoots per m^2; and (3) sites were selected to ensure representation of habitats with different canopy vegetation and slope aspect. At each of these sites, we marked 30 sampling points along a 100 m transect. The starting point of the transect, its direction, and the spacing of the sampling points were all determined using a random number table. At each point, the distance to the nearest *T. canadensis* shoot and the distance from that shoot to its nearest neighbor were measured. These distances were used to estimate density according to the formula derived by Batcheler (1971): $\log(\text{density}) = \log(n/\pi(\Sigma r_a^2)) - (0.1416 - 0.1613(\Sigma r_a/\Sigma r_b))$; where r_a is the distance from the point to the nearest shoot, r_b is the distance from that shoot to its nearest neighbor, and n is the number of shoots sampled. This method avoids the biases inherent in using random quadrat methods to sample a clumped distribution like that of a vegetatively spreading species such as *T. canadensis* (Batcheler, 1971).

Because *T. canadensis* spreads vegetatively, the delineation of an individual (genet) is impossible without tracing the root system. Therefore, we used the shoot (ramet) as our unit of measurement. A ramet was defined as a single emergent stem of the plant, disconnected from neighboring stems at a soil depth of 2 cm. For each shoot, we measured the basal diameter and the diameter of all branches greater than or equal to 3.0 mm on these shoots. These values were converted to grams dry weight by comparison with a standard curve of biomass versus branch diameter determined previously for *Taxus canadensis* [mass = 0.685 − 1.02 (diameter) + 0.539 (diameter)^2; r^2 = 0.99 (J. J. Stachowicz, unpubl. data)]. Biomass per shoot was multiplied by the density of each population (shoots per m^2) to obtain an estimate of biomass for each population.

Annual growth increments on *T. canadensis* are indicated by terminal bud scars on the stem and are often apparent as far back as five years. To estimate aboveground growth for each population, we measured the stem diameter just above the third terminal bud scar (Figure 1) from the apex of ten randomly selected branches on each shoot used for biomass estimates. Growth measurements were made in late fall, at the end of the growing season, so the measurement should represent three full years of growth. By measuring growth for the most recent three-year period, and then dividing by three to convert to an annual rate, we attempted to minimize the effects of year-to-year variability on our growth estimates. The annual diameter increment was converted to biomass using the standard curve of diameter versus mass, and an average annual biomass increment per branch was calculated. Total annual growth was estimated by multiplying the average annual biomass increment per branch by the total number of branches per shoot.

We estimated removal rates by deer (in grams of tissue per year) by measuring the diameter of all branches browsed within the past year at the point of removal, estimating biomass of removed tissue from the diameter-biomass relationship described above, and summing over all browsed branches for the entire shoot. Both annual growth and removal rates per shoot were multiplied by density to obtain areal estimates per m^2.

The nearest canopy and understory individuals to each shoot were recorded and environmental data taken as previously described. The canopy at each site was classified based on whether the majority of the nearest canopy individuals recorded were coniferous or deciduous. At all of the locations we sampled, either conifers or deciduous trees greatly outnumbered the other, so determination of canopy type was unambiguous and no mixed canopy areas were sampled.

DATA ANALYSIS

Relationships between environmental variables and *T. canadensis* presence were examined using Chi-Square tests (Sokal and Rohlf, 1981), testing the null hypothesis that the frequency of occurrence was the same in all categories. Biomass, annual growth, and deer removal rates for different habitats were evaluated by ANOVA with site characteristics as fixed effects. Data on species presence-absence in the 200 sample plots were analyzed by divisive classification using TWINSPAN (Hill, 1979a) to determine associations among different species and *T. canadensis.* Species presence-absence data were also analyzed by correspondence analysis (CA), an ordination technique, using DECORANA (Hill,

