

Predicting Long-Term Forest Development Following Hemlock Mortality

Jennifer C. Jenkins^{1,3}, Charles D. Canham², and Paul K. Barten^{1,4}

Abstract

The hemlock woolly adelgid (*Adelges tsugae* Annand.), an introduced pest specializing on eastern hemlock (*Tsuga canadensis* (L.) Carr.), threatens to cause widespread hemlock mortality in New England forests. In this study, we used a stem-based model of forest dynamics (SORTIE) to predict forest development in a northeastern forest both with and without eastern hemlock. In all simulations, forest development was explained by species-specific life-history characteristics such as growth, mortality, and recruitment as they relate to light availability. Forest composition after 500 years depended on the relative abundances of late-successional species: eastern hemlock was long-lived but did not easily gain or yield space; American beech (*Fagus grandifolia* Ehrh.) gained dominance quickly and soon comprised nearly all basal area in a stand unless hemlock was present; and yellow birch (*Betula alleghaniensis* Britton) persisted if beech and hemlock were absent. Early-successional species thrived in the forest if late-successional species were not present. We conclude that the long-term impact of the hemlock woolly adelgid on forest composition in northeastern forests will depend both on initial species composition and on the extent of hemlock death. If 50% of the overstory basal area in hemlock is removed by the adelgid, and if the adelgid does not persist at densities high enough to cause extended damage, hemlock stands will continue to be dominated by hemlock. Mixed hemlock - hardwood stands will be dominated by the late-successional species remaining. If hemlock death is near 90% of overstory basal area, hemlock is likely to continue to persist in low densities while the other late-successional species gain dominance. If hemlock death is complete, all stands will be dominated by beech and yellow birch where they are present, no matter what their initial abundances. Hardwood stands will not be affected by the adelgid.

Introduction

Northeastern forests are currently threatened by an outbreak of hemlock woolly adelgid, a defoliating insect pest specializing on eastern hemlock. Because of its extreme virulence, its unusually high fecundity (McClure 1989), and its rapid dispersal via wind and animals (McClure 1990), the

adelgid's arrival in a healthy forest stand often foreshadows the death of all hemlock (McClure 1991). Eastern hemlock often grows in pure stands or in mixed stands with deciduous species (Kelty 1986); adelgid infestation in southern New England has thus initiated a rapid shift from mixed and coniferous to deciduous forest (Jenkins et al. 1999, Orwig and Foster 1998). The consequences of hemlock mortality, however, are likely to be visible at a much larger scale, as the selective removal of a dominant forest species is often accompanied by landscape-level reorganization of forest structure (Shugart and West 1977, Twery and Patterson 1984). In this study we used a modeling approach to assess the potential long-term impact of eastern hemlock mortality on forest composition for a small watershed in southern New England.

Methods

SORTIE model

The SORTIE model tracks individual trees on a spatially explicit basis, generating light indices for each stem as a function of its nearest neighbors. In this way, dispersal, growth, mortality, and recruitment rates are based on species-specific responses to resource availability (Canham et al. 1994, Kobe et al. 1995, Pacala et al. 1993, 1996, Ribbens et al. 1994). The model is uniquely appropriate for this study for two reasons: 1) its emphasis on life-history characteristics at the individual tree level allowed us to focus on the effects of selective removal of one species, and 2) SORTIE's species-specific functions were parameterized at the study site in northwestern Connecticut. Nutrient and water limitations are not represented in this version of the model. We do not consider this a limitation of this analysis, as previous field studies have suggested that such limitations are indeed rare at the study site (S. Pacala, pers. comm.).

Study site

The Camp Pond watershed (41°58' N and 73°15' W) encompasses approximately 130 hectares in the northern portion of the Great Mountain Forest in the northwestern corner of Connecticut (Figure 1). Elevation ranges from 420 to 530 meters. Soils are derived from glacial till, range from 10 to about 100 cm thick, and are extremely rocky. The forest lies within the transition hardwood - hemlock - white pine forest vegetation zone (Westveld 1956), though white pine (*Pinus strobus* L.) is absent from the Camp Pond watershed. Most of the forest is between 80 and 100 years old; in parts of the northeast, northwest, and southernmost portions of the watershed, selective harvesting took place within the last 30 years. Hemlock woolly adelgid is not yet present at the site.

Forest survey

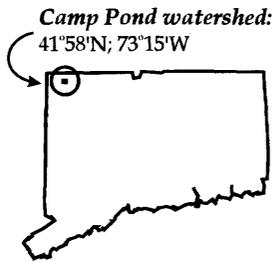
We conducted a detailed forest inventory to assess current forest composition by species and 10 cm size class. Sample

¹Yale University School of Forestry and Environmental Studies, 205 Prospect St., New Haven, CT 06511

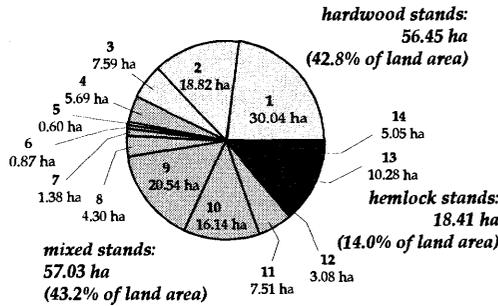
²Institute of Ecosystem Studies, Rte 44A, Box AB, Millbrook, NY 12545

³Corresponding author, current address: USDA Forest Service Northern Global Change Program, 705 Spear St., South Burlington, VT 05403

⁴Current address: University of Massachusetts, Department of Forestry and Wildlife Management, PO Box 34210, Amherst, MA 01003

