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REGENERATION OF THREE SYMPATRIC BIRCH SPECIES ON EXPERIMENTAL HURRICANE BLOWDOWN MICROSITES

G. C. CARLTON[1] AND F. A. BAZZAZ

Department of Organismic and Evolutionary Biology, Harvard University,
Cambridge, Massachusetts 02138 USA

Abstract. Tip-up mounds, pits, and other microsites created by hurricanes may promote diversity in many forests by providing opportunities for different species to regenerate. To see if we could detect differences in microsite preference among closely related species, we studied the regeneration of three sympatric *Betula* species on five types of microsites on experimental mound–pit complexes. Microsites were created by pulling down canopy trees to simulate damage from past hurricanes in southern New England. Seeds were collected in litter traps and experimentally released over mounds and pits to determine effects of microtopography on fine-scale dispersal patterns. The fate of naturally germinating seedlings was monitored on the disturbed site, and seedlings were also transplanted onto microsites to examine growth patterns, causes of mortality, and leaf-level physiology.

Seed rain onto the disturbed site was abundant and spatially heterogeneous because of scattered residual canopy trees and surviving uprooted trees. Seeds tended to disperse away from vertically oriented surfaces of mounds and to accumulate in pits. Most seedlings germinated on scarified level areas rather than on mounds or in pits, but mounds became more favorable for germination the second year following disturbance. Two fundamentally different types of mortality were observed in transplanted seedlings. Extrinsic factors such as frost heaving, burial by soil and litter, and browsing were dominant on some microsites. Mortality due to these factors occurred primarily during the winter and was unrelated to seedling size. On other microsites, resource limitation (low light levels and lack of water or nutrients) was the major cause of death. Small seedlings were most susceptible to mortality on these microsites, and most deaths occurred during the growing season.

White birch (*Betula papyrifera* Marsh.) exhibited the fastest growth and most flexible photosynthetic response to changing light levels but suffered greatest mortality on shaded microsites. Black birch (*B. lenta* L.) showed increased leaf area ratio in shaded conditions. Yellow birch (*B. alleghaniensis* Britt.) was least flexible and grew more slowly than the other species but was best able to survive on shaded microsites. All species attained maximum growth on tip-up mounds. After three growing seasons, the tallest seedlings reached nearly 3 m above the forest floor, enabling us to predict which individuals would ultimately reach the canopy to complete the regeneration process.

Key words: Betula; *coexistence; disturbance; germination; growth; Massachusetts; microsites; mortality; mound–pit complex; regeneration; seed dispersal; windthrow.*

INTRODUCTION

Plant communities persist through the process of regeneration, a broad and rather imprecise term widely used in the ecological literature. Regeneration may refer to the recruitment of a particular species population into a community, the replacement of a stand of trees of one or more species, the cycling of dominant species in a community, or the recovery of an entire community (Watt 1947, Smith 1962, Harper 1977). Regardless of the usage, regeneration normally depends upon some disturbance event that causes damage or death to one or more individuals in the community and thereby releases space and resources (White 1979, Bazzaz 1983, Pickett and White 1985). The newly available resources are then taken up by surviving individuals already present in the community or by new individuals recruited from seed (Grubb 1977). Response of surviving individuals, which occurs through lateral extension of crowns, deployment of new leaves, or basal sprouting, is often very rapid (Hibbs 1983, Canham 1989, Whitmore 1989). Recruitment from seed occurs much more slowly and may be precluded on sites with abundant surviving vegetation (Hibbs 1982, Runkle 1982).

Regeneration from seed is a complex process involving a number of stages (Grubb 1977). The first stage is the production and dispersal of viable seed. Seed production for most species varies both spatially and temporally, depending on the abundance and vigor of mature adults and on environmental conditions (Cavers 1983). Dispersal patterns are determined by

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[1] Present address: Biological Sciences Department, California State Polytechnic University, 3801 West Temple Avenue, Pomona, California 91768 USA.

the availability of suitable biotic vectors or by the vagaries of wind movement or water flow (Fenner 1985, Johnson and Fryer 1992). The second stage, germination and emergence of shoots from the soil surface, may commence immediately after seeds disperse or following a period of dormancy (Cook 1980). Many species have very specific germination requirements that are only satisfied on particular "safe sites" (Harper et al. 1965, Hartgerink and Bazzaz 1984). The third stage is seedling establishment, during which the seedling becomes a viable, independent organism capable of producing its own food (Fenner 1985). The final stage, growth and development of the established seedling to maturity, may require several decades and is often excluded from regeneration studies. Because each of the four stages involves the interaction between specific biological processes and particular environmental conditions, many unique regeneration niches are possible (Grubb 1977). Differences in regeneration requirements may therefore provide opportunities for similar species to coexist in natural communities (Schmida and Ellner 1984, Denslow 1985, Petraitis et al. 1989).

In the forests of southern New England, hurricanes are an important disturbance agent (Foster and Boose 1992). Severe hurricanes have caused extensive damage and initiated regeneration of forests throughout this region (Foster 1988*b*). The susceptibility of forests to hurricane damage depends on stand age, species composition, aspect, soil depth, and slope position. Forests on exposed south-facing slopes are most severely damaged, and white pine (*Pinus strobus* L.) is more susceptible to breakage and uprooting than hardwood species (Rowlands 1939). All forests, however, become more vulnerable with increasing stand age, and many hardwood forests >50 yr old have suffered extensive damage in past hurricanes (Foster 1988*b*, Foster and Boose 1992).

Hurricanes not only remove most of the forest canopy but also create tip-up mounds, pits, and other forest floor microsites that provide a window of opportunity for recruitment from seed (Spurr 1956, Henry and Swan 1974, Oliver and Stephens 1977, Schaetzl et al. 1990). This is especially important for species such as birches (*Betula*) that do not sprout readily from the base of damaged stems. Birches, in fact, are strongly associated with microsites created by windthrow and may depend on such sites for persistence in the community (Hutnik 1952, Peterson and Pickett 1990, Schoonmaker 1992). Although the affinity of birches for specific microsites is widely recognized, the influence of microsites on the various stages of birch regeneration is poorly understood. Furthermore, subtle ecological differences among birch species may create slightly different regeneration requirements following a disturbance event such as a hurricane blowdown.

In the temperate deciduous forests of New England, for example, black birch (*Betula lenta* L.) and yellow birch (*B. alleghaniensis* Britt.) are frequently observed growing on old tip-up mounds (Henry and Swan 1974). These species are intermediate in shade tolerance, regenerating primarily in canopy gaps but able to persist as seedlings and saplings in the forest understory (Erdmann 1990, Lamson 1990). Although closely related and ecologically similar, black birch and yellow birch differ in response to experimental light, water, and nutrient treatments under controlled conditions (Wayne 1992, Crabtree and Bazzaz 1993, Bazzaz and Wayne 1994). White birch (*B. papyrifera* Marsh.) is a shade-intolerant, early successional species that also regenerates on old tip-up mounds but may occur on level scarified areas where vegetation and litter have been removed (Safford et al. 1990). All three species consistently produce moderate to abundant seed crops, the seeds being dispersed by wind, primarily during the fall and winter (Marquis 1969, Matlack 1989, Houle and Payette 1990, Lamson 1990, Safford et al. 1990). Most germination occurs from May through July for all three species, and seedling mortality rates are typically high (Marquis 1969, Tubbs 1969, Safford 1983, Houle 1994).

In this paper we describe the regeneration from seed of these three birch species on five types of forest floor microsites. The microsites were created by an experimental hurricane blowdown treatment that simulated the effects of past hurricanes in southern New England. We had two primary objectives in this study. We wanted first to determine if microsites influenced birch seed dispersal or the ability of dispersed seeds to germinate. Secondly, we wanted to identify differences among the three species in survival and growth of established seedlings on the five types of microsites.

