Forest Response to the Introduced Hemlock Woolly Adelgid in Southern New England, USA

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Forest response to the introduced hemlock woolly adelgid in southern New England, USA[1]

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ORWIG, D. A. AND D. R. FOSTER (Harvard University, Harvard Forest, Petersham, Massachusetts 01366). Forest response to the introduced hemlock woolly adelgid in southern New England, USA. J. Torrey Bot. Soc. 125:60–73. 1998.—Hemlock woolly adelgid (HWA), *Adelges tsugae*, an introduced aphid-like insect from Asia, is expanding its range across the northeastern United States through the range of *Tsuga canadensis* (eastern hemlock) and can severely reduce or eliminate this important late-successional species. As part of a study investigating stand- and landscape-level forest dynamics resulting from HWA infestation, we examined initial community response of eight *T. canadensis* stands in south-central Connecticut. Our major objectives were to assess mortality patterns in *T. canadensis*, evaluate subsequent changes in stand microenvironment, and relate these and stand composition to initial patterns of regeneration, understory response, and community reorganization. *Tsuga canadensis* damage varied broadly across the study area ranging from near zero to greater than 95% mortality. All size and age classes sampled were attacked by HWA, although smaller trees exhibited higher mortality rates than larger trees. All remaining *T. canadensis* sampled in seven of the eight stands were infested with HWA and over 90% suffered at least 50% foliar loss. Substantial accumulations of downed woody debris have developed in stands with severe HWA damage. Canopy gaps created by HWA damage significantly increased the amount of light reaching the forest floor and resulted in rapid understory vegetation responses. Prolific *Betula lenta* (black birch) establishment occurred in stands with moderate to severe *T. canadensis* mortality. In addition, opportunistic herbaceous species (*Erechtites hieracifolia*, *Phytolacca americana*) and exotic species (*Ailanthus altissima*, *Microstegium vimineum*) have recently invaded these stands. Due to mortality from HWA, *T. canadensis* seedlings were scarce in sampled stands, suggesting that advance regeneration and seedbanks will not be important mechanisms for *T. canadensis* reestablishment. *Tsuga canadensis* cannot sprout following defoliation and has no apparent resistance to HWA. Therefore, dramatic reductions in *T. canadensis* across broad geographical areas appear imminent if HWA dispersal continues unimpeded and no effective natural enemies of HWA are found.

Key words: pest infestation, successional dynamics, tree mortality, *Tsuga canadensis*.

The invasion of exotic pathogens and forest pests into forest ecosystems is an important ecological, economic, and evolutionary process that alters forest structure, composition, productivity, and dynamics (Liebhold et al. 1995). Introductions of forest pests may result in major changes in forest stand and landscape patterns and may have devastating impacts on aesthetic conditions and important natural resources (Castello et al. 1995). Although the history of pathogen introductions are often well documented, the response of temperate forest ecosystems to the selective decimation of a dominant tree species is poorly understood (Ehrlich and Mooney 1983; Lawton 1994; Castello et al. 1995). Major questions include the following: What are the spatial and temporal patterns of infestation at stand and landscape levels and what factors control them? What role does a dominant species, or its elimination, play in controlling the microenvironment of light, wind speed, and temperature in forest stands? What patterns of response and recovery are exhibited by the different species and structural layers of a forest as a dominant species is selectively removed? Answers to these fundamental questions are essential for understanding the history, dynamics, and function of forests world-wide but are especially pertinent for the northeastern U.S., where pathogen and pest outbreaks have occurred through geological time and with increasing regularity during the past century. We specifically focus on the latter two questions in this study.

The New England landscape has been repeatedly affected by a variety of forest pests. Approximately 4800 years B.P., *Tsuga canadensis* (eastern hemlock) experienced a dramatic decline in abundance throughout the eastern U.S.,

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presumably as a result of insect outbreaks (Davis 1981; Allison et al. 1986; Bhiry and Filion 1996). In the 20th century, eastern forests experienced widespread mortality and decline of *Castanea dentata* (chestnut), *Ulmus* spp. (elm), *Quercus* spp. (oak), and *Fagus grandifolia* (American beech) as a result of exotic pathogens and insect pests (Liebhold et al. 1995). Currently, forests of southern New England are being impacted by the introduction of another major forest pest, the hemlock woolly adelgid (HWA, *Adelges tsugae*). HWA outbreaks provide an analog for the historic *T. canadensis* decline as well as a comparison with other forest pathogens, and they present the opportunity to document the dynamics and processes resulting from a destructive pest as they unfold.

ECOLOGY OF HEMLOCK AND THE HEMLOCK WOOLLY ADELGID. The HWA is a small, aphid-like insect that was introduced into Virginia presumably from Japan during the early 1950s (Souto, Luther and Chianese 1996). Since its introduction, HWA has spread to 10 states, from North Carolina to Massachusetts, and has created extensive decline and mortality of *T. canadensis* and *Tsuga caroliniana* (Carolina hemlock) in Virginia, Pennsylvania, New Jersey, and Connecticut (Fig. 1). HWA apparently reached Connecticut forests sometime during 1985 (McClure 1987), and resulted in widespread mortality by 1988 (McClure 1990). HWA is currently documented in 147 towns (87%) in Connecticut and at least 36 towns (10%) in Massachusetts (B. Lapin unpublished data; C. Burnham pers. comm.). Adelgids settle on young *Tsuga* twigs and feed on ray parenchyma cells via a long stylet, causing needle loss, bud mortality, and branch and tree mortality within 4 years (McClure 1991; Young et al. 1995). HWA populations can increase rapidly because they complete two generations each year, have no known natural enemies in eastern North America and can disperse rapidly via wind, birds, deer, and human activity such as logging (McClure 1989, 1990). In addition, *T. canadensis* has shown no resistance to HWA and injured trees apparently have little chance for recovery (McClure 1995a). The current growing stock volume of *T. canadensis* in Connecticut forests exceeds 6.5 million m^3 (Dickson and McAfee 1988a), and since the rate of HWA spread is approximately 30 km/yr, it is expected that much of this resource will be lost to HWA if effective biological controls are not found (McClure 1995a, 1995b). With over 800,000 ha of forest classified as *T. canadensis* or *T. canadensis-Pinus strobus* (white pine) type in New England, representing over 85 million m^3, the potential ecological impacts and financial losses are enormous (Dickson and McAfee 1988a, 1988b, 1988c; Frieswyk and Malley 1985a, 1985b; Powell and Dickson 1984).