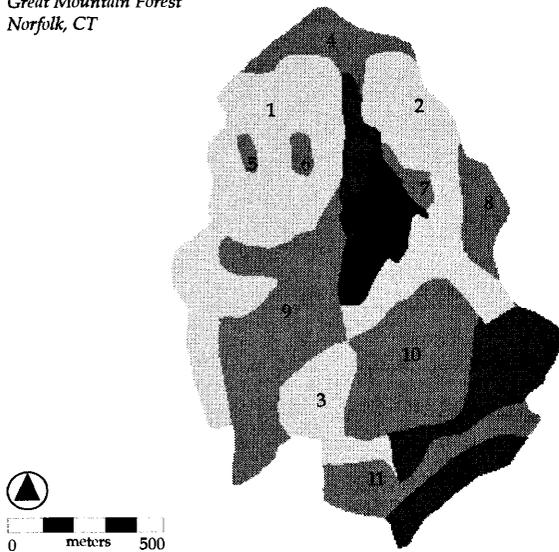


Stand Areas:



Site Map:

Camp Pond watershed
Great Mountain Forest
Norfolk, CT



land cover types:
hardwood stands ■
mixed stands ■
hemlock stands ■
Camp Pond ■

Figure 1.—Site description: location within Connecticut, watershed map, and stand descriptions.

points were located along east-west transects roughly 100 m from each other; transects were established 100 m apart. At each of 124 sample points, variable-radius plots were measured, using a prism with a basal area factor of 2.3 m² ha⁻¹. Species and diameter at breast height (dbh) were recorded for each tree counted "in" by the prism. Plots were located with a global positioning system using differential correction (Trimble Pathfinder Basic Plus; 2 to 5 m accuracy). An external antenna was mounted on a 40-foot telescoping stadia rod to alleviate interference from the forest canopy. The Universal Transverse Mercator (UTM) coordinates of each point were registered to a geographic information system (GIS) for further analysis.

Stand delineation

To facilitate modeling forest succession in stands with different species compositions, we used the forest inventory data to divide the watershed into stands. Stands containing less than 10% relative basal area (RBA) in overstory (dbh >= 10 cm) hemlock were classified as hardwood, those containing more than 60% RBA overstory hemlock were classified as hemlock, and stands with 10 to 60% RBA

overstory hemlock were classified as mixed hemlock-hardwood stands. Each plot was assigned to one of the three forest cover categories, and stand boundaries were drawn around groups of plots assigned to the same category using the onscreen digitizing function in Idrisi (Eastman 1992). We delineated fourteen stands within the watershed (Figure 1): three hemlock, eight mixed, and three hardwood (Table 1).

Simulations

Each stand was treated separately in the model simulations. In order to initialize the model with current conditions for each stand, we used the forest survey data to calculate the number of trees per hectare in each 10-cm size class for each species, rounded to the nearest integer. Several species were present in the study area but were ignored: striped maple (*Acer pensylvanicum* L.), which made up less than 5% of overstory basal area in the six stands where it occurred; gray birch (*Betula papyrifera* Marsh.), which made up less than 2% of overstory basal area in the three stands where it occurred; and black birch (*Betula lenta* L.), which made up less than 5% of overstory basal area in the five

Table 1.—Current overstory (dbh \geq 10 cm) forest composition for 14 stands delineated using plot-based forest inventory of Camp Pond watershed, Great Mountain Forest, Norfolk, CT. See Figure 1 for stand map. Bold values refer to the most abundant species in each stand. Absence of data indicates zero RBA (relative basal area) value. Species abbreviations are as follows: BE, American beech (*Fagus grandifolia* Ehrh.); HM, Eastern hemlock (*Tsuga canadensis* Carr.); SM, sugar maple (*Acer saccharum* Marsh.); YB, yellow birch (*Betula alleghaniensis* Britton); BC, black cherry (*Prunus serotina* Ehrh.); RM, red maple (*Acer rubrum* L.); WA, white ash (*Fraxinus americana* L.); RO, northern red oak (*Quercus rubra* L.).

Stand type	Hardwood			Mixed			
	1	2	3	4	5	6	7
Total BA (m ² ha ⁻¹)	24.13	23.16	29.77	29.77	26.06	19.27	20.04
RBA values							
by species	BE	0.29	0.30	0.16			0.06
	HM	0.01	0.05	0.49	0.48	0.33	0.32
	SM	0.10	0.10	0.02			0.09
	YB	0.03	0.02	0.11		0.06	0.03
	BC	0.09	0.08	0.11	0.04	0.11	0.12
	RM	0.14	0.14	0.22	0.17	0.12	0.25
	WA	0.05	0.05			0.28	0.03
	RO	0.40	0.19	0.12	0.11	0.23	0.09

Stand type	Mixed				Hemlock		
	8	9	10	11	12	13	14
Total BA (m ² ha ⁻¹)	36.18	28.12	33.89	30.54	21.72	31.29	32.06
RBA values							
by species	BE	0.07	0.18	0.22	0.05	0.06	0.14
	HM	0.45	0.41	0.39	0.62	0.76	0.69
	SM	0.08	0.03	0.03	0.05		
	YB	0.02	0.07	0.04	0.11	0.04	0.02
	BC	0.04	0.06	0.03	0.08	0.02	0.02
	RM	0.27	0.30	0.26	0.20	0.07	0.01
	WA		0.01	0.02	0.01		
	RO	0.04	0.05	0.04	0.06	0.04	0.02

stands where it occurred. Black oak (*Quercus velutina* Lam.) occurred in three of the stands and was treated as red oak. All other species had been parameterized in SORTIE and accounted for 100% of the overstory basal area.

While many stands infested with hemlock woolly adelgid have eventually experienced complete hemlock mortality, it is possible that: a) a natural enemy might be found which could be released to keep the population in check (Cheah and McClure 1996, Lyon and Montgomery 1995, McClure 1987, 1995, Montgomery and Lyon 1996); b) the adelgid population would remain too low to cause extensive damage in areas with extremely cold temperatures (but see Parker et al. 1998); c) some localized hemlock trees would prove resistant; or d) site factors would render the pest less virulent in some forests than in others. In these cases, hemlock mortality might be incomplete. To predict the impacts of partial hemlock mortality on northeastern forests, we performed simulations with partial (50% and 90%) hemlock removal in addition to the simulations with complete (100%) mortality. For each of the 11 non-hardwood stands, five 500 year simulations (each using a different random number seed to initialize the stochastic functions in the model) were performed under four sets of conditions: current conditions, 50% hemlock mortality, 90% hemlock mortality, and complete hemlock mortality. We removed hemlock from

the community by fixing its initial density at 50%, 10%, or 0% of its current density while holding all other variables constant. We assumed that standing hemlock trees died immediately upon infestation, and that they fell to the forest floor directly after their mortality. This scenario is not truly representative of the "gradual" canopy gaps created in eastern hemlock forests by the adelgid (Jenkins et al. 1999, Krasny and Whitmore 1992), so we may overestimate the light available to understory trees following hemlock mortality. Over the long term, however, we expect that this would have little effect on forest development.