To meet the first objective we designed a set of seed dispersal and germination experiments to address the following questions:

1) Is birch seed rain onto the disturbed site reduced because of the loss of canopy trees, and do surviving trees create a spatially heterogeneous seed dispersal pattern?

2) Does mound-and-pit microtopography influence fine-scale seed dispersal patterns?

3) How do the five microsites influence the germination and survival of birch seedlings and to what extent is survival related to seedling size?

To meet the second objective, which focused on differences among the three species in microsite preference, we transplanted seedlings onto the five microsites and addressed the following questions:

4) What are the causes of seedling mortality on the different microsites and what effect would elimination of specific causes of mortality have on survival?

5) To what extent do differences among the three species in height growth, final biomass, carbon allocation patterns, and leaf-level physiology explain regeneration patterns?

6) Can we predict the ultimate regeneration success

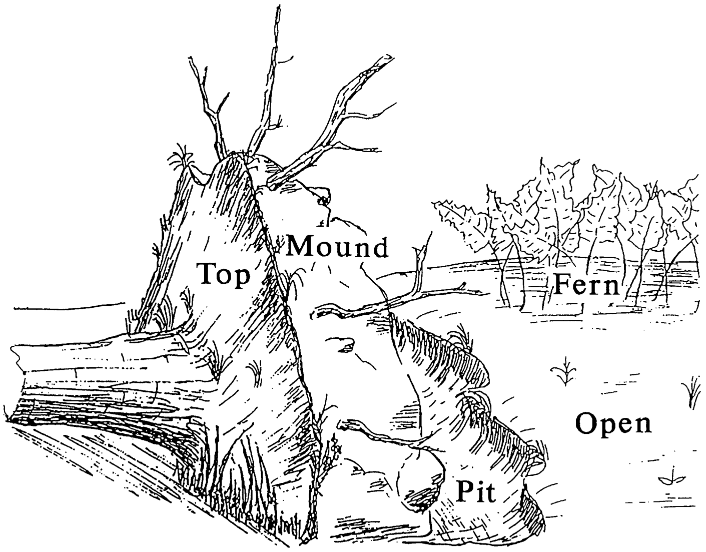


FIG. 1. Five microsites created by experimental hurricane blowdown treatments. The root plate microsite mentioned in seed dispersal results is the vertical portion of the mound rising above the pit and is not visible in this figure.

of each species by observing the growth of the largest individual seedlings on each microsite?

METHODS

Study sites

This study was conducted at the Harvard Forest within the Transition Hardwoods–White Pine–Hemlock vegetation zone of north-central Massachusetts (Westveld 1956). Soils are acidic loams derived primarily from glacial till and variable in texture, depth, and drainage. The regional climate is cool temperate (summer mean 20°C, winter mean −4°C) with mean annual precipitation of 105 cm distributed evenly throughout the year (D. R. Foster, *unpublished records*). The forest disturbance regime is characterized by hurricane blowdowns at ~100-yr intervals, by disease and insect epidemics, and recently by timber harvesting, clearing of land for cultivation, and other human activities (Foster 1992).

Seed dispersal and germination were studied on the Long-Term Ecological Research (LTER) site located in the Tom Swamp tract. This site was located near the top of a gently sloping, northwest-facing hill formed by glacial deposition, as evidenced by uniformly distributed stones and boulders (Lutz and Cline 1947). The productive stony loam soils overlie an impermeable fragipan layer 50–75 cm below the surface, which restricts water movement and causes localized ponding in the winter and spring (Lyford et al. 1963). The relatively even-aged stand was ~75 yr old and consisted primarily of hardwoods released after removal of old-field pine in 1915 (Lutz and Cline 1947). Northern red oak (*Quercus rubra* L.) and red maple (*Acer rubrum* L.) dominated the stand at the time of this study, but white ash (*Fraxinus americana* L.), eastern white pine (*Pinus strobus* L.), white birch (*Betula papyrifera* Marsh.), black birch (*B. lenta* L.), and yellow birch (*B. alleghaniensis* Britt.) were fairly common.

In September 1990, a 0.80-ha (50 × 160 m) experimental hurricane blowdown was created in the stand by pulling down randomly selected canopy trees. Trees were pulled down in a northwesterly direction to simulate the orientation of blowdown damage resulting from hurricanes striking the forest in 1788, 1815, and 1938 (Foster and Boose 1992). Selection of trees to be uprooted was based on data from the 1938 hurricane, including relationships between species, height, and susceptibility to damage (Rowlands 1939, Foster 1988*a*, *b*). Trees were pulled over by fastening a cable around the bole at a height of 3–5 m and applying force with a logging skidder located 100 m northwest of the experimental site. Force was applied until the roots failed or the bole snapped and trees came to rest against the forest floor or other standing or uprooted trees.

Mortality, growth, and leaf-level physiology of established seedlings were studied on the Prospect Hill tract of the Harvard Forest. This study site was located on a gentle, east-facing slope in a 60-yr-old stand dominated by red oak and red maple with an admixture of white pine and birches. In September 1989, a 0.25-ha (50 × 50 m) experimental hurricane blowdown was created in the stand by pulling down randomly selected canopy trees as described above for the Tom Swamp site.

Five distinct types of microsites were identified on both experimental blowdown sites (Fig. 1). Uprooted trees created tip-up mounds, pits, and north-facing vertical forest floor surfaces referred to as top microsites. Level areas relatively free of competing vegetation were designated open sites, and level areas covered by ferns or other understory vegetation were called fern sites. Each of these microsites provides a unique environment for seedling growth. Effects of microsites on climatic and soil factors are presented in another paper (G. C. Carlton and F. A. Bazzaz, *unpublished manuscript*). In this paper we focus on the effects of each microsite on seed dispersal and seedling germination and growth.

Seed dispersal experiments

Birch seed rain onto the disturbed site in the Tom Swamp tract and adjacent forest understory was sampled using conical muslin litter traps with an opening of 0.2 m^2 suspended from a triangular frame of PVC (polyvinyl chloride plastic) welding rod (a modification of traps described in Hughes et al. 1987). Sixteen traps were randomly placed along each of four transects, three on the experimental blowdown site and one in the forest understory. Transects were 120 m long and oriented east and west parallel to the long axis of the experimental blowdown. The north blowdown transect was 10 m from the northern edge of the blowdown, the south blowdown transect was 10 m from the southern edge of the blowdown, and the center transect was 25 m from each edge in the center of the simulated blowdown. The understory transect was 50 m south of the southern edge of the blowdown. Seed rain was sampled from May 1991 to April 1992.

Data for black birch were normally distributed with equal variance among transects. Therefore, differences in seed rain among transects were tested with one-way ANOVA. Post hoc pairwise tests were conducted using Fisher's protected least significant difference (FPLSD), which is recommended when the F test for treatments is significant (Carmer and Swanson 1973, Petersen 1985). Because white birch data were heteroscedastic, differences between transects were tested using single-degree-of-freedom linear contrasts. Linear contrasts were also used to test for differences between blowdown and understory seed rain of each birch species. All statistical tests were performed with SYSTAT (Wilkinson 1990).