Tsuga canadensis plays a unique rôle in the eastern forest landscape. It is an extremely long-lived, shade-tolerant conifer that may grow in dense monospecific stands or in combination with *P. strobus* and deciduous hardwood species. *Tsuga canadensis* creates important structural diversity at the stand and landscape level and provides habitat and cover for a variety of wildlife species (DeGraaf et al. 1992; Benzinger 1994b). In the absence of major disturbance, *T. canadensis* stands are characterized by a cool, damp microclimate, low light levels, depauperate understory vegetation cover, and relatively stable forest composition (Lutz 1928; Rogers 1978, 1980; Benzinger 1994a). These characteristics may be attributed to the influence *T. canadensis* has on the immediate forest environment by casting deep shade and depositing acidic litter (Godman and Lancaster 1990). Across the New England landscape, *T. canadensis* stands are frequently found on exposed slopes as well as on more protected sites such as ravines and stream bottoms (Rogers 1978; Kessell 1979). Due to its shallow rooting habit and relatively thin bark, *T. canadensis* is very sensitive to wind, fire, drought, and anthropogenic disturbances (Whitney 1990; Foster et al. 1992; Foster and Zebryk 1993; Abrams and Orwig 1996), and therefore many present-day *T. canadensis* stands are found on historically protected or inaccessible sites (Rogers 1978; Foster and Zebryk 1993; Mladenoff and Stearns 1993).

STUDY OBJECTIVES. Much is now known about the life cycle and biology of HWA (McClure 1987, 1989, 1990, 1991; Young et al. 1995), and efforts to develop biological and chemical control methods continue (McClure 1992, 1995a, 1995b; Steward and Horner 1994; USDA 1996). However, little information exists on the short and long term effects of HWA on forest ecosystems (cf. Evans et al. 1996) and we do not know how the loss of *T. canadensis*, a late-successional conifer species that exerts a strong control over stand microclimate and soil conditions, will affect vegetation organization, successional dynamics, species diversity, and microenvironmental characteristics.

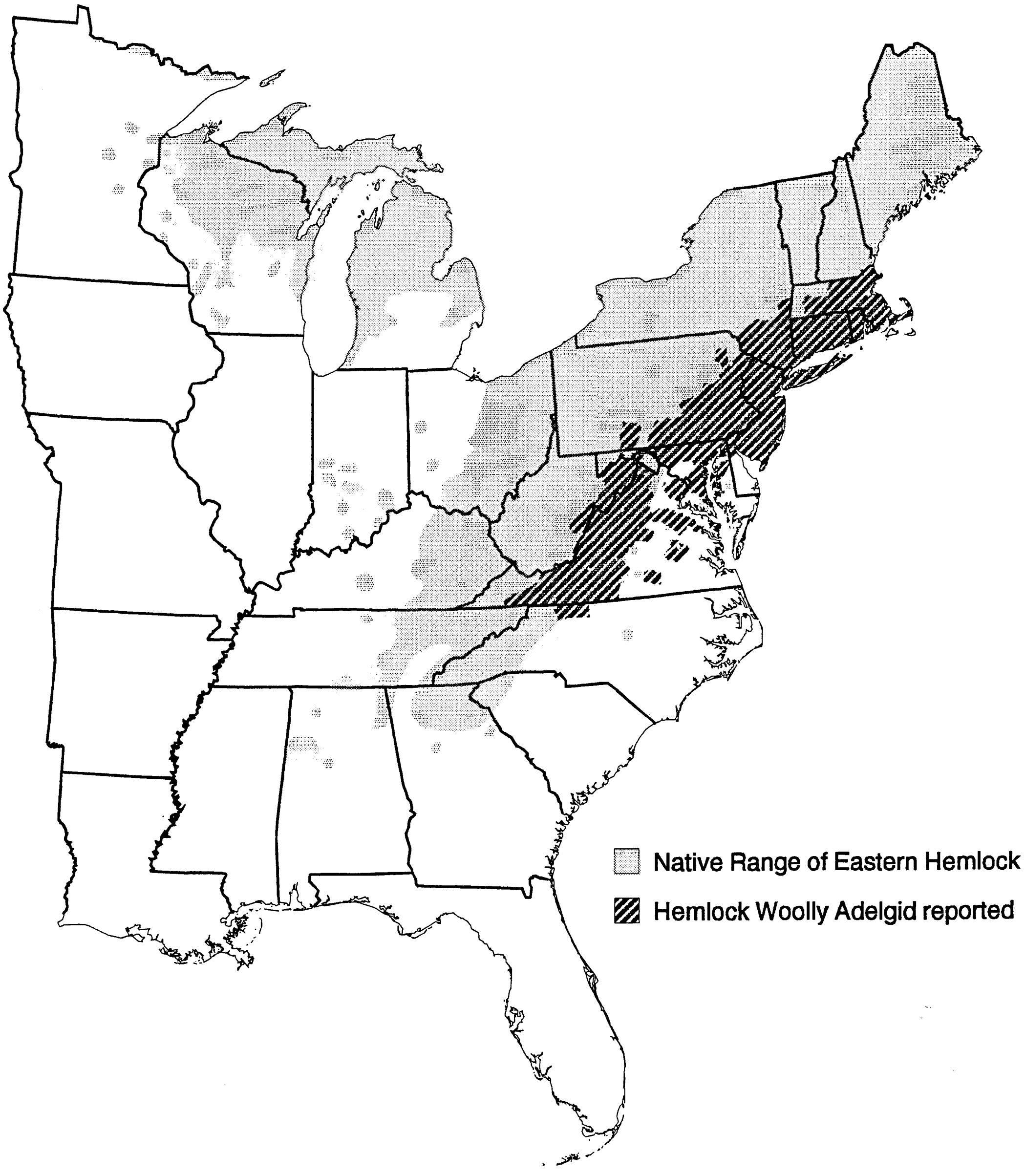

Fig. 1. Hemlock Woolly Adelgid distribution in the eastern United States during 1996 (Luther 1997).