Since hemlock mortality is not likely to alter forest development in hardwood stands, simulations of current forest conditions only were performed for the three stands classified as hardwood. The averages of each species' RBA in the five simulations for each set of species compositions are reported here with their associated standard deviations. In this analysis, we focus on RBA rather than raw basal area (BA) values because a) we were skeptical about the very high raw BA values generated by the model at this stage in model development (subsequent model revisions have addressed this issue), and b) the relative abundance of individual species (and not their absolute BA values) was truly the variable of interest.

Results

Current conditions

In simulations representing future development from existing conditions in the hardwood stands (Table 2), initial RBA of early-successional and shade-intolerant species were replaced by beech, yellow birch, and sugar maple (*Acer saccharum* Marsh.). In simulations representing future development from existing conditions in the hemlock stands (Table 2), the RBA of hemlock remained roughly constant or increased slightly; beech RBA also increased slightly. At the same time, in these stands the RBA of early successional species such as red oak (*Quercus rubra* L.), red maple (*Acer rubrum* L.), and black cherry (*Prunus serotina* Ehrh.) declined. Similar trends were seen in the development of the mixed stands through time (Table 2). In general, where beech, hemlock, and yellow birch were present, they increased dramatically in RBA at the expense of other species, especially red maple and black cherry.

Hemlock removal

When hemlock was completely removed from the three hemlock stands (Table 3), the remaining late-successional species dominated stand development. Beech and yellow birch were present, and they gained dramatically in RBA over time with a concomitant decrease in basal area of early-successional species. When hemlock was removed completely from mixed stands the situation was similar: if beech or yellow birch was present it gained significantly. Under these conditions, though, each species had a greater advantage where it was the only late-successional species present.

When hemlock was partially removed from both hemlock and mixed stands, the remaining late-successional species dominated forest structure at year 500 (Tables 4 and 5). Overall, in simulations representing partial hemlock death, beech made dramatic gains while the remaining hemlock and yellow birch were slower to increase RBA.

Dynamics of late-successional species

The long-term dynamics of succession depended on the initial relative abundances of the species present. In particular, the presence or absence of yellow birch, hemlock, and beech strongly influenced community composition after 500 years of undisturbed succession. When beech was the only species remaining, it dominated by year 50 (Table 3, stand 4); when yellow birch remained alone, it dominated within 300 years (Table 3, stand 6). When hemlock was the only species present of the three (Tables 4 and 5, stand 5), it gained steadily though its RBA increase was not as rapid.

When two of the three species occurred together, dynamics were less predictable. For example, when beech and yellow birch occurred together in the absence of hemlock (Table 3, stands 4-14; Table 2, stand 1), both species were present and had gained RBA in year 500. Beech was quicker to gain basal area, becoming the most abundant in late succession

no matter what its initial abundance. In the one case where yellow birch was more abundant than beech at year 500 (Table 5, stand 9), both species were equally abundant initially, suggesting that yellow birch remained competitive in late succession only when its initial abundance was high enough for it to remain competitive with beech. When hemlock occurred with beech but not yellow birch, of course, beech was most likely to be predominant in the stand within 20 years (Tables 2, 4, and 5, stand 4).

More common, however, were simulations in which all three species occurred simultaneously. Under these conditions hemlock was most likely to gain dominance by year 20, but the composition of the remaining forest and the initial abundances of all three late-successional species were better predictors of late-successional outcome.

Dynamics of early-successional species

When none of the three late-successional species were present, early-successional species persisted in the stand through year 500 (Figure 2; Table 3, stand 5). When both types of species were present, however, the trend from year zero was predictable: the early-successional species steadily lost relative basal area while the late-successional species gained (Figure 3).

At year 500, if white ash (*Fraxinus americana* L.) persisted, it was present in very low densities. Black cherry and red oak, while not dominant, were common in the original forest. While they dominated late in succession when no other late-successional species was present (Figure 2), they were largely excluded from late-successional dynamics. Red oak, however, gradually gained basal area in several of the simulations, reaching its peak density between years 100 and 150 (Figure 4) and remaining dominant even in the presence of hemlock in one simulation (Table 5, stand 5). Unlike the early-successional species mentioned so far, red maple was initially common in the forest at Camp Pond. In all of the model simulations, however, red maple steadily lost RBA.

Discussion

Consequences of hemlock mortality

If the current spreading pattern of hemlock woolly adelgid infestation in southern New England reaches Great Mountain Forest, and if a suitable natural enemy or an insecticide practical for forest use does not become available, it is possible that virtually all hemlock in this community will be lost. Forest development after adelgid infestation will depend on the composition of the forest community when the adelgid arrives. The stands that do not currently contain hemlock will continue to develop as predicted, with a gradual decline in early-successional species and an accompanying increase in late-successional species. In predominantly hemlock stands, the loss of hemlock will be accompanied by an increase in yellow birch, a gap-phase species. If beech is present when hemlock dies, the model predicts that beech will increase

Table 2.—Comparisons of current relative basal area (RBA) with RBA predicted by SORTIE after 500 years of undisturbed succession. Initial data are based on 1994 field measurements. Final values refer to the mean (standard deviation) of five 500-year SORTIE simulations. Proportions may not add to 1.00 due to rounding. Bold type indicates the most dominant species. See Figure 1 for stand map. Species are listed in order of decreasing shade tolerance (as described by Canham et al. 1994). Absence of data indicates zero RBA value.

