A modelling approach to assess the long-term impact of beech bark disease in northern hardwood forest

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Abstract: This study proposes a modelling approach to assess the effect of beech bark disease on species demographic dynamics and structure of stands using SORTIE, a spatially explicit and individual-based forest succession model. The original model was modified to account for the increased mortality rate of infected *Fagus grandifolia* Ehrh. (American beech) and for some resistance to the disease. Two different scenarios, modeling species behaviour with and without the disease, respectively, were compared over a period of 300 years. Results reveal significant differences in species global demographic dynamics between both scenarios. Analyses of tree diameter-class distribution indicate that 50 years after the infestation, large *F. grandifolia* trees disappear, while the number of trees with a DBH between 11 and 50 cm considerably increases. At 300 years, the density of *F. grandifolia* with a DBH greater than 30 cm in the diseased scenario is superior or close to that in the nondiseased scenario, suggesting a progressive reestablishment of the species population structure. Eastern hemlock (*Tsuga canadensis* (L.) Carrière) is the species that largely benefits from beech bark disease. The study demonstrates the potential of a modelling approach to acquire quantitative insights about the long-term ecological impact of the disease.

Résumé : Cette étude propose une approche de modélisation pour évaluer l'effet de la maladie corticale de *Fagus grandifolia* Ehrh. (hêtre à grandes feuilles) sur la dynamique démographique des espèces et la structure des peuplements en utilisant SORTIE, un modèle de succession forestière spatialement explicite qui considère les tiges individuellement. Le modèle original a été modifié pour prendre en considération le taux accru de mortalité des hêtres infectés ainsi qu'une certaine résistance à la maladie. Deux différents scénarios, simulant respectivement le comportement des espèces avec et sans la maladie, ont été comparés sur une période de 300 ans. Les résultats révèlent des différences significatives dans la dynamique démographique globale des espèces entre les deux scénarios. Les analyses de la distribution des classes de diamètre des arbres indiquent que 50 ans après l'infestation, les gros individus de *F. grandifolia* disparaissent alors que le nombre de hêtres ayant un DHP compris entre 11 et 50 cm augmente considérablement. À 300 ans, la densité de *F. grandifolia* dans le scénario infesté pour les arbres ayant un DHP supérieur à 30 cm est supérieure ou semblable à celle du scénario non-infesté, ce qui suggère un ré-établissement progressif de la structure de la population de l'espèce. *Tsuga canadensis* (L.) Carrière est l'espèce qui bénéficie largement de la maladie. L'étude démontre le potentiel d'une approche de modélisation pour acquérir des informations quantitatives détaillées sur l'impact à long-terme de la maladie corticale du hêtre.

Introduction

Forest ecosystems are maintained in equilibrium with the presence of pathogens inherent in natural processes (Dinoor and Eshed 1984). These forest pathogens are biotic agents that lead to disease development. They eliminate the less vigorous or not genetically adapted individuals of a community through natural selection by causing mortality or decreasing a tree's ability to compete for resources. Pathogens are part of forest succession, since they control species maintenance and genetic diversity (Castello et al. 1995). Though native pathogens are usually beneficial to forest ecosystems, exotic ones may contribute to a loss in forest equilibrium. In fact, foreign pathogens can considerably modify natural forest dynamics by reducing the number of individuals within a species and changing the structure and succession pattern of the forest.

Beech bark disease (BBD) is caused by a complex consisting of an exotic insect, *Cryptococcus fagisuga* Lind., and either one of two bark-killing fungi: *Nectria coccinea* var. *faginata*, an exotic species, or *Nectria galligena*, a native pathogen common on many other hardwood hosts (Ehrlich 1934; Shigo 1972; Houston 1975; Mahoney et al. 1999). The fungi invade bark tissues previously altered by the feeding activity of the beech scale, *C. fagisuga*. Sometimes, a red-

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brown liquid oozes from the bark tissues killed by the fungi. Foliage of severely affected trees may become sparse and turn yellow. The bark of American beech, *Fagus grandifolia* Ehrh., weakened by the scale attack is predisposed to invasions by *Nectria* spp. Massive invasions can result in tree death (Shigo 1972; Lavallée 1985; Burns and Houston 1987; Brisson and Le Sauteur 1997). The disease progresses according to three subjectively defined stages. The establishment of scale populations corresponds to the advancing front, while high mortality rates of *F. grandifolia* represent the killing front. The aftermath stage is reached when the disease is endemic (Shigo 1972; Houston 1994).

BBD constitutes a serious problem for northern hardwood forests in North America and raises considerable concerns for ecologists and forest managers. First discovered in Nova Scotia in 1911, the disease rapidly invaded New England, the Maritimes, and southern Quebec (Ehrlich 1934; Lachance 1982; Houston 1994; Brisson et al. 1996). Spatiotemporal patterns of BBD spread and development have been documented. A forest stand with a high density of mature *F. grandifolia* is considered to be a major source of dispersion, and the disease can spread rapidly. In Quebec, between 1965 and 1974, BBD progressed in the southern and western directions at a speed of 32 km/year (Lavallée 1974). In a study conducted in an old-growth forest of southern Quebec, Brisson et al. (1996) reported that in 1995 78% of the *F. grandifolia* population with a DBH of 10 cm or more were infested by the beech scale; a year later, the insect was found on 97% of the population. Patterns of scale infestation are related to distance from a large old tree, wind direction, and site topography (Houston et al. 1979). The disease is associated with high mortality rates; in some regions, 20% of the *F. grandifolia* population died because of the disease (Lavallée 1974; Gavin and Peart 1993). Although its course may take several years, trees can be killed after 2 years of severe infection (Houston 1975). Most disease-caused mortality occurs among trees with a large diameter (Mize and Lea 1979; Jones and Raynal 1987; Fernandez and Boyer 1988). The impact on growth of surviving trees is much less clear. Mize and Lea (1979) found a significant but weak effect, while two studies respectively conducted by Gavin and Peart (1993) and Gove and Houston (1996) demonstrated that BBD reduced the growth of second- and old-growth *F. grandifolia* for several decades.