We have pursued this question by investigating the initial forest response to the selective mortality of *T. canadensis* in southern New England. In this study our specific objectives are: (1) to assess the extent of *T. canadensis* damage and/or mortality associated with HWA; (2) to determine the initial floristic response to adelgid infestation and the variation in this response across sites; (3) to evaluate vegetation recovery processes and mechanisms; (4) to gain insight into the susceptibility of forests to HWA damage and the likelihood of *T. canadensis* survival and/or recovery; and (5) to assess the potential ecological implications of *T. canadensis* decline and mortality on ecosystem structure and function. This is the first paper documenting stand response to HWA and therefore this research is of fundamental importance for understanding and predicting the effects of forest pathogens and insect pests on forest ecosystems and for ensuring sound management decisions concerning restoration of affected stands.

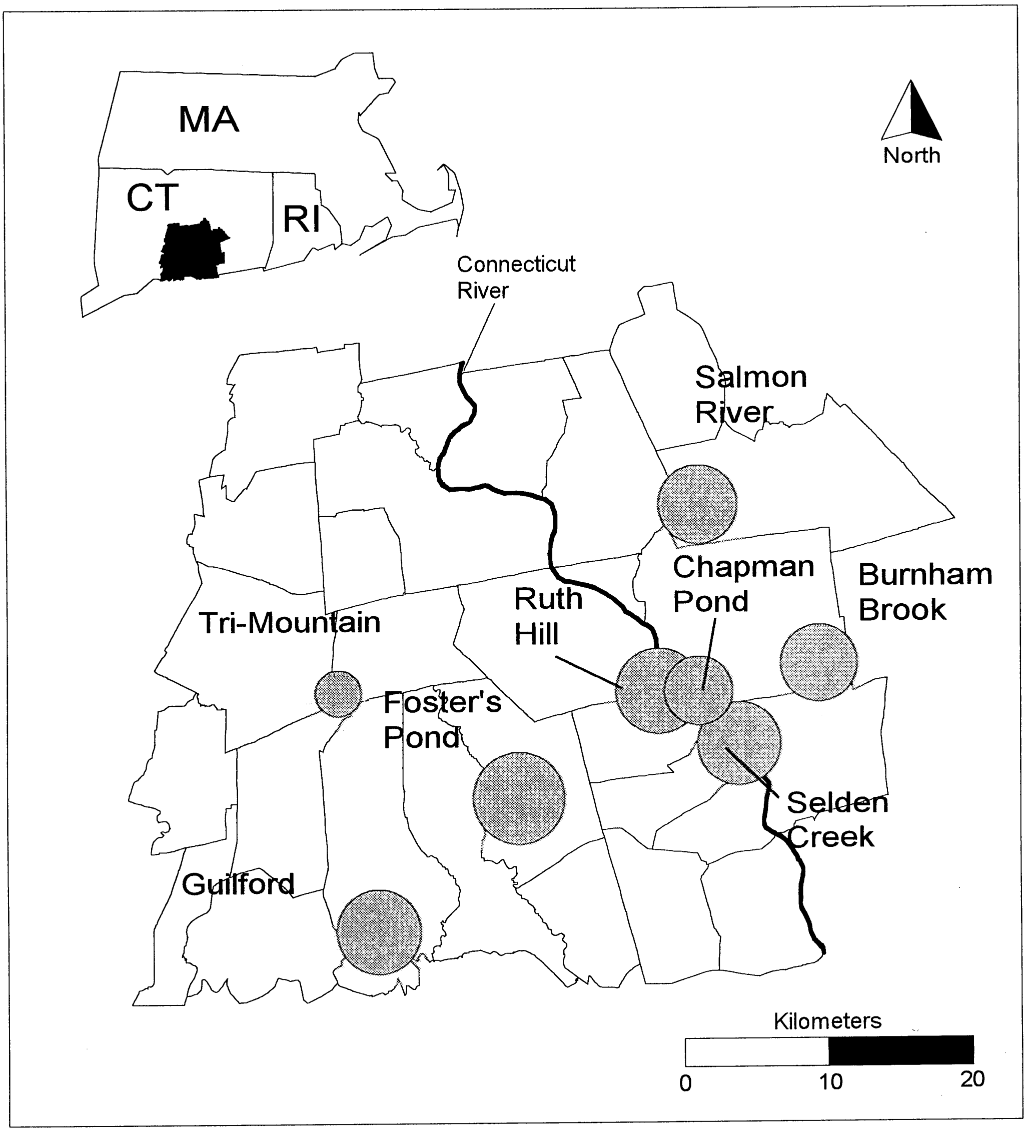

Fig. 2. Location of central Connecticut *Tsuga canadensis* study sites. The relative abundance of overstory *T. canadensis* at each site is indicated by the size of the circle (range = 50–90%).

