Effects of an introduced pathogen on resistance to natural disturbance: beech bark disease and windthrow

Michael J. Papaik, Charles D. Canham, Erika F. Latty, and Kerry D. Woods

Abstract: In forests of eastern North America, introduced pathogens have caused widespread declines in a number of important tree species, including dominant species such as American beech (*Fagus grandifolia* Ehrh.). Most studies have focused on changes in forest composition and structure as a direct result of mortality caused by a pathogen. Our field studies of windthrow resistance in forests of northern New York and northern Michigan demonstrate that resistance of beech trees to windthrow is severely reduced by beech bark disease (BBD). This reduced resistance was primarily due to the increase in the probability of stem breaks of moderately and highly infected beech trees. The severity of BBD infection on individual trees has a significant negative effect on resistance to windthrow. We tested potential consequences of this for long-term composition and structure in these forests by using a simulation model, SORTIE. We found that species such as yellow birch (*Betula alleghaniensis* Britt.) and eastern hemlock (*Tsuga canadensis* (L.) Carr.) increased in basal area primarily because of the effect BBD had on the creation of new seedbed substrates. Our results highlight the indirect effects that host-specific pathogens can have on community dynamics and species coexistence in forests.

Résumé : Des agents pathogènes non indigènes ont causé des dépérissements généralisés chez plusieurs espèces importantes d'arbres dans les forêts de l'est de l'Amérique du Nord, incluant des espèces dominantes telles le hêtre à grandes feuilles (*Fagus grandifolia* Ehrh.). La plupart des études ont mis l'accent sur les changements dans la structure et la composition de la forêt qui sont le résultat direct de la mortalité causée par l'agent pathogène. Les travaux de terrain des auteurs sur la résistance au chablis dans les forêts du nord des États de New York et du Michigan démontrent que la résistance des hêtres au chablis est sévèrement réduite par la maladie corticale du hêtre. Cela est dû principalement à l'augmentation de la probabilité que la tige des hêtres modérément à sévèrement infectés se brise. La sévérité de l'infection a un effet négatif important sur la résistance au chablis des arbres affectés par la maladie. Ils ont testé les conséquences possibles de cette situation sur la composition et la structure de ces forêts à long terme à l'aide du modèle de simulation SORTIE. Ils ont trouvé que les espèces comme le bouleau jaune (*Betula alleghaniensis* Britt.) et la pruche du Canada (*Tsuga canadensis* (L.) Carr.) ont augmenté leur surface terrière principalement à cause de l'effet de la maladie corticale du hêtre sur la création de nouveaux substrats de lits de germination. Leurs résultats mettent en évidence les effets indirects que les agents pathogènes spécifiques à un hôte peuvent avoir sur la dynamique de la communauté et la coexistence des espèces dans les forêts.

[Traduit par la Rédaction]

Introduction

Introduced pests and pathogens, such as chestnut blight fungus (*Cryphonectria parasitica* (Murr.) Barr), Dutch elm disease fungus (*Ophiostoma ulmi* (Buism.) Nannf.), hemlock woolly adelgid (*Adelges tsugae* Annand), and beech bark disease (BBD) (*Cryptococcus fagisuga* Lind., with *Nectria* spp.), have caused widespread declines of trees in forests of eastern North America. Chestnut and elm often dominated in their communities, and their removal resulted in major changes in forest dynamics and composition (Harlan 1976; Harper 1977; Burdon and Shattock 1980; Liebhold et al. 1995). American beech (*Fagus grandifolia* Ehrh.) is also a dominant species in many regions of eastern North America (McIntosh 1972). Once BBD is present in a stand, it spreads rapidly, killing >50% of beech trees >25 cm diameter at

Received 7 April 2004. Accepted 20 May 2005. Published on the NRC Research Press Web site at http://cjfr.nrc.ca on 6 September 2005.

M.J. Papaik.[1,2] Institute of Ecosystem Studies, Box AB, Millbrook, NY 12545, USA; Department of Natural Resources Conservation, Holdsworth Natural Resources Center, University of Massachusetts, Amherst, MA 01003, USA.
C.D. Canham. Institute of Ecosystem Studies, Box AB, Millbrook, NY 12545, USA.
E.F. Latty. Institute of Ecosystem Studies, Box AB, Millbrook, NY 12545, USA; Department of Biology, Hollins University, P.O. Box 9615, Roanoke, VA 24020, USA.
K.D. Woods. Bennington College, 1 College Drive, Bennington, VT 05201, USA.

[1] Present address: Université du Québec à Montréal, C.P. 8888, succursale Centre-ville, Montréal, QC H3C 3P8, Canada.
[2] Corresponding author (e-mail: papaikm@ecostudies.org).

doi: 10.1139/X05-116

1.35 m (diameter at breast height (DBH)) (Houston 1994), skewing the size structure of beech populations to smaller classes (Gavin and Peart 1993; Forrester et al. 2003). Some stands are then characterized by dense thickets of beech sprouts and deformed trees that are only slowly killed by BBD (Houston 1975). However, BBD does not significantly change sprout vigor (Jones and Raynal 1987). Thus, beech may remain an important species and inhibit a dramatic reorganization of the canopy community (Twery and Patterson 1984).

Recent studies examining changes in canopy composition in the aftermath of BBD reinforce this conclusion. Leak and Smith (1996) determined that natural succession was the dominant factor governing change in forest composition since the introduction of BBD at Bartlett Experimental Forest in the White Mountains of New Hampshire in the 1950s; the modest decline of beech was due to timber management, and BBD accounted for only minor changes. Fahey (1998) found that in a 110-year-old stand in Arnot Forest in south-central New York, where BBD has been present since about 1970, forest change was consistent with the Oliver and Larson (1996) model of a stand undergoing transition from the understory reinitiation stage to the old-growth stage. Other studies drew more nuanced conclusions. DiGregorio et al. (1999) found that sugar maple growth was stimulated in the nongap understory by as much as 30%, presumably as a result of the thinning of the canopy due to the diffuse disturbance caused by BBD. Forrester et al. (2003) concluded that BBD, present at Huntington Forest, New York, since the 1960s, has hastened the onset of uneven-aged conditions, but in contrast to the findings of Fahey (1998), without the stand undergoing the understory reinitiation phase.

Secondary effects of BBD may lead to long-term changes not anticipated by any of these studies. In forests of the southeastern United States that are free of BBD, beech persistence is largely due to the high resistance of intermediate-sized beech trees (20–40 cm DBH) to windthrow (Batista et al. 1998). In stands where BBD is present, however, beech trees in this size class have a high susceptibility to windthrow (Canham et al. 2001), suggesting that these beech populations may be at risk over the longer term. Further, several studies noted an apparent increase in snapped stems of diseased beech and attributed it to the effects of BBD (e.g., Houston and O'Brien 1983). Overall, coarse woody debris (CWD) increases two to four times in stands affected by BBD (McGee 2000), and rotting CWD is an important seedbed substrate for small-seeded species, such as yellow birch (*Betula alleghaniensis* Britt.) and eastern hemlock (*Tsuga canadensis* (L.) Carr.) (Gilbert 1965; Godman and Lancaster 1990; Peterson and Pickett 1995; McGee 2001). Higher CWD loads, combined with higher understory light levels due to the canopy thinning effects of BBD (Digregorio et al. 1999) and windstorm gaps (Peterson and Pickett 1995), could have long-term impacts on beech persistence and subsequent community dynamics that may not be evident in short-term (≤60 years) studies of the impact of the disease.

In this paper, we (1) quantify how the presence of BBD in forests of eastern North America alters the resistance of beech to both uprooting and stem break; (2) determine whether beech trees in New York show progressively higher susceptibility to windthrow as BBD severity increases; and (3) incorporate the results into SORTIE, a spatially explicit model of forest dynamics (Pacala et al. 1996), to investigate the consequences of the change in windthrow mortality of beech for long-term forest composition and structure in beech–hemlock stands of northern hardwood forests of northeastern North America.