Stand type	Hardwood						Mixed							
	1		2		3		4		5		6		7	
Species	initial	final (SD)												
BE	0.18	0.83 (0.06)	0.29	0.72 (0.06)	0.30	0.72 (0.12)	0.16	0.52 (0.11)					0.06	0.38 (0.07)
HM			0.01	0.01 (0.02)	0.05	0.01 (0.03)	0.49	0.43 (0.09)	0.48	0.86 (0.02)	0.33	0.71 (0.10)	0.32	0.35 (0.08)
SM	0.10		0.21	0.18 (0.05)	0.10	0.03 (0.03)	0.02						0.09	0.01 (0.02)
YB	0.03	0.05 (0.05)	0.02	0.03 (0.04)	0.11	0.18 (0.12)					0.06	0.10 (0.10)	0.03	0.13 (0.04)
BC	0.09	0.03 (0.03)	0.08	0.02 (0.03)	0.11	0.01 (0.02)	0.04	0.01 (0.02)	0.16	0.05 (0.05)	0.11	0.07 (0.05)	0.12	0.08 (0.05)
RM	0.14	0.05 (0.03)	0.14	0.02 (0.03)	0.22	0.04 (0.05)	0.17	0.03 (0.03)	0.12	0.03 (0.06)	0.28	0.04 (0.03)	0.25	0.03 (0.03)
WA	0.05	0.01 (0.02)	0.05	0.01 (0.02)										0.03
RO	0.40	0.03 (0.04)	0.19	0.02 (0.04)	0.12		0.11	0.01 (0.02)	0.24	0.05 (0.05)	0.23	0.09 (0.04)	0.09	0.01 (0.01)

Stand type	Mixed						Hemlock							
	8		9		10		11		12		13		14	
Species	initial	final (SD)												
BE	0.10	0.31 (0.11)	0.07	0.15 (0.03)	0.18	0.34 (0.05)	0.22	0.51 (0.07)	0.05	0.06 (0.04)	0.06	0.17 (0.09)	0.14	0.25 (0.13)
HM	0.45	0.51 (0.12)	0.41	0.58 (0.15)	0.39	0.49 (0.06)	0.30	0.24 (0.13)	0.62	0.88 (0.07)	0.76	0.78 (0.08)	0.69	0.67 (0.10)
SM	0.08	0.05 (0.03)	0.03		0.03		0.03		0.05	0.01 (0.01)				
YB	0.02	0.06 (0.05)	0.07	0.18 (0.15)	0.04	0.1 (0.04)	0.11	0.17 (0.09)	0.02		0.04	0.05 (0.03)	0.02	0.03 (0.03)
BC	0.04		0.06	0.03 (0.04)	0.03	0.01 (0.01)	0.08				0.02		0.02	0.01 (0.03)
RM	0.27	0.06 (0.05)	0.30	0.04 (0.03)	0.26	0.07 (0.07)	0.20	0.03 (0.04)	0.18	0.05 (0.08)	0.07	0.01 (0.01)	0.11	0.03 (0.08)
WA			0.01		0.02		0.01	0.01 (0.02)						
RO	0.04	0.01 (0.02)	0.05	0.02 (0.03)	0.04		0.06	0.04 (0.06)	0.08		0.04	0.01 (0.01)	0.02	

Table 3.—Comparisons of RBA with hypothetical complete eastern hemlock mortality due to woolly adelgid infestation with RBA predicted by SORTIE after 500 years of undisturbed succession following eastern hemlock mortality. Simulations were performed for Mixed and Hemlock stands only (stands 4-14). See Figure 1 for stand map. Initial data are based on 1994 field measurements minus eastern hemlock. Final values refer to the mean (standard deviation) of five 500-year SORTIE simulations. Proportions may not add to 1.00 due to rounding. Bold type indicates the most dominant species; absence of data indicates a zero RBA value. Species are listed in order of decreasing shade tolerance (as described by Canham et al.1994).

Stand type	Mixed											
	4		5		6		7		8		9	
Species	initial	final (SD)										
BE	0.32	0.91 (0.03)					0.09	0.57 (0.10)	0.18	0.81 (0.08)	0.12	0.39 (0.11)
HM												
SM	0.04	0.01 (0.02)					0.14	0.03 (0.03)	0.15	0.02 (0.03)	0.05	
YB					0.08	0.71 (0.07)	0.05	0.23 (0.13)	0.03	0.08 (0.06)	0.12	0.53 (0.11)
BC	0.08	0.02 (0.04)	0.31	0.32 (0.07)	0.17	0.09 (0.02)	0.17	0.07 (0.04)	0.08	0.05 (0.05)	0.10	0.03 (0.02)
RM	0.34	0.05 (0.03)	0.23	0.25 (0.06)	0.41	0.06 (0.04)	0.37	0.07 (0.03)	0.48	0.04 (0.04)	0.50	0.05 (0.02)
WA							0.05	0.01 (0.02)				0.02
RO	0.22	0.01 (0.02)	0.46	0.42 (0.08)	0.34	0.14 (0.07)	0.13		0.08			0.09

Stand type	Mixed		Hemlock							
	10		11		12		13		14	
Species	initial	final (SD)								
BE	0.30	0.78 (0.08)	0.31	0.65 (0.08)	0.14	0.37 (0.07)	0.27	0.59 (0.13)	0.47	0.76 (0.14)
HM										
SM	0.06	0.01 (0.01)	0.04	0.01 (0.02)	0.14	0.20 (0.02)				
YB	0.07	0.09 (0.03)	0.15	0.22 (0.06)	0.05	0.41 (0.10)	0.17	0.23 (0.08)	0.06	0.13 (0.09)
BC	0.05	0.02 (0.01)	0.12	0.06 (0.02)			0.09	0.02 (0.02)	0.06	0.02 (0.03)
RM	0.43	0.09 (0.07)	0.28	0.06 (0.05)	0.47	0.12 (0.04)	0.31	0.05 (0.04)	0.35	0.08 (0.05)
WA	0.03	0.01 (0.03)	0.01							
RO	0.06		0.09		0.21	0.08 (0.07)	0.16	0.11 (0.08)	0.06	0.01 (0.02)