The influence of the disease on species composition and structure of stands has also been investigated, but generally it has not been exhaustively quantified and is mostly restricted to a relatively short period of time owing to field study limitations. Two important questions have been raised and are still subject to speculation: (1) what is the long-term effect of BBD on the *F. grandifolia* population and diameter-class structure and (2) which species benefit(s) the most from BBD and how long does it take for this (these) species to increase its (their) competitiveness in the presence of the disease? Field studies conducted so far indicate that *F. grandifolia* is likely to replace itself for at least one generation due to its regeneration by root sprouts, its high shade tolerance, and its ability to take advantage of small openings (Houston 1975; Twery and Patterson 1984; Runkle 1990). It has been shown that mortality of diseased trees often leads to the development of dense stands of *F. grandifolia* originating from root sprouts and seedlings (Houston 1994). However, in stands dominated by eastern hemlock (*Tsuga canadensis* (L.) Carrière) where the greater mortality of *F. grandifolia* occurs, *F. grandifolia* may become even less significant in the stand. Furthermore, if the species that replace *F. grandifolia* in these stands are susceptible to BBD, their growth may be slowed enough to prevent the next generation from competing successfully (Twery and Patterson 1984). Tolerant species, such as hemlock and sugar maple (*Acer saccharum* Marsh.), are expected to increase their competitiveness owing to the presence of BBD. Field studies have shown that hemlock benefits the most in stands where BBD is present (Twery and Patterson 1984; Runkle 1990).

Valentine (1982) suggested that one way to quantify the effects of BBD is to use a model to simulate changes in a stand over time, with and without the presence of BBD. Since no model was available to explicitly study BBD influence, he proposed some modifications to an existing model of forest growth and transition called FORTNITE (Aber and Melillo 1982). However, the modelling that was envisioned has never been completed (H.T. Valentine, personal communication, 2002).

In this study, we modified and used SORTIE, a spatially explicit and individual-based model of forest dynamics (Pacala et al. 1993), to assess the effect of BBD on species demographic responses and structure of stands over 300 years. Based on the literature review, we formulated two hypotheses. First, *F. grandifolia* does not disappear following the invasion of the disease, but its demographic structure is substantially changed. More specifically, BBD transforms a long-lived dominant canopy tree species of northern hardwood forest into an abundant subcanopy species by causing high mortality rates of larger stems. Given the fact that mortality stimulates the production of *F. grandifolia* seedlings by root sprouting, the disease creates a relatively dense subcanopy layer of foliage that does not progress to canopy height. Second, since hemlock is the most shade-tolerant tree present in the simulated stands, it is the species that will benefit the most from the infestation. A significant advantage of using a dynamic model like SORTIE for BBD research is the possibility to go beyond field study limitations and to exhaustively quantify the long-term impact of the disease on species dynamics by comparing different scenarios.

Methodology

SORTIE BC version 4.1 (Pacala et al. 1993, 1996) is a mechanistic and stochastic model that simulates succession in a northern hardwood forest composed of nine dominant and subdominant species: *Acer rubrum* L. (red maple), *A. saccharum*, *Betula alleghaniensis* Britt. (yellow birch), *F. grandifolia*, *T. canadensis*, *Fraxinus americana* L. (white ash), *Prunus serotina* Ehrh. (black cherry), *Pinus strobus* L. (white pine), and *Quercus rubra* L. (red oak). The model has been developed using sites and species located in and around Great Mountain Forest in northwestern Connecticut, U.S.A., at elevations varying between 450 and 510 m. These sites contain second-growth stands that are predominantly between 80 and 120 years in age, and they are found on sandy, acidic Inceptisols and Spodsols on glacial till derived from schist–gneiss bedrock (Pacala et al. 1996).

SORTIE is composed of four submodels, namely light resource, growth, mortality, and recruitment, that simulate the life cycle of each tree based on estimated functions that were determined according to tree size and competition for light among trees. The temporal simulation unit is 5 years. The quantity of light available to each individual is calculated first, taking into account the shadow created by neighbouring trees. The light resource determines the growth of seedlings and saplings, while the growth of adult trees is calculated using a growth function that was empirically established for each species. Mortality of each individual is then estimated according to its inverse growth rate (Kobe et al. 1995) and to a random probability function. Finally, recruitment is based on the number of seeds and root sprouts produced by each adult tree as a function of its size. Seedlings are dispersed around the parent tree using a density distribution that is inversely proportional to the distance from their parent (Ribbens et al. 1994). The reader is referred to Pacala et al. (1996) for additional details.