Effects of mound-and-pit microtopography on seed dispersal patterns were determined by experimentally releasing labeled yellow birch seeds over two mound–pit complexes and mapping their distribution. Seeds were labeled with a small spot of white paint on each side. Tests demonstrated that the paint did not influence dispersal patterns. Seeds of white birch and black birch were too small to test microdispersal patterns. Because seeds of these species are morphologically similar to those of yellow birch, we assumed they would exhibit similar dispersal characteristics. We also mapped dispersal patterns for red oak and red maple, the two dominant species on the study site, and have presented the results for these species to contrast with the yellow birch results. Yellow birch and red oak seeds were released in October 1992, and seeds of red maple were released in July 1991 and April 1993. Seeds were released on dry days with light winds.

To conduct this experiment, we erected a 2.3 × 2.3 m wooden frame ~2.5 m above the forest floor over each of the two replicate mound–pit complexes. The frame was horizontally oriented and subdivided into a grid of one hundred 23 × 23 cm squares, using twine stretched across the frame. From the corners and midpoints of each grid square, we measured the vertical distance from the frame to the ground surface using a plumb bob. We then marked the position of the plumb bob on the ground to project the planar grid to the ground surface. Using this procedure, we established a grid of 400 11.5 × 11.5 cm squares on a large mound–pit complex and a grid of 320 11.5 × 11.5 cm squares on a small mound–pit complex. We then released individual seeds from the center of each 23 × 23 cm grid square in the frame and mapped where the seeds landed. Between 300 and 500 seeds of each species were released above each mound–pit complex to obtain a sufficient number of seeds within the mapped area to determine dispersal patterns.

We used data from the plumb bob projections to construct contour maps for each mound–pit complex and superimposed seed dispersal patterns on each map. We also estimated the horizontally projected planar surface area (as seen from above) and the three-dimensional surface area of each microsite type and counted the number of seeds distributed onto each microsite. To determine if dispersed seeds were associated with specific microsites, we tested the goodness-of-fit of the observed frequency distribution of seeds to the distribution of both the horizontally projected planar area and the actual three-dimensional surface area of the different microsites. The log-likelihood ratio test with Williams' correction factor was used to estimate the chi-square distribution (Sokal and Rohlf 1981).

Germination surveys

We surveyed the recruitment, survival, and growth of tree seedlings germinating during the 1991 growing season on each blowdown type and in the undisturbed forest understory. For this purpose, 24 replicate sets of mound–pit pairs were randomly selected and five 0.1-m^2 circular plots were randomly located within each microsite. The first four 0.1-m^2 plots on each microsite were used to sample tree seedlings, understory vegetation, and forest floor substrate. The fifth plot was reserved for micrometeorological measurements (G. C. Carlton and A. L. Lezberg, *unpublished data*). In addition to mound, pit, top, open, and fern microsites, sampling was conducted on the vertical root plate rising above pit microsites and in the adjacent undisturbed forest understory. Data are therefore presented from 672 0.1-m^2 plots (24 replicate sets of microsites × 7 microsites per set [including the forest understory] × 4 plots per microsite).

In July 1991 we estimated the percent cover of different types of substrate on each plot. Then in October 1991 we estimated the percent cover of understory vegetation and conducted surveys of tree seedlings. Measurements on each seedling included basal diameter, stem length, crown dimensions, crown density, and the number and stage of development of all leaves. Crown dimensions and crown density were used to calculate projected leaf area (i.e., the total seedling leaf area minus overlap when viewed from directly above the seedling). In July 1992 we measured surviving 1991 seedlings and tallied but did not measure new seedlings on the plots.

Data are presented only for birch seedlings, which constituted ~90% of all seedlings. Because birch seedlings could not be consistently identified to species, data for all three birch species were pooled. Differences among microsites in number of seedlings were tested by constructing the following four classes of seedling numbers: 0, 1–3, 4–15, and $\geq$16 seedlings per microsite. Likelihood-ratio chi-square tests of association were then applied to test for interactions between microsite and class frequencies (Sokal and Rohlf 1981).

We tested for differences among microsites in growth parameters measured in July 1992. Birch growth variables, which were all lognormally distributed and homoscedastic, were analyzed using one-way ANOVA with FPLSD post hoc tests for variables with significant microsite effects. To assess the relationship between growth and mortality, seedlings were divided into two groups: those that survived through July 1992 and those that died between October 1991 and July 1992. Differences between the two groups in first-season growth were tested using *t* tests for variables meeting assumptions of ANOVA and Mann-Whitney *U* tests for other variables.

Seedling transplant experiment

Experimental design.—In June 1990, we selected three sets of microsites on the Prospect Hill experimental blowdown site for a preliminary experiment to test transplanting methodology. The preliminary experiment revealed that relatively large mounds and pits were required to ensure that all seedlings were adequately spaced and experienced similar conditions (e.g., elevation above the forest floor or type of soil). Based on these results, we selected eight additional sets of microsites for the experiment, each set containing one each of five types of microsites: open, fern, mound, pit, and top. For this experiment, we did not distinguish a root plate microsite and did not plant seedlings in the forest understory. We then located nine planting positions on each of the 40 microsites (8 sets of microsites × 5 microsites per set) and extracted a soil core from each planting position. Soil cores were sieved to remove rocks and coarse roots and then mixed together by microsite type for transplanting of experimental seedlings.

Seedlings of the three birch species were germinated in flats in a greenhouse in June 1990 and transplanted 1 mo later into peat pots filled with soil taken from the microsites. Before transplanting to the field, we assigned each seedling to one of three size classes based on stem length and leaf area. In August 1990, we transplanted three seedlings of each species to each experimental microsite, for a total of 360 seedlings (8 sets of microsites × 5 microsites per set × 3 species × 3 seedlings per species). For each species, one seedling of each of the three size classes was transplanted to each microsite. We identified three general locations on each microsite and at each location planted one seedling per species, all in the same size class. Size classes were randomly assigned to locations on each microsite. Peat pots were removed from soil cores before transplanting, and seedlings with intact soil cores were planted into the holes from which the soil had been extracted.

Measurements.—Seedling dimensions were measured while seedlings were growing in peat pots and immediately after transplanting to the experimental blowdown microsites. Subsequent measurements were made in October 1990, once every two months during the 1991 growing season, and at the end of the 1992 growing season. On each seedling we measured basal diameter, total height, and lengths of main stem, branches, and individual leaves. Basal diameter was measured with calipers to the nearest 0.1 mm. Total height and lengths of branches and leaves were measured to the nearest 0.1 cm. We also estimated the amount of damage to each leaf due to herbivory. In some cases, herbivores had removed nearly all of the leaf blade, but the petiole and midrib were always present to indicate that herbivory had occurred. In 1992 we collected all senescing leaves to calculate total leaf area and leaf biomass produced during the growing season. Near selected seedlings, we measured ambient light levels, CO_2 concentrations, air temperature, soil water content, water potential, and organic matter content, and nitrogen and nitrate supply rate (G. C. Carlton and F. A. Bazzaz, *unpublished manuscript*).

We then selected one seedling per species from each of five replicate microsites of each type for physiological measurements (5 sets of microsites × 5 microsites per set × 3 species = 75 seedlings). In September 1992, net photosynthesis under light-saturated and light-limiting conditions was measured on these seedlings. High light levels were obtained by using large mirrors to focus direct beam radiation on seedlings. With this method we achieved photosynthetic photon flux densities (PPFD) of at least 850 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for all seedlings, levels that are above the saturation point for these species (Wayne 1992). Low light levels were obtained by placing black umbrellas above seedlings to reduce photon flux densities to 45 ± 5 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Photosynthetic acclimation to high and low light levels was tested on three individuals of each species. Gas exchange was measured immediately before imposing the light treatment and then at intervals of 3, 8, 15, 30, and 60 min after imposing the treatment. For both high-and low-light treatments, net photosynthetic rates at 3 min were similar to those at 60 min. We therefore assumed that 3 min was adequate acclimation time, although most seedlings were allowed to acclimate for at least 5 min before gas exchange measurements were made. All measurements of seedling gas exchange were made on the first fully developed leaf using portable gas exchange systems (Model LI-6200, Li-Cor, Lincoln, Nebraska). Relative humidity was maintained near ambient levels during photosynthesis measurements.