Materials and methods

Field data

This research is based on data collected after separate windstorms in New York and Michigan. The New York site, where BBD has been present since the 1960s, was used for most of the data analysis and simulations. The Michigan site, where BBD was absent at the time of the study, was used to compare the windthrow resistance of beech to that of sugar maple in BBD-free stands.

In July 1995, an intense windstorm crossed northern New York state, affecting old-growth and second-growth stands in the Five Ponds Wilderness Area of the western Adirondack Mountains. Forty-three 20-m-radius circular plots (0.126 ha) along a swath crossing the storm path were censused a year after the storm (Canham et al. 2001). BBD severity on each beech tree was assessed in 18 of the 43 plots, but that information was not used in the original analyses reported by Canham et al. (2001). All trees >10 cm DBH and rooted within plots were tallied by species, DBH, and condition (tipped up, snapped below crown, or damaged crown). A tree was considered removed from the canopy (i.e., dead for the purposes of the simulations) if it was uprooted, tipped >45° from perpendicular, or broken below the crown. Disease severity was based on a visual assessment of bark defect (Burns and Houston 1987; Latty et al. 2003). Four levels of infection were scored: no indication of defect (none); the presence of *C. fagisuga* or discrete bark lesions <3 cm in diameter (low); obvious necrotic tissue with blocky patches on <50% of the circumference of the tree (moderate); and obvious necrotic tissue with blocky patches on >50% of the circumference of the tree (high). A total of 1116 trees within the 18 plots were scored for windthrow. This included 705 beech trees that were also scored for BBD (Table 1).

In July 2002, an intense, local storm affected an old-growth stand in the upper peninsula of Michigan, where BBD was absent at the time of the storm (the 100-ha Dukes Research Natural Area of the Hiawatha National Forest) (Woods 2001, 2004). Eighty-three circular, 0.2-acre (0.08-ha) permanent inventory plots in a 2.9-ha mapped stand were remeasured following the storm. Of 3894 stems with DBH >5 cm, about 7% were tipped up or broken below the crown; the mortality rate increased with size. Storm-caused mortality varied between plots from 0% to nearly 50% of canopy stems.

Data analysis

We used the same nonlinear logistic regression model developed by Canham et al. (2001) to estimate windthrow susceptibility parameters for both the Michigan site with no BBD and the 18 plots in New York in which BBD was assessed. Canham et al. (2001) defined windthrow to include both snapped stems and trees tipped >45° from zenith. The method estimates species-specific parameters that determine

Table 1. Basic statistics on demographics, tree size, and windstorm damage of all stems ≥10 cm DBH in the 18 plots in New York in which beech bark disease (BBD) level was recorded.

	n	Density (no./ha)	Basal area (m^2/ha)	Max. DBH (cm)	Total windthrow (%)	Stem break (%)	Tipped (%)
All beech	705	313.3	9.2	60	24.8	12.5	12.3
No BBD	381	169.3	3.5	60	17.1	7.1	10
Low BBD	127	56.4	1.5	48	18.9	7.9	11
Moderate BBD	88	39.1	1.5	37.3	31.8	15.9	15.9
High BBD	109	48.4	2.8	570	53.2	33.9	19.3
Sugar maple	138	61.3	5.8	83	37.7	12.3	25.4
Red spruce	213	94.7	7	67.1	47	16.4	30.5
Yellow birch	60	26.7	5.1	83	33.3	8.3	25
Subtotal	1116	496	27.2	83	31.1	13.1	18.1
Other species	72	32	3.3	79	58.3	9.7	48.6
Total	1188	528	30.4	83	32.7	12.8	20

the probability of windthrow as a function of species and DBH and as an index of local storm severity:

$$[1] \qquad \log\left(\frac{P_{isj}}{1-p_{isj}}\right) = a_s + c_s S_i \mathrm{DBH}_{isj}^{b_s}$$

where p_{isj} is the probability of windthrow for the *j*th individual of species *s* in plot *i*; S_i is the estimated storm severity index for plot *i* (scaled between 0 and 1); DBH_{isj} is diameter at breast height of the *j*th individual of species *s* in plot *i*; and a_s, b_s, and c_s are estimated, species-specific parameters. The storm severity index (S_i) is estimated by the likelihood procedure and allowed to vary between 0 and 1, with 0 representing no windthrow damage and with 1 representing the most severe level of windthrow damage observed in the data set. Four species, beech, sugar maple, red spruce (*Picea rubens* Sarg.), and yellow birch (*B. alleghaniensis*), were sufficiently abundant in the New York plots to be included in the analyses.

To estimate separate susceptibility parameters for each of the four levels of BBD, we treated each infection level as a separate beech "species". Thus, the full disease model has seven "species": beech (×4 levels of BBD), sugar maple, yellow birch, and hemlock. The nondisease model uses the four biological species. We tested alternative disease models that looked for evidence of threshold effects of BBD by pooling infection classes according to BBD severity. This set of alternative models was used in four separate analyses with different dependent variables: overall mortality, stem snap, tip-up, and crown damage.

We used the Akaike information criterion (AIC), corrected for small data sets ($\mathrm{AIC_c}$), to determine the most parsimonious model in each analysis (Burnham and Anderson 2002). The model with the lowest $\mathrm{AIC_c}$ has the strongest support in the data, and the difference in AIC between two models ($\Delta\mathrm{AIC_c}$) provides a measure of the relative strength of evidence in the data for the two different models. We report $\Delta\mathrm{AIC_c}$ as

$$[2] \qquad \Delta\mathrm{AIC_c} = \mathrm{AIC_c}(\text{alternative}) - \mathrm{AIC_c}(\text{best})$$

SORTIE simulation model

We used SORTIE (Pacala et al. 1996) to test stand-level consequences of increased susceptibility to windthrow in beech trees with BBD. SORTIE is a spatially explicit, individual-based neighborhood model that forecasts tree population dynamics by predicting the fate of individual trees in 5-year time steps. It consists of species-specific functions that predict each tree's available light (Canham et al. 1994), growth (Pacala et al. 1994), mortality (Kobe et al. 1995), wind-related mortality (Papaik 1998, 2005), and contribution to regeneration (Ribbens et al. 1994).

Regeneration is defined as the number of new seedlings that would be produced by a "standardized" tree with 30 cm DBH if the entire area of the seed shadow consisted of favorable substrate (following the notation of Ribbens et al. (1994)). The regeneration model consists of a dispersal function that determines the spatial positions of all new recruits produced by every tree with DBH ≥10 cm (Ribbens et al. 1994); and a seedling establishment function that calculates the number of seeds, their germination, and 1-year seedling establishment success as a species-specific function of tree size, seed mass, and seedbed substrate type (Greene and Johnson 1998). If a seedling establishes, SORTIE evaluates its persistence through the first and each subsequent 5-year time step as a function of available light. The seedling establishment function has three components: (1) substrate creation; (2) species-specific seed germination and seedling establishment probabilities for different substrates; and (3) substrate changes over time. First, substrate creation is driven by tree mortality. When trees die, some fall over, creating fresh CWD. We assume, for simplicity, that trees that die from causes other than windthrow die standing and disappear from the stand without any further contribution to community dynamics. This is a conservative assumption that underestimates CWD creation. All windthrown trees fall at the time of death and create fresh CWD; 50% of them uproot, and the rest snap. The area of fresh CWD created by a fallen tree is calculated as (0.5 × DBH × tree height), which is equivalent to a triangle that is the height of the tree, with DBH as the width of the base.

The second component of the substrate model defines the species-specific probabilities of seed germination and seedling establishment for three different seedbed substrate types: fresh CWD, rotting CWD, and litter. Substrate favorability is a function of seed mass and is based on field experiments by Greene and Johnson (1998) (parameters reproduced in Table 2*a*). A substrate is either unfavorable for seedling estab-

Table 2. Substrate parameters used in the simulations.