Modeling the impact of beech bark disease

Three aspects must be considered in attempts to model the impact of BBD. The first one is the increased mortality rate of larger diseased trees. The second is the slower growth of diseased trees before they die. The third is the ability of *F. grandifolia* to regenerate by root sprouting. A close examination of SORTIE reveals that the recruitment function of *F. grandifolia* generates seedlings regardless of whether they originated from seed or from a root sprout as a function of distance from a parent. The function can be considered as more appropriate for reproduction from sprouts than for reproduction from seeds, since it is known that root sprouts only occur within some finite distance from a parent, while a small proportion of seeds can be dispersed at very long distances from the parent (C.D. Canham, personal communication, 2000). Jones and Raynal (1986, 1987) showed that reduced parent vigour has little effect on sprout production and survival as long as the parent tree remains alive. For these reasons, SORTIE was considered appropriate for a good estimation of *F. grandifolia* recruitment, and the corresponding submodel was not modified.

The slower growth of diseased trees is a more complex issue. Gavin and Peart (1993) conducted a study to measure the effects of BBD on the growth of *F. grandifolia*. They found that growth of severely infected trees fell significantly below that of uninfected trees in second- and old-growth stands. Growth of severely infected trees was reduced by more than 40% relative to that of healthy trees. However, in a similar study, Mize and Lea (1979) found a significant but low reduction in annual DBH of infested trees. Based on the fact that very little detailed information was available to correctly evaluate the growth reduction of infested trees, the *F. grandifolia* growth function currently available in SORTIE was not modified. This decision was also supported by the fact that trees can be killed after 2 years of severe infection (Houston 1975). Since the temporal unit of simulation in SORTIE is 5 years, it seemed reasonable to assume that most infested trees will die in a short period of time during the simulation even though it is known that some severely infected trees can survive for a longer period of time.

A decisive factor to assess the impact of BBD is the change in the mortality rate of adult trees. In SORTIE, the adult mortality function is expressed by a curve that illustrates a constant annual probability of mortality of 1%. A logistic equation allows the use of a variety of curve shapes to modify parameter values of the random mortality function:

$$[1] \qquad \mathrm{Prob(m)} = \mathrm{rand} + \frac{e^{\alpha+\beta(\mathrm{DBH}-E)}}{1+e^{\alpha+\beta(\mathrm{DBH}-E)}}$$

where Prob(m) is the probability of mortality at each time step, rand is the constant annual mortality for all tree sizes (1%/year), DBH is the diameter at breast height (centimetres), α is the random mortality expressed by the slope after the inflection point of the curve, β is the random mortality expressed by the slope at the inflection point of the curve, E is the elderly mortality or DBH at the inflection point of the curve. Parameters α, β, and E are species specific.

Adult tree mortality parameters can be set to produce an increase in the probability of *F. grandifolia* mortality with increasing tree size. Studies undertaken to investigate *F. grandifolia*'s vulnerability to disease have revealed that the probability of mortality increases drastically for trees with a DBH >25 cm in northern hardwood forests (Jones and Raynal 1987; Fernandez and Boyer 1988). Also, Houston (1994) mentioned that more than 50% of *F. grandifolia* trees >10 in. (1 in. = 2.54 cm) in diameter are killed and many more are severely damaged. Based on this information, several tests were performed to find the best possible mortality function for infested *F. grandifolia*. We multiplied Prob(m) of the random mortality curve by 1.5 for trees with a DBH ≥25 cm. This curve was then used to adjust the original curve by changing its α, β, and E values and to obtain a modified mortality curve (Fig. 1). The values of α, β, and E were changed so that mortality varied with tree size. The modified mortality curve shows a slight increase in the probability of mortality beginning for trees >25 cm DBH. The maximum increased probability of mortality is reached at about 100 cm DBH. At about 110 cm, the mortality is equivalent in the two curves. Beyond 110 cm DBH, the modified curve shows considerably lower mortality than the original one. This is to account for the fact that under the modified scenario, the trees that reach such a size are indeed more likely to survive because of their resistance to BBD and the reduced competition from other *F. grandifolia*. The respective parameter values of the modified mortality curve are –5, 0.05, and 60. The original and modified curves are asymptotic at a probability of mortality of 1.

In addition to the major aspects previously described, the modelling is based on four other assumptions:

1. The initial distributions were computer generated. They do not reflect the current state of an existing forest, but rather a hypothetical situation in a northern hardwood forest similar to the sites where the model was calibrated.
2. The species distributions do not reflect all the forest types where *F. grandifolia* occurs or where the disease occurs (e.g., some affected forests do not include hemlock and therefore are not represented in this study).

Fig. 1. Modified adult mortality curve.