STUDY AREA. The study area in south-central Connecticut encompasses the lower Connecticut River Valley and portions of the eastern uplands and coastal slopes (Fig. 2), and is characterized by a humid, continental climate with long, cool winters and short, mild summers (Hill et al. 1980). Elevations range from 0 to 180 m a.s.l. and soils are predominantly sandy loams formed from weathered gneiss, schist, and granite (Reynolds 1979). The region is located at the southern limits of the *T. canadensis-P. strobus*-northern hardwood vegetation type (Nichols 1935) and the northern extent of the *Quercus-Castanea* type described by Braun (1950). We selected this area because *T. canadensis* is broadly distributed and is the predominant conifer in the region and because HWA is becoming widespread.

Methods and Analysis. Forty-six 0.04-ha plots were established in eight stands varying in size from 8 to 175 ha in south-central Connecticut (Fig. 2). Since HWA migrated rapidly across southern and central Connecticut in only a few years, the exact timing of HWA infestation and tree mortality in our stands is uncertain.

However, site selection was carefully based on information and recommendations from Connecticut State Foresters (H. Hurlock, R. Rocks, pers. comm.), The Nature Conservancy (B. Lapin, pers. comm.) and research scientists with the U.S. Forest Service (T. Odell, pers. comm.), who documented recent HWA infestations and subsequent *T. canadensis* decline and/or mortality in these specific sites. All stands appeared completely intact with full tree canopies in 1990 black and white aerial photographs (1:12,000 scale) obtained from the State Department of Environmental Protection. In addition to good historical background on the sequence of infestation, we also developed the following criteria for the establishment of permanent plots within these areas: access and long-term protection of the stand from salvage logging, wide variation in *T. canadensis* mortality and timing of HWA infestations, and broad geographic distribution across the study region.

Within each stand, five 0.04-ha plots were systematically located at 20 to 30 m intervals along transects orientated along the central axis of each stand. In one stand of more than 100 ha, ten overstory plots were established. All plots were permanently marked with iron pipe. All trees (stems at least 8 cm diameter breast height (dbh)) were tallied by species and dbh, and assigned a canopy position based on the amount of intercepted light received by the tree crown (Smith 1986). *Tsuga canadensis* that died within the last 2–3 years, which were identified by extensive retention of fine twigs in the dead crown, were also tallied in order to determine species composition prior to HWA infestation. Eight randomly selected live trees were cored at 1.37 m in each plot for age determinations. Crown vigor was estimated for each *T. canadensis* tree based on the amount of retained foliage. Presence of HWA and other insect pests was noted during this sampling.

We attribute *T. canadensis* damage and mortality observed in these stands to HWA, although several additional factors may have exacerbated *T. canadensis* mortality in our study area including summer drought and insects such as hemlock loopers (*Lambdina fiscellaria* and *L. athasaria*) and hemlock scales (*Fiorinia externa* and *Nuculaspis tsugae*) (Benzinger 1994a; Evans et al. 1996). Scale insects have been observed in several stands and moderate looper defoliation was reported in our study region in 1991 and 1992 (USDA 1994). The extent to which insects affect *T. canadensis* susceptibility to HWA or vice-versa is still unclear (Evans et al. 1996).

A list of all vascular plant species occurring in each plot was recorded, as were slope, aspect, and topographic position. Nomenclature follows Gleason and Cronquist (1991). Saplings (less than 8 cm dbh and over 1.4 m tall) were also tallied by species within the 0.04 ha plots. In ten 1 m^2 subplots randomly established in each overstory plot, cover of seedling, herb, and shrub species was estimated using a modified Braun-Blanquet scale and seedling heights were determined for a sub-sample of the tallest stems in each subplot. The depth of the soil organic horizon to the nearest 0.5 cm was also measured in each subplot.

Stand level variability of light environment was characterized during relatively clear days with photosensitive paper sensors (Friend 1961; Sullivan and Mix 1982), which have been used successfully in several recent studies to measure integrated photosynthetically active radiation (PAR) (Kitajima and Augspurger 1989; MacDougall and Kellman 1992; Wayne and Bazzaz 1993). Sensors were constructed with 20 sheets (2.5×2.5 cm^2) of Proprint sepia paper wrapped in a black cardboard jacket with a 0.6 cm diameter hole in the center for light penetration and placed in plastic, waterproof bags. Five light sensors were placed horizontally at the height of the seedling layer in each overstory plot for seven 24-hr periods. Light sensors were calibrated using Li-Cor Quantum sensors (LI-190SZ) connected to data loggers (LI-1000) placed beneath an intact forest canopy (low light) and in a partial clearing (gap) to include variable light environments.

One-way ANOVAs with Tukey's multiple comparison procedure were used to assess differences in average seedling density, seedling height, and forest floor light conditions among the eight stands. Multiple linear regression analysis was used to identify independent site factors that had a significant effect on these dependent variables. Tests were performed on log-transformed variables to reduce heteroscedastic variances.

Results. Stands ranged in age from 73 to 109 years and most sites were located on west- or northwest-facing hillsides with moderate slopes (<20%) (Table 1). Prior to HWA infestations, the importance of overstory *T. canadensis* ranged from 49 to 88 percent and stands could be classified as being nearly pure *T. canadensis*

Table 1. Overstory species composition and stand characteristics in central Connecticut *Tsuga canadensis* study sites prior to HWA infestation. Stands are arranged in order of decreasing *Tsuga canadensis* mortality as presented in other tables.

	Burnham Brook	Chapman Pond	Guilford	Selden Creek	Ruth Hill	Foster's Pond	Tri-Mountain	Salmon River
Relative Importance Values[a]								
Tsuga canadensis	66	58	75	69	74	88	49	77
Betula lenta	6	17	1	18	12	1	16	—
Quercus velutina	2	15	—	5	1	1	—	13
Quercus prinus	—	—	9	—	—	2	12	—
Acer rubrum	11	—	6	7	4	6	4	3
Elevation (m)	91–123	0–80	0–40	0–46	30–98	30–60	123–168	30–76
Aspect(s)	NW	W-SW	NW-SE	W-NW	NW	NE	NW	N
Slope (%)	15	6	7	9	15	12	25	5
Size (ha)	175	60	54	85	31	8	15	16
Overstory density (ha^{-1})	713	663	1355	740	605	595	740	710
Overstory basal area (m^2 ha^{-1})	43	32	44	45	45	49	37	43
Mean age ± SE (n = 40)	91 ± 5	85 ± 3	68 ± 3	85 ± 6	73 ± 3	84 ± 4	109 ± 6	68 ± 3

[a] Includes the most common tree species in each stand calculated as: (Relative basal area + Relative density)/2. *T. canadensis* I.V. was based on live and dead trees in 1995.

or *T. canadensis*-hardwood mixtures with species such as *Betula lenta* (black birch) and *Quercus* sharing overstory importance (Table 1).