(*a*) Substrate favorability parameters.

Species	Probability of establishing on unfavorable substrate
Yellow birch	0.039
Hemlock	0.056
Red maple	0.111
Sugar maple	0.169
Black cherry	0.217
Beech	0.282

(*b*) Substrate decay parameters.

Substrate	α	β
Fresh CWD decaying to rotting CWD	–0.5	2.6
Fresh CWD decay × 0.5 (sensitivity test)	–0.2	2
Rotting CWD (proportion decay/5 years)	0.45	

Note: Favorability parameters are derived from Greene and Johnson (1998); decay parameters, from M. Beaudet (unpublished data) for eq. 4. CWD, coarse woody debris.

lishment of all species (i.e., fresh CWD and litter) or differentially favorable for seedling establishment of some species (e.g., rotting CWD is favorable for the establishment of small-seeded species, such as hemlock and yellow birch (Gilbert 1965; Runkle 1985; Harmon and Franklin 1989; Godman and Lancaster 1990; McGee 2001)).

The final component of the substrate model calculates how substrates decay (i.e., change into other substrates). Substrate is created by tree fall that creates fresh CWD. Fresh CWD decays to rotting CWD as a logistic function of time in 5-year time steps, according to

$$[3] \qquad \text{Substrate} = e^{-\alpha t^{\beta}}$$

where t is time in time steps since the creation of fresh CWD; and α and β are decay parameters. A constant proportion of rotting CWD decays to forest litter in each time step. Parameter values are based on observations of a postharvest chronosequence in managed stands in mixed-hardwood forests in southern Quebec (M. Beaudet, unpublished data). Beaudet estimated that within 10 years ~95% of fresh CWD decays to rotting CWD, and after 5 years, ~45% of rotting CWD "decays" to forest litter (Table 2*b*).

The wind disturbance submodel integrated into SORTIE (Papaik 1998) requires that the user specify (1) a wind disturbance regime, consisting of return intervals for storms of a wide range of severity; and (2) parameters that define species-specific resistance to windthrow as a function of an index of storm severity (Canham et al. 2001). We based our wind disturbance regime on Frelich and Lorimer's (1991) reconstruction of long-term wind disturbance in forests of the upper midwest region of the United States (Table 3).

BBD lowers the growth rate of infected trees (Twery and Patterson 1984; Gavin and Peart 1993), but we did not have appropriate data to directly model this effect. For this reason, together with a second one discussed in the substrate model below, our simulations of the effects of BBD are conservative and do not capture reduced growth or increased mortality of larger beech trees that is directly due to the effects of BBD. It should be noted that the original parameterization of SORTIE used data from stands in northwestern Connecticut in which the disease had been present for several decades.

Table 3. Windstorm disturbance regime used in all simulations, showing the expected storm mortality for the six different return intervals used in these simulations.

	Return interval (years)					
	40	80	160	320	640	1280
Storm index × 100 (% mortality)	2.8	13.2	23.7	34.1	44.5	54.9

Note: Derived from Frelich and Lorimer (1991).

Table 4. Maximum-likelihood estimates for stands in New York in which beech bark disease (BBD) or a high level of BBD (HBBD) was present for parameters in eq. 1 that were used in the simulations (see text for full explanation) and for stands in the upper peninsula of Michigan in which BBD was absent.

Species	a_s	b_s	c_s
New York stands			
Fagus grandifolia			
Stands without BBD	–1.960	0.68	0.19
Stands with BBD	–3.057	0.94	0.23
Stands with HBBD	–1.028	0.9	0.1
All stands			
Tsuga canadensis	–1.599	1.47	0
Betula alleghaniensis	–3.302	0.19	2.34
Prunus serotina	–2.752	0.68	0.66
Acer saccharum	–1.960	0.68	0.19
Acer rubrum	–2.261	0.43	1.14
Michigan stands			
Fagus grandifolia	–7.565	0.13	4.86
Acer saccharum	–7.148	0.1	4.96

Estimating the impact of BBD on community structure and composition

We evaluated the implications for communities of the change in the windthrow susceptibility of beech; for this we used three different windthrow resistance parameter sets for *F. grandifolia* (Table 4). For stands with high levels of BBD on beech trees (HBBD), we used parameter values estimated in our analysis of the 18 plots in New York that were scored for BBD level. For stands simulating the presence of BBD, we used parameter values derived from all 43 plots from Canham et al. (2001). For stands simulating the absence of BBD, we set beech parameter values for windthrow to be the same as those for sugar maple. There were two reasons for our assumption that beech windthrow parameters would closely resemble those of sugar maple in the absence of BBD. First, Batista et al. (1998) found that small and medium-sized beech trees were among the most wind-firm trees in BBD-free forests of the southeastern United States. Second, our Michigan data revealed that windthrow parameters for beech and sugar maple in forests free of BBD were virtually identical (Woods 2004). For all species other than

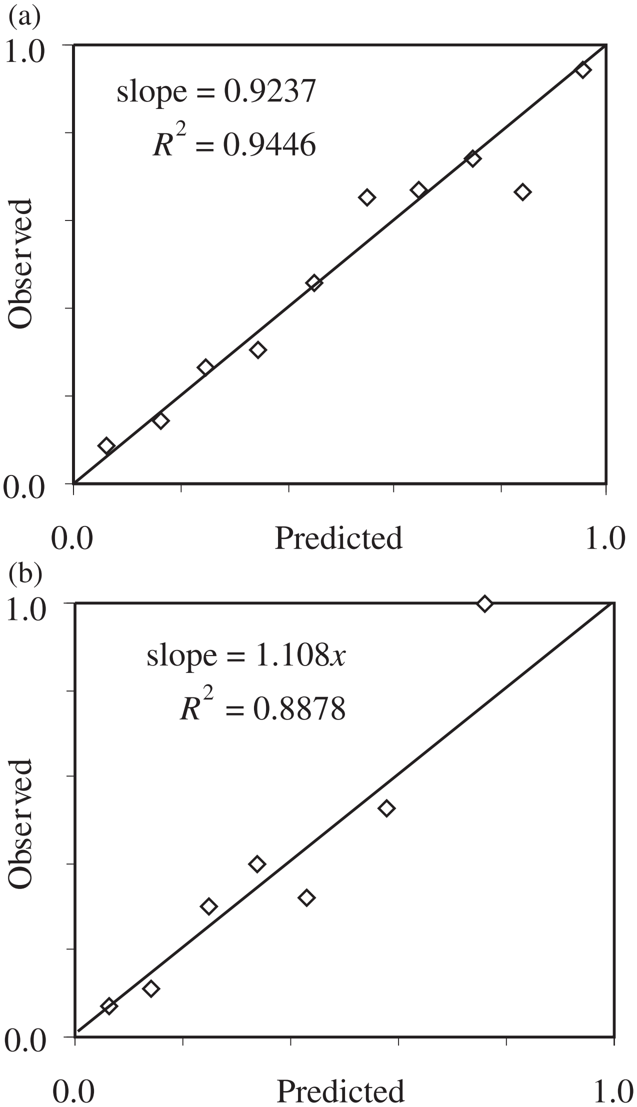


Fig. 1. Goodness of fit of the maximum-likelihood analysis of probability of windthrow as a function of storm severity index, species, and size for the data set where level of beech bark disease infestation was noted: (*a*) full-mortality model; (*b*) stem-snap model. Data points represent the observed proportion of all species of dead trees (vertical axis) as a function of predicted probability of windthrow (horizontal axis). The solid diagonal line indicates a 1:1 correspondence between observed and expected. The greater deviations from 1:1 at higher predicted probabilities are due to the relatively few observations in that class.