Table 4.—Comparisons of RBA with hypothetical 50% eastern hemlock mortality due to woolly adelgid infestation with RBA predicted by SORTIE after 500 years of undisturbed succession following 50% eastern hemlock mortality in each 10 cm size class. Simulations were performed for Mixed and Hemlock stands only (stands 4-14). See Figure 1 for stand map. Initial data are based on 1994 field measurements minus 50% of eastern hemlock. Final values refer to the mean (standard deviation) of five 500-year SORTIE simulations. Proportions may not add to 1.00 due to rounding. Bold type indicates the most dominant species; absence of data indicates a zero RBA value. Species are listed in order of decreasing shade tolerance (as described by Canham et al.1994).

Stand type	Mixed											
	4		5		6		7		8		9	
Species	initial	final (SD)										
BE	0.21	0.70 (0.05)					0.08	0.46 (0.12)	0.13	0.46 (0.05)	0.09	0.33 (0.05)
HM	0.33	0.23 (0.07)	0.32	0.74 (0.08)	0.20	0.50 (0.04)	0.19	0.19 (0.04)	0.29	0.46 (0.06)	0.27	0.37 (0.04)
SM	0.03	0.01 (0.03)					0.11	0.03 (0.03)	0.11		0.03	0.01 (0.01)
YB					0.07	0.30 (0.09)	0.04	0.16 (0.14)	0.02	0.01 (0.01)	0.09	0.21 (0.08)
BC	0.05	0.04 (0.05)	0.21	0.14 (0.06)	0.13	0.08 (0.03)	0.14	0.08 (0.03)	0.06	0.03 (0.03)	0.07	0.03 (0.03)
RM	0.23		0.16	0.06 (0.05)	0.33	0.02 (0.02)	0.30	0.05 (0.03)	0.34	0.02 (0.04)	0.36	0.05 (0.04)
WA							0.04				0.01	
RO	0.15	0.02 (0.04)	0.31	0.05 (0.06)	0.27	0.11 (0.09)	0.10	0.01 (0.02)	0.06	0.01 (0.02)	0.06	0.01 (0.02)
Stand type	Mixed				Hemlock							
	10		11		12		13		14			
Species	initial	final (SD)										
BE	0.23	0.51 (0.12)	0.25	0.58 (0.09)	0.08	0.11 (0.04)	0.10	0.23 (0.03)	0.22	0.33 (0.10)		
HM	0.22	0.32 (0.13)	0.21	0.16 (0.07)	0.45	0.78 (0.14)	0.62	0.69 (0.03)	0.54	0.48 (0.08)		
SM	0.04	0.01 (0.01)	0.03		0.08	0.02 (0.03)						
YB	0.05	0.08 (0.09)	0.12	0.17 (0.06)	0.03	0.03 (0.07)	0.06	0.04 (0.03)	0.03	0.09 (0.03)		
BC	0.04	0.02 (0.02)	0.10	0.01 (0.02)			0.03		0.03	0.03 (0.03)		
RM	0.33	0.04 (0.07)	0.22	0.05 (0.06)	0.26	0.03 (0.03)	0.12	0.03 (0.03)	0.16	0.06 (0.04)		
WA	0.03	0.02 (0.04)	0.01									
RO	0.05		0.07	0.02 (0.04)	0.11	0.03 (0.04)	0.06	0.01 (0.02)	0.03	0.01 (0.02)		

Table 5.—Comparisons of RBA with hypothetical 90% eastern hemlock mortality due to woolly adelgid infestation with RBA predicted by SORTIE after 500 years of undisturbed succession following 90% eastern hemlock mortality in each 10 cm size class. Simulations were performed for Mixed and Hemlock stands only (stands 4-14). See Figure 1 for stand map. Initial data are based on 1994 field measurements minus 90% of eastern hemlock. Final values refer to the mean (standard deviation) of five 500-year SORTIE simulations. Proportions may not add to 1.00 due to rounding. Bold type indicates the most dominant species; absence of data indicates a zero RBA value. Species are listed in order of decreasing shade tolerance (as described by Canham et al.1994).

Stand type	Mixed											
	4		5		6		7		8		9	
Species	initial final (SD)											
BE	0.29	0.81 (0.06)					0.09	0.56 (0.08)	0.17	0.74 (0.07)	0.12	0.36 (0.07)
HM	0.09	0.14 (0.08)	0.09	0.28 (0.08)	0.04	0.11 (0.03)	0.07	0.08 (0.02)	0.07	0.07 (0.05)	0.05	0.11 (0.04)
SM	0.04						0.13	0.02 (0.04)	0.14	0.01 (0.02)	0.04	
YB					0.08	0.63 (0.05)	0.05	0.15 (0.10)	0.03	0.05 (0.02)	0.12	0.42 (0.05)
BC	0.07	0.02 (0.03)	0.28	0.27 (0.09)	0.16	0.06 (0.01)	0.16	0.06 (0.04)	0.07	0.01 (0.01)	0.10	0.06 (0.06)
RM	0.31	0.01 (0.03)	0.21	0.14 (0.03)	0.40	0.08 (0.02)	0.35	0.07 (0.08)	0.45	0.10 (0.06)	0.47	0.05 (0.02)
WA							0.04	0.01 (0.03)			0.02	
RO	0.20	0.02 (0.03)	0.41	0.30 (0.12)	0.32	0.12 (0.04)	0.12	0.04 (0.04)	0.08	0.02 (0.03)	0.08	

