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# Changes in a hemlock-dominated forest following woolly adelgid infestation in southern New England[1]

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SMALL, M. J., C. J. SMALL (Department of Botany, Connecticut College, New London, Connecticut 06320), AND G. D. DREYER (Goodwin-Niering Center for Conservation Biology and Environmental Studies, Connecticut College, New London, Connecticut 06320). Changes in a hemlock-dominated forest following woolly adelgid infestation in southern New England. J. Torrey Bot. 132: 458–470. 2005.—The hemlock wooly adelgid (HWA; *Adelges tsugae*), a small aphid-like insect introduced from Japan, has caused widespread hemlock (*Tsuga canadensis*) mortality throughout the mid-Atlantic and southern New England region over the last twenty years. We examined long-term (1952–2002) changes in hemlock-dominated stands before and after the appearance of the HWA in 1987 in the Connecticut College Arboretum, southeastern Connecticut. With HWA infestation, basal area of *T. canadensis* declined dramatically, dropping 70% from 1982 to 2002. Forest communities responded to the elimination of the dominant species by quickly filling various sized gaps. Black oaks (*Quercus velutina*, *Q. coccinea*, *Q. rubra*) increased from 28% of canopy basal area in 1982 to 41% in 2002. Sapling density increased markedly following HWA infestation, from 80 stems/ha in 1982 to nearly 5600 in 2002, with greatest increase in *Sassafras albidum* (0 to 1900 stems/ha) and *Acer rubrum* (4 to 1100 stems/ha). Ledge and ravine communities, formerly dominated by *T. canadensis*, became more compositionally distinct, with greater importance of black oaks on more xeric ledge sites and mixed canopy dominance in mesic ravine sites. Major trends associated with the decline of *T. canadensis* included a shift in canopy dominance to oak and mixed hardwoods, considerable understory development, including greater herb richness and abundance and increased density of clonal saplings, and expansion of several invasive shrubs and woody vines.

Key words: *Tsuga canadensis*, *Adelges tsugae*, central hardwood forests, long-term vegetation change, forest recovery

Over the last 100 years, forests in the northeastern United States have changed dramatically, due in part to the extensive removal of dominant tree species by introduced pathogens and insects. In the early twentieth century, chestnut blight (*Cryphonectria parasitica*), a fungal pathogen, removed the canopy dominant *Castanea dentata* from upland forests (Delcourt and Delcourt 2000). *Ulmus americana*, once a common urban shade tree and a major component of deciduous wetland forests, was attacked in the 1930s by Dutch elm disease (*Ophiostoma ulmi*), a beetle transmitted fungus (Wesley 1998). In a disturbance of similar magnitude, eastern hemlock (*Tsuga canadensis* (L.) Carr.) is being eliminated from the canopy and understory of forests of the central Atlantic and New England states by an exotic insect pest, the hemlock woolly adelgid (*Adelges tsugae* Annand.; hereafter HWA).

The HWA is a 2–3 mm long insect, believed to have been introduced from Japan (McClure 1987). Its eggs are laid on *T. canadensis* twigs in woolly white secretions and are easily dispersed by wind, birds, and mammals (McClure 1989, 1990, 1991). The adult insect feeds on the sap of young *T. canadensis* shoots in late winter and early spring and may also inject toxic spittle into the branches (McClure 1987). Main limbs often die within one year of infestation and whole trees within four to ten years (McClure 1991). First reported in West Virginia in the 1950s, the HWA has now spread in *T. canadensis* stands along the east coast north through southern New England (McClure 1987, 1990;

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Colbert et al. 2002). In 1985, the HWA arrived in south central Connecticut, possibly blown in with Hurricane Gloria. Since its arrival, high *T. canadensis* mortality has occurred in Connecticut, but the infestation is not as well established in the northern part of the state (Orwig 2002).

Pollen data show that *T. canadensis* experienced a dramatic decline in the northeast during the mid-Holocene, approximately 5400 years ago (Davis 1969, 1958; Fuller 1998), possibly due to an invasive pathogen (Allison et al. 1986). The tree recovered to its former population levels only after 2000 years (Davis 1969, Allison et al. 1986, Fuller 1998). Today, *T. canadensis* is a slow-growing, shade tolerant conifer that extends in range from Quebec south to Alabama and west to northeastern Minnesota (Godman and Lancaster 1990). It is found in cool, moist habitats as well as high rocky ledges, often in association with *Acer saccharum*, *Fagus grandifolia*, *A. rubrum*, various *Quercus* and *Betula* species, as well as in pure stands (Godman and Lancaster 1990). Thin bark, shallow roots, and slow regeneration rates make *T. canadensis* particularly sensitive to disturbance. Low seed viability and slow growth retard recolonization after disturbance (Godman and Lancaster 1990). In southern New England, mature *T. canadensis* stands are now limited to protected sites that have been relatively free of anthropogenic disturbances such as fire and timber harvesting, including wetland borders, ravines, and rocky ridge tops (Godman and Lancaster 1990).

Hemlocks have many important functions at the ecosystem level, and the consequences of its disappearance over large regions are poorly understood. For example, 96 avian species are associated with hemlock, eight of which prefer hemlock stands (Yamasaki et al. 1999). Forty-seven mammal species are associated with hemlock, 10 of which prefer hemlock habitat (Yamasaki et al. 1999). As the only common evergreen tree in southern New England forests, hemlock provides important thermal protection for some species in winter (Yamasaki et al. 1999), and it is a large source of winter seed for bird populations (Yamasaki et al. 1999). The evergreen habit of hemlock has also been shown to be important in maintaining the quality of forest streams (Jenkins et al. 1999).

Studies examining the effects of HWA-induced mortality of *T. canadensis* in southern New England forests have found that *Betula* spp., *A. rubrum*, *Quercus* spp., and other deciduous hardwoods often replace *T. canadensis* in the forest canopy (Orwig and Foster 1998, E. Largay, unpublished manuscript). Such changes alter understory microclimates and change the leaf litter from slowly decomposing coniferous needles to more rapidly decaying deciduous litter. The density of standing dead *T. canadensis* has been shown to increase, as has the amount of coarse woody debris on the forest floor (Orwig and Foster 1998). Large gaps in the forest canopy form, allowing more light to reach the ground (Orwig and Foster 1998), which may increase soil surface temperatures and decrease moisture content (Jenkins et al. 1999). Increased nitrogen cycling (Jenkins et al. 1999) and rates of nitrification have also been found in areas with *T. canadensis* mortality (Jenkins et al. 1999, Yorks 2002, Cobb and Orwig 2002). This may increase nitrogen loss to soil water, decrease nutrient availability within stands, and possibly compromise stream water quality (Jenkins et al. 1999, Yorks 2002).