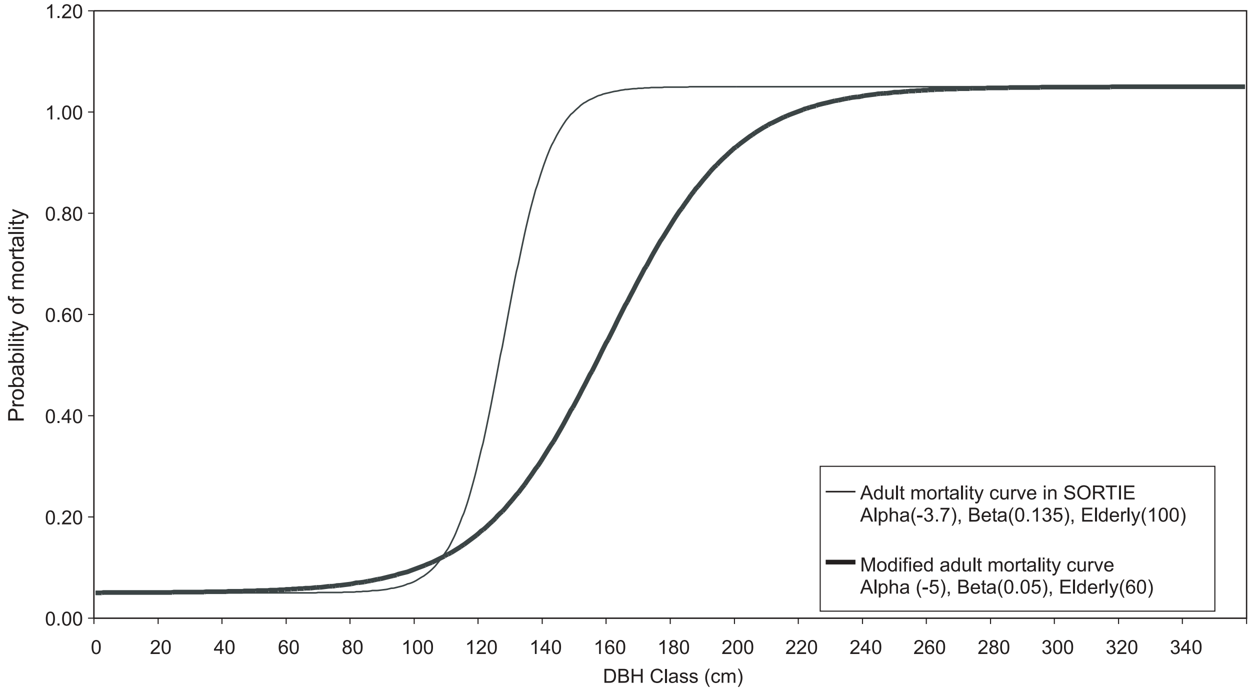
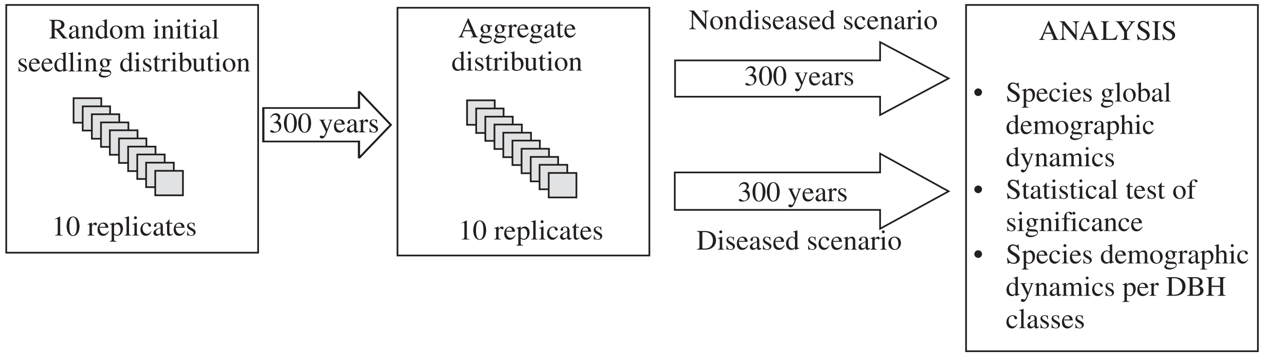


Fig. 2. Outline of the simulation and analytical steps.



(3) No major stand-altering disturbances other than BBD known to affect root sprouting and (or) seeding are included in the simulation. In southern temperate forests, the disturbance regime is better characterized by the death of scattered individuals (Runkle 1985), and larger-scale disturbances such as tornadoes or fires are very infrequent. Thus, for our 300-year simulations, individual tree mortality is the only type of disturbance considered.

(4) The small proportion of *F. grandifolia* that is highly resistant to the disease is not taken into consideration. Some trees have been found to be resistant to the disease, but they usually constitute less than 1% of the population (Houston 1994); therefore, differential resistance to the disease is not considered in the model.

Also, the recently understood role of blue jays in the dispersal, reintroduction, and reestablishment of *F. grandifolia* was not modelled.