Tsuga canadensis damage varied widely across the study area ranging from nearly zero to greater than 95% mortality (Table 2). A few stands lost only a small percentage of overstory or sapling sized individuals as a result of HWA (e.g., Salmon River, Tri-Mountain), whereas the most severely damaged sites (e.g., Chapman Pond, Burnham Brook) lost over 95% of overstory *T. canadensis* trees, up to 90% of saplings, and from 50 to 69% of total stand density and basal area. With the exception of the uninfested Salmon River stand, all surviving *T. canadensis* trees sampled at our sites were infested with HWA, contained varying amounts of chlorotic foliage, and suffered at least 25% foliage loss (Figs. 3, 6). There was no apparent relationship between *T. canadensis* mortality and average stand size or age, as stands with nearly identical age structures exhibited widely dissimilar mortality percentages. In moderately damaged stands, tree mortality was related to canopy class (Fig. 4). A higher percentage of overtopped and intermediate canopy trees was killed at these sites.

Levels of integrated light reaching the forest floor and seedling regeneration response were closely related to stand structure associated with infestation level (Fig. 5). Several stands with severe and moderate levels of damage experienced significantly ($P < 0.05$) higher average light levels than slightly affected stands. Burnham Brook and Foster's Pond sites had significantly ($P < 0.05$) higher seedling densities and seedling heights than all other stands. On these two sites, seedling densities averaged 16 m^{-2} and seedling heights averaged 66 cm, while sites with low damage levels had average seedling densities less than 1 m^{-2} and average heights of only 5 cm. *Betula lenta* seedlings were ubiquitous and represented 76% of all seedlings encountered in our plots (Fig. 6). Additional common seedling species included *Acer rubrum* (red maple), *Prunus serotina* (black cherry), and several *Quercus* species. Multiple regression analysis indicated that understory light level had significantly positive relationships with average seedling density and height (Table 3). Depth of soil organic matter also had a significant and positive relationship with seedling density, while overstory density had a marginally significant but negative relationship with seedling height growth. Depth of organic layer varied among stands (Table 4) and

Table 2. Stand damage associated with HWA infestations in central Connecticut *Tsuga canadensis* study sites. Values for each parameter are expressed as the relative percent of *T. canadensis* or all trees (stand) lost due to HWA-inflicted mortality. Stands are arranged in order of decreasing HWA impact.

	Burnham Brook	Chapman Pond	Guilford	Selden Creek	Ruth Hill	Foster's Pond	Tri-Mountain	Salmon River[a]
T. canadensis overstory density	97	96	69	62	40	32	14	5
Stand overstory density	62	55	54	45	28	27	7	4
T. canadensis overstory basal area	99	91	60	37	28	25	19	4
Stand overstory basal area	69	53	44	24	21	23	9	3
T. canadensis importance value	63	50	23	17	9	4	4	<1
T. canadensis sapling density	92	71	55	83	71	8	28	37
Stand sapling density	72	61	35	79	56	<1	19	36

[a] No HWA was observed on trees or saplings in 1995. Losses were due to several windthrows and unknown causes.

appeared to correspond well with overstory *T. canadensis* importance value.

Sapling densities and overall understory species richness varied widely and paralleled individual stand differences in structure and composition (Table 4). The only notable sapling layer occurred at Foster's Pond, contained a high density of *B. lenta*, and became established subsequent to canopy dieback. Average shrub cover values were low across all sites, rarely exceeding 4%. Common shrub species included *Toxicodendron radicans* (poison ivy), *Parthenocissus quinquefolia* (Virginia creeper), *Mitchella repens* (partidgeberry), and several *Vitis* (grape) species. Similarly, herbaceous species were scarce in most stands with the exception of Ruth Hill, which had an abundance of *Dennstaedtia punctilobula* (hay-scented fern). *Dryopteris spinulosa* (spinulose wood fern), *Polystichum acrostichoides* (Christmas fern), *Erechtites hieracifolia* (fireweed), and several *Carex* (sedge) species were also common in the herb layer. Interestingly, several damaged stands contained invasive exotic species such as *Berberis thun-*