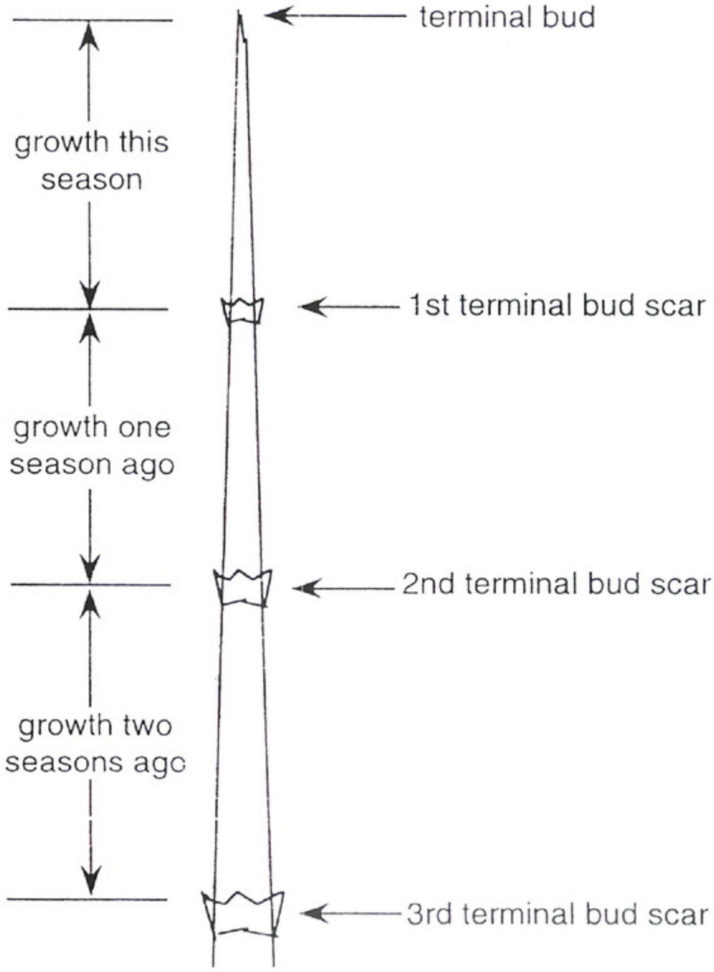

Figure 1. Branch tip of *Taxus canadensis* showing bud scars marking annual growth increments. Measurements of growth were made over the most recent three-year period by measuring the branch diameter just above the third terminal bud scar (see text).

1979b). This analysis represents plots or species graphically, on a two (or greater) dimensional set of axes, placing those with the most similar patterns of occurrence closest together, and thereby allowing relationships between many samples or species to be easily recognized. To test if the axis values generated by DECORANA were predictive of *T. canadensis* presence, we correlated them, along with environmental parameters (slope, aspect, elevation, etc.), with *T. canadensis* presence by multiple logistic regression (Kleinbaum et al., 1988). This analysis is similar to standard multiple linear regression, with the exception that the dependent variable (in this case *T. canadensis* occurrence) is dichotomous (yew is either present or absent).

RESULTS AND DISCUSSION

Taxus canadensis occurred in 37 out of 200 plots sampled (18.5%). The only understory or forest floor species that occurred more frequently was striped maple (*Acer pensylvanicum* L., 43.5%). Several other forest floor species were similar in frequency to *T. canadensis.* These include *Rubus* sp., 17%; *Lycopodium obscurum* L., 16.5%; *Lycopodium clavatum* L., 14.5%; *Lycopodium annotinum* L., 14.5%; *Aster divaricatus* L., 13.5%; and *Mitchella repens* L., 13%. The frequency of occurrence of *T. canadensis* in Hanover is higher than that in north-central Massachusetts. *Taxus canadensis* occurred in seven of 74 (9.5%) plots in the Harvard Forest and surrounding area of Petersham, Massachusetts (Gerhardt, 1993), and a survey of a 40 township region in north-central Massachusetts found *T. canadensis* in 17 out of 360 plots, less than five percent (C. Mabry and D. R. Foster, unpubl. data). These studies used 20 m × 20 m plots in which presence/absence of all vascular plant species was recorded, so general methods are comparable to this study. The land-use history and topography of these central-Massachusetts sites are similar to those of Hanover, New Hampshire, and both receive ample precipitation throughout the year. However, Hanover has a shorter growing season and more of the precipitation comes as snowfall than at the Harvard Forest, suggesting that the primary difference between these sites is related to temperature and latitude.