F. grandifolia, we used the parameter values in all simulations that were estimated by Canham et al. (2001) (Table 4).

The plot size for each simulation was 16 ha, with 10 replicate runs of 500 years each. The initial population of trees was determined by randomly dispersing 1-cm-DBH saplings of each species throughout the plot at a density of 25 saplings/ha.

CWD creation and decay were important parts of this model and difficult to parameterize precisely. We ran two different sets of tests to explore the sensitivity of the model to different substrate creation and decay rates. First, we doubled and quadrupled the area of CWD with each treefall (CWD × 2 and CWD × 4). Second, we delayed the creation of rotting CWD by halving the decay rate of CWD (fresh decay × 0.5) such that 95% of fresh CWD became rotting CWD after 20 years, instead of 10 years. This test effectively increases the delay between the creation of canopy gaps at the time of the windstorm and the creation of rotting CWD. In what follows, "baseline" refers to baseline substrate conditions.

Results

Effects of BBD on susceptibility of beech to windthrow

Our data collected following the 1995 storm in the Adirondacks demonstrate that the probability of windthrow increases as a function of severity of BBD (see Table 1). This is primarily due to increased stem breakage; the most severely infected trees were almost twice as likely to experience stem break as to experience uprooting (Table 1). The best mortality models produced excellent fits to the data (Fig. 1*a*). Two mortality models had virtually identical support in the data (models 5 and 6, $\Delta\mathrm{AIC_c}$ = 0.26, Table 5), and both had considerably more support than the nondisease model for mortality (model 1, $\Delta\mathrm{AIC_c}$ = 5.21); therefore, we conclude that there is clear evidence that beech windthrow mortality is a function of disease severity. In particular, there is considerable support in the data for an increase in the probability of stem snap for trees with BBD ($\Delta\mathrm{AIC_c}$ = 4.41) and less support for an increased probability of uprooting ($\Delta\mathrm{AIC_c}$ = 2.04). The most parsimonious stem-snap model (model 3, Table 5) indicates that low levels of BBD have no effect on stem snap, but moderate and high levels of BBD do. Therefore, we infer that the increase in total windthrow mortality of beech trees in BBD stands (Fig. 2*a*) is due primarily to the increased probability of stem breaks in moderately and highly infected beech trees.

The estimated resistance of medium-sized beech (30 cm DBH) to windthrow was dramatically reduced with respect to other species (Fig. 2*a*). However, smaller beech trees (10 cm DBH) remained highly resistant to windthrow, even when infested with BBD (Fig. 2*b*). This was especially evident as storm severity increased. In New York, the resistance to windthrow of the entire population of beech trees was dramatically different from that of the subset that showed no external sign of infection (Fig. 3*a*). The resistance of these putatively disease-free trees in New York was similar to that of sugar maple (Fig. 3*a*), just as it was in the disease-free stands in the upper peninsula of Michigan (Fig. 3*b*). Note that because the storm severity index is scaled independently for each data set, similar values of the index for different sites do not equate to similar storm intensity or probability of mortality. For this reason, we used the Michigan results to infer that the resistance of beech to windthrow prior to the presence of BBD in New York was similar to the resistance of sugar maple.

Effects of windthrow and BBD on long-term forest dynamics

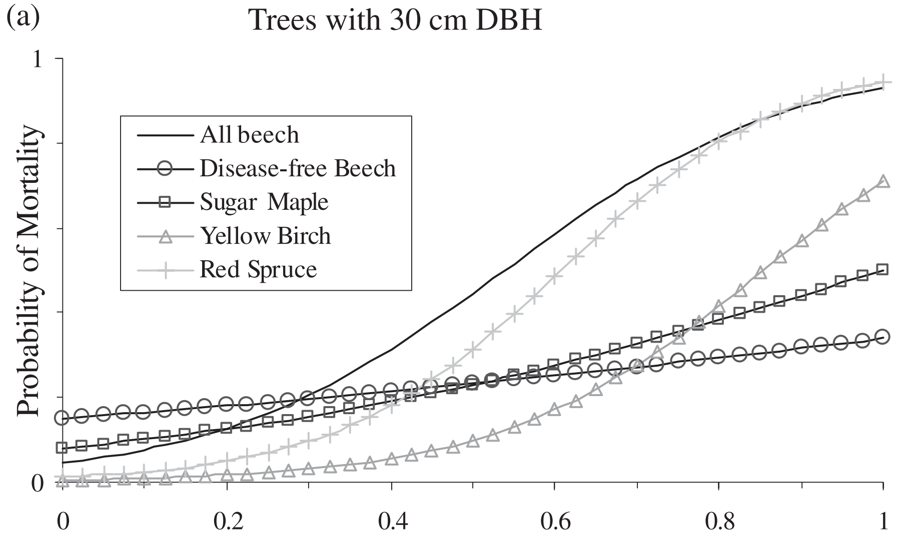
We simulated changes in community dynamics to three different levels of BBD in the context of the same long-term wind disturbance regime. In the absence of BBD, beech was the long-term competitive dominant among the six major

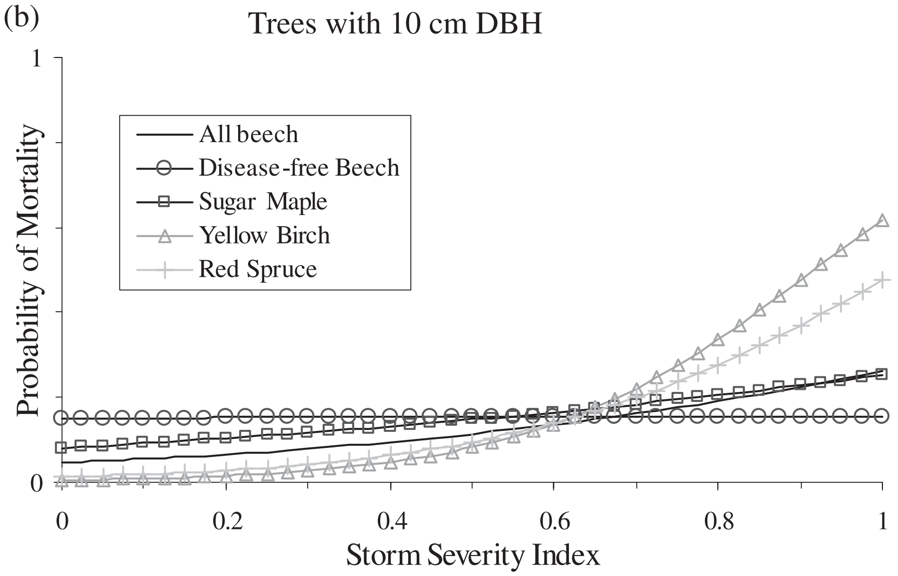
Table 5. Determining the best models for estimating the effect of beech bark disease (BBD) on wind damage.

BBD model	ΔAIC_c Mortality	 Stem snap	 Tipover
(1) No effect of BBD	5.21	4.41	2.04
(2) Any level of BBD has the same effect	3.45	8.2	0
(3) Low level of BBD has no effect; moderate and high levels of BBD have the same effect	3.44	0	1.4
(4) Low level of BBD has no effect; moderate and high levels of BBD have different effects	6.25	2.71	8.05
(5) Low and moderate levels of BBD have the same effect; high level of BBD has a different effect	0	4.33	6.54
(6) The effect of BBD is a function of the level of BBD	0.26	3.78	6.69

Note: The best model has $\Delta AIC_c = 0$; a difference of <2 suggests that we should expect to see a lot of variation in which model would be the best if we could draw multiple independent samples; a difference of >4 suggests that the model with the larger AIC_c has considerably less support (Burnham and Anderson 2002). AIC_c, Akaike information criterion, corrected for small data sets.