As part of an on-going, long-term ecological research program, this study examined HWA induced changes in a *T. canadensis* dominated forest stand in southern New England. Such long-term studies are particularly important in coastal New England, where disturbances such as fire, hurricanes, and infestation by exotic pests have had strong influences on community structure in the past and are likely to continue in the future. The objectives of this study were to examine: (1) the response of canopy, shrub, and ground layer vegetation to hemlock decline; (2) changes in woody regeneration as an indicator of future canopy composition following the appearance of the HWA; and (3) variations in the responses of hemlock-dominated communities across distinct site types (rocky ledges and moist, sheltered ravines). Viewed in the context of vegetation change over a fifty-year period, future trends in forest dynamics were also considered.

**Materials and Methods.** STUDY SITE. The Bolleswood Natural Area (BNA), located in the Connecticut College Arboretum, New London, Connecticut, was established in 1952 as a natural area preserve and as a location for long-term ecological studies. As a preserve, the study site has been maintained with minimal human disturbance since its establishment, to serve as an unmanaged control against a largely managed landscape (Niering and Goodwin 1962). The BNA covers ~65 ha and is located 6.4 km north of the Long Island Sound (USGS 1984). The terrain of the BNA is characterized by a series of north-south running ledges. Mamacoke gneiss (USGS 1967) is overlain by a thin, weakly developed ground moraine and numerous granitic glacial erratics (USGS 1960) left as the Wisconsin glaciation receded ~15,000 years ago (Niering and Goodwin 1962). A thin soil of sandy loam covers much of the area, with abundant bedrock outcrops (Morgan 1939).

The BNA includes various natural community types such as oak (*Quercus*), oak-hemlock (*Quercus*-*Tsuga*) and hemlock-hardwood dominated forests, red maple (*Acer rubrum*) swamps, former agricultural areas (today dominated by *Quercus* spp., *Carya* spp., *Betula* spp., *Prunus serotina*, and *Smilax* spp.), open fields, peat bogs, and a small, artificially constructed lake. Located in the central hardwoods-hemlock forest region (Westveld 1956), the forest vegetation of the BNA exhibits greatest importance of oak species (e.g., *Quercus velutina*, *Q. rubra*, and *Q. alba*), with local abundance of *Tsuga canadensis*. A major hurricane in 1938 blew down most of large *T. canadensis* stems (Avery et al. 1940). By 1972, the *T. canadensis* population had recovered to approximately 30% of its former stem density (Hemond et al. 1983) and continued to increase through the early 1980s, until the introduction of the HWA in approximately 1987 (E. Largay, unpublished manuscript).

SAMPLING PROCEDURES. Between 1952 and 1954, four east-west transects were established in the BNA (Niering and Goodwin 1962). Three transects extended 305 m (1000 ft) and one 427 m (1400 ft), each spaced at 122 m (400 ft) intervals. The transects were sampled at ten year intervals from 1952 to 2002, with additional sampling in 1997 (Goslee 1998). Contiguous 3 $\times$ 3 m (10 $\times$ 10 ft) square quadrats ($N$ = 890) were established on both sides, along the entire length of each transect. These long-term vegetation quadrats encompass all major community types in the BNA. The current study concentrated on a subset of these plots ($N$ = 280) in which *T. canadensis* was particularly abundant, those classified as ''oak-hemlock'' or ''hemlock-hardwoods'' communities by Hemond et al. (1983).

Presence data were recorded for all shrub and herbaceous species in each 3 $\times$ 3 m quadrat. To measure the composition and abundance of tree species, quadrat data were compiled for 15.2 m (50 ft) sections of each transect (2 plots $\times$ 5 plots). Thus, species and diameter of all trees (woody stems greater than 2.5 cm in diameter at breast height (DBH), measured at 1.37 m) were recorded in continuous 6 $\times$ 15 m (20 $\times$ 50 ft) rectangular plots ($N$ = 89 for all BNA plots; $N$ = 28 for *T. canadensis*-dominated plots). Woody individuals were placed in one of the following tree height classes and data similarly compiled: individuals > 1.8 m (6 ft) tall and < 2.5 cm DBH; 0.6 to 1.8 m (2 to 6 ft) tall; 5 to 61 cm (2 in to 2 ft) tall. Seedlings were individuals < 5 cm tall. Nomenclature for all species follows Gleason and Cronquist (1991).

DATA ANALYSIS. All tree data were analyzed across the 28–90 m$^2$ (6 $\times$ 15 m) plots. For all analyses, *Quercus rubra*, *Q. velutina*, and *Q. coccinea* were grouped as ''black oaks.'' Density, basal area, and frequency were calculated for tree species reaching breast height. Importance values (IV) for trees were calculated as the average of relative density, relative basal area, and relative frequency. Frequency of shrub and herbaceous species in the 90 m$^2$ blocks was also calculated. Simple least squares linear regressions were fitted to basal area data for dominant canopy species from 1952 to 1982 and from 1992 to 2002 to project future trends in canopy composition.

Compositional variation and vegetation response were compared between plots established on two adjacent site types: ledges (oak-hemlock communities on rocky sites; $N$ = 14) and ravines (hemlock-hardwood communities on moist, sheltered sites; $N$ = 14). Non-metric, multidimensional scaling (NMS) ordination was used to examine compositional trends across study plots for 1982 and 2002 (McCune and Mefford 1999). Presence-absence data for all vegetation layers (herbs, shrubs, saplings, and trees) were used in the ordination analyses.

**Results.** The HWA first appeared in the BNA in 1987. The next scheduled survey in 1992 began to reflect the *Tsuga canadensis* decline, although little *T. canadensis* mortality had occurred. The results are therefore divided into before and after infestation sections, to highlight the different vegetation change trajectories directly before the HWA and at present.

BEFORE HWA INFESTATION (1952–1992). The early BNA surveys reflected the forest's recovery from the nearly complete devastation of the 1938 hurricane, with the basal area of nearly all tree species increasing steadily from 1952 to 1992 (19.6 m$^2$/ha in 1952, 42.1 in 1992; Fig. 1).

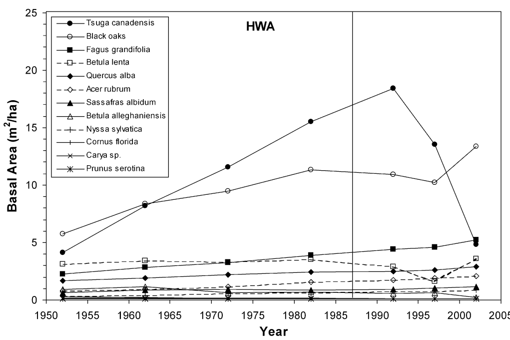


FIG. 1. Average total basal area of dominant tree species from 1952–2002 in hemlock-dominated sample plots in the BNA of the Connecticut College Arboretum. Vertical line indicates first observation of the hemlock woolly adelgid in the Arboretum in 1987.