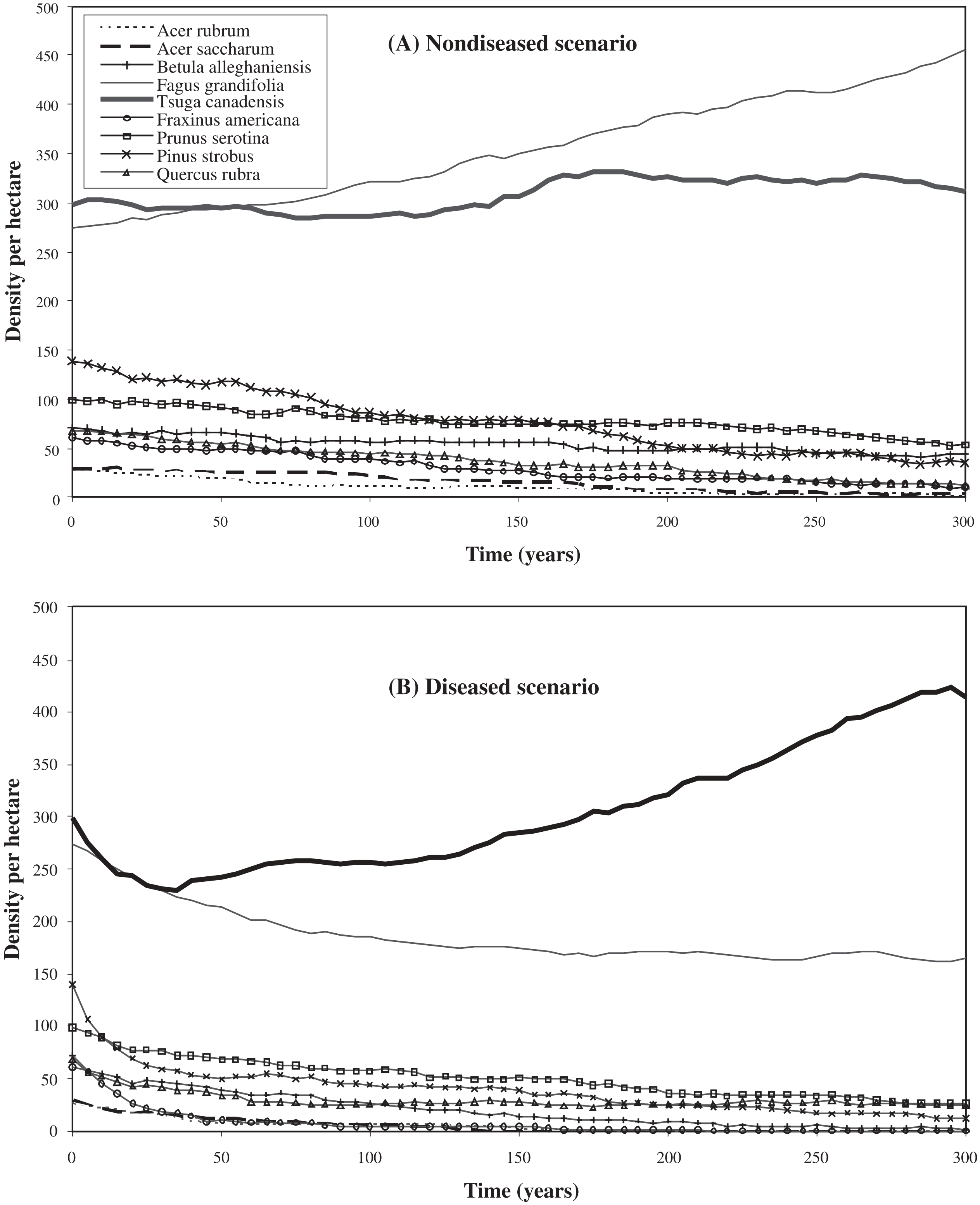
Finally, two scenarios were established. The first one simulates forest dynamics without the effect of BBD. The second scenario models a decline in *F. grandifolia* population by increasing the mortality of *F. grandifolia* trees using the modified adult mortality function.

Initial conditions and simulation scenarios

The nine species available in the SORTIE model were used to create a hypothetical species composition and stand structure of the northern hardwood forest. Simulations were generated using a toroïdal matrix of 100 m × 100 m over a temporal extent of 300 years or 60 time steps. The two scenarios were replicated 10 times each. For the diseased scenario, we applied the modified parameter values of the *F. grandifolia* random mortality function to simulate the second stage (killing front) and the aftermath stage of BBD. To isolate the impact of BBD, we used 10 different seeds in the pseudorandom number generator of SORTIE for the nondiseased scenario, and the exact same seeds were imposed on the diseased scenario. We therefore replicated for both scenarios 10 simulations that were different only in terms of *F. grandifolia* random mortality parameter values.