After gas exchange measurements were completed, all seedlings were harvested. We removed and counted remaining leaves, excavated and washed roots, and measured basal diameter and length of the main stem and the length of all branches. Total leaf area of each seedling was determined by running all leaves through a leaf area meter (Li-Cor Model LI-3200). Shoots, roots, and leaves were then separated and dried at 70°C for a minimum of 4 d. After drying, four to six leaves from each seedling on which photosynthesis was measured were crushed and analyzed for nitrogen content. Total Kjeldahl nitrogen was determined with a Tecator Kjeltec Auto 1030 Analyzer system.

Multiple-decrement life tables.—Because cause of death could be identified for nearly all seedlings that died, multiple-decrement life tables were used to quantify the impact of different mortality agents on the experimental birch populations (Preston et al. 1972). In using the multiple-decrement approach, the probability of death by a given cause in the absence of other causes is approximated mathematically. For the case of two causes, A and B, we wanted to determine q_A and q_B, the probability of death by each cause independent of the other, given that we know D_A and D_B, the proportion of individuals dying from each of the two causes. The probability of surviving both causes of death is then

$$1 - (D_A + D_B) = (1 - q_A)(1 - q_B). \quad (1)$$

Because we have two unknowns, q_A and q_B, we need a second equation to find a solution. If we assume that the relative number of deaths by either cause is equal to the relative probability of death by that cause, then

$$q_A/q_B = D_A/D_B \quad (2)$$

and we are able to solve for q_A and q_B by substituting

$$q_A = (q_B \times D_A)/D_B$$

into Eq. (1) to yield

$$1 - (D_A + D_B)$$
$$= 1 - (q_B \times D_A)/D_B - q_B + q_B^2 \times (D_A/D_B). \quad (3)$$

Eq. (3) simplifies to the quadratic equation

$$D_A \times q_B^2 - (D_A + D_B) \times q_B + D_B \times (D_A + D_B)$$
$$= 0 \quad (4)$$

which can then be solved for q_B by using the quadratic formula and for q_A by substitution. Solution for three or more causes is accomplished by considering each cause against the combined effects of all other causes (Carey 1989).

Analysis of growth and leaf-level physiology.—Estimates of individual leaf area were obtained by measuring leaf length and leaf area of leaves on 30 seedlings of each of the three birch species. From these measurements the following regression equations were developed relating leaf length (L) to area (A):

$$A = 0.5367 \times L^{1.8767}\ R^2 = 0.979 \text{ [White birch]} \quad (5)$$

$$A = 0.2597 \times L^{2.0584}\ R^2 = 0.969 \text{ [Black birch]} \quad (6)$$

$$A = 0.3070 \times L^{1.9832}\ R^2 = 0.970 \text{ [Yellow birch]} \quad (7)$$

Estimated area of individual leaves was summarized to obtain total leaf area per seedling. Validation tests of leaf area models on small seedlings with few leaves indicated that predicted leaf area was within 10% of actual leaf area for 90% of seedlings. Predictive ability for larger seedlings with more leaves should be greater.

Calculation of growth parameters for individual seedlings enabled us to estimate experimental error and test for differences among species and microsites (McGraw and Garbutt 1990). All analysis of variance and regression procedures were done with MGLH routines in SYSTAT (Wilkinson 1990). Repeated-measures ANOVA methodology was used to analyze diameter, height, biomass, and leaf area data. The experiment was analyzed as a 5 × 3 split-plot fixed-effects model, with microsites as the main effect, replicated eight times, and species as the subplot effect. Values from the three replicate individuals of each species on each microsite were pooled for statistical analysis to minimize occurrence of missing data. For some analyses it was still necessary to impute values for missing data to meet assumptions of repeated-measures ANOVA (Wilkinson 1990).

Distributions of all variables were checked and variables were transformed when necessary to meet assumptions of ANOVA. A preliminary factorial ANOVA and scatterplot of residuals was used to identify outliers. For all variables with outliers, separate ANOVAs were run before and after deleting outliers. In the few cases where deletion of outliers influenced ANOVA results, we conducted a Kruskal-Wallis nonparametric analysis of variance. However, deletion of outliers did not affect the outcome of ANOVA for any of the variables reported here. After deleting outliers, a second factorial ANOVA was run to provide residuals for Levene's test. This test consists of merging absolute values of residuals with original grouping variables and conducting an ANOVA on the absolute residuals (Levene 1960). Significant results for a factor indicate unequal variances among levels of that factor (Wilkinson

1990). For factors with unequal variance, single-degree-of-freedom contrasts were used instead of the ANOVA F value for tests of significance (Milliken and Johnson 1984).

In addition to standard assumptions, repeated-measures ANOVA requires that covariances across all pairs of cells be equivalent. This assumption was tested by comparing Huynh-Feldt multivariate F statistics with univariate statistics. When discrepancies occurred, signifying departure from the covariance assumption, the more conservative multivariate statistics (Pillai's trace) were used (Wilkinson 1990). When F values for microsite or species effects were significant, pairwise tests were conducted using Fisher's protected least significant difference (FPLSD) (Carmer and Swanson 1973, Petersen 1985).

To examine time trends in growth of species on different microsites, we analyzed coefficients of the response curves generated by individual seedlings (Meredith and Stehman 1991). By using separate tests for each microsite, which differed markedly in their effects on growth, differences among species in growth trends could be detected more readily. Linear and quadratic coefficients were obtained by calculating the weighted sum of all measurements on an individual, with orthogonal polynomial coefficients as the weights (Gurevich and Chester 1986). Coefficients of response curves were then used as the raw data for one-way analysis of variance to test for linear or quadratic growth trajectories. Examination of variable distributions, identification and deletion of outliers, tests for equality of variance among cells, and FPLSD pairwise tests were conducted as described above.

To examine the relationship between growth rate and mortality, we pooled all species and calculated mean diameter and height in October 1991 and October 1992. For each of these sampling dates, we compared growth rates of seedlings that died before the end of the next growing season with rates of those that survived ≥ 1 yr after the measurement date. Differences between classes were tested with Student's t values calculated for unequal sample sizes (Sokal and Rohlf 1981).

Final yield data were analyzed as a split-plot design, with microsites as the main effect and species as the subplot effect (Wilkinson 1990). Data from surviving replicate seedlings were pooled to form the experimental units for ANOVA and variables were transformed as necessary to meet assumptions of ANOVA. As described above in this subsection, equality of variance among levels of each factor was tested by conducting an ANOVA on absolute residuals (Levene 1960), and equality of covariance across cells was tested using Huynh-Feldt multivariate F statistics (Wilkinson 1990). Linear contrasts were used to test for differences among species and microsites. For variables with unequal variance among cells, single-degree-of-freedom contrasts were used in lieu of the F statistic. We investigated patterns of carbon allocation by calculating the following ratios for each combination of microsite and species : stem mass ratio, root mass ratio, leaf mass ratio, leaf area ratio, and specific leaf mass (Causton and Venus 1981, Hunt 1990). Mean ratios were obtained from ratios calculated for individual seedlings.

Five replicate individuals per species on each microsite type were used for all physiological measurements. Physiological data were analyzed as a split-plot design, with microsites as the main effect and species as the subplot effect as described above for growth and yield data. Relationships among physiological parameters and between physiological and growth parameters were then examined using correlation analysis. Possible effects of variation in light levels on photosynthesis measurements were tested using analysis of covariance.