By 1962, black oaks (*Quercus rubra*, *Q. velutina*, and *Q. coccinea*) and *Tsuga canadensis* were canopy co-dominants, each having a total basal area of 8.0 $m^2$/ha. *Tsuga canadensis* expanded rapidly, reaching 18 $m^2$/ha basal area and 43% importance value (IV) by 1992 (Table 1; Fig. 1). From 1972 until the arrival of the HWA, *T. canadensis* was the dominant canopy species, exceeding all others in stem density, basal area, and frequency (Table 1; Fig. 1).

Total basal area of black oaks and *Fagus grandifolia* increased gradually as the forest aged (Fig. 1). *Betula lenta* (as well as *Q. alba* and *Acer rubrum*) showed only minor increases in basal area during this period but, with black oaks, reached secondary importance by 1982 (IV = 12.2% and 19.2%, respectively; Table 1). After 1982, *B. lenta* slowly began to decline in density, basal area, and importance, as a well-developed canopy of *T. canadensis* formed.

In conjunction with the maturation of the forest canopy from 1952 to 1982, density of all sapling species decreased (Table 2). Total density declined from nearly 600 saplings/ha to 80, and sapling richness dropped by nearly 60%. Density of *T. canadensis* saplings decreased by 75% but remained most numerous of all species through 1982. Saplings of *B. lenta*, *Quercus* spp., *F. grandifolia*, and *A. rubrum* experienced similar declines. By 1982, the understory was almost devoid of saplings other than *T. canadensis* (Table 2).

In the decade prior to the HWA, few shrub species were found in the understory. *Smilax rotundifolia* and *Kalmia latifolia* were most common, present in more than 50% of plots in 1982 (Table 3). Also common were *Clethra alnifolia*,

Table 1. Density (DEN; stems/ha), mean basal area (BA; $m^2$/ha), frequency (FRQ; %) and importance value (IV; %) for trees taller than breast height in BNA hemlock plots from 1982–2002. "Black oaks" include *Quercus rubra*, *Q. velutina*, and *Q. coccinea.* Data sorted by IV for 1982.

| | 1982 | | | | 1992 | | | | 1997 | | | | 2002 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | DEN | BA | FRQ | IV | DEN | BA | FRQ | IV | DEN | BA | FRQ | IV | DEN | BA | FRQ | IV |
| *Tsuga canadensis* | 1065.4 | 15.5 | 89.3 | 39.2 | 1037.7 | 18.4 | 89.3 | 43.2 | 583.8 | 13.5 | 85.7 | 37.2 | 190.0 | 4.7 | 64.3 | 16.4 |
| Black oaks | 224.1 | 10.8 | 78.6 | 19.2 | 162.6 | 10.4 | 71.4 | 17.9 | 138.9 | 10.0 | 67.9 | 19.6 | 162.6 | 13.5 | 67.9 | 24.6 |
| *Betula lenta* | 152.7 | 3.5 | 85.7 | 12.2 | 96.1 | 2.9 | 64.3 | 10.0 | 69.2 | 1.5 | 53.6 | 8.5 | 76.9 | 3.6 | 60.7 | 11.6 |
| *Fagus grandifolia* | 152.7 | 3.9 | 28.6 | 8.2 | 175.7 | 4.4 | 28.6 | 9.5 | 176.3 | 4.5 | 28.6 | 11.9 | 332.3 | 5.1 | 42.9 | 19.1 |
| *Acer rubrum* | 103.8 | 1.5 | 57.1 | 7.5 | 100.0 | 1.7 | 50.0 | 7.9 | 100.0 | 1.8 | 50.0 | 9.3 | 88.4 | 2.0 | 46.4 | 9.0 |
| *Quercus alba* | 26.9 | 2.4 | 21.4 | 4.1 | 23.1 | 2.5 | 17.9 | 4.0 | 23.1 | 2.6 | 17.9 | 4.7 | 23.1 | 2.8 | 17.9 | 5.2 |
| *Betula alleghaniensis* | 29.7 | 0.6 | 25.0 | 2.9 | 15.4 | 0.5 | 10.7 | 1.7 | 11.5 | 0.5 | 10.7 | 1.9 | 69.2 | 0.1 | 10.7 | 3.2 |
| *Sassafras albidum* | 30.8 | 0.8 | 21.4 | 2.8 | 23.1 | 0.8 | 14.3 | 2.4 | 23.1 | 0.9 | 14.3 | 2.9 | 103.8 | 1.1 | 28.6 | 6.9 |
| *Nyssa sylvatica* | 34.6 | 0.6 | 7.1 | 1.6 | 34.6 | 0.6 | 7.1 | 1.8 | 34.6 | 0.7 | 7.1 | 2.3 | 34.6 | 0.8 | 7.1 | 2.5 |
| *Carya* sp. | 11.5 | 0.1 | 10.7 | 1.1 | 3.8 | 0.0 | 3.6 | 0.4 | 3.8 | 0.0 | 3.6 | 0.5 | 3.8 | 0.0 | 3.6 | 0.5 |
| *Cornus florida* | 7.7 | 0.0 | 7.1 | 0.7 | 3.8 | 0.0 | 3.6 | 0.4 | 3.8 | 0.0 | 3.6 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Prunus serotina* | 3.8 | 0.01 | 3.6 | 0.3 | 19.2 | 0.0 | 3.6 | 0.7 | 15.4 | 0.0 | 3.6 | 0.8 | 23.1 | 0.0 | 3.6 | 1.1 |
| **Total** | **1844.0** | **39.5** | **435.6** | **99.8** | **1695.0** | **42.1** | **364.4** | **99.9** | **1183.0** | **36.1** | **346.6** | **100.1** | **1107.8** | **33.7** | **353.7** | **100.1** |

Table 2. Density (stems/ha) and richness of saplings in BNA hemlock plots from 1952–2002. Note arrival of the hemlock woolly adelgid (HWA) to the BNA in 1987.

| Species | 1952 | 1962 | 1972 | 1982 | 1992 | 1997 | 2002 |
|---|---|---|---|---|---|---|---|
| *Tsuga canadensis* | 390 | 201 | 136 | 64 | 235 | 133 | 19 |
| *Betula lenta* | 80 | 19 | 4 | 0 | 68 | 104 | 148 |
| Black oaks | 34 | 0 | 0 | 0 | 49 | 775 | 705 |
| *Fagus grandifolia* | 23 | 4 | 4 | 4 | 262 | 269 | 421 |
| *Acer rubrum* | 15 | 0 | 0 | 4 | 72 | 165 | 1129 |
| *Quercus alba* | 15 | 4 | 4 | 0 | 30 | 11 | 57 |
| *Cornus florida* | 8 | 0 | 4 | 4 | 8 | 4 | 11 |
| *Prunus serotina* | 8 | 4 | 4 | 4 | 303 | 171 | 879 |
| *Sassafras albidum* | 8 | 0 | 0 | 0 | 254 | 1236 | 1942 |
| *Betula populifolia* | 4 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Carya* spp. | 4 | 4 | 4 | 0 | 0 | 23 | 244 |
| *Castanea dentata* | 4 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Betula alleghaniensis* | 0 | 0 | 0 | 0 | 57 | 11 | 4 |
| *Nyssa sylvatica* | 0 | 4 | 4 | 0 | 4 | 19 | 34 |
| **Total** | **591** | **239** | **163** | **80** | **1342** | **2920** | **5594** |
| **Species Richness** | **12** | **7** | **8** | **5** | **11** | **12** | **12** |

*Hamamelis virginiana*, *Smilax glauca*, and *Viburnum acerfolium* (30–39% of plots). At that time, *Euonymus alatus* was the only non-native invasive species present.