Presence-absence data (Table 1), collected during our vegetation survey, show that *T. canadensis* occurs more frequently on sites with concave slopes, at slope bases, at low elevations, on north- and east-facing slopes, or on level ground (slope <10%) than in locations with other physiographic characteristics. The sampling of *T. canadensis* populations showed that, where this species grew, density was greatest in level areas (0.83 shoots/m^2) and lowest on south-facing slopes (0.23 shoots/m^2). Shoots growing on north-facing slopes have the greatest standing crop or biomass ($F = 4.52$; $P < 0.001$) and growth rates or production equal to shoots on level ground but greater than those on south slopes ($F = 6.09$; $P < 0.001$; Figure 2A). Production of *T. canadensis* did not differ under deciduous versus coniferous canopies, although biomass was slightly greater under deciduous canopies (Figure 2B).

The distribution of *T. canadensis* in upland forests of Hanover

Table 1. Occurrence of *Taxus canadensis* by habitat characteristics for 200 plots in Hanover, New Hampshire.

	Taxus present	*Taxus* absent	Frequency
Slope Shape			
Concave	21	28	42.9
Planar	15	65	18.8
Convex	1	70	1.4
	$\chi^2 = 33.04$	df = 2; $P < 0.0001$	
Slope Position			
Slope Base	16	16	50.0
Lower Third	20	32	38.5
Middle Third	0	57	0
Upper Third	1	50	2.0
Ridge Top	0	8	0
	$\chi^2 = 49.09$	df = 4; $P < 0.0001$	
Elevation (meters)			
100–200	10	0	100
200–300	6	17	26.1
300–400	19	45	29.7
400–500	2	94	2.1
>500	0	7	0
	$\chi^2 = 68.99$	df = 4; $P < 0.0001$	
Aspect			
North	23	59	28.0
East	12	33	26.7
South	0	31	0
West	2	40	4.8
	$\chi^2 = 19.24$	df = 3; $P = 0.0002$	
Percent Slope			
0–9°	15	26	36.6
10–19°	8	53	13.1
20–29°	7	44	13.7
>30°	7	40	14.9
	$\chi^2 = 11.244$	df = 3; $P = 0.0105$	
Time since abandonment[1]			
less than 30 years	0	42	0
30–120 years	6	15	28.6
>120 years or never cleared	31	106	22.6
	$\chi^2 = 12.50$	df = 2; $P = 0.0019$	

[1] Time since the land was last cultivated or intensively cut.