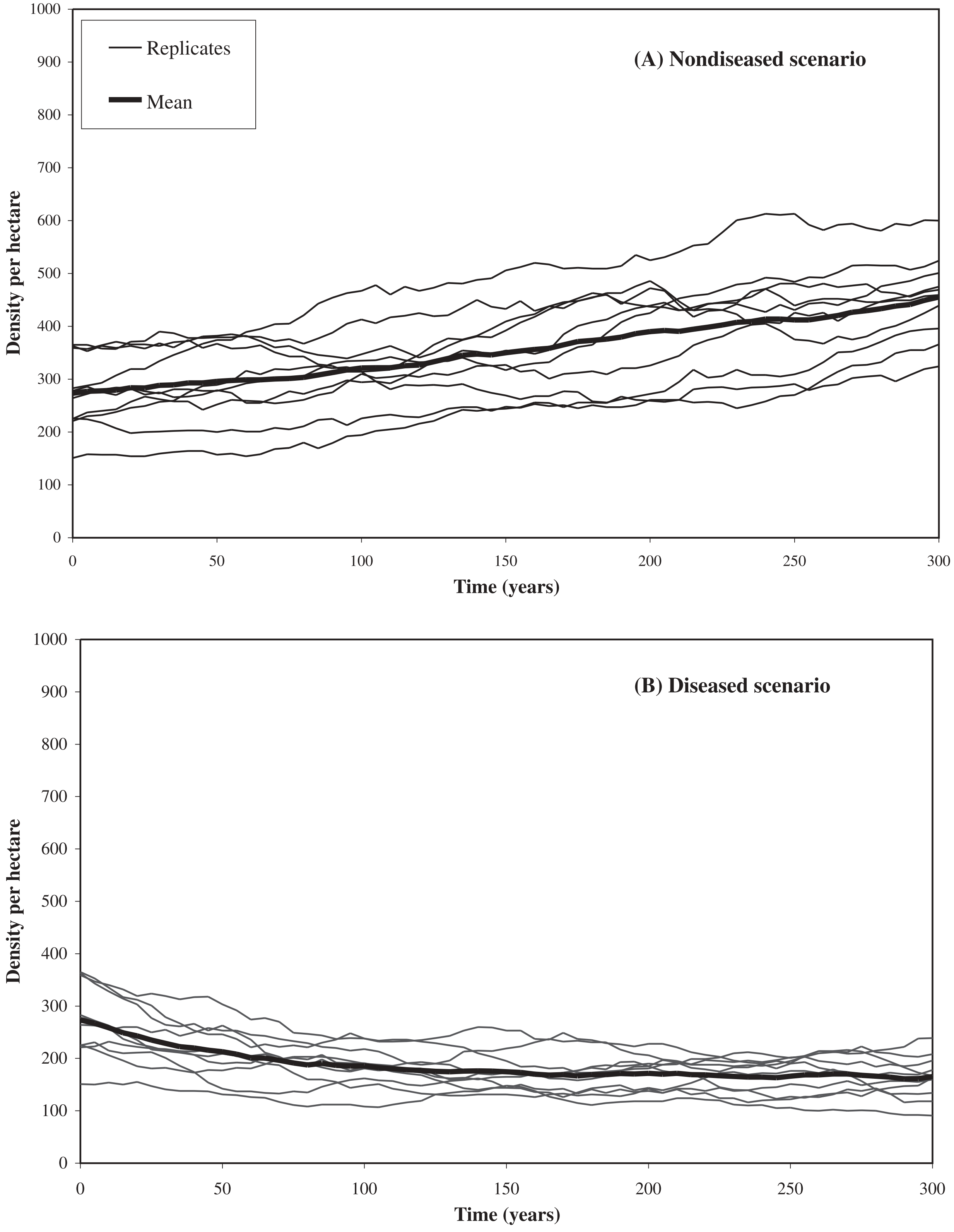
Each simulation was started with a random initial seedling

Fig. 3. Species global averaged demographic density results for both scenarios.



distribution of the nine species and a seedling density of 100 individuals/ha for each species (Fig. 2). After 300 years of simulation (60 time steps), the SORTIE Tree Map File, containing the spatial coordinates and attributes of each tree, was extracted and used for initial conditions. This was done to restart the simulation with an aggregate spatial structure of trees to avoid sensitivity to initial conditions. Previous studies have shown that SORTIE generates such an aggregate pattern after 300 years of simulation regardless of species initial spatial configuration (Dubé et al. 2001; Ménard

Fig. 4. Replicate variability for *Fagus grandifolia* for both scenarios.



et al. 2002*a*). Temporal demographical outputs and playback files were generated for each replicate. Playback files give information on species type, spatial coordinates, and DBH for each individual in the matrix at each time step of the simulation.

Once the simulations with SORTIE were completed, two

Table 1. Results of the Kolmogorov–Smirnov goodness-of-fit test for all replicate comparison between both scenarios.

	Replicates									
Species	1	2	3	4	5	6	7	8	9	10
Acer rubrum	0.388	0.049*	0.164	0.258	0.054*	0.000*	0.218	0.119	0.134	0.084*
Acer saccharum	0.278	0.328	0.094*	0.044*	0.313	0.209	0.333	0.169	0.000*	0.313
Betula alleghaniensis	0.547	0.442	0.502	0.696	0.711	0.144	0.815	0.358	0.333	0.119
Fagus grandifolia	0.980	0.990	0.995	0.985	0.995	0.980	0.995	0.995	0.990	0.925
Tsuga canadensis	0.462	0.786	0.631	0.557	0.751	0.616	0.751	0.517	0.701	0.567
Fraxinus americana	0.462	0.403	0.134	0.602	0.288	0.134	0.099	0.228	0.223	0.223
Prunus serotina	0.253	0.253	0.323	0.328	0.383	0.427	0.338	0.731	0.537	0.467
Pinus strobus	0.253	0.452	0.194	0.209	0.189	0.243	0.139	0.139	0.199	0.393
Quercus rubra	0.258	0.447	0.134	0.791	0.427	0.179	0.338	0.099	0.442	0.179

Note: Values with an asterisk indicate no significant difference between both scenarios of initial conditions.

types of analysis were performed. First, the species global demographic dynamics were evaluated, regardless of tree size. Time series were produced to observe and to characterize the impact of BBD on forest dynamics over 300 years. A nonparametric statistical test was applied on the extracted demographic outputs for each species to compare the diseased and nondiseased scenarios. The two-sample Kolmogorov–Smirnov goodness-of-fit test (Sokal and Rohlf 1981) was used to verify whether two replicates, one of each scenario, having the same seed in the pseudorandom number generator of SORTIE, were significantly different from one another. We compared each of the 10 replicates as well as the average of the replicates for each scenario. Second, the distribution of tree diameter classes was extracted at different moments in the simulation, namely 0, 50, 200, and 300 years. A detailed analysis of the density of trees in each DBH class was made to better evaluate the impact of BBD on species composition and structure.