Lowest richness (25 species) and frequency (64%) of herbaceous species was found in *T. canadensis*-dominated plots during the last survey prior to HWA arrival (1982; Table 4).

Table 3. Percent frequency of shrub and vine species in BNA hemlock plots from 1982–2002. Non-native invasive species denoted by an asterisk (*).

| | 1982 | 1992 | 1997 | 2002 |
|---|---|---|---|---|
| *Smilax rotundifolia* | 61 | 71 | 68 | 86 |
| *Kalmia latifolia* | 57 | 46 | 46 | 57 |
| *Smilax glauca* | 39 | 61 | 61 | 82 |
| *Viburnum acerifolium* | 39 | 36 | 29 | 25 |
| *Clethra alnifolia* | 36 | 21 | 18 | 21 |
| *Hamamelis virginiana* | 32 | 29 | 29 | 32 |
| *Lindera benzoin* | 18 | 18 | 11 | 21 |
| *Toxicodendron radicans* | 18 | 18 | 18 | 18 |
| *Vaccinium corymbosum* | 14 | 0 | 7 | 14 |
| *Vaccinium angustifolium* | 7 | 0 | 0 | 0 |
| *Amelanchier* spp. | 4 | 0 | 4 | 25 |
| *Euonymus alatus** | 4 | 4 | 4 | 4 |
| *Gaylussacia baccata* | 4 | 0 | 0 | 0 |
| *Gaylussacia frondosa* | 4 | 0 | 0 | 0 |
| *Rubus* spp. | 4 | 7 | 4 | 18 |
| *Viburnum dentatum* | 4 | 4 | 14 | 4 |
| *Viburnum prunifolium* | 4 | 4 | 4 | 4 |
| *Berberis thunbergii** | 0 | 4 | 4 | 7 |
| *Celastrus orbiculatus** | 0 | 7 | 0 | 14 |
| *Cornus* spp. | 0 | 4 | 0 | 0 |
| *Decodon verticillatus* | 0 | 0 | 4 | 0 |
| *Ilex verticillata* | 0 | 4 | 0 | 18 |
| *Lonicera japonica** | 0 | 0 | 0 | 4 |
| *Parthenocissus quinquefolia* | 0 | 7 | 11 | 11 |
| *Rosa multiflora** | 0 | 4 | 0 | 0 |
| *Sambucus canadensis* | 0 | 4 | 0 | 0 |
| *Vaccinium pallidum* | 0 | 4 | 11 | 36 |
| *Vaccinium* spp. | 0 | 0 | 0 | 4 |
| *Viburnum* spp. | 0 | 0 | 0 | 11 |
| *Vitis labrusca* | 0 | 4 | 4 | 0 |
| *Vitis* spp. | 0 | 0 | 0 | 7 |
| **Species Richness** | **17** | **21** | **19** | **23** |

Table 4. Percent frequency of herbaceous species in BNA hemlock plots from 1982–2002. Data sorted by 1982 herb frequency. Only species with frequency > 5% for any sample year shown.

| | 1982 | 1992 | 1997 | 2002 |
|---|---|---|---|---|
| *Maianthemum canadense* | 36 | 46 | 43 | 50 |
| *Chimaphila maculata* | 14 | 29 | 25 | 29 |
| *Carex* spp. | 11 | 29 | 29 | 53 |
| *Gaultheria procumbens* | 11 | 11 | 7 | 14 |
| *Symplocarpus foetidus* | 11 | 18 | 18 | 18 |
| *Viola* spp. | 11 | 14 | 7 | 11 |
| *Aralia nudicaulis* | 7 | 7 | 4 | 4 |
| *Arisaema* spp. | 7 | 11 | 14 | 21 |
| *Aster* spp. | 7 | 14 | 18 | 25 |
| *Dennstaedtia punctilobula* | 7 | 14 | 11 | 21 |
| *Mitchella repens* | 7 | 11 | 11 | 11 |
| *Osmunda cinnamomea* | 7 | 4 | 7 | 7 |
| *Thelypteris noveboracensis* | 7 | 18 | 21 | 18 |
| *Anemone quinquefolia* | 4 | 18 | 14 | 7 |
| *Impatiens capensis* | 4 | 18 | 18 | 11 |
| *Lycopodium obscurum* | 4 | 7 | 4 | 8 |
| *Medeola virginiana* | 4 | 11 | 11 | 14 |
| *Polypodium virginianum* | 4 | 21 | 11 | 7 |
| *Smilacina racemosa* | 4 | 7 | 7 | 11 |
| *Solidago* spp. | 4 | 11 | 7 | 7 |
| *Dryopteris carthusiana* | 0 | 7 | 7 | 7 |
| *Galium palustre* | 0 | 0 | 0 | 13 |
| Grasses | 0 | 7 | 7 | 7 |
| *Melampyrum lineare* | 0 | 4 | 0 | 7 |
| *Monotropa uniflora* | 0 | 0 | 11 | 11 |
| *Onoclea sensibilis* | 0 | 7 | 7 | 7 |
| *Polygonum* spp. | 0 | 4 | 0 | 7 |
| *Uvularia sessilifolia* | 0 | 4 | 4 | 7 |
| **Species Richness** | **25** | **29** | **27** | **38** |
| **Frequency of Herbaceous Species (%)** | **64** | **79** | **89** | **89** |

*Maianthemum canadense* was the most frequent species in 1982 (36% of plots). *Chimaphila maculata*, *Carex* spp., *Gaultheria procumbens*, *Symplocarpus foetidus*, and *Viola* spp. were also common (11–14% of plots; Table 4).

After the HWA Infestation (1992–2002). In 1992, five years after the HWA was first recognized in the BNA, there was little to no mortality of mature *T. canadensis* (Table 1, Fig. 1) but trees were rapidly defoliating (E. Largay, unpublished manuscript). Over the next five years, the density of living *T. canadensis* tree stems decreased by over 40%. By 2002, less than 20% of the 1982 stems were still alive, declining from >1,000 stems/ha in 1992 to fewer than 200 in 2002 (Table 1). Total basal area of living *T. canadensis* in hemlock-dominated plots decreased by 75%, from a peak of 18.4 $m^2$/ha in 1992 to only 4.7 $m^2$/ha in 2002 (Table 1; Fig. 1), similar to 1952 post-hurricane levels.