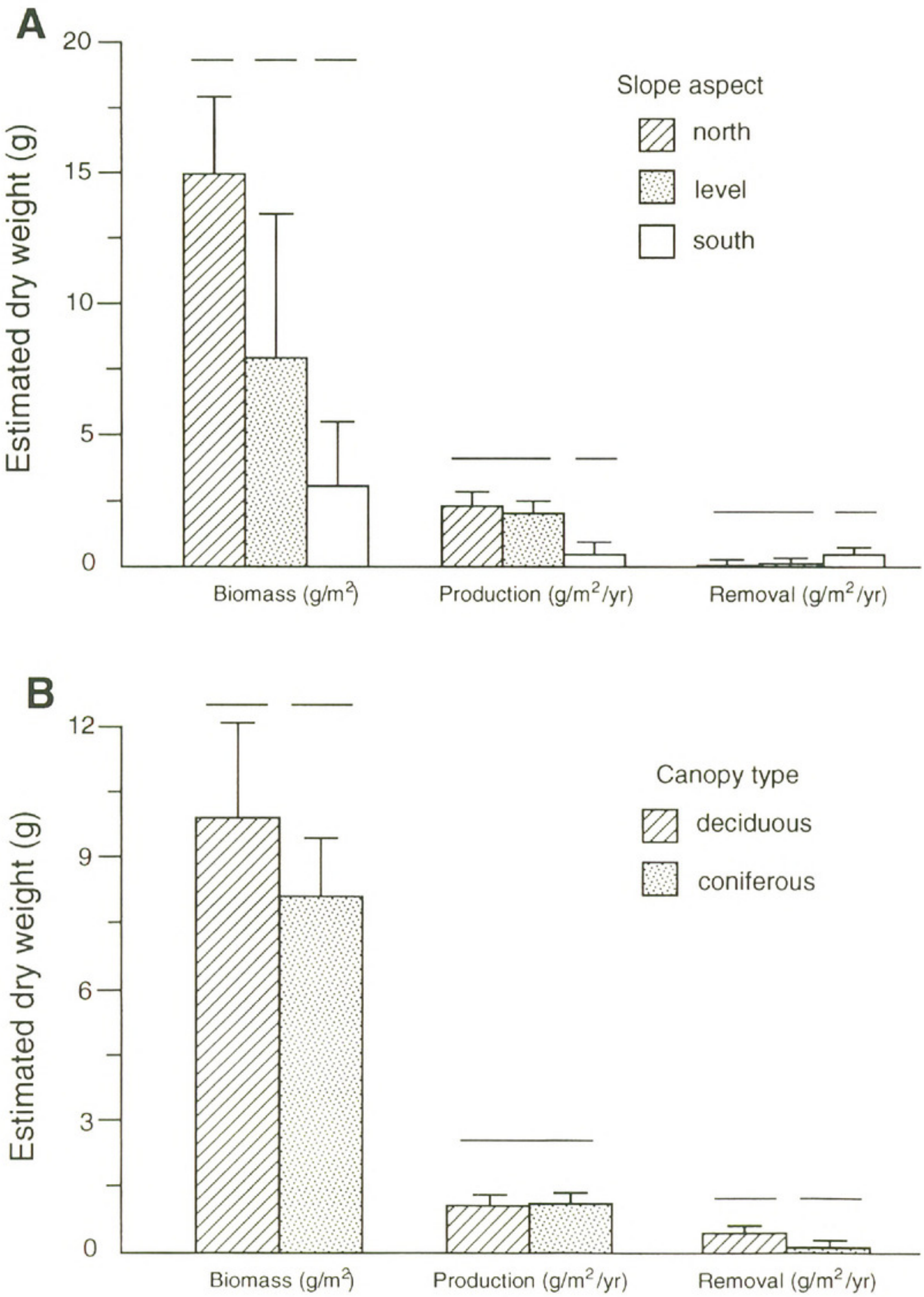

Figure 2. *Taxus canadensis* biomass, production (annual growth), and removal by deer per m^2 (mean + 1 SE) at sites with various aspects (A) and canopy types (B). Lines above bars indicate means that do not differ significantly at $P > 0.05$ by ANOVA.

is linked strongly to environmental variables, such as slope shape, slope position, elevation, aspect, and percent slope, that affect soil moisture and relative humidity. This is consistent with the hypothesis of habitat preference as a determinant of the distribution of this species. In north-temperate locations, north-facing slopes are generally cooler and have higher relative humidity and soil moisture than comparable south-facing slopes (Geiger, 1965; Oke, 1978). Cold air drainage can also account for a similar pattern of increased moisture and decreased temperature on the lower portions of a slope compared to upper regions (Oke, 1978). These facts are in accord with what has been observed anecdotally for *T. canadensis* in the southern portion of its range. Nichols (1913), for example, noted that in Connecticut, *T. canadensis* was much more common in "lower ground." In north-central Massachusetts, it is not uncommon to find *T. canadensis* at the boundary between upland and wetland or on steep rock ledges where "moisture conditions are favorable" (Hosley and Ziebarth, 1935; T. D. Allison and J. J. Stachowicz, unpubl. data). Populations in southern Minnesota and northern Iowa are typically found at the talus base of north-facing limestone cliffs (T. D. Allison, pers. obs.).

Our survey data also indicated a potential impact of deer browsing on *T. canadensis* distribution and an interaction of browsing with habitat. Browsing rate (removal) was higher under deciduous than coniferous canopies (Figure 2B). However, because a large proportion of the areas where *T. canadensis* grew under a deciduous canopy were on south-facing slopes, it is unclear whether this difference is attributable directly to canopy or if it is an indirect effect because deer are more likely to winter on south-facing slopes than on north-facing ones. Where *T. canadensis* occurred on south-facing slopes, browse damage was greatest ($F = 4.081$; $P < 0.001$), with removal nearly equaling annual growth or production (Figure 2A). North-facing slopes and level areas did not differ in removal rates. High deer populations have been implicated in limiting *T. canadensis* distribution in Michigan, Wisconsin, and New York (e.g., Spiker, 1935; Beals et al., 1960), but similar reports have not been made for New England. Despite the fact that removal equals annual growth on south-facing slopes, *Taxus canadensis* may persist in these areas if there is high annual variability in browse pressure that could allow the population to recover following an episode of intense browsing. Thus deer browsing may not result in extirpation of local *T. canadensis*