Results

Assessment of the species global demographic densities

Averaged curves of the 10 replicates for the nondiseased scenario suggest coherent species global demographic behaviours (Fig. 3A). *Fagus grandifolia* and *T. canadensis* are the co-dominant species. This situation typically corresponds to a nondisturbed forest dominated by the two most shade-tolerant species of the model (Pacala et al. 1996). Brisson et al. (1994) found a similar trend in an old-growth forest of southern Quebec. *Prunus serotina* appears as the third competitor. The low competitiveness of *A. saccharum*, a very shade-tolerant species, can be explained by the type of soil at the sites where SORTIE was calibrated. Its survival on sandy and acidic soils at low light is lower than it is on calcareous soils (Pacala et al. 1996). Also, SORTIE does not simulate major disturbances that usually contribute to a higher competitiveness of that species. These long-term species dynamics are in accordance with previous studies undertaken with SORTIE (Pacala et al. 1996; Dubé et al. 2001; Ménard et al. 2002*a*, 2002*b*).

The species global demographic dynamics represented by the averaged curves for both scenarios reveal important differences in species behaviour as simulations progress with time (Fig. 3). In the diseased scenario, *F. grandifolia* density reduces rapidly within the first 50 years of the simulation; then, a continuous slow decline in density is observed until about 170 years, followed by stabilization (Fig. 3B). *Tsuga canadensis* is the species that benefits the most from *F. grandifolia* decline. Its density decreases during the first 25 years, but it definitely increases until the end of the simulation. *Prunus serotina* becomes the third species in importance very early in the simulation. *Pinus strobus* and *Fraxinus americana*, two intolerant species, are the species that seem the most affected in the diseased scenario, showing a more rapid decline compared with the nondiseased scenario.

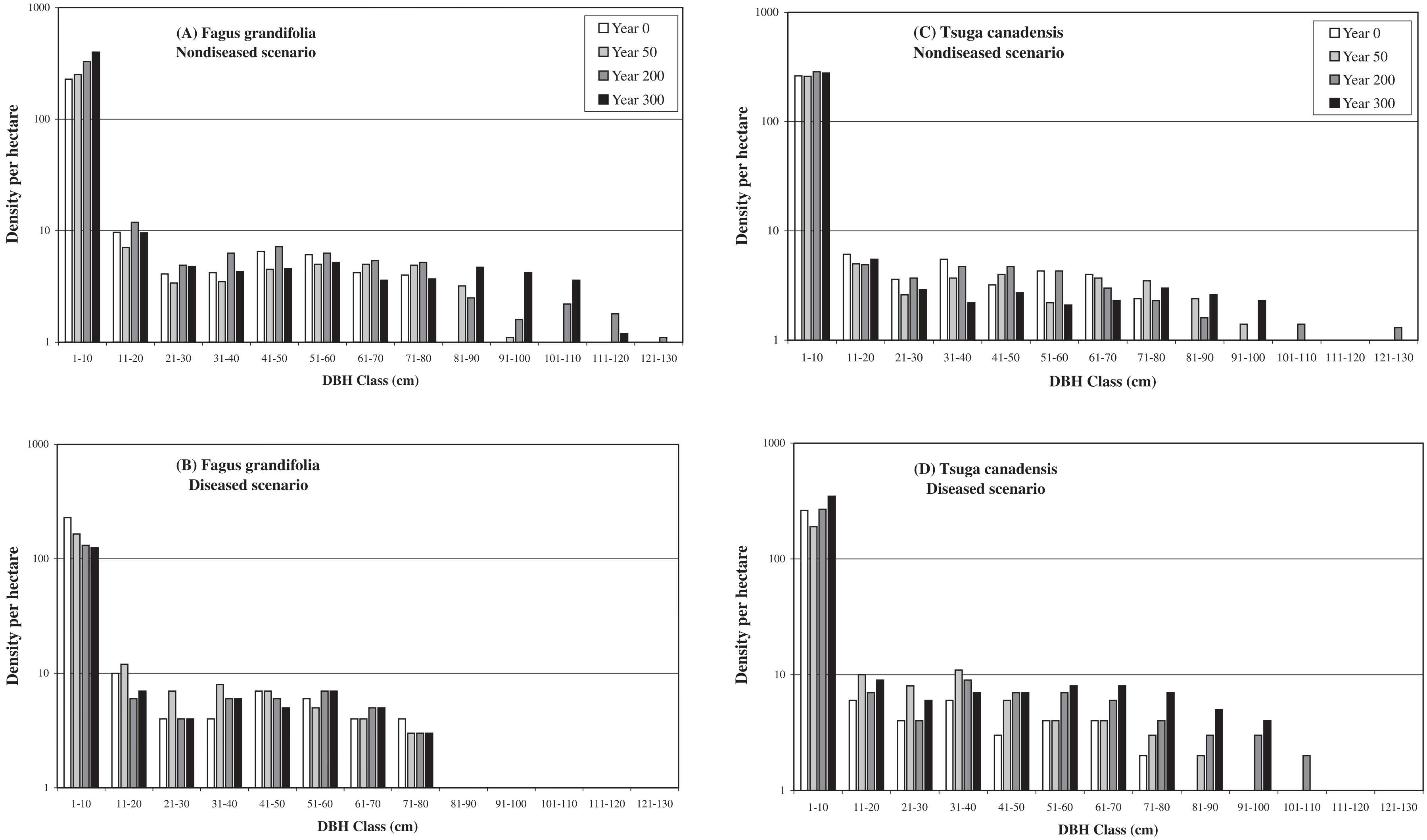
Table 2. Results of the Kolmogorov–Smirnov (K–S) goodness-of-fit test for the average of replicate comparison between both scenarios.