Accompanying the *T. canadensis* decline, black oaks and *F. grandifolia* basal area increased. For the first time since 1952, *T. canadensis* was surpassed in importance by hardwood species (2002 IV: *T. canadensis* = 16.4%, black oaks = 24.6%, *F. grandifolia* = 19.1%; Table 1). Black oaks reached their greatest total basal area of 13.5 $m^2$/ha in 2002 (Table 1, Fig. 1). Relatively shade intolerant species such as *B. lenta* and *B. alleghaniensis* had shown gradual declines in all measures of tree growth from 1982 to 1997 (Table 1, Fig. 1). Following *T. canadensis* mortality, basal area of *B. lenta* increased 140%, from a low of 1.5 $m^2$/ha in 1997 to a high of 3.6 in 2002. Density of *B. alleghaniensis* increased more than 500%, from 11.5 stems/ha in 1997 to 69.2 in 2002. Importance of both species also increased during this period (Table 1). *Acer rubrum*, *Sassafras albidum*, and *Prunus serotina* showed associated increases in importance in 2002.

After HWA infestation, total density of saplings increased dramatically in *T. canadensis*-dominated plots, from 80 stems/ha in 1982 to nearly 5600 in 2002 (Table 2). Total sapling richness more than doubled, from 5 species in 1982 to 12 in 2002 (Table 2). The most pronounced increases during this period were evi-

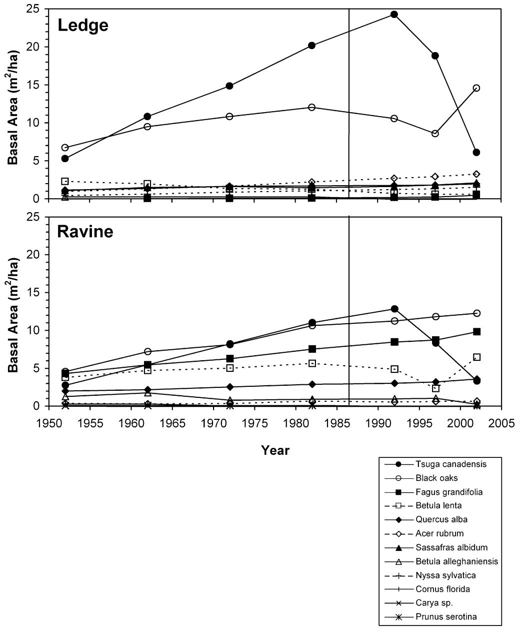


FIG. 2. Average total basal area of dominant tree species in hemlock-dominated ravine and ledge plots in the BNA (1952–2002). Vertical line indicates first observation of the hemlock woolly adelgid in the Arboretum in 1987.

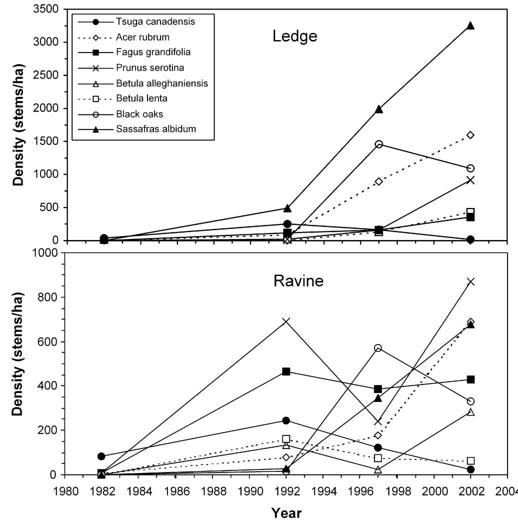


FIG. 3. Average density of dominant sapling species in hemlock-dominated ravine and ledge plots in the BNA (1982–2002). Note differing scales of the *y*-axes.

dent in *S. albidum* (0 to 1942 stems/ha), a root suckering species comprising 35% of all saplings in 2002, *A. rubrum* (4 to 1129 stems/ha), *Prunus serotina* (4 to 879 stems/ha), and black oaks (0 to 705 stems/ha). Dramatic increases were also seen in *F. grandifolia*, *Carya* spp., *B. lenta*, and *Q. alba* over these two decades. *Tsuga canadensis* sapling density increased initially to 235 stems/ha in 1992 but declined dramatically by 2002 (19 stems/ha; Table 2).

With *T. canadensis* mortality, shrub richness increased from 17 species in 1982 to 23 in 2002 (Table 3). Species dominant in 1982 remained common. In addition, the frequency of *Amelanchier* spp. more than quadrupled from 4% before the infestation to 25% in 2002. *Smilax rotundifolia*, *Ilex verticillata*, *Vaccinium pallidum*, and *Rubus* spp. also more than doubled in frequency from 1982 to 2002 (Table 3). Non-native invasive species such as *Berberis thunbergii*, *Celastrus orbiculatus*, *Lonicera japonica*, and *Rosa multiflora* also appeared in plots for the first time after *T. canadensis* began to decline.

In the herbaceous layer, previously abundant species such as *Maianthemum canadense*, *Chimaphila maculata*, and *Carex* spp. increased in frequency between 1982 and 2002 (Table 4). Many less abundant species, including ferns (e.g., *Dennstaedtia punctilobula*, *Thelypteris noveboracensis*, *Polypodium virginianum*), forbs (e.g., *Aster* spp., *Medeola virginiana*, *Solidago* spp., *Smilacina racemosa*), and graminoids (*Carex* spp. and grasses) also increased in frequency (Table 4). The frequency of herbs across all plots increased from 64% to 89%, and total herb richness increased from 25 to 38 species (Table 4).

SITE INFLUENCES. More xeric, exposed ledges and more mesic, protected ravine sites differed in response to *T. canadensis* mortality (Fig. 2). In 1982, ravine plots had mixed dominance of black oaks, *F. grandifolia*, *Q. alba*, *B. lenta*, *A. rubrum*, and *T. canadensis*. Ledge plots were clearly dominated by *T. canadensis* and black oaks (Fig. 2). Introduction of the HWA caused dramatic basal area decline by 2002, particularly on ledge sites (28.8% decline ledge vs. 13.2% ravine), and greatly reduced *T. canadensis* importance on both ledges and ravines (65–70% IV decline; data not shown). With the loss of *T. canadensis*, dominance in both communities shifted to black oaks. On ravine sites, secondary importance also was shared by *F. grandifolia* and *B. lenta* (Fig. 2).