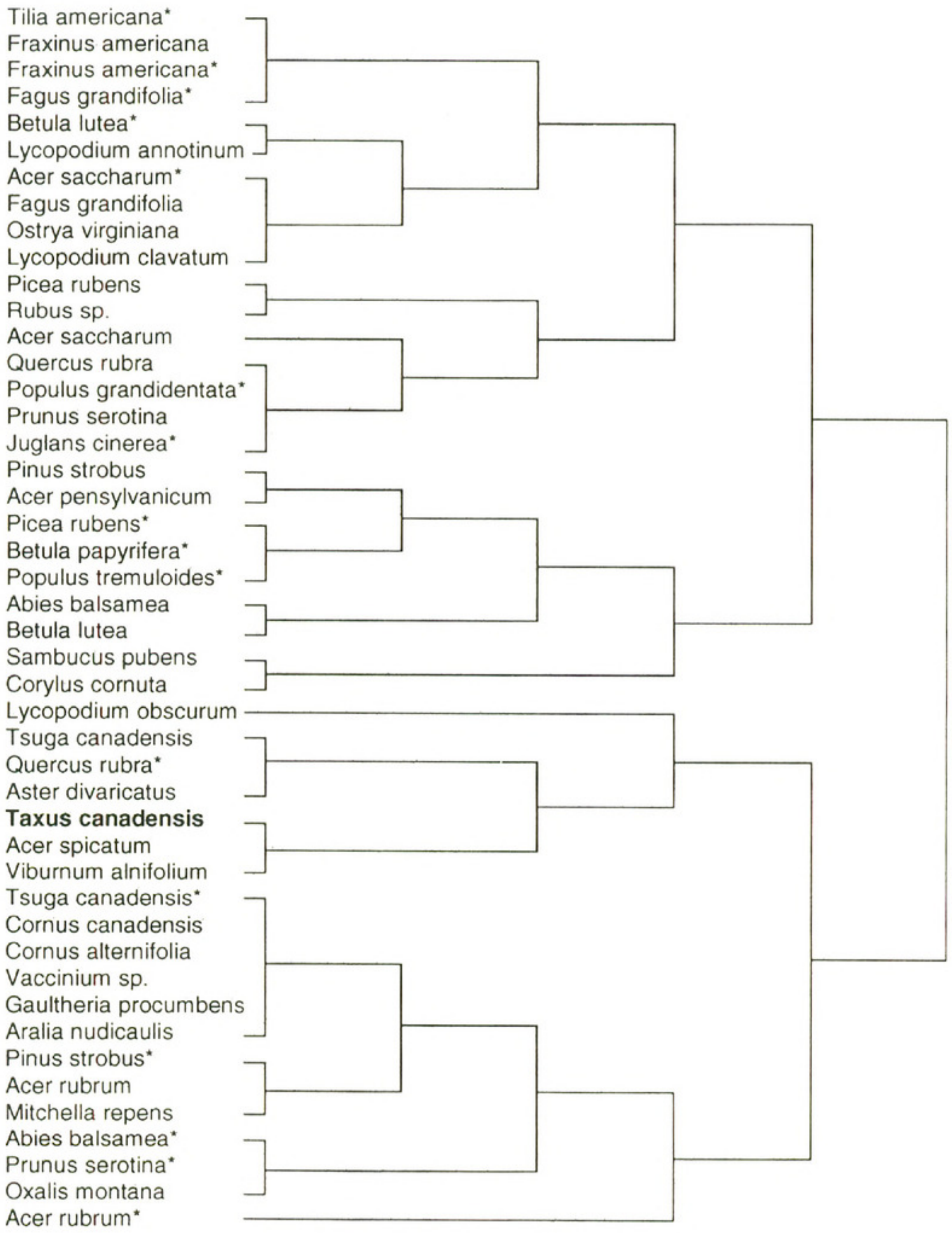

Figure 3. Results of TWINSPAN divisive classification of presence-absence data from survey of 200 plots (see text). Species with asterisks are canopy representatives; the same species without asterisks are understory representatives.

populations, although our data indicate that in certain habitats browsing may retard expansion of existing populations by reducing clonal expansion and seed production (Allison, 1990).