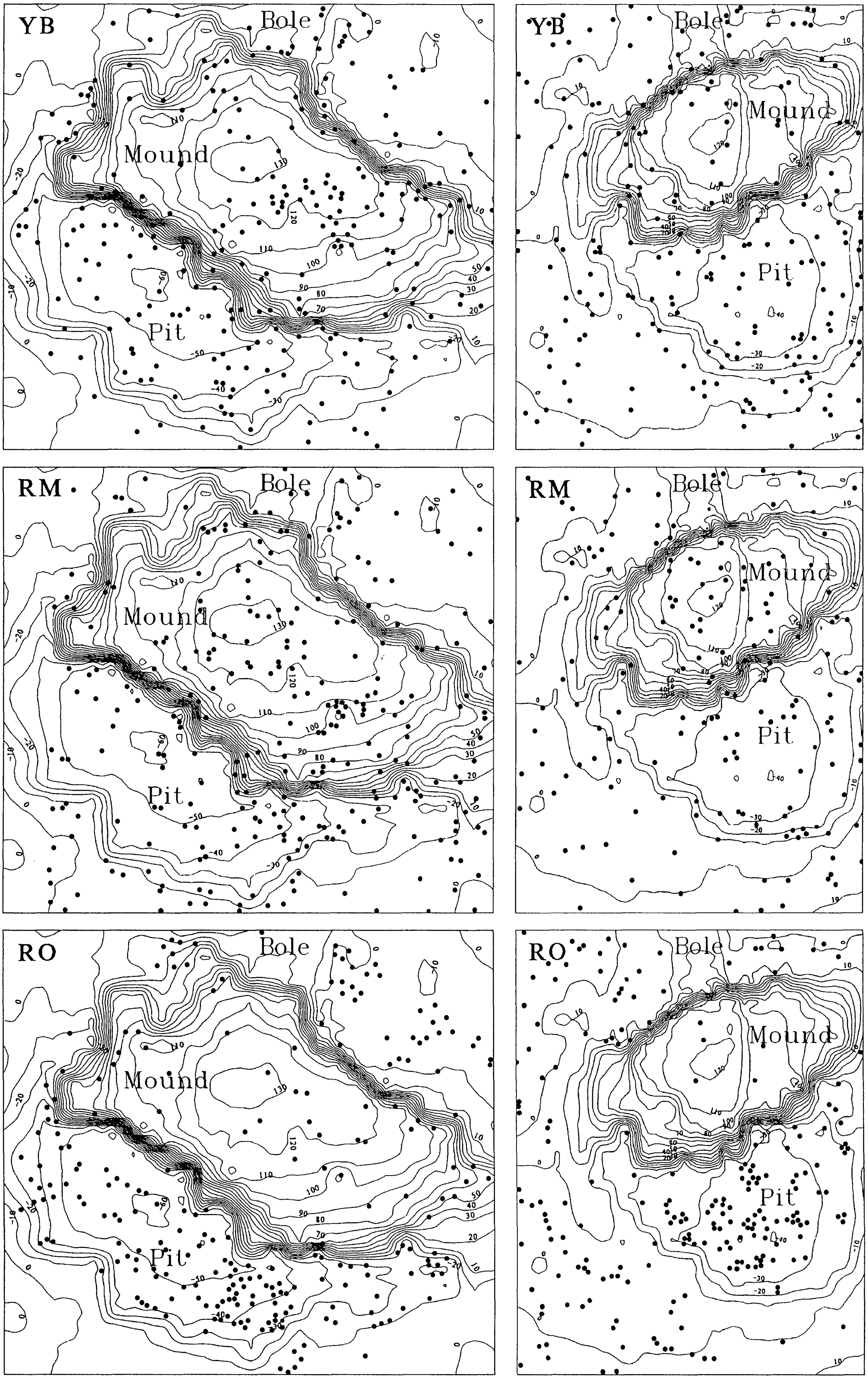
RESULTS

Seed dispersal

The simulated blowdown in 1990 reduced the density of black birch canopy trees from 47.5 stems/ha to 22.5 stems/ha. However, there were still 37.5 living black birch trees/ha on the blowdown site in 1993 because several uprooted trees remained alive. Density of overstory black birch in the adjacent undisturbed forest was 55.0 stems/ha before the simulated blowdown (D. R. Foster and A. L. Lezberg, *unpublished data*). Seed rain of black birch was greater in the understory of the undisturbed forest than in the blowdown during the winter of 1991–1992. The three blowdown transects received 66.7–76.9 seeds/m^2, significantly less than the 122.5 seeds/m^2 in the understory transect ($P < 0.004$ for all FPLSD tests).

The simulated blowdown reduced the density of white birch canopy trees from 32.5 stems/ha to 5.0 stems/ha, but 12.5 stems/ha remained alive on the blowdown site in 1993. Density of white birch in the adjacent undisturbed forest was 20.0 stems/ha before the simulated blowdown (D. R. Foster and A. L. Lezberg, *unpublished data*). From this pool of mature trees, white birch dispersed significantly more seed into the blowdown than into the understory of the undisturbed forest ($P < 0.030$ for all single-degree-of-freedom contrasts). White birch seed rain along the northern, central, and southern blowdown transects was 956.6, 864.8, and 494.0 seeds/m^2, respectively, whereas only 383.5 seeds/m^2 fell in the understory.

Seed rain of black birch was only slightly more variable in the blowdown than the understory: coefficient of variation (CV) = 44%, 49%, 61%, and 42% along the north, central, south, and understory transects, respectively. However, seed rain of white birch was much more variable along the northern and central blowdown transects (CV = 116% and 112%, respectively) than in the understory (CV = 64%). Seed rain from the few yellow birch trees in the stand was negligible.


YB
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The larger of the two mounds selected for experimental seed dispersal reached 130 cm above the forest floor and created a pit 60 cm deep (Fig. 2, left side). The smaller mound was nearly as tall but much narrower, creating a pit only 40 cm deep (Fig. 2, right side). The root plate of both mound–pit complexes was oriented toward the southeast and the top microsite faced the northwest. The distribution of yellow birch seeds was significantly different from the distribution of microsites by either planar area ($P < 0.01$ for chi-square tests on both mound–pit complexes) or actual surface area ($P < 0.001$ for chi-square tests). More than 31% of all yellow birch seeds landed in the two pits, which made up only 23.2% of the total planar area and 16.4% of the actual surface area on the two mound–pit complexes (Table 1, Fig. 2). Red maple seeds tended to remain on the mound more than seeds of yellow birch and were distributed in proportion to the planar area of the different microsites on the small mound–pit complex (Table 1, Fig. 2). Distribution of red oak acorns was significantly different from the distribution of either planar or surface area ($P < 0.001$ for both complexes). At least half of the acorns came to rest in pits on both complexes (Table 1, Fig. 2). Conversely, only 15% of the acorns remained on the large mound and <3% remained on the small mound. Only one of the 500 acorns dispersed remained on a root plate and none remained on a top microsite.

Germination and seedling survival

The type of substrate, which is thought to be an important controller of germination for most species, varied appreciably among microsites. Substrate on open and fern microsites in the blowdown was similar to substrate on the understory sites, with almost 90% covered by litter and the remainder covered by woody debris, living roots, and rocks (Fig. 3). However, on both open and fern sites there were a few patches of exposed soil, which were not present in the understory sites. The majority of the surface of top microsites and pits was also covered with litter, but these sites were characterized by more exposed soil (Fig. 3). More than half of the surface of mounds and 90% of root plates was exposed mineral subsoil. Many mounds, however, had a fringe of organic horizon exposed near the edge of the uprooted portion of the forest floor. Mounds also tended to trap more leaf litter and other organic debris than root plates (Fig. 3). The percent cover of living vegetation also varied among microsites. Total cover of all vegetation on open microsites (29.9%) was similar to the forest understory (28.3%). Fern microsites, which were located in patches of dense vegetation, had the greatest cover (47.9%). Vegetative cover was intermediate on top microsites (17.0%) and lowest on the recently exposed mounds (5.4%), pits (2.1%), and root plates (1.0%).