Stand type	Mixed		Hemlock							
	10		11		12		13		14	
Species	initial final (SD)									
BE	0.29	0.80 (0.11)	0.31	0.62 (0.10)	0.12	0.29 (0.07)	0.21	0.43 (0.07)	0.37	0.70 (0.06)
HM	0.06	0.10 (0.06)	0.03	0.07 (0.04)	0.12	0.33 (0.12)	0.24	0.32 (0.06)	0.21	0.17 (0.06)
SM	0.05	0.01 (0.01)	0.04		0.12 0.04 (0.04)					
YB	0.06	0.04 (0.03)	0.14	0.25 (0.07)	0.04	0.19 (0.13)	0.13	0.18 (0.08)	0.05	0.08 (0.07)
BC	0.05	0.01 (0.02)	0.12	0.01 (0.02)			0.07	0.03 (0.03)	0.05	0.01 (0.02)
RM	0.40	0.05 (0.07)	0.27	0.03 (0.03)	0.42	0.07 (0.07)	0.24		0.27	0.01 (0.03)
WA	0.03		0.01							
RO	0.06		0.08	0.01 (0.02)	0.18	0.08 (0.06)	0.12	0.04 (0.05)	0.05	0.02 (0.02)

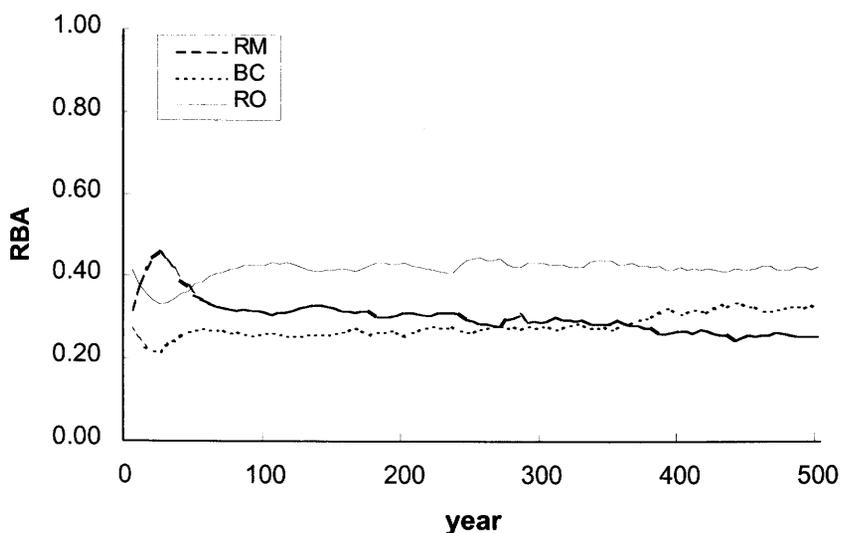
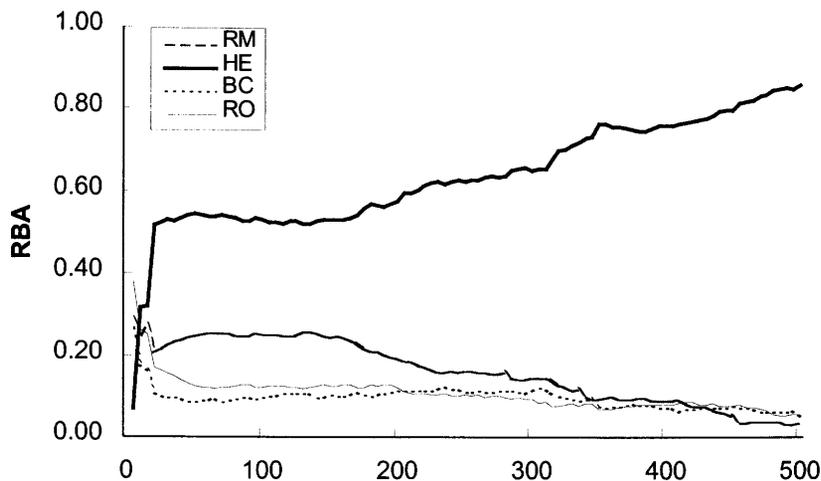


Figure 2.—Predicted effect of complete hemlock mortality in a stand with no other late-successional species (stand 5; see Tables 2, and 3 for initial and final conditions). Top panel shows succession through year 500 with no mortality, and bottom panel shows succession through year 500 with 100 % mortality. Line traces mean RBA values at 5-year time steps. Species abbreviations are as defined in Table 1.

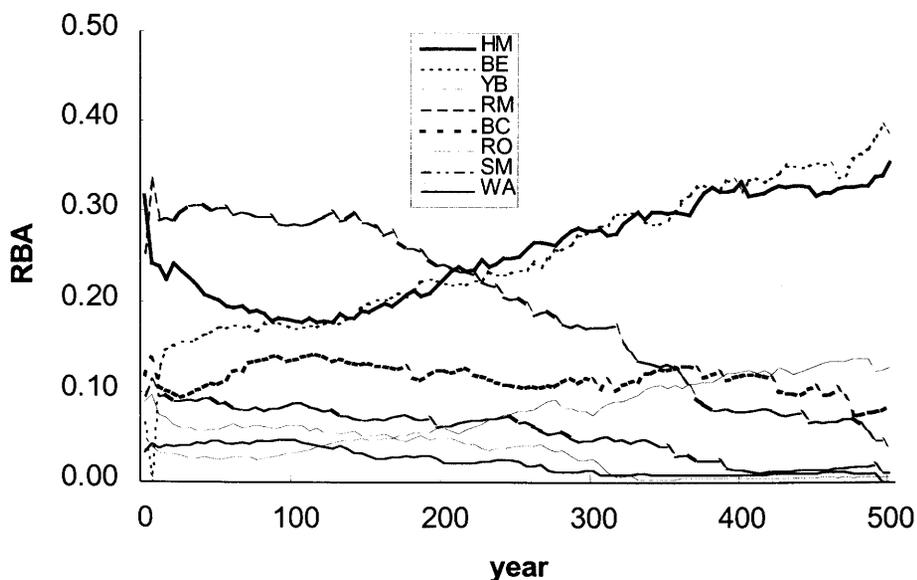


Figure 3.—Typical successional development with all three late-successional species (stand 8; see Table 2 for initial and final conditions). Lines trace RBA values at 5-year time steps. Species abbreviations are as defined in Table 1.