Species	K–S
Acer rubrum	0.283
Acer saccharum	0.333
Betula alleghaniensis	0.736
Fagus grandifolia	0.995
Tsuga canadensis	0.776
Fraxinus americana	0.452
Prunus serotina	0.283
Pinus strobus	0.218
Quercus rubra	0.482

Figure 4 shows the variability among the 10 replicates for *F. grandifolia*. This variability is greater in the nondiseased scenario (Fig. 4A). In the diseased scenario, there is no sign of a cyclical pattern in *F. grandifolia*, but rather a slow decline during the first years followed by stabilization (Fig. 4B).

The nonparametric Kolmogorov–Smirnov test was applied to verify if the difference between the scenarios was significant for each species. The test was performed on each replicate and on the average of the 10 replicates at a 5% alpha level (treshold value of the test (D_c) = 0.096). We reject the null hypothesis for each replicate except for replicates 2, 5, 6, and 10 for *A. rubrum* and for replicates 3, 4, and 9 for *A. saccharum* (Table 1). We also reject the null hypothesis for the average of replicates (Table 2) and conclude that there are significant differences between the nondiseased and the diseased scenarios for each species.

Fig. 5. Demographic dynamics of *Fagus grandifolia* and *Tsuga canadensis* for both scenarios in terms of DBH classes at years 0, 50, 200 and 300. Note that the *y* axis has a logarithmic scale.



Assessment of the species demographic densities in terms of DBH classes

To assess the impact of BBD on the composition and structure of stands, a detailed analysis of the demographic responses of *F. grandifolia* and *T. canadensis* is presented in terms of DBH classes for four critical moments in time during the 300 years of simulation (Fig. 5). Results are shown at year 0 where the simulation begins, at year 50 where *F. grandifolia* surpasses *T. canadensis* in the nondiseased scenario (Fig. 3A), at year 200 where *T. canadensis* is more abundant in the diseased scenario than in the nondiseased scenario (Fig. 3), and finally, at 300 years, which corresponds to the end of the simulation.

A first obvious observation is the disappearance of *F. grandifolia* with a DBH greater than 80 cm in the diseased scenario (Fig. 5B), while trees can reach a DBH of 130 cm in the nondiseased scenario (Fig. 5A). Fifty years after the disease onset, a higher proportion of the smaller number of stems from the 1–10 cm class grow into the 11–50 cm class. Over the whole period of 300 years, there are fewer seedlings and saplings (DBH smaller than 10 cm) in the diseased scenario, but a greater number of them reach a DBH varying between 11 and 50 cm. This reveals that areas occupied by veteran trees before the introduction of the disease are replaced by a dense subcanopy layer of smaller trees.

It takes 200 years for *T. canadensis* to considerably increase its density in all classes of DBH in the diseased scenario (Figs. 5C and 5D). At year 50, we observe a slight decrease of *T. canadensis* with a diameter lower than 10 cm, but it is followed by an increase in this DBH class up to year 300. This confirms that this species is largely advantaged by the presence of BBD in the forest stand.

Conclusions

The results obtained in this study show that the long-term impact of BBD is in accordance with the short-term impact and hypotheses already documented and suggested by previous field studies. The demographic structure of *F. grandifolia* is strongly affected by the disease, producing a strong decline in large trees to the benefit of younger trees with diameter varying mainly between 11 and 50 cm. The disease creates a dense subcanopy layer. Therefore, *F. grandifolia* does not go to extinction over a long-term period. The simulation shows that its population declines during the first 50 years and then stabilizes over 300 years. After 200 years, *T. canadensis* largely benefits from the infestation, being the most shade-tolerant species present in the stand.

Our modelling approach represents a first attempt at exhaustively quantifying the impact of BBD on the demographic structure of dominant species composing the stand by comparing two scenarios, one with and one without the presence of the disease. Even though a model is always a crude approximation of the complexity of the real world, the modelling approach used in this study allows a systematic investigation of several possible scenarios that can lead to the formulation of new hypotheses to be further tested in the field. Potential questions that can be examined are (1) what is the long-term impact of the disease on tree growth and sprout production, (2) is there an increase of resistance to the disease over several generations of trees, and (3) what happens to seedling development for nonbeech species in stands that have a dense *F. grandifolia* understory? Also, the parameters and simulated forest composition are based on data collected around Great Mountain Forest in northwest Connecticut. It would be interesting to simulate the long-term effect of BBD using other forest types to evaluate how the changes in diameter-class distribution and species composition resulting from BBD may vary across *F. grandifolia*'s entire range.

Additional improvements of the original model SORTIE could be made to better assess the impact of BBD. The growth function of *F. grandifolia* could be modified to simulate the progressive growth decline of the infested trees. It would then be interesting to see how reducing the growth rate of *F. grandifolia* would affect the dynamics of the forest stands. Another important aspect to take into consideration is the fact that a small percentage of *F. grandifolia* is resistant to the disease complex and show no signs of damage, growth reduction, or increased mortality. Finally, since the model already provides the location of all the trees composing the stand at each step of the simulation, it could allow a detailed investigation of the spatiotemporal pattern of infestation, which can significantly contribute to a better understanding of a major aspect of the disease propagation and can facilitate management decisions to preserve our forests.

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