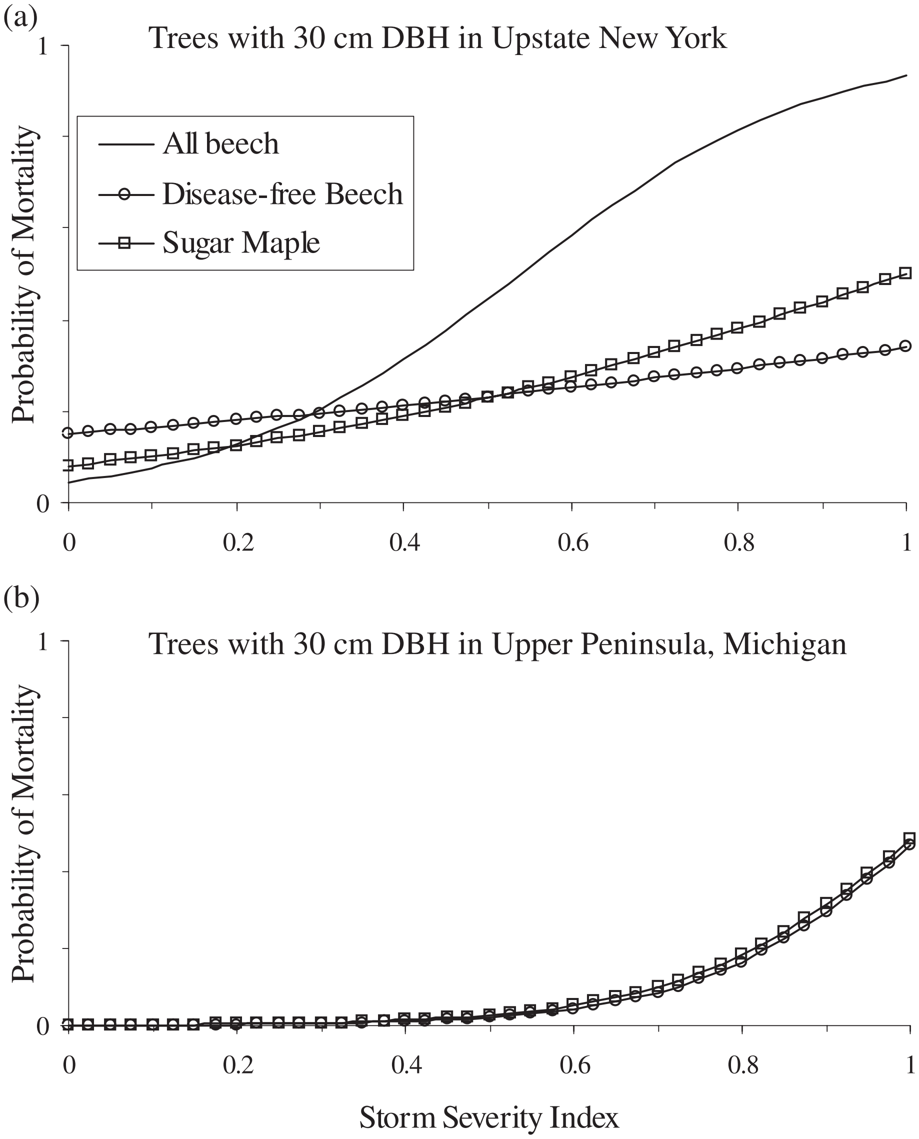
Fig. 2. Predicted probabilities of wind mortality as a function of storm severity index, determined by using eq. 1 and parameters reported in Table 4: (*a*) 30 cm DBH; (*b*) 10 cm DBH.





tree species in northern New York (Fig. 4*a*). Yellow birch and hemlock persisted but in gradually declining importance throughout the simulation period. Although beech remained the long-term dominant species in simulations in which BBD was present (Fig. 4*b*), its basal area was 15%–25% lower (see Fig. 5: no BBD vs. BBD). The model predicted that yellow birch and hemlock both become more important in late-successional stands, as a result of the presence of BBD

Fig. 3. Graphical display of predicted probabilities of windthrow as a function of storm severity index for sugar maple and beech trees with a DBH of 30 cm, determined by using eq. 1, in (*a*) upstate New York forests, including the wind resistance of beech in all 43 plots with parameters as estimated by Canham et al. (2001); (*b*) upper peninsula of Michigan forests with parameters as reported in Table 4.



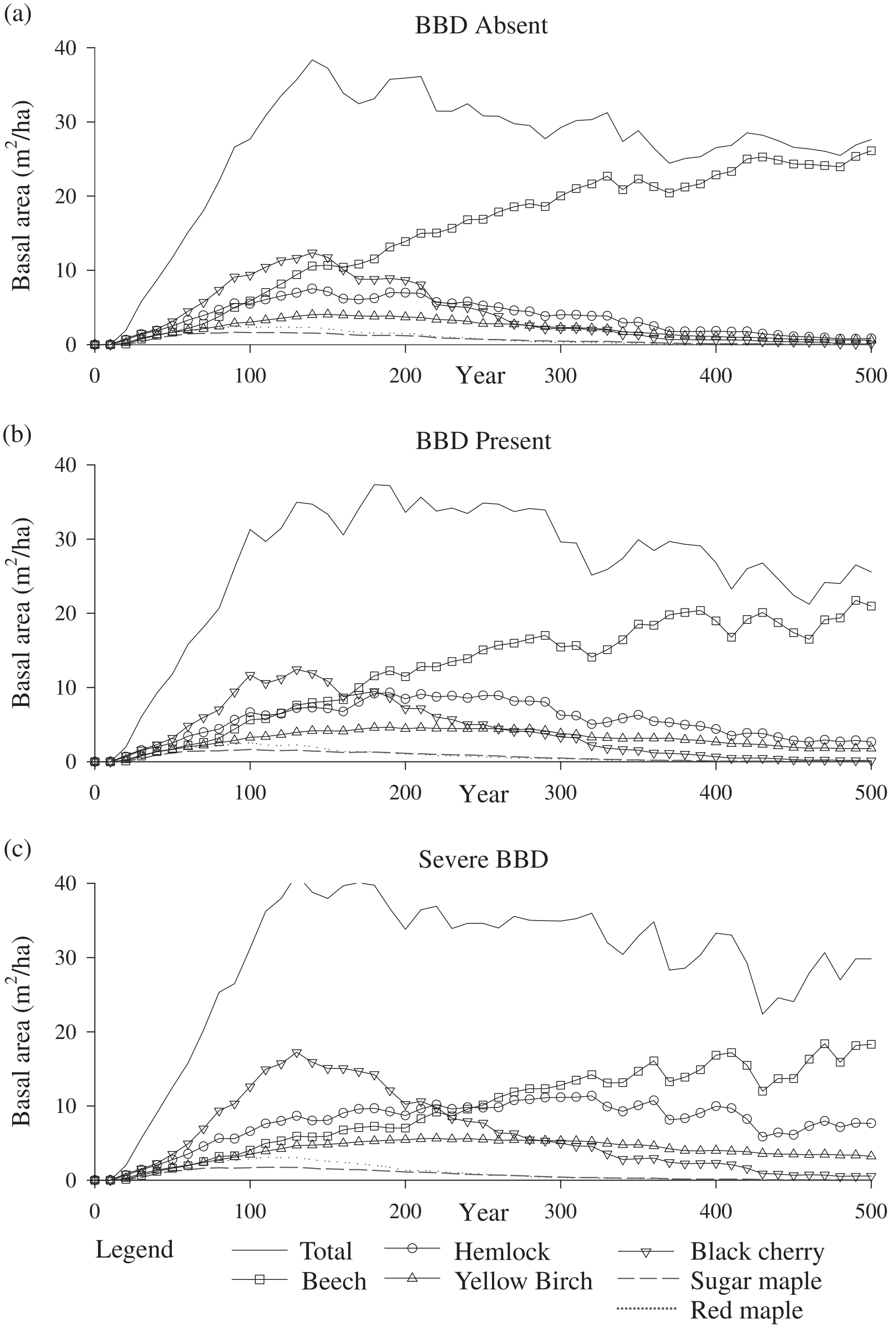
(Fig. 4*b*), and even more so in the most severely impacted stands (i.e., HBBD) (Fig. 4*c*). Beech decline was 1.5–3 times greater in HBBD stands than in BBD stands (Table 6).