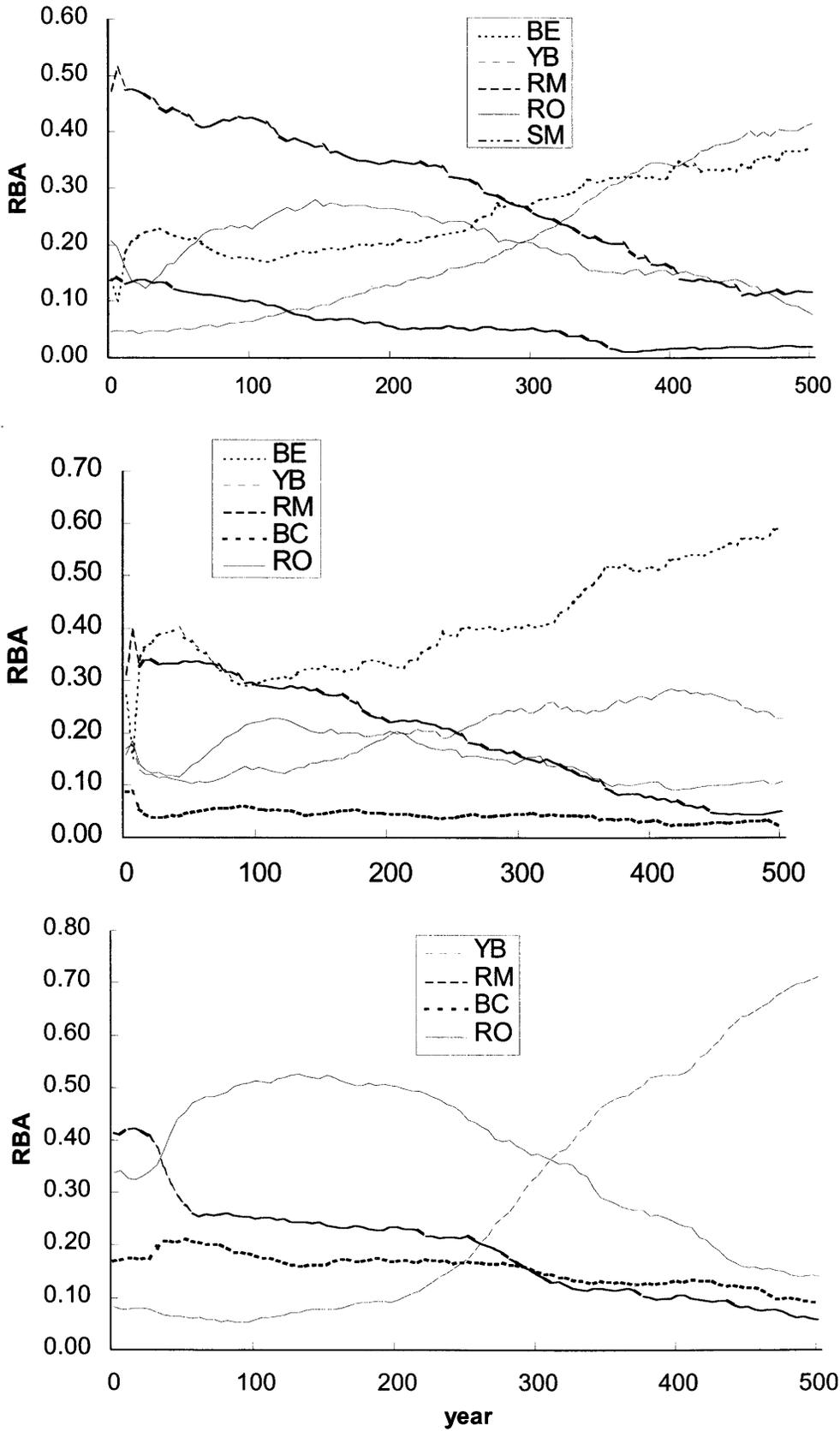


Figure 4.—Typical red oak peak and decline around year 100 (top panel: stand 12, no hemlock; middle panel: stand 13, no hemlock; bottom panel: stand 6, no hemlock; see Table 3 for initial and final RBA values). Lines trace RBA at 5-year time steps. Species abbreviations are as defined in Table 1.

Table 6.—Metrics summarizing interspecific variation among competitive strategies (from Pacala et al. 1996). See Table 1 for species abbreviations.

Species	Years to 3 m height in full sun	Years to 3 m height in 1% sun	Mean dispersal distance (m)	5-year survivorship of a 1 cm sapling in full sun
BE	19.4	55.0	5.9	0.92
HM	15.5	75.3	4.1	0.91
SM	18.4	31.7	8.1	0.69
RM	14.6	92.8	10.6	0.35
YB	13.9	29.3	31.0 ¹	0.65
RO	11.9	125.4	8.7	0.38
BC	11.4	49.5	8.0	0.53
WA	11.9	100.6	16.3	0.20

¹The estimated value was > 65 m; Pacala et al. (1996) chose the lower value based on statistical considerations and because their field plots were not large enough to ensure reliability of estimates this high (see Ribbens et al. 1994).

dramatically and quickly in these stands as well. In mixed stands, the sequence of development will depend upon the initial presence or absence of the other two late-successional species. If beech or yellow birch are present, they will increase in abundance following the loss of hemlock. If neither late-successional species is present, early-successional species will coexist in the undisturbed forest at least to year 500.

If hemlock is not completely lost from the community it is likely to remain at very low densities. In fact, pollen records show that despite the dramatic decline of eastern hemlock in northeastern forests several times throughout history, it has recovered after each decline to be dominant in certain areas of the northeast (Foster and Zebryk 1993).