There were 451 new birch seedlings on all plots in 1991 and 587 new seedlings in 1992. In both years more than half of all new seedlings germinated on open sites (55.9% in 1991 and 52.0% in 1992). Seedling density on other sites varied between years. In 1991 seedling density was second highest on fern microsites (20.4% of all seedlings), but in 1992 20.8% of seedlings germinated on mounds and only 10.4% of new seedlings were found on fern microsites. Fewer than 8% of seedlings germinated on pit, top, or root plate microsites, and only four seedlings germinated in the forest understory during the study.

Of the 451 birch seedlings that germinated in 1991, 52% survived through July 1992, with greatest survival on mounds (67%) and open sites (66%) (Table 2). Survival on fern, pit, and top microsites was similar (47%, 44%, and 38%, respectively). None of the seedlings germinating on root plates or understory sites survived. Surviving birch seedlings were significantly larger in October 1991 than were seedlings that died between October 1991 and July 1992 (Table 2). Mean basal diameter of survivors was greater than diameter of nonsurvivors on all microsites. Height, leaf number, and projected leaf area were also greater for survivors on open sites, and survivors on fern, pit, and top sites were either taller or had more foliage than nonsurvivors (Table 2).

Performance of transplanted seedlings

Patterns and causes of mortality.—Survival of transplanted seedlings was very similar for the three species: 72 of 120 white birch seedlings and 77 of 120 seedlings of both black and yellow birch were still alive after 3 yr (Table 3). Total impact of mortality at different periods was obtained by summarizing k-values, which quantify mortality rate (Begon and Mortimer 1986). Using white birch as an example, the sum of winter k-values (October 1990 and October 1991) was 0.098, which was 44.1% of the total k-value of 0.222 (Table 3, k_x column). In contrast, winter mortality accounted for 66.8% and 60.6% of the total k-value for black birch and yellow birch, respectively (Table 3). Mortality during the 1991 growing season was much greater in white birch (42.8% of the total k-value) than in black birch or yellow birch (21.8%, and 22.8% of the total k-value, respectively) (Table 3).

Seedling mortality was lowest on open sites and highest in pits (Fig. 4). Timing of mortality also dif-

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FIG. 2. Dispersal of experimentally released seeds of three species onto a large (left) and a small (right) mound–pit complex. The right side of each large map is oriented toward magnetic north, and the upper right corner of each small map is oriented toward magnetic north. The scale on all maps is 1:31, and contour intervals are 10 cm. Species are yellow birch (YB), red maple (RM), and red oak (RO).

TABLE 1. Distribution of microsite areas and experimentally released seeds on two mound–pit complexes. Values are percentage of the mound–pit complex in each of the five microsite types and the percentage of yellow birch, red maple, and red oak seeds that came to rest on each microsite.

Mound–pit complex	Microsite	Planar area†	Surface area	Species		
				YB	RM	RO
Large	Open	37.1	16.7	27.9	25.7	33.1
	Mound	34.1	37.8	36.1	38.4	15.1
	Pit	24.2	18.4	30.1	29.2	52.2
	Top	1.3	11.1	1.9	0.7	0.0
	Root plate	3.3	16.0	4.1	6.0	0.4
Small	Open	53.4	32.1	49.3	44.7	47.6
	Mound	17.8	22.9	15.0	21.7	2.4
	Pit	22.1	14.4	32.4	27.3	50.0
	Top	1.0	5.0	1.4	0.6	0.0
	Root plate	5.7	25.6	1.9	5.6	0.0

Notes: In addition to mound, pit, and top microsites, we distinguished the root plate (the vertical portion of the mound immediately above the pit). All area around each mound–pit complex was considered an open microsite. Fern microsites were not included in this experiment. Species are yellow birch (YB), red maple (RM), and red oak (RO).

† Planar area = area as seen from above.

fered among microsites, with mortality occurring primarily during the growing season on fern and top microsites but primarily during the winter on mounds and in pits. In fact, 66.2% of all seedlings planted in pits died during the first winter (Fig. 4). The sum of winter k-values was 81.6% of the total k-value for mounds and 69.2% of the total for pits but only 18.6% of the total for fern microsites and 34.4% of the total for top microsites. On open microsites, where >90% of seedlings survived, the sum of winter k-values was 59.1% of the total k-value.

Differences among species in survival were apparent only under ferns and, to a lesser extent, on top microsites (Fig. 4). White birch fared poorly in the deep shade cast by ferns and other herbaceous vegetation, with 50% mortality by the end of the third growing season. In contrast, all yellow birch seedlings survived the first two growing seasons under ferns, and total mortality for yellow birch was no greater under ferns than on open sites. Mortality rates on top sites were greater in yellow birch than in black birch, particularly during the first two years of the experiment (Fig. 4).

Microsites differed markedly in causes of mortality. The heavy mortality in pits was due almost entirely to burial by soil and rocks eroding from adjacent tip-up mounds and by leaf litter accumulating during the fall and winter (Fig. 5). Seedlings on mounds were exposed to severe frost heaving, particularly during the first winter when snowfall was light. Browsing of main stems and branches by snowshoe hares (*Lepus americanus*) was the only important cause of mortality on open sites. Most mortality under ferns and on top microsites was apparently caused by resource limitation rather than the action of biotic or physical factors although some seedlings died from browsing, burial, and frost heaving on these sites (Fig. 5).

The three species did not differ appreciably in susceptibility to specific causes of mortality. Mortality due to resource limitation was greatest in white birch (15.8%) and lowest in yellow birch (8.3%). Yellow

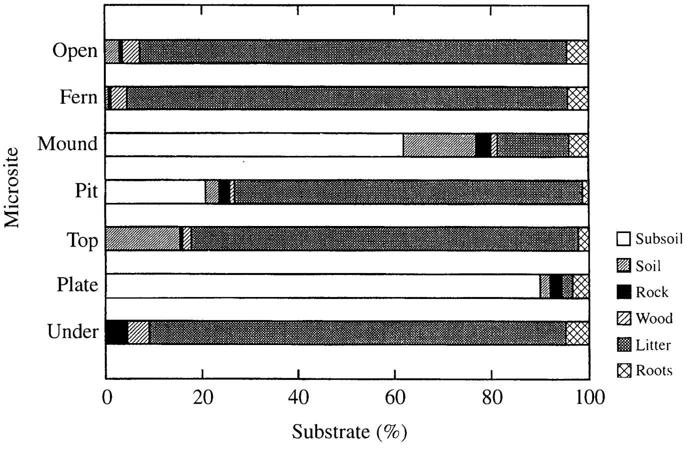

FIG. 3. Substrate of experimental blowdown microsites and adjacent forest understory in July 1991. Types of substrate are subsoil mineral horizon, surface organic horizon, rock, woody debris, leaf litter, and living roots.

TABLE 2. Relationship between growth and survival for first-year birch seedlings germinating naturally on microsites of experimental blowdown.