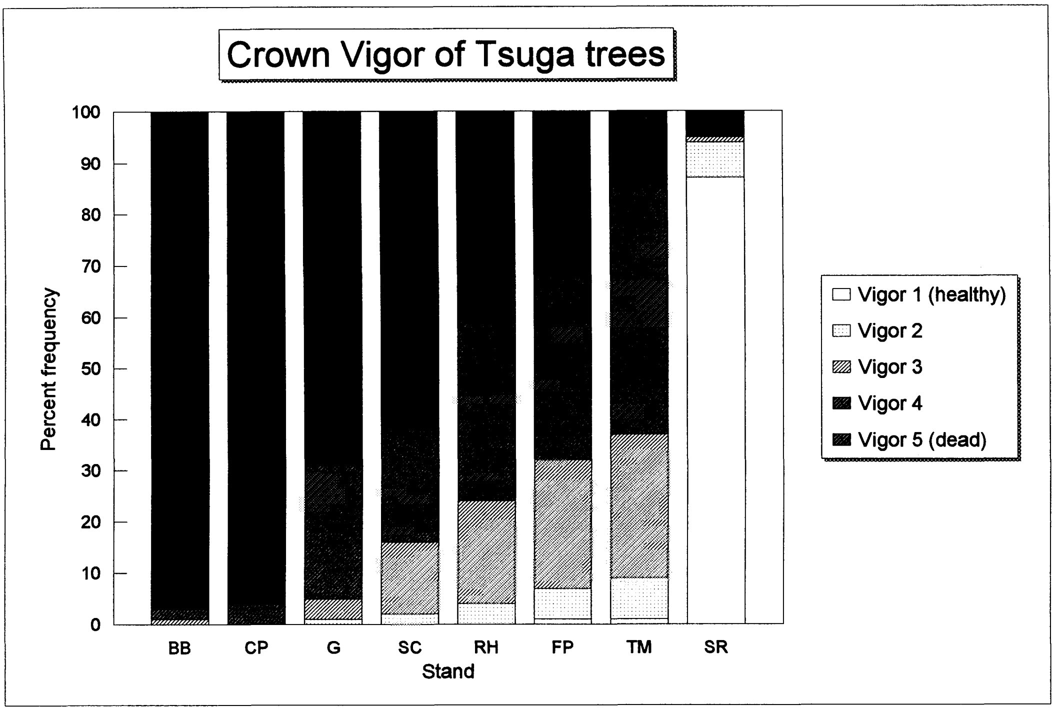

Fig. 3. Percentage of overstory *Tsuga canadensis* by vigor class among central Connecticut study sites in 1995. Tree vigor classes are designated according to the amount of foliage remaining: 1 = 76–100%; 2 = 51–75%; 3 = 26–50%; 4 = 1–25%; 5 = dead. Stand abbreviations correspond to Table 1.

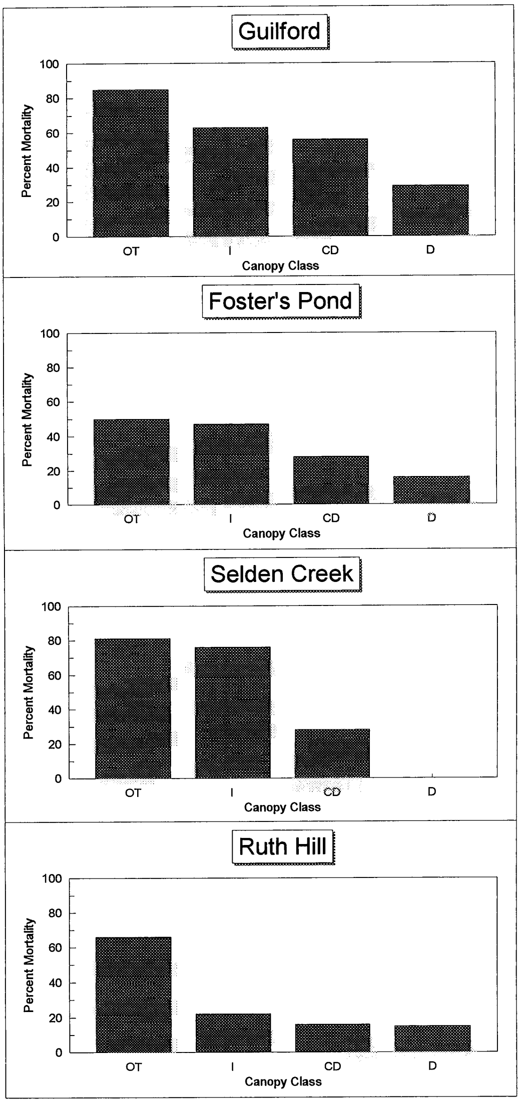

Fig. 4. Canopy percentage of overstory *Tsuga canadensis* mortality for four moderately-damaged study sites in central Connecticut. Canopy classes are designated according to Smith (1986) as: OT, overtopped; I, intermediate; CD, codominant; D, dominant.

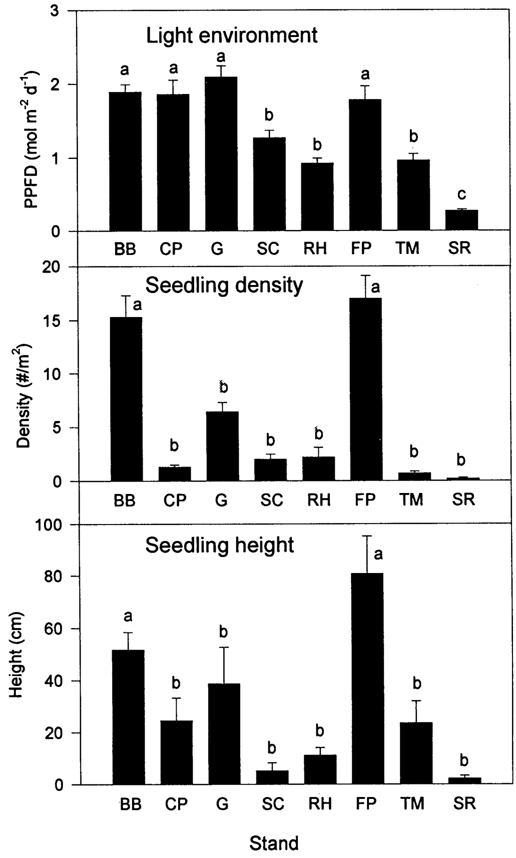

Fig. 5. Relationship between daily understory light environment and average seedling characteristics in central Connecticut *Tsuga canadensis* study sites. Site values with the same letter are not significantly different at $P < 0.05$.

bergii (Japanese barberry), *Celastrus orbiculatus* (Asiatic bittersweet), *Ailanthus altissima* (tree of heaven) and *Microstegium vimineum* (Japanese stilt grass).