Both ledge and ravine sites experienced large surges in sapling density following introduction of the HWA (Fig. 3). By 2002, ledge sites had considerably greater total density of saplings

(7700 stems/ha) than ravine sites (2900 stems/ha; Fig. 3). *Sassafras albidum* dominated ledge understories from 1992 (490 stems/ha) to 2002 (3200 stems/ha; Fig. 3). *Acer rubrum*, black oaks, *Prunus serotina* were also abundant. During this same period in ravine sites, *S. albidum* shared understory dominance with black oaks, *Prunus serotina*, *F. grandifolia*, and *A. rubrum*.

Non-metric multidimensional scaling (NMS) ordination of 1982 presence-absence data for all species showed marked compositional separation of ledge and ravine plots (Fig. 4a). The 1982 NMS ordination was best fit by a two-axis solution, as determined by a Monte Carlo randomization test ($P < 0.05$) and visual examination of the NMS scree plot. The first two NMS axes accounted for 65.6% of the variability in the data (axis 1 = 33.2%, axis 2 = 32.4%). Ledge plots generally were located high on axes 1 and 2 (Fig 4a). These plots grouped tightly on the NMS ordination, indicating high compositional similarity, and each shared dominance of *S. albidum*, *T. canadensis*, and *B. lenta*. Plots established on ravine sites showed greater variation in species composition, with plots forming two discrete clusters around ledge plots. The first cluster of ravine plots was located high on axis 1 and low on axis 2 (lower right portion of the ordination), associated with high richness of trees, shrubs, and herbaceous layer species (Fig. 4a). Species typical of more mesic to hydric habitats, such as *Symplocarpus foetidus*, *Impatiens capensis*, *Arisaema triphyllum*, *Viola* spp., *Maianthemum canadense*, and *Osmunda cinnamomea*, were particularly prevalent in these plots. Many of the woody species common in these plots, including *Lindera benzoin*, *A. rubrum*, *P. serotina*, and *Liriodendron tulipifera*, also suggested more mesic sites.

A second cluster of ravine plots was located lower on axis 1 and high on axis 2 (upper left portion of the ordination; Fig. 4a). These plots were characterized by low species richness in all vegetation strata and very low abundance of common species such as black oaks, *S. albidum*, *Kalmia latifolia*, *Clethra alnifolia*, *Smilax* spp., and *M. canadense*, rather than shared abundance of any particular species.

Ordination of ledge and ravine data collected two decades later, following HWA infestation, showed even stronger compositional separation of ledge and ravine plots (Fig. 4b). The 2002 NMS ordination was again best fit by a two-axis solution (Monte Carlo randomization test ($P < 0.05$), visual examination of NMS scree plot). The first two NMS axes accounted for 69.5% of the variability in the data (axis 1 = 39.7%, axis 2 = 29.8%). The first ordination axis represented a gradient of decreasing soil moisture, negatively correlated with herbaceous richness and importance of more mesic species such as *L. benzoin*, *Toxicodendron radicans*, *S. foetidus*, *A. triphyllum*, *I. capensis*, *Viola* spp., and *Carex* spp. (Fig. 4b). Plots located high on axis 1 had lowest herbaceous richness and greatest frequency of *Q. alba* and ericaceous herbs such as *Chimaphila maculata* and *Gaultheria procumbens*, species common to drier, acidic soils.

Ordination axis 2 showed strong separation of ledge and ravine plots, again indicating marked difference in species composition (Fig. 4b). As in 1982, ledge plots were clustered tightly on the ordination, located high on axis 2. These plots exhibited greater tree and shrub richness than ravine plots, including greater frequency of *A. rubrum*, *T. canadensis*, *S. albidum*, black oaks, *K. latifolia*, *Vaccinium* spp., and *Smilax* spp. Interestingly, *A. rubrum*, *K. latifolia*, and *Clethra alnifolia*, species abundant in the BNA, occurred almost exclusively in ledge plots in 2002.

Ravine plots in 2002 were located low on axis 2, entirely distinct from ledge plots (Fig. 4B). As in 1982, these plots showed much greater variability in species composition than ledge plots but no longer formed two discrete groups. Compositional differences between ledge and ravine plots largely resulted from lower richness of trees and shrubs and greater richness of herbaceous species. Ravine plots showed greater frequency of shrubs such as *L. benzoin*, *Viburnum* spp., and *T. radicans* and many herbaceous species (*Viola* spp., *Arisaema triphyllum*, *Aster* spp., *Smilacina racemosa*, *I. capensis*) and ferns (*Thelypteris noveboracensis*, *Dennstaedtia punctilobula*). A number of rare herbs (very low frequencies) were present in ravine plots, and all invasive non-native plants occurring in *T. canadensis*-dominated plots in 2002 were restricted to ravine sites (See Table 3 for invasive species).

**Discussion.** HEMLOCK. Although the HWA was first recognized on the site in 1987, actual *Tsuga canadensis* mortality took some years to occur. The 1992 survey indicated extensive defoliation but little *T. canadensis* mortality; but by 1997, 45% of the population was dead (Table 1). Other studies of heavily infested stands in central Connecticut also found that trees remained alive for ten or more years after infestation (Orwig 2002). *Tsuga canadensis* saplings