Divisive classification (Figure 3) indicated that *T. canadensis* was most closely associated with mountain maple (*Acer spicatum* Lam.) and hobblebush (*Viburnum alnifolium* Marsh.). *Quercus* *rubra* was the most closely associated canopy species (Figure 3). Red oak is generally common in mesic woodlands which were logged but not cleared for agriculture, a land-use category in which *T. canadensis* occurred frequently (Table 1). The divisive classification (Figure 3) also indicated that *T. canadensis* is not closely linked with *Acer saccharum, Tilia americana* L., *Betula lutea,* or *Fagus grandifolia* although these species are characteristic of the northern hardwoods forest found in the lower elevations of Hanover. The apparent absence of any association of *T. canadensis* with late-successional northern hardwoods and its association with red oak, a species that occurs in mid-successional forests around Hanover (see Study Site description), suggest that *T. canadensis* may not be restricted to late-successional forests.

In Hanover, *T. canadensis* was absent from areas which were logged within the past 30 years, but was not limited to primary woodlands (Table 1). One of the densest populations we observed was located on a floodplain at the base of a northwest-facing slope that was cultivated as recently as the 1880's. We have also observed *T. canadensis* populations growing in old-field white pine stands in north-central Massachusetts. An effect of past land use on *T. canadensis* distribution was indicated in a 1930's survey of vegetation in Petersham, Massachusetts, where this species was restricted to primary woodlands (Whitney and Foster, 1988). Any such effect should diminish with time as *T. canadensis* recolonizes suitable habitat, as has been suggested in more recent forest surveys of north-central Massachusetts (Gerhardt, 1993; C. Mabry and D. R. Foster, unpubl. data). Because our data on land-use history lacked detail on the time of abandonment or reforestation, we cannot determine the length of time required by *T. canadensis* for recolonization, except that it is a minimum of 30 years.

The divisive classification (Figure 3) suggests that *T. canadensis* is associated with red oak, and thus not necessarily linked to old-growth forests, but the ordination of the vegetation survey data with DECORANA indicates an affinity for a more coniferous canopy. The ordination produced four vegetation axes, only two of which were significantly correlated with *T. canadensis* occurrence (Table 2). The first vegetation axis corresponds to an increasing importance of *Abies balsamea* and a decreasing importance of *Betula papyrifera* Marsh. The second axis was positively correlated with low elevation coniferous forests near the base of north and northwest slopes, and negatively correlated with high

Table 2. Results of multiple logistic regression analysis. Measured independent variables predict the outcome of the dichotomous dependent variable *Taxus canadensis* presence (only variables with significant contribution to the final model are listed). Positive values of estimates indicate a positive association of *T. canadensis* presence with that variable (e.g., *T. canadensis* occurs more frequently on slopes that are concave rather than convex or planar). Negative values of estimates indicate a negative association of *T. canadensis* with that variable (e.g., *T. canadensis* occurs less frequently with distance upslope). The magnitude of the estimate suggests the relative importance of that factor in predicting the presence of *T. canadensis*. Tolerance statistics for all independent variables fall within the allowable limits, so no significant collinearities ($P > 0.05$) between predictors are apparent. CA = correspondence analysis.

		95% confidence interval of estimate			
Factor (indep. variable)	**Estimate**	**Lower**	**Upper**	**G**	***P***
Slope position	−1.282	−1.919	−0.646	49.31	0.0005
Slope shape (concavity)	2.601	1.203	4.000	21.55	0.0005
Slope aspect	−0.011	−0.022	0.000	4.40	0.05
CA Axis #1	0.647	0.234	1.061	8.77	0.005
CA Axis #2	1.101	0.423	1.780	12.05	0.001

elevation deciduous forests on south-facing slopes. Neither of these axes give any evidence for an association of *T. canadensis* with climax northern hardwood forests. In addition to these two vegetation axes, the final logistic regression model of *T. canadensis* presence-absence was influenced strongly by slope shape, aspect, and position (Table 2), environmental variables that influence moisture levels (Geiger, 1965; Oke, 1978). The model indicates that *Taxus canadensis* occurs most frequently near the base and on the lower portions of north- and east-facing concave slopes and that its frequency is lower in plots higher upslope, on a convex-shaped slope, and with a more southerly aspect (Tables 1, 2).