Discussion. Tree population declines over broad geographical areas are not unprecedented. A rapid, rangewide decline in *Ulmus* (elm) occurred in Europe during the mid-Holocene, possibly resulting from a pathogenic attack in conjunction with cutting by Neolithic people (Peglar 1993). Following the rangewide *T. canadensis* decline in North America 4800 years ago, large increases in *Betula* pollen were initially observed followed by increases in *Quercus*, *Fagus*, and *Acer* (Davis 1981; Allison et al. 1986; Foster and Zebryk 1993). Similar results were observed in sediments following the elimination of *C. dentata* in eastern North America during the early 20th century (Brugam 1978; Davis 1981; Allison et al. 1986). The current *T. canadensis* decline provides an analog to the historic declines of *T. canadensis* and other species and enables us to examine the potential consequences and processes involved as *T. canadensis* is replaced.

We observed variation in HWA-induced damage and mortality at several different scales in central Connecticut. Within-stand mortality was spatially patchy, although our canopy vigor results suggest that this initial pattern will gradually lead to complete *T. canadensis* mortality. Smaller trees at our sites exhibited higher mortality rates than larger trees, perhaps due to less extensive root systems, higher root competition, lower stem capacitance and insufficient carbohydrate reserves (Jacquart et al. 1992; Vose and Swank 1994). Across our study area *T. canadensis* distribution was patchy. Although we only examined a small number of stands in this study, the range of damage contained therein is largely representative of *T. canadensis* stand conditions observed in dozens of stands located throughout south-central Connecticut (D. Orwig et al., unpubl. data). In a related study, all *T. canadensis* stands >3 ha are being mapped within a 6000 km^2 transect that spans the entire Connecticut River valley in Connecticut (D. Orwig et al. unpubl. data). This information has been incorporated into a landscape level GIS analysis of *T. canadensis* distribution versus edaphic, topographic, and biological factors in order to examine the distribution and pattern of HWA spread and to determine whether damage patterns observed in the present study are consistent across the landscape. In addition, the response of ecosystem processes to HWA-related damage and mortality will be measured in a subset of these stands.

The HWA:*T. canadensis* system operates very differently from some historical pathogen and pest systems. Tree damage associated with HWA is unlike that resulting from chestnut blight, gypsy moth, dutch elm disease, or the related balsam woolly adelgid (*Adelges piceae*) because HWA defoliates overstory trees, saplings, and seedlings, and therefore has the potential to eliminate *T. canadensis* from a site within a few years (Witter and Ragenovich 1986; McClure 1991; Castello et al. 1995). Moreover, *T. canadensis* trees lack the ability to sprout or refoliate after defoliation and consequently reestablishment can only occur from seed transported from surviving trees or from the seedbank. The duration of viable *T. canadensis* seed in forest soils is typically only one growing season (Marquis 1975), although a few references have documented seed viability for up to four years (USDA 1948; Olson et al. 1959). It is believed that on most sites, episodic establishment of *T. canadensis* occurs infrequently, only under unusual conditions related to seedbed, moisture, and seed availability (Mladenoff and Stearns 1993; Benzinger 1994a). *Odocoileus virginianus* (white-tailed deer) may provide an additional obstacle for regeneration of *T. canadensis* and other species in these forests. Many studies have shown that deer browse can severely reduce *T. canadensis* seedling densities (summarized in Mladenoff and Stearns 1993). Studies in Connecticut have shown that the state deer herd density has more than doubled since 1980, resulting in high local population densities that impact understory composition and structure (Kittredge and Ashton 1995; Ward 1996). These circumstances raise concerns about the long-term viability, stability and composition of *T. canadensis* ecosystems. As stated previously, many *T. canadensis* stands are currently scattered across the landscape in sites that have been protected historically from intensive human and natural disturbance. If *T. canadensis* is effectively removed from even a portion of these sites, the seed source will be drastically reduced or eliminated across broad geographic areas. In that regard it is interesting to note that the recovery period of *T. canadensis* following the mid-Holocene decline lasted one to two thousand years (Davis 1981; Allison et al. 1986).

All surviving trees in our stands except those at Salmon River are infested with HWA and contain moderate to severe canopy damage. Consequently, many of our study sites currently contain a high proportion of standing dead snags or trees with only tufts of foliage at the outer ends of upper branches remaining. In severely damaged stands, many dead tree tops and boles have snapped off during several recent wind storms and deterioration has continued due to the presence of observed secondary organisms such as hemlock borer (*Melanophila fulvogut-*

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Fig. 6. Photographs of key ecological aspects of Hemlock Woolly Adelgid (HWA) infestations in central Connecticut *Tsuga canadensis* study sites. (a) *Tsuga canadensis* branch covered with HWA ovisacs located along twigs at the base of the needles. Each woolly tuft may contain up to 50 eggs; (b) Severe HWA damage located within the Guilford study site. Note dead *T. canadensis* trees in foreground and background adjacent to trees with only sparse canopies remaining. Trees typically die with intact branch structure and gradually fall apart over a 3–10 year period; (c) Prolific *Betula lenta* establishment under HWA-damaged *T. canadensis* trees; (d) aerial view of widespread *T. canadensis* mortality near Burnham Brook. Dead *T. canadensis* have conical form and fine patterning of intact branches and are surrounded by healthy hardwood species.


a
b
c
d

Table 3. Multiple regression results of average seedling density and height on various stand characteristics in central Connecticut *Tsuga canadensis* study sites. For each pair of values, the top number represents the standardized regression coefficient of the independent variable; the bottom number represents the significance of the variable in the model.