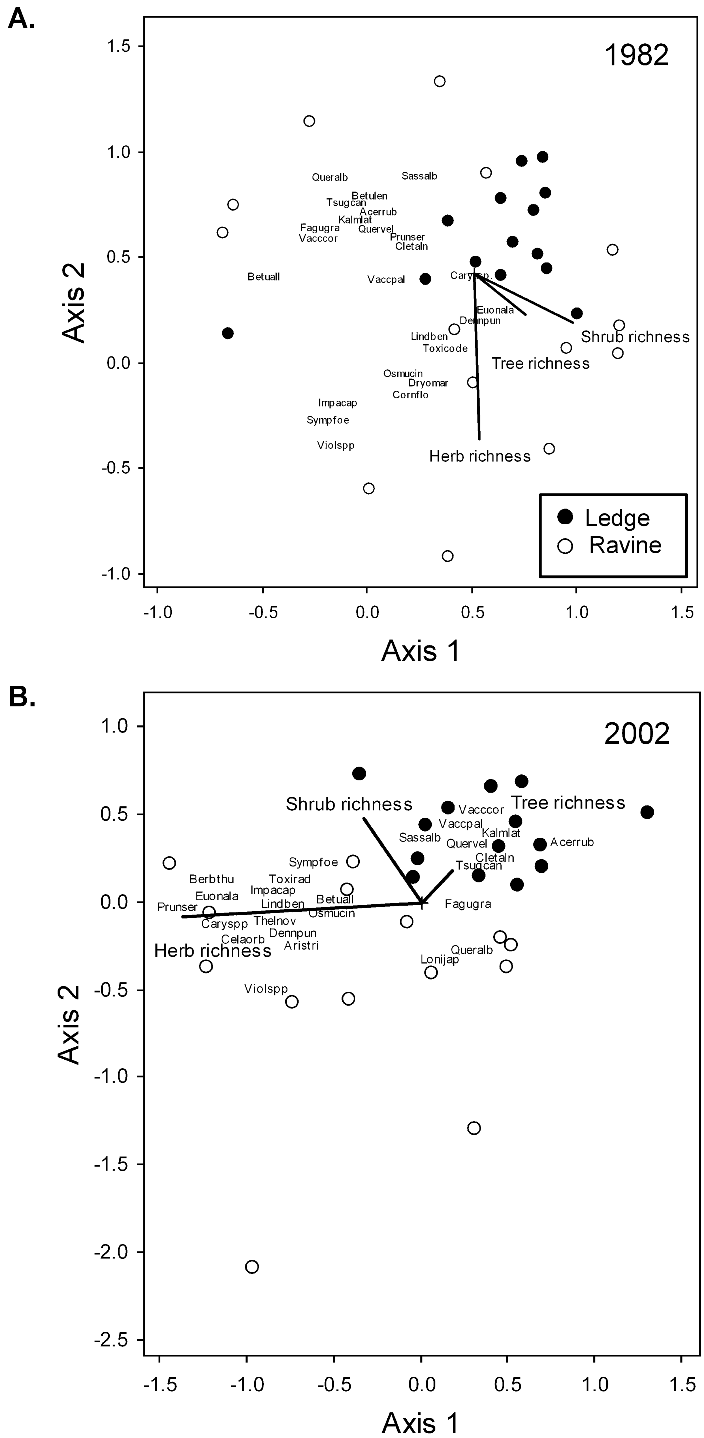


FIG. 4. NMS ordinations of BNA ravine ($N$ = 14) and ledge ($N$ = 14) plots based on presence-absence data for all vascular plant species (a) 1982 data (pre-HWA); (b) 2002 data (post-HWA).

initially responded to the decline of the dominant canopy species like other understory trees, by increasing in density for a short time after HWA infestation (Table 2). However, by 2002 there were relatively few *T. canadensis* of any size alive.

OTHER TREE SPECIES. Before the infestation, basal area of black oaks and *Fagus grandifolia* was slowly increasing, whereas *Betula lenta* exhibited a slow decline. Mature *B. lenta*, relatively intolerant of shade, were probably declining remnants from the recovery of the BNA forest after the 1938 hurricane. As *T. canadensis* increased and formed a dense canopy, *B. lenta* reproduction and growth was limited by shade (George and Bazzaz 1999).

As *T. canadensis* stems died and basal area declined, hardwood species in the canopy became increasingly important. Black oaks and other hardwoods, particularly *B. lenta* and *F. grandifolia*, increased in basal area after HWA infestation (Fig. 1). Other studies have shown similar growth increases, with annual growth ring widths of hardwoods increasing three to five times after HWA infestation (Orwig 2002). In addition to increases in stem diameter, crowns of existing hardwoods typically extend into canopy gaps and eventually return shade to the forest floor. Documented rates of crown expansion into canopy gaps created by chestnut blight, the 1938 hurricane, and selective cutting at Harvard Forest, Massachusetts, have ranged from 6 to 14 cm/year (Hibbs 1982). Additionally, density of *B. lenta* and black oaks increased between 1997 and 2002 (Table 1), suggesting that basal area increases also resulted from new stems that reached advanced height classes. Eventually, the rate of lateral canopy closure could be great enough in small gaps to prevent younger stems from reaching the canopy (Hibbs 1982).

The advantage of vegetative reproduction by root suckering was clear in the BNA. *Sassafras albidum* tree density increased by almost 400%, and *F. grandifolia* density nearly doubled between 1997 and 2002 (Table 1). During the same period the canopy population of the less common root suckering species *Nyssa sylvatica* remained static. Dramatic density increases also occurred with *F. grandifolia* and *S. albidum* saplings. (Table 2). *Sassafras*, absent from the sapling strata prior to the HWA infestation, increased to nearly 2000 stems/ha. *Fagus* saplings also increased, but to a lesser extent. One advantage of rootsuckering species is that distant but connected sprouts may increase the ability of the ''parent'' stem to survive suppression by canopy dominants for long periods of time. When a disturbance occurs and conditions improve, the ability to sprout from extensive existing root systems allows the colonization of new space quickly, without the production of great quantities of seed and the difficulties of germination and establishment. The abundance of tree reproduction by vegetative means in this study also emphasizes the importance of pre-existing individuals to the future composition of the canopy.

Although we do not present tree seedling data here (due to dramatic annual fluctuations), it is clear from the sapling information in Table 2 that many trees did successfully reproduce by seed. Non-rootsuckering trees including Black oaks, *Acer rubrum*, *Cornus florida*, *Carya* spp. and especially *Prunus serotina* all had sizeable increases in sapling density by 2002. This finding agrees with other studies that tracked tree reproduction following the introduction of the HWA in southern New England (Orwig and Foster 1998, Orwig 2002, Orwig and Kizlinski 2002).

BNA hemlock forest communities thus responded to the elimination of the dominant species by quickly filling the various sized gaps left by dead trees. In many ways, this behavior was similar to stands recovering from other types of disturbance, such as fire, high winds, and elimination of other species. For example, after the 1938 hurricane, Hibbs (1982) found *Prunus pennsylanica*, *A. rubrum* and black oaks dominant in the understory at Harvard Forest. After a tornado in northern Pennsylvania, species richness and tree density increased rapidly, with notable increases in *F. grandifolia*, *Betula* spp., *Rubus alleghaniensis*, and *Dennstaedtia punctilobula* (Peterson and Pickett 1995). Following the removal of *Castanea dentata* from the canopy in New Jersey, North Carolina, and Tennessee by the chestnut blight, other canopy species enlarged to fill in gaps, while *Betula* spp. seedlings and saplings dominated the understory (Keever 1953, Woods and Shanks 1959, Good 1968). Sediment cores taken from lakebeds in southern Ontario, New Hampshire, and southern Connecticut have shown that during the mid-Holocene hemlock decline 5400 years ago, percentages of hemlock pollen dropped concurrently with pollen influxes of *Pinus strobus* L. (white pine), black oaks (*Quercus velutina*, *Q. rubra*,and *Q. coccinea*, *F. grandifolia*, *A. sac-*

*charum*, *Castanea dentata* and *B. lenta* (Davis 1958, 1969; Fuller 1998).

SHRUB SPECIES. Shrub and vine species also responded quickly to the overstory changes, increasing in both richness and abundance, with expansion of preexisting species and the influx of nine additional species of shrubs and vines. In particular, species of *Smilax* and *Amelanchier* increased dramatically in frequency; *Kalmia latifolia* and *Hamamelis virginiana* remained common. The invasive exotic species *Berberis thunbergii*, *Celastrus orbiculatus*, and *Lonicera japonica* all first appeared in the plots after HWA infestation, and all subsequently increased in frequency. Only one exotic invasive, *Euonymus alatus*, was present prior to the infestation, and its frequency remained constant over the past twenty years.