Micro-site	Number living and dying	Basal diameter (mm)	Height (cm)	Number of leaves	Projected leaf area (cm^2)
Open	166	0.77***	2.31***	4.42***	2.89***
	86	0.42	1.38	3.24	0.70
Fern	42	0.60***	2.19	4.83***	2.26**
	50	0.37	1.67	3.37	0.50
Mound	22	1.16*	4.39	4.64	7.84
	11	0.67	2.93	3.60	3.57
Pit	8	0.91*	4.04	4.12**	10.20*
	10	0.49	3.06	1.80	1.07
Top	20	0.68**	2.40*	2.85	1.33
	33	0.44	1.67	3.85	1.00

Notes: The top value in each pair refers to seedlings that survived $\geq$1 yr after being measured in October 1991, and the bottom value refers to seedlings that died in $<$1 yr. There were no surviving seedlings on root plate or understory microsites. Diameter, height, and leaf number values are means, with significance of *t* tests indicated by asterisks. Values for projected leaf area are medians, with significance of Mann-Whitney *U* tests indicated by asterisks.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

birch was slightly more susceptible to browsing than the other species (5.8% compared to 2.5% mortality rate). Effects of burial and frost heaving were very similar for all three species. Because of the similarity in response of the three species to different mortality agents, we pooled data for all species for multiple-decrement analysis, judging that assumptions of this analysis were reasonably well satisfied with pooled data. Separate analyses were conducted for each microsite, however, since microsites differed substantially in both rates and causes of mortality.

Age- and cause-specific mortality probabilities in the absence of all other causes were generally similar to those in the presence of other causes. This was due to relatively low mortality rates on most microsites and to the dominant effect of burial in pits. The most striking difference was the predicted increase in mortality due to resource limitation in the absence of other causes. In pits, for example, only 1.4% of seedlings died from resource limitation but 6.2% were predicted to die if resource limitation was the only cause of death (Table 4). On top microsites, effects of both browsing and resource limitation would increase in the absence of other mortality agents. If there had been adequate snow cover on mounds to prevent frost heaving, mortality would have been reduced from 25.0% to 8.1%. Protecting seedlings against browsing by snowshoe

TABLE 3. Survivorship tables for three birch species growing on experimental hurricane blowdown microsites.

Date	Age, x (mo)	Interval, D_x (mo)	No. alive, a_x	Proportion surviving, l_x	No. dying, d_x	Mortality rate, q_x	Monthly mortality, q_x/D_x	ln(a_x)	k_x
White birch									
Aug 1990	0	2	120	1.000	0	0.000	0.000	2.079	0.000
Oct 1990	**1**	**6**	**120**	**1.000**	**18**	**0.150**	**0.025**	**2.079**	**0.070**
Apr 1991	2	2	102	0.850	11	0.108	0.054	2.009	0.050
Jun 1991	3	2	91	0.758	4	0.044	0.022	1.959	0.019
Aug 1991	4	2	87	0.725	5	0.057	0.029	1.940	0.026
Oct 1991	**5**	**7**	**82**	**0.683**	**5**	**0.061**	**0.009**	**1.914**	**0.028**
May 1992	6	5	77	0.642	5	0.065	0.013	1.886	0.029
Oct 1992	7		72	0.600				1.857	0.222
Black birch									
Aug 1990	0	2	120	1.000	0	0.000	0.000	2.079	0.000
Oct 1990	**1**	**6**	**120**	**1.000**	**22**	**0.183**	**0.031**	**2.079**	**0.088**
Apr 1991	2	2	98	0.817	3	0.031	0.015	1.991	0.014
Jun 1991	3	2	95	0.792	5	0.053	0.026	1.978	0.023
Aug 1991	4	2	90	0.750	1	0.011	0.006	1.954	0.005
Oct 1991	**5**	**7**	**89**	**0.742**	**8**	**0.090**	**0.013**	**1.949**	**0.041**
May 1992	6	5	81	0.675	4	0.049	0.010	1.908	0.022
Oct 1992	7		77	0.642				1.886	0.193
Yellow birch									
Aug 1990	0	2	120	1.000	4	0.033	0.017	2.079	0.015
Oct 1990	**1**	**6**	**116**	**0.967**	**22**	**0.190**	**0.032**	**2.064**	**0.091**
Apr 1991	2	2	94	0.783	4	0.043	0.021	1.973	0.019
Jun 1991	3	2	90	0.750	2	0.022	0.011	1.954	0.010
Aug 1991	4	2	88	0.733	3	0.034	0.017	1.944	0.015
Oct 1991	**5**	**7**	**85**	**0.708**	**5**	**0.059**	**0.008**	**1.929**	**0.026**
May 1992	6	5	80	0.667	3	0.038	0.008	1.903	0.017
Oct 1992	7		77	0.642				1.886	0.193

Notes: $d_x = a_x - a_{x+1}$; $q_x = d_x/a_x$; $k_x = \ln(a_x) - \ln(a_{x+1})$. Age classes ($x$) span different numbers of months, as indicated by the interval D_x. Overwinter values are in boldface type. The bottom value in the k_x column for each species is the sum of all k_x values for that species.

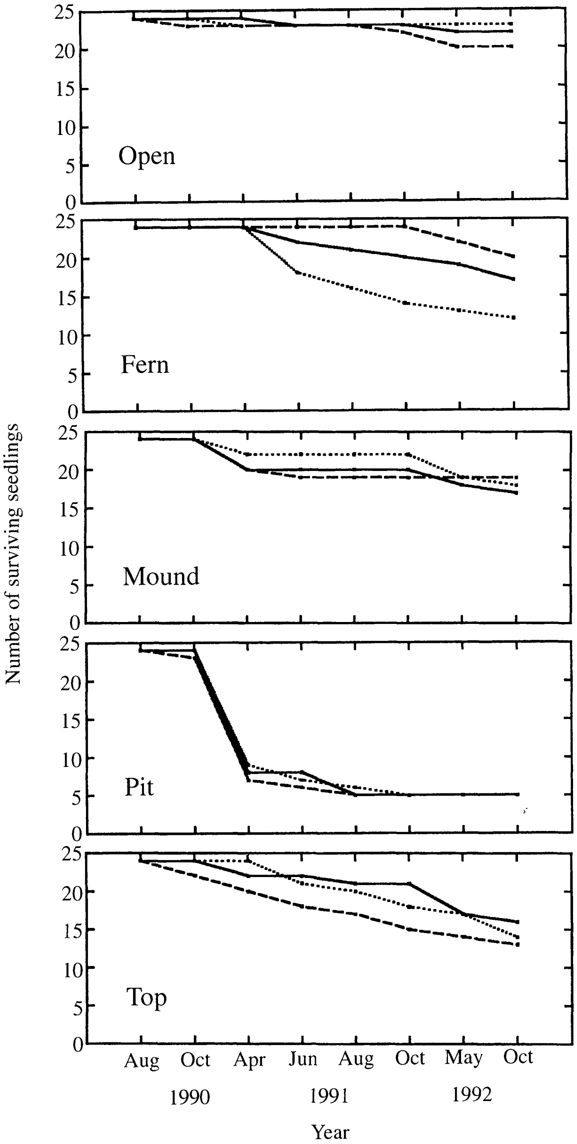

FIG. 4. Survival of seedlings of white birch (········), black birch (———), and yellow birch (– – –) during three seasons of growth on microsites created by an experimental hurricane blowdown treatment. Twenty-four seedlings of each species were planted on each microsite in August 1990, and all surviving seedlings were harvested in October 1992.

hares would virtually eliminate mortality on open sites (Table 4).