Importance of seedbed substrate

The substrate sensitivity tests illustrated how BBD changes the importance of CWD dynamics in these forests. In the absence of BBD, community dynamics were resistant to changes in CWD, showing only minor decreases in beech and minor increases in hemlock and yellow birch basal area as CWD successively doubled (Fig. 5). With BBD present, community dynamics were more sensitive to changes in CWD (Fig. 5). There was a notable increase in hemlock and yellow birch with the first doubling of CWD. A second doubling of CWD resulted in significant differences in stand trajectory, with hemlock and yellow birch codominating with beech. Beech basal area decreased throughout as BBD increased, such that the amount of decrease became more sensitive to CWD dynamics as BBD increased. Nevertheless, beech remained a dominant species in all except the most extreme test (Fig. 5: HBBD).

In our last sensitivity test, we doubled the decay time of fresh CWD to decaying CWD and reran the simulations shown in Fig. 4. This mimicked the delay in the decay of fresh CWD of trees overlying other fallen trees. It spread out the pulse of regeneration of small-seeded species following a storm event, and gaps created by windstorms closed before most of the fresh CWD became decaying CWD. Neither the successional patterns nor the relative basal area of each species differed from those shown in Fig. 4 (results not shown). This implies that in the presence of BBD, favorable seedbed substrate (i.e., decaying CWD) plays a more important role in canopy dynamics than in healthy stands.

Fig. 4. Changes in forest community basal area dynamics as a result of the change in probability of beech windthrow due to beech bark disease (BBD). Results show the mean response of 10 replicate runs using windthrow resistance parameters from Table 4: (*a*) BBD absent; (*b*) BBD present; and (*c*) severe BBD present.



Discussion

Effects of BBD on susceptibility of beech to windthrow

Our analyses of field data revealed that any level of BBD infection increased the susceptibility of medium-sized and large beech trees to windthrow across the entire range of storm severity. Beech trees infected with BBD were presumably more susceptible to stem snap because woodborers and decay fungi weaken the wood beneath phloem tissue killed by BBD (Houston and O'Brien 1983). These results suggest

Fig. 5. Changes in forest community basal area dynamics as a result of the change in probability of beech windthrow, highlighting how sensitivity to coarse woody debris (CWD) dynamics increases with beech bark disease (BBD) level. Bars show the average and standard deviation of the basal area over 100-year intervals for each species and for each BBD test condition.

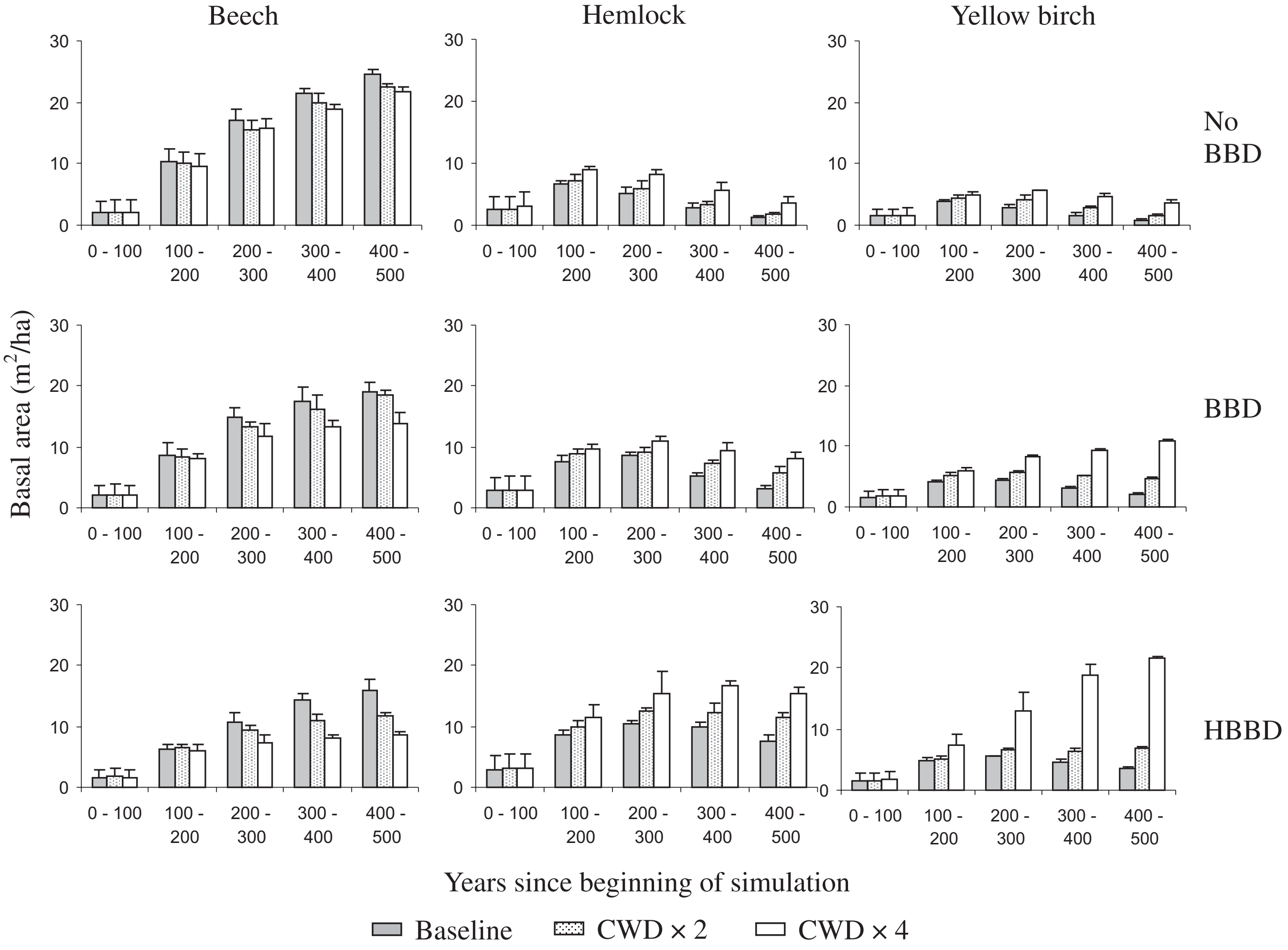


Table 6. Percent change in beech basal area relative to stands that are free of beech bark disease (BBD) or free of a high level of BBD (HBDD) for stands of various ages.

	Stand age (years)				
	0–100	100–200	200–300	300–400	400–500
BBD	–6.5%	–15.8%	–13.6%	–18.0%	–22.8%
HBBD	–20.9%	–40.2%	–38.5%	–33.5%	–34.9%

that BBD does not significantly weaken root systems, a finding that is consistent with Houston's (2001) observation that root sprouting remains a viable mode of beech regeneration in diseased trees. The increase in susceptibility to wind is also consistent with observations of higher CWD in old-growth northern hardwood forests in which BBD is present than in old-growth stands where it is absent. Up to 64% of beech CWD in old-growth stands in Adirondack Park is due to BBD (McGee 2000). By providing additional seedbed substrate, more CWD can differentially favor small-seeded species, such as yellow birch and hemlock (Gilbert 1965; Godman and Lancaster 1990; McGee 2001). Further, the larger and more frequent windthrow gaps that result from increased beech mortality (Krasny and DiGregorio 2001) allow more light to penetrate to the understory, which could increase regeneration opportunities for light-demanding species, such as black cherry and yellow birch (Canham et al. 1994).