Similar increases in shrub and vine cover were found in other studies following HWA outbreaks in the northeast (Orwig and Foster 1998, Orwig 2002, Orwig and Kizlinski 2002, Yorks 2002), as were increases in invasive species (Orwig and Foster 1998). The invasibility of a site is thought to depend on both fluctuations in the availability of resources and the availability of propagules (Davis et al. 2000). A concern is that opportunistic invasive exotic plant species such as *C. orbiculatus*, *B. thunbergii* and *Lonicera* spp., common and highly problematic in this region, may take advantage of the increased resource availability following hemlock decline and invade former hemlock stands. The increase in abundance of invasive species in formerly *T. canadensis* dominated plots should be monitored closely in the future, as they have been shown to displace native species elsewhere in the BNA and other regions (Fike and Niering 1999).

HERBACEOUS SPECIES. Herbaceous species reacted more quickly than canopy species to HWA infestation. Defoliation allowed more light to reach the forest floor, even while the hemlocks remained alive. Herbaceous species having the greatest frequency in 2002 were primarily preexisting shade tolerant species, including *Maianthemum canadense*, *Dennstaedtia punctilobula*, *Chimaphila maculata* and *Carex* spp., all of which increased in frequency since 1982 (Table 3). Herbaceous species in our *Tsuga*-dominated plots were similar to those found in other HWA infested stands in the northeast (Orwig and Foster 1998, Yorks 2002, Orwig 2002, Orwig and Kizlinski 2002,).

SITE DIFFERENCES. Ledge and ravine sample sites were quite different prior to the HWA infestation. Both plots contained many of the same species, but in different abundances. In ravine plots, *Tsuga canadensis* shared the canopy with black oaks and *Fagus grandifolia*, although other species were also relatively common. In ledge plots, the canopy was very much dominated by *T. canadensis*, with black oaks as the only other common tree. With the decline of *T. canadensis*, both ravine and ledge sites came to be dominated by pre-existing black oaks. In ravine plots, *F. grandifolia* maintained co-dominance with black oaks, and *Betula lenta* and *Quercus alba* were also relatively important. Saplings in ledge and ravine plots behaved similarly in both sites, with regeneration particularly abundant on ledge sites. *Sassafras albidum* dominated regeneration on the ledge, whereas *Prunus serotina* dominated in the ravine (Fig. 3). Based on the NMS ordinations, it is clear that vegetation composition of ravine and ledge sites became more distinct between 1982 and 2002 (Fig. 4), particularly in terms of herb richness. Presumably, increased light at ground level, combined with greater moisture availability, led to the greater herb richness in ravine plots.

The decline of hemlock can be compared in many ways to the decline of chestnut in the early 1900s. In both cases, a single species was involved and mortality was relatively gradual as trees defoliated, allowing neighboring canopy trees to fill in gaps (Keever 1953, Woods and Shanks 1959, Good 1968, Orwig 2002,). However, hemlocks of all age classes were susceptible to the HWA while only larger, reproductive chestnut became infected by chestnut blight. Further, *T. canadensis* has been the dominant, or often the only, evergreen forest tree in many parts of its range. With its disappearance from the canopy, the microclimate of the forest floor has changed dramatically, with greater levels of light, increased temperatures and changes in moisture content. Given the nearly complete local mortality of *T. canadensis* expected in the near future and the rapid spread of the HWA (20–30km/year; Orwig and Foster 1998), it seems unlikely that southern New England *T. canadensis* populations will recover during the 21$^{st}$ century.

FUTURE FORESTS. The contemporary and future forests would be very different without the influence of the HWA. Based on pre-HWA basal area data from 1952–1982, projections of the fu-

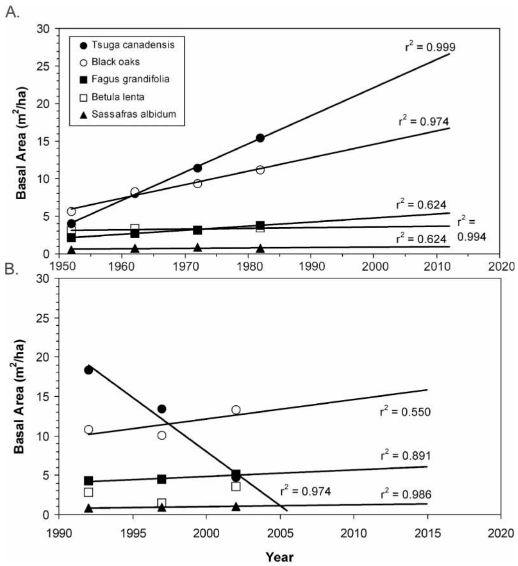


FIG. 5. Projections of future basal area for dominant canopy species in BNA hemlock-dominated plots based on a) data collected prior to the HWA (1952–1982) and b) data collected after the HWA (1992–2002). Trendline for *Betula lenta* after the HWA not shown ($r^2 = 0.120$).

ture forest canopy in BNA hemlock plots showed *Tsuga canadensis* continuing to increase in dominance, with black oaks as co-dominants (Fig. 5). Shade tolerant *Fagus grandifolia* would also continue to increase in basal area. Other less common species such as *Quercus alba*, *Sassafras albidum*, *Nyssa sylvatica*, and *Acer rubrum* would maintain a constant level or decline slightly. In terms of plant succession models, the healthy, mature hemlock forest is perhaps a classic example of the inhibition model (Connell and Slatyr 1977), in which one species physically dominates a site and prevents the intrusion of other species.

Projections based on data collected since the HWA infestation indicate that all *T. canadensis* stems in the BNA will die by 2006 (Fig. 5B), 19 years after HWA was first recognized on the site. Black oaks, *F. grandifolia*, and *S. albidum* are expected to increase in basal area and dominance, producing a mixed hardwood community. Larger gaps will be available to early successional species, while smaller gaps are likely to be filled by mid to late successional trees and saplings already present (Connell and Slatyr 1977). Rootsuckering species are something of a wildcard, as they can quickly dominate locations in close proximity to a ''parent'' tree. Contrasting two projections from the same location before and just following a disturbance such as the HWA highlights the dynamic and unpredictable nature of vegetation development.

Clearly caution must be used when predicting future vegetation patterns, even when based on long-term data. Particularly in southern New England, the role of periodic stand-level disturbance cannot be ignored. Disturbances such as hurricanes often have a return interval of less than 200 years in this area (Niering 1998). Given our history of Dutch elm disease, chestnut blight, repeated gypsy moth defoliations, and the HWA, all in the twentieth century, the return interval of natural and exotic pest disturbance appears to be well within the maturation time of our forest communities and may be getting shorter. In addition, the proliferation of invasive plants and animals, particularly in response to stand level natural and anthropogenic disturbances, is also having a profound and unpredictable effect on future forest composition.

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