Height growth, biomass, and carbon allocation.— During the course of the transplant experiment, mean height growth of all three birch species was linear on top microsites, quadratic with negative curvature on open and fern sites, and quadratic with positive curvature on mound sites (Fig. 6, Table 5). In other words, absolute growth rates were constant on top microsites, decreasing on open and fern sites, and increasing on mounds. High mortality and variable growth rates in pits obscured temporal patterns. The slope of the white birch height growth curve on mounds was significantly greater than the slope of the other species ($P = 0.001$ for both black and yellow birch; FPLSD test). White birch seedlings on mounds were also taller throughout the course of the experiment than seedlings of black and yellow birch (Table 5, Total F) ($P = 0.002$ and $P = 0.001$, respectively; FPLSD test). The same trends were observed on top, pit, and open microsites, although differences were not significant. Patterns of diameter growth were similar to height growth patterns and are not presented.

Biomass and allocation patterns of the 226 surviving seedlings differed substantially among microsites and species. Seedlings under ferns were smaller than seedlings on all other sites in stem, root, and total biomass ($P < 0.007$ for all single-degree-of-freedom contrasts) and had lower specific leaf mass (SLM) than seedlings on open sites or mounds. Seedlings on open sites were smaller in all biomass components than were seedlings on mounds ($P < 0.05$ for all single-degree-of-freedom contrasts). White birch were larger than the other species in all biomass components, but only differences in stem mass were significant ($P < 0.01$). White birch also had higher SLM than black birch ($P = 0.013$).

The proportion of carbon allocated to leaves, the leaf mass ratio (LMR), was similar across all microsites. Stem mass ratios (SMR) were significantly higher under ferns and on tops than on the other three microsites ($P < 0.001$). Large seedlings of all three species tended to allocate more to stems than small seedlings on all microsites except pits (Carlton 1993). Leaf area ratio

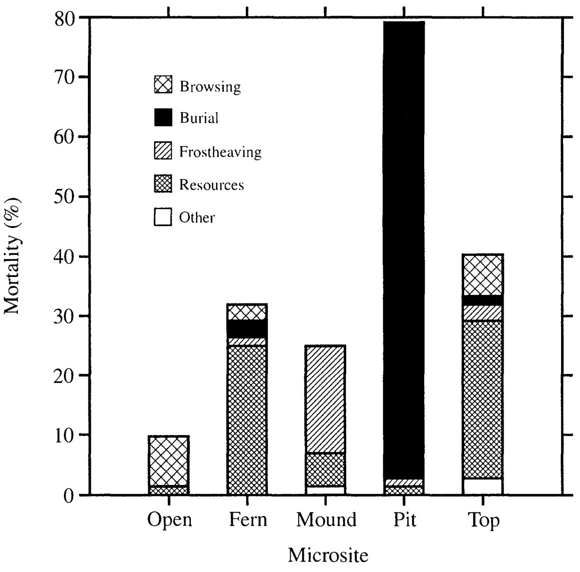

FIG. 5. Mortality rate and cause of death for birch seedlings during three seasons of growth on five microsites of experimental hurricane blowdown. Seedlings of all three birch species were pooled for this analysis. Causes of death are browsing by snowshoe hares, burial by litter and soil, frost heaving, resource limitation, and other causes that could not be identified.

TABLE 4. Percent mortality by cause for birch seedlings grown on microsites of experimental blowdown.

Microsite	Total	Browsing	Burial	Frost	Resource	Other
Open	9.72	8.33	0.00	0.00	1.39	0.00
		8.39	0.00	0.00	1.45	0.00
		1.45	9.72	9.72	8.39	9.72
Fern	31.94	2.78	2.78	1.39	25.00	0.00
		3.04	2.84	1.41	26.60	0.00
		29.69	29.84	30.86	7.12	31.94
Mound	25.00	0.00	0.00	18.06	5.56	1.39
		0.00	0.00	18.38	6.80	1.41
		25.00	25.00	8.11	19.53	23.93
Pit	79.17	0.00	76.39	1.39	1.39	0.00
		0.00	77.46	1.43	6.25	0.00
		79.17	7.59	78.87	77.78	79.17
Top	40.28	6.94	1.39	2.78	26.39	2.78
		9.05	1.75	2.96	29.11	2.78
		34.28	39.17	38.41	15.69	38.52

Notes: Causes of death are browsing by snowshoe hares, burial by soil and litter, frostheaving, resource limitation, and other causes that could not be identified. Values in the first of the three rows associated with each microsite are percent mortality attributed to the specified cause. Values in the second row are estimated mortality rates due to the specified cause in the absence of all other causes. Values in the third row are estimated mortality rates of all other causes in the absence of the specified cause.

(LAR) was significantly higher in black birch than in either white birch ($P = 0.018$) or yellow birch ($P = 0.023$), particularly on fern microsites. Yellow birch seedlings allocated more to roots than black birch ($P = 0.012$). There were no other significant differences among species in allocation ratios.

Leaf-level physiology.—Mean leaf nitrogen concentration did not differ significantly among microsites, although seedlings on mound tops tended to have higher nitrogen levels (2.15%) than those in pits (1.80%). Over all microsites, yellow birch had the lowest nitrogen concentration (1.73%), less than black birch (1.94%) ($P = 0.068$) and significantly less than white birch (2.07%) ($P = 0.011$). Differences between white and yellow birch were greatest on open, fern, and mound microsites.

For all three species, light-saturated (PPFD > 850 $\mu mol \cdot m^{-2} \cdot s^{-1}$) net photosynthetic rates (P_{max}) were lower for seedlings growing under ferns than for seedlings on open ($P = 0.007$), mound ($P = 0.006$), pit ($P = 0.060$), or top microsites ($P = 0.023$). Under high light, white birch achieved significantly higher photosynthetic rates than yellow birch ($P = 0.049$) and consistently higher rates than black birch ($P = 0.081$) (Fig. 7A). Black and yellow birch were very similar in their photosynthetic response to high light. Under light-limiting conditions (PPFD 45 ± 5 $\mu mol \cdot m^{-2} \cdot s^{-1}$), seedlings of all three species had net photosynthetic rates of ~1 $\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$, regardless of the microsite on which they had been growing (Fig. 7B).

Because photosynthetic rates at such low light levels are sensitive to slight variations in PPFD, we tested for effects of light levels on gas exchange rates. The slope of the regression of photosynthetic rate on light level for all microsites and species combined was not significant ($P = 0.381$). Slopes for separate regressions by microsite were also not significant, but the slopes of species-specific equations for black birch and yellow birch were significant ($P = 0.031$ and $P = 0.041$, respectively). Because the slopes of equations for the two species were different ($P = 0.036$), effects of light levels on gas exchange were tested separately for each species. For these tests, we used analysis of covariance of microsite effects adjusted for light. For both species there was a significant interaction term in the ANCOVA, suggesting differences in experimental light levels among microsites. However, microsite effects on net photosynthesis adjusted for light were still not significant for either black birch ($P = 0.886$) or yellow birch ($P = 0.492$).

White birch seedlings exhibited a stronger relationship between net photosynthesis rates and growth parameters than the other species. Basal diameter, stem mass, and leaf mass of white birch were all significantly correlated with P_{max} ($R = 0.78$, 0.73, and 0.74, respectively). Specific leaf mass (SLM) was also highly correlated with P_{max} ($R = 0.78$, $P = 0.002$), indicating that high-light photosynthetic rates were directly related to leaf morphology. The only significant relationship in yellow birch seedlings was a positive correlation between total leaf biomass and P_{max} ($R = 0.72$). There were no significant correlations between net photosynthesis rates and growth parameters in black birch.

Growth of largest individuals.—By the end of the experiment, the largest seedlings of all three species were ~2 m tall and weighed >100 g. The tallest individuals were growing on mounds or top microsites, which effectively increased their height above the forest floor and improved their competitive position. Of the 40 seedlings comprising the five tallest on each of