Ecological context of the simulations

SORTIE growth, growth-dependent mortality, and dispersal parameters were all estimated in beech–hemlock stands at Great Mountain Forest (GMF), in Connecticut, where sugar maple was present but not dominant. The sites were on nutrient-poor, acidic, sandy loamy soils derived from glacial till and schist and gneiss bedrock (Kobe et al. 1995). Sugar maple fared poorly in our simulations because of their poor low-light survival at these sites (Kobe et al. 1995). At a nearby site with richer soils, Kobe (1996) showed that sugar maple survival dramatically improves; in SORTIE simulations sugar maple went from being a nonpersistent species at GMF to being the dominant species at the richer site, solely because of increased low-light survival. Thus, we are not using these simulations to make specific predictions about what will happen in all northern hardwood stands. We are predicting that similar changes in CWD loading will result in trends similar to those we discuss below. The sensitivity of the stand to changes in CWD will vary, depending on variation in the development of beech thickets and on how parameter estimates respond to ecosystem factors that are not explicitly modeled.

A second consideration is that each seedling is subject to shading effects from all neighboring trees tall enough to have a DBH (1.35 m tall), but seedlings do not cast shade. Under normal seedling densities SORTIE results are not sensitive to this simplification. However, beech stands stressed by BBD can sometimes develop dense thickets of root sprouts that exclude species that are less shade tolerant (Houston 1994). If a thicket were to form, shade cast by trees <1.35 m tall could be an important factor. We would not expect yellow birch basal area to increase, as our results show, because it is a mid-shade-tolerant species. Hemlock, on the other hand, is almost as shade tolerant as beech and may persist or increase modestly in such stands over the time spans of our simulations. Thickets were not explicitly included in our simulations because (1) there was considerable stand-to-stand variation in the development of thickets and a lack of robust data to parameterize it; and (2) we were primarily interested in the logical consequences for community dynamics of changes in the windthrow resistance of beech trees.

Effects of windthrow and BBD on long-term community structure and composition

Our simulations showed that the net effect of BBD on windthrow in stands in which beech is the dominant species was to make diseased forests more disturbance prone, even in the absence of a change in the frequency and intensity of windstorms. The rates of canopy tree turnover and gap formation increased; the forest shifted to an earlier successional condition, in which species that are less shade tolerant, such as hemlock and yellow birch, increased in importance. In this more disturbance prone forest, there will be persistent differences in the dynamics of the herbaceous community and tree seedlings (Woods 2004).

Batista et al. (1998) found that windthrow resistance of subcanopy and canopy trees with 20–40 cm DBH was critical to the persistence of beech populations in regions subject to hurricane disturbance. Our results show that BBD dramatically increases the susceptibility of beech to windthrow in that size range (see Fig. 2*a*) and reduces the importance of beech in the baseline (see Fig. 4) and all sensitivity tests (Fig. 5) but does not threaten its persistence. The persistence of beech is a result of continued high survival of beech saplings (DBH <15 cm), which is due to (1) high windthrow resistance (see Fig. 2*b*); (2) continued vigor of beech sprouts in infested stands (Jones and Raynal 1987); and (3) very high low-light survival (Kobe et al.1995).

The response of the other species in our simulations depended on their shade tolerance and seedling recruitment characteristics. Black cherry basal area did not change in stands with BBD, whereas both hemlock and yellow birch increased (see Fig. 4). Windstorms open up the canopy, but leave the subcanopy and understory less disturbed, such that there is only a modest increase in the average light regime for seedlings. Black cherry regeneration remained minimal in simulations with BBD, because black cherry is not sensitive to changes in substrate conditions induced by BBD, and the improvement in the understory light regime was not enough to increase seedling survival in the understory.

Both hemlock and yellow birch increased in importance because of greater seedling establishment on rotting CWD in BBD-infested stands, but differences in light limitation, resistance to windthrow, and dispersal explain the differences in their responses. Hemlock basal area increased because low-light survival was higher for this species than for all other species in these simulations except beech (Kobe et al. 1995). Yellow birch basal area increased because of high windthrow survival of birch trees, especially large birch trees in intermediate-severity windstorms (Canham et al. 2001; Woods 2004), and because of high mean dispersal distance of birch seeds (Ribbens et al. 1994). As the stand matured, the greater mean dispersal and windthrow resistance of yellow birch relative to the other species allowed it to become widely established in gaps and on favorable substrates created by tree fall and, under certain conditions, to become the dominant species in a stand (Fig. 5). Hemlock basal area increased more than that of yellow birch in stands with BBD (see Fig. 4) because of its superior low-light survival under the understory trees that survive windstorms. Recently, Greene et al. (2004) argued that Ribbens et al. (1994) underestimated the mean dispersal of hemlock. If so, our results likely underestimate the increase in hemlock basal area in BBD-infested stands, because underestimating the local dispersal kernel of a species underestimates the basal area of that species (Papaik 2005).

Importance of seedbed substrate

The distribution of seedbed substrates plays a critical role in the relative seedling abundance of different species but has less influence on overall canopy composition dynamics because of the importance of light to the survival of seedlings to the sapling stage (McGee 2001). Our results show that the distribution of seedbed substrates plays a much more important role in determining canopy community dynamics because of the increase in CWD caused by BBD. Beech CWD increases three- to four-fold because of the increase in all BBD related mortality (McGee 2000). Our simulations underestimated the change in CWD creation due to the effects of BBD, because they reflect only changes in CWD that are due to beech windthrow mortality. This suggests that windthrow is not the dominant source of beech mortality in BBD stands and implies that the results from the CWD × 2 or CWD × 4 sensitivity test may be more indicative of the net effect of BBD on forest community dynamics.

Conclusions

BBD dramatically increases the probability of stem breakage in beech trees in windstorms, leading to greater rotting CWD and higher seedling abundances in species that depend on rotting CWD for regeneration. Beech continues to be a dominant canopy tree species in all our simulations, because small beech trees (i.e., less than approx. 15 cm DBH) remain highly resistant to windthrow and form a dense understory of beech saplings. However, windstorms result in pulses of CWD creation that are greater in stands with BBD. Greater amounts of rotting CWD lead to increased seedling establishment in small-seeded species. Windstorms also create larger gaps that persist longer than single-tree gaps. Thus, even 20 years or more after a windstorm, seedlings of small-seeded species both are more abundant and have a greater probability of reaching canopy status in stands with BBD. As a result, canopy tree community dynamics become more sensitive to CWD dynamics in stands with BBD than in stands without BBD.

Our results highlight impacts of BBD on long-term competitive dynamics and species coexistence that are not evident in short-term studies. Our simulations suggest that the change in beech windthrow resistance alone can potentially reduce the importance of beech. Beech-dominated stands are more disturbance prone in the presence of BBD, and the relative basal area of species that are less shade tolerant will increase in stands where beech is the competitive dominant. However, complex community responses do not necessarily favor pioneer species, despite increased rates of canopy gap formation. We conclude that this invasive pathogen has complex community- and site-specific effects on forest composition and structure, over and above the immediate short-term impact on the affected species.

Acknowledgements

This research was supported by National Science Foundation (NSF) grant DEB-0087214 and by the US Environmental Protection Agency (EPA) through the STAR Graduate Fellowship Program award U91578401-0. The views expressed here are those of the authors and do not represent positions taken by the EPA. Research at the Michigan site was supported by NSF, US Forest Service, and Andrew Mellon Foundation grants. This study is a contribution to the program of the Institute of Ecosystem Studies, Millbrook, New York. We thank Dr. D.F. Greene for feedback and two anonymous reviewers for helpful comments on previous versions of the manuscript.

References

Batista, W.B., Platt, W.J., and Macchiavelli, R.E. 1998. Demography of a shade-tolerant tree (*Fagus grandifolia*) in a hurricane-disturbed forest. Ecology, **79**: 38–53.

Burdon, J.J., and Shattock, R.C. 1980. Disease in plant communities. Appl. Biol. **5**: 145–219.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York.