Late-successional species: life history characteristics

The continued presence of hemlock in forests for sustained periods of time is evidence of its remarkably high survivorship under low-light and low-growth conditions (Canham et al. 1994, Pacala et al. 1996) (Table 6). Hemlock grows relatively quickly when light is plentiful, but it can also survive while suppressed for long periods of time in the understory. Despite this flexibility, it does not produce and disperse recruits as successfully as the other species that comprise this community (Pacala et al. 1996, Ribbens et al. 1994). As a result, hemlock basal area in this study stayed relatively constant: while it did not lose basal area, it did not gain basal area either, especially when present in a community where it had an initially low abundance and competed with other species. However, the recruitment parameters used in the model may affect these results. In SORTIE, all species except beech are assigned the same number of new recruits per 100 cm diameter tree (Pacala et al. 1996). This may bias these simulations toward more hemlock than was realistic because under natural conditions, hemlock seeds experience a 15 to 25% germination rate and hemlock seedlings are extremely susceptible to failure (Godman and Lancaster 1990,

Mladenoff and Stearns 1993, Swartley 1984). Because of its low regeneration rate, hemlock in the field may actually take much longer to dominate than it did in these simulations. However, certain site conditions may favor hemlock: for example, hemlock is quite successful in ravines and on rocky slopes (Black and Mack 1976, Rogers 1978, Whitney 1990).

Beech was quick to gain basal area in this forest. While beech grows more slowly than hemlock in full sun, it grows more quickly than hemlock under low light conditions (Table 6). In addition, it survives well under its own deep canopy while saplings of other species are more severely limited by its shade than by the shade of any other species (Canham et al. 1994). It also disperses over a larger distance, though still largely by sprouts, and has even higher low-light survivorship than hemlock (Table 6). As a result, once it is established beech is likely to continue increasing in basal area until it dominates the stand either by itself or with hemlock. Another reason for the quick increase of beech is its reproduction by root sprouting. In fact, in SORTIE the number of recruits per 100 cm beech tree is lower than the number of recruits per 100 cm tree of all other species in order to compensate for this method of reproduction, which is common at Great Mountain Forest (Pacala et al. 1996). While it is possible that these recruitment parameters actually make beech more prolific in SORTIE than in nature, a lower recruitment rate would simply lengthen the temporal scale of the dynamics. Beech saplings will still survive for an exceptionally long time beneath the shade of their conspecifics regardless of how quickly they colonize available space.

After the simulated loss of a significant amount of hemlock in hemlock stands, yellow birch was quick to occupy the space made available. This gap-phase species grows very quickly in full sun (Table 6). It also grows quickly in low light (Table 6), a trait which makes yellow birch uniquely able to take advantage of a small and short-lived gap. However, yellow birch has a low-growth mortality rate intermediate between those of early- and late-successional species (Pacala et al.

Table 7.—Predicted mortality rate (%/5 years) for sapling of each species under ambient light levels predicted for each canopy species (from Canham et al. 1994). Canopy species are listed horizontally across the top of the table. Species are listed in order of decreasing shade tolerance. See Table 1 for species abbreviations.

Sapling species	BE	HM	SM	YB	BC	RM	WA	RO
BE	2.6	2.5	2.2	2.2	2.1	2.2	2.1	2.1
HM	3.0	1.2	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
SM	11.8	4.8	0.6	0.6	0.2	0.4	0.2	0.2
YB	20.4	11.2	2.3	2.4	1.0	1.7	1.0	1.0
BC	25.0	8.5	0.1	0.1	<0.1	<0.1	<0.1	<0.1
RM	56.0	34.4	2.7	3.1	0.1	0.1	0.1	0.1
WA	68.1	46.8	5.9	6.5	0.5	2.6	0.5	0.4
RO	76.8	57.3	6.6	7.5	0.1	2.1	0.1	0.1

1996). Mortality rate determined the successional status of yellow birch in these stands: after early-successional species, yellow birch was next to die when light became limiting. And under conditions of full sun, yellow birch RBA was outpaced by the early-successional species because its mortality curve lay above those of the early-successional species (Pacala et al. 1996). In field studies, yellow birch seeds are as likely to travel 1 m as 100 m. Incorporated into SORTIE, this flat dispersal function enables it to colonize distant gaps, thereby preventing the species from disappearing.

Early-successional species: life history characteristics

The early dominance of species such as red maple, black cherry, red oak, and white ash can be attributed to quick growth in full sun while their speedy decline resulted from high rates of mortality in low sun (Table 6). These species disperse well and grow quickly, but late-successional species grow almost as quickly in full sun. The late-successional species cast more shade and have lower mortality and more rapid growth in the low-light conditions they create (Canham et al. 1994). Thus, if even one late-successional tree is established, it will survive and produce recruits until the early-successional species no longer have access to light (Table 7).

Conclusions

While the results from this analysis can be used to predict forest development in other forested watersheds with similar species and size structures, the specific predictions presented here are not directly applicable to every southern New England forest. For example, research in central Connecticut has shown that black birch recruitment is quite common following hemlock mortality (Jenkins et al. 1999, Orwig and Foster 1998). The SORTIE model is not currently parameterized to predict black birch dynamics, and black birch is not common at our study site, so our analysis

excludes this early-successional species. Also not considered here is the potential recruitment and migration of species across stand boundaries. Finally, this analysis does not account for the effects of any other disturbance. It is rare that 500 years of autogenic succession would occur without logging, windthrow, or invasion by another forest pest; these events would interrupt the long-term predictions we present here.

Still, this general pattern of succession will follow the mortality of a dominant species in any forest where light is the factor most limiting to growth. Immediately following mortality, shade-intolerant and gap-phase species will experience an increase due to enhanced light in newly-formed gaps. Where late-successional shade-tolerant species are present, they will slowly gain in dominance and continue to persist for years after the disturbance. In essence, selective removal of the dominant species will “restart” succession by increasing the RBA of early-successional shade-intolerant species; over time, late-successional and shade-tolerant species will increase in abundance at the expense of the early-successional species. Because variations in light transmission and shade tolerance can explain growth and mortality of individual tree species, they are excellent predictors of succession (Peet and Christensen 1980, Pickett et al. 1987).

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