No consistent association between *T. canadensis* and tree species was observed; the ordination, divisive classification, and literature search each suggested different canopy associates. For example, the divisive classification (Figure 3) indicated that the most closely associated canopy species was *Quercus rubra*, while the ordination (axes scores from DECORANA) suggested association with *Abies balsamea* and other conifers. Further, the literature search suggested that in the northeastern United States, *T. canadensis* is associated with a northern hardwoods canopy of

Acer saccharum and *Betula lutea* (e.g., Heimburger, 1934; Egler, 1940; Cline and Spurr, 1942; Stearns, 1951; Leak, 1973; Siccama, 1974). In contrast, the association of *T. canadensis* with other understory shrubs was much more consistent. Understory species were generally too rare to influence the ordination greatly, but both the divisive classification (TWINSPAN results, Figure 3) and limited understory literature (Heimburger, 1934; Egler, 1940) suggest that *Viburnum alnifolium* and *Acer spicatum* are closely associated with *Taxus canadensis.* Additionally, the divisive classification (Figure 3) suggests that none of these three species is particularly closely associated with any canopy species.

The differences in the strength and consistency of *T. canadensis* associations with understory shrubs vs. canopy trees may be the result of differences in the duration of the influence of past land-use in the different layers of vegetation. Long-lived canopy species in secondary woodlands, such as *Quercus rubra,* could be first generation individuals which have not been replaced by later successional northern hardwoods. *Taxus canadensis* may have been eliminated by forest clearing and plowing, but once reforestation began, this species was eventually able to recolonize environmentally suitable sites. Later-successional tree species, however, have to wait for removal of the overstory containing earlier-successional species before succeeding to the canopy. This process is suggested by the closer association of *Taxus canadensis* with understory individuals of *Tsuga canadensis* than with canopy individuals (Figure 3).

CONCLUSIONS

As we predicted, *T. canadensis* is most abundant and productive on north-facing slopes. Although we did not find *T. canadensis* in any south-facing plots in our vegetation survey, it is not completely excluded from south-facing sites (we were able to find some populations for biomass, production, and removal estimates), but it is considerably less abundant and productive when present. Our survey was limited to upland forests, and we specifically excluded open and wet habitats, such as old fields and swamps. Our own observations indicate that *T. canadensis* does not grow in recently abandoned old fields, but may be found in swamps and on slopes surrounding bogs. Therefore, our conclusions about the ecological status of *T. canadensis* are limited to upland habitats.

There are clear differences in the frequency, abundance, and productivity of this species in the upland forests of Hanover: *Taxus canadensis* does best in sites with physiographic characteristics that promote high humidity and soil moisture. Our data indicate that it is most common at or near the base of concave slopes with northerly aspects and is often associated with *Acer spicatum* and *Viburnum alnifolium. Taxus canadensis* is not restricted to primary woodlands, although it is apparently excluded from recently logged sites. It is unclear whether deer browsing restricts *T. canadensis* distribution, and the impact of browsing may be confounded with habitat because deer may be more likely to winter on south-facing slopes. However, browsing is greatest on south-facing slopes and may limit the spread of *T. canadensis* in these habitats. Our data also suggest that *T. canadensis* is more abundant in Hanover than in north-central Massachusetts. This may be related to the cooler climate of Hanover, which results in a wider range of habitats available for use by *T. canadensis.*

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J. J. S.[1]
DARTMOUTH COLLEGE
HANOVER, NH 03755

T. D. A.[2]
HARVARD FOREST
PETERSHAM, MA 01366

Present addresses:

[1] University of North Carolina at Chapel Hill, Institute of Marine Sciences, 3431 Arendell St., Morehead City, NC 28557

[2] Department of Forestry and Wildlife, University of Massachusetts, Amherst, MA 01003