Burns, B.S., and Houston, D.R. 1987. Managing beech bark disease: evaluating defects and reducing losses. North. J. Appl. For. **4**: 28–33.

Canham, C.D., Finzi, A.C., Pacala, S.W., and Burbank, D.H. 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. Can. J. For. Res. **24**: 337–349.

Canham, C.D., Papaik, M.J., and Latty, E.J. 2001. Interspecific variation in susceptibility to windthrow as a function of tree size and storm severity for northern hardwood tree species. Can. J. For. Res. **31**: 1–10.

DiGregorio, L.M., Krasny, M.E., and Fahey, T.J. 1999. Radial growth trends of sugar maple (*Acer saccharum*) in an Allegheny northern hardwood forest affected by beech bark disease. J. Torrey Bot. Soc. **126**: 245–254.

Fahey, T.J. 1998. Recent changes in an upland forest in south-central New York. J. Torrey Bot. Soc. **125**: 51–59.

Forrester, J.A., McGee, G.G., and Mitchell, M.J. 2003. Effects of beech bark disease on aboveground biomass and species composition in a mature northern hardwood forest, 1985 to 2000. J. Torrey Bot. Soc. **130**: 70–78.

Frelich, L.E., and Lorimer, C.G. 1991. A simulation of landscape-level stand dynamics in the northern hardwood region. J. Ecol. **79**: 223–233.

Gavin, D.G., and Peart, D.R. 1993. Effects of beech bark disease on the growth of American beech (*Fagus grandifolia*). Can. J. For. Res. **23**: 1566–1575.

Gilbert, A.M. 1965. Yellow birch *(Betula alleghaniensis* Britton). *In* Silvics of forest trees of the United States. *Edited by* H.A. Fowells. USDA Agric. Handb. 271. pp. 104–109.

Godman, R.M., and Lancaster, K. 1990. *Tsuga canadensis* (L.) Carr. eastern hemlock. *In* Silvics of North America. Vol. 1: Conifers. *Edited by* R.M. Burns and B.H. Honkala. USDA Agric. Handb. 654. pp. 604–612.

Greene, D.F., and Johnson, E.A. 1998. Seed mass and early survivorship of tree species in upland clearings and shelterwoods. Can. J. For. Res. **28**: 1307–1316.

Greene, D.F., Canham, C.D., Coates, K.D., and LePage, P.T. 2004. An evaluation of alternative dispersal functions for trees. J. Ecol. **92**: 758–766.

Harlan, J.R. 1976. Diseases as a factor in plant evolution. Annu. Rev. Phytopathol. **14**:31–51.

Harmon, M.E., and Franklin, J.F. 1989. Tree seedlings on logs in *Picea–Tsuga* forests of Oregon and Washington. Ecology, **70**: 48–59.

Harper, J.L. 1977. Population biology of plants. Academic Press, London, UK.

Houston, D.R. 1975. Beech bark disease — aftermath forests are structured for a new outbreak. J. For. **73**: 660–663.

Houston, D.R. 1994. Major new tree disease epidemics — beech bark disease. Annu. Rev. Phytopathol. **32**: 75–87.

Houston, D.R. 2001. Effect of harvesting regime on beech root sprouts and seedlings in a north-central Maine forest long affected by beech bark disease. USDA For. Serv. Res. Pap. NE-717.

Houston, D.R., and O'Brien, J.T. 1983. Beech bark disease. USDA For. Serv. For. Insect Dis. Leafl. 75.

Jones, R.H., and Raynal, D.J. 1987. Root sprouting in American beech: production, survival, and the effect of parent tree vigor. Can. J. For. Res. **19**: 539–544.

Jones, R.H., and Raynal, D.J. 1988. Root sprouting in American beech (*Fagus grandifolia*): effect of root injury, root exposure, and season. For. Ecol. Manage. **25**: 79–90.

Kobe, R.K. 1996. Intraspecific variation in sapling mortality and growth predicts geographic variation in forest composition. Ecol. Monogr. **66**: 181–201.

Kobe, R.K., Pacala, S.W., Silander, J.A., Jr., and Canham, C.D. 1995. Juvenile tree survivorship as a component of shade tolerance. Ecol. Appl. **5**: 517–532.

Krasny, M.E., and DiGregorio, L.M. 2001. Gap dynamics in Allegheny northern hardwood forests in the presence of beech bark disease and gypsy moth disturbances. For. Ecol. Manage. **144**: 265–274.

Latty, E.J., Canham, C.D., and Marks, P.L. 2003. Beech bark disease in northern hardwood forests: the importance of nitrogen dynamics and forest history for disease severity. Can. J. For. Res. **33**: 257–268.

Leak, W.B., and Smith, M.L. 1996. Sixty years of management and natural disturbance in a New England forested landscape. For. Ecol. Manage. **81**: 63–73.

Liebhold, A.M., Macdonald, W.L., Bergdahl, D., and Maestro, V.C. 1995. Invasion by exotic forest pests: a threat to forest ecosystems. For. Sci. Monogr. **30**: 1–49.

Logan, J.A., Regniere, J., and Powell, J.A. 2003. Assessing the impacts of global warming on forest pest dynamics. Front. Ecol. Environ. **1**: 130–137.

McGee, G.G. 2000. The contribution of beech bark disease-induced mortality to coarse woody debris loads in northern hardwood stands of Adirondack Park, New York, U.S.A. Can. J. For. Res. **30**: 1453–1462.

McGee, G.G. 2001. Stand-level effects on the role of decaying logs as vascular plant habitat in Adirondack northern hardwood forests. J. Torrey Bot. Soc. **128**: 370–380.

McIntosh, R.P. 1972. Forests of the Catskill Mountains, New York. Ecol. Monogr. **42**: 143–161.

Oliver, C.D., and Larson, B.C. 1996. Forest stand dynamics. John Wiley & Sons, New York.

Pacala, S.W., Canham, C.D., Silander, J.A., Jr., and Kobe, R.K. 1994. Sapling growth as a function of resources in a northern temperate forest. Can. J. For. Res. **24**: 2172–2182.

Pacala, S.W., Canham, C.D., Saponara, J., Silander, J.A., Jr., Kobe, R.K., and Ribbens, E. 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. Ecol. Monogr. **66**: 1–43.

Papaik, M.J. 1998. Effects of windstorm in northern temperate forests. M.Sc. thesis, Bard College, Annandale-on-Hudson, N.Y.

Papaik, M.J. 2005. Modeling disturbance and competition in temperate forests of northeastern North America. Ph.D. dissertation, University of Massachusetts, Amherst, Mass.

Peterson, C.J., and Pickett, S.T.A. 1995. Forest reorganization: a case study in an old-growth forest catastrophic blowdown. Ecology, **76**: 763–774.

Ribbens, E., Silander, J.A., Jr., and Pacala, S.W. 1994. Seedling recruitment in forests: calibrating models to predict patterns of tree seedling dispersion. Ecology, **75**: 1794–1806.

Runkle, J.R. 1985. Disturbance regimes in temperate forests. *In* The ecology of natural disturbance and patch dynamics. *Edited by* S.T.A. Pickett and P.S. White. Academic Press, New York. pp. 17–34.

Twery, M.J., and Patterson, W.A. 1984. Variations in beech bark disease and its effects on species composition and structure of northern hardwood stands in central New England. Can. J. For. Res. **14**: 565–574.

Wargo, P.M. 1988. Amino nitrogen and phenolic constituents of bark of American beech, *Fagus grandifolia*, and infestation by beech scale, *Cryptococcus fagisuga*. Eur. J. For. Pathol. **18**: 279–290.

Woods, K.D. 2001. Long-term change and spatial pattern in a late-successional hemlock – northern hardwood forest. J. Ecol. **88**: 267–282.

Woods, K.D. 2004. Intermediate disturbance in a late-successional hemlock – northern hardwood forest. J. Ecol. **92**: 464–476.