	Overstory basal area (m^2/plot)	*T. canadensis* mortality (%)	Organic horizon depth (cm)	Overstory density ($plot^{-1}$)	Light (mol m^{-2})
Seedling density (m^{-2})	0.10656 (0.38092)	0.82982 (0.57316)	0.31732 (0.01644)	−0.13722 (0.27836)	0.51899 (0.00114)
Seedling height (cm)	−0.01834 (0.88149)	0.03788 (0.80181)	0.11909 (0.36036)	−0.25326 (0.05302)	0.68632 (0.00006)

tata), shoestring fungi (*Armillaria mellea*), and conk fungi (*Ganodernia lucidum*). The consequences of this mortality will be substantial pulses of woody debris, dramatic changes in age, structural, and compositional attributes of these forests, and altered wildlife habitat (Benzinger 1994b). In addition, light availability, above and below-ground space, and other resources should increase as HWA spreads across the landscape (Canham and Marks 1985; Oliver and Larson 1990).

Our results indicate that changes in the understory microenvironment and the subsequent vegetation response due to HWA damage has been dramatic in some stands. Gaps created by thinning *T. canadensis* canopies increased the amount of light reaching the previously shaded forest floor and created conditions that facilitated the prolific establishment of *B. lenta* seedlings. This was particularly evident in stands with a high percentage of *T. canadensis* in the overstory (e.g., Foster's Pond). In addition, the soil organic layer present under *T. canadensis* canopies appeared to be an ideal germination substrate for this light, wind-dispersed species (Leak 1958). Several researchers have reported similar *Betula* increases following partial cutting (Kittredge and Ashton 1990; Ward and Stephens 1996) and tree mortality due to *Cryphonectria parasitica* (chestnut blight) and windthrow (Good 1968; Hemond et al. 1983). Abundant *B. lenta* regeneration is also anticipated in moderately damaged stands in the future, owing to its copious seed production and presence in the overstory (Ward and Stephens 1996).

Seedlings of *A. rubrum* and several *Quercus* species were also present in low densities in most of our study sites and may be important species in the future. The overall scarcity of *T. canadensis* seedlings in these forests suggests that advance regeneration and seedbanks will not be important mechanisms for *T. canadensis* reestablishment. Very few shrub species have colonized these stands except for bird-dispersed *Vitis* species and *Parthenocissus quinquefolia*. Several opportunistic herbaceous species have recently become established in low abundance throughout the study area including *Erechtites hieracifolia* and *Phytolacca americana* (pokeweed) (pers. obs.). These species exhibit a buried seed strategy and can rapidly increase in abundance following disturbance (Del Tredici 1977; Peterson and Pickett 1990, 1995). HWA damage has also resulted in the invasion of several exotic tree, shrub, and herbaceous species which may increase in the future and further affect revegetation processes and dynamics (Cronk and Fuller 1995). The ultimate composition and rate of vegetation response will be further determined by many factors including pre-HWA site and soil characteristics, *T. canadensis* mortality rates, herbivore pressure, and the percentage of overstory space occupied by hardwood species.

Healthy hemlock stands appear to be fairly resistant to plant species' invasion and stand replacement owing to the lack of advance regeneration, acidic soil environment, nutrient poor, thick humus, and seedbanks with low percentages of overstory tree species (Rogers 1978, 1980; Mladenoff 1990). Therefore, the extreme rapidity of invasion observed in our stands was unexpected. The process of invasion primarily by wind-dispersed *B. lenta*, occurred regardless of its overstory importance (e.g., Foster's Pond) and suggests that only a few overstory *B. lenta* are necessary to provide an adequate seed supply under these conditions. Establishment of *B. lenta* occurred without soil scarification and appeared to only require a high light environment for successful germination.

Conclusions. We have gained valuable insight into the initial recovery processes and mechanisms of forests as a dominant species is removed from the landscape by documenting

Table 4. Average understory vegetation and soil organic layer characteristics in central Connecticut *Tsuga canadensis* study sites.

	Burnham Brook	Chapman Pond	Guilford	Selden Creek	Ruth Hill	Foster's Pond	Tri-Mountain	Salmon River
Sapling density (ha^{-1})	125	117	865	310	135	8635	1010	510
Shrub cover (% ± SE)	0.4 ± 0.3	3.1 ± 1.1	2.5 ± 1.2	4.8 ± 2.7	0.5 ± 0.2	1.2 ± 0.5	0.3 ± 0.2	*
Herb cover (% ± SE)	4.3 ± 1.6	5.0 ± 2.2	—	2.9 ± 1.5	22.3 ± 4.3	5.6 ± 2.2	1.4 ± 0.5	—
Understory richness (plot average ± SE)	6.5 ± 0.8	14.0 ± 1.8	10.0 ± 1.0	8.2 ± 2.7	11.8 ± 2.3	15.0 ± 1.9	11.0 ± 1.5	1.8 ± 0.4
Organic layer depth (cm ± SE)	3.7 ± 0.2	0.7 ± 0.1	4.8 ± 0.5	3.1 ± 0.3	1.6 ± 0.2	6.6 ± 0.5	1.3 ± 0.2	4.1 ± 0.3

* <0.1%.

damage patterns and changes in forest structure and composition resulting from an introduced forest pest as they unfold. The results of this study and direct observations in dozens of stands throughout the state indicate that Connecticut forests are being severely impacted by HWA. To date, the rate and intensity of infestation is not attributable to any site factor or stand characteristic and there is no apparent impediment to the widespread expansion of HWA and devastation of *T. canadensis* across its range. Varying degrees of HWA infestation at the stand level resulted in high *T. canadensis* mortality rates, pulses of downed woody debris, and dramatic changes in microenvironment characteristics due to overstory canopy gaps. These structural changes have initiated rapid vegetation responses in understories typically devoid of vegetation. In addition, our results suggest that some sites may experience a complete change in cover type from *T. canadensis* to forests dominated by *Betula*, *Quercus*, and *Acer* species. Under this scenario, forest composition and structure at the landscape level would become increasingly more homogenous. The outlook for *T. canadensis* persistence in southern New England forests is bleak. If HWA dispersal continues unimpeded, dramatic reductions of *T. canadensis* across broad geographical areas appear imminent unless natural or introduced predators of HWA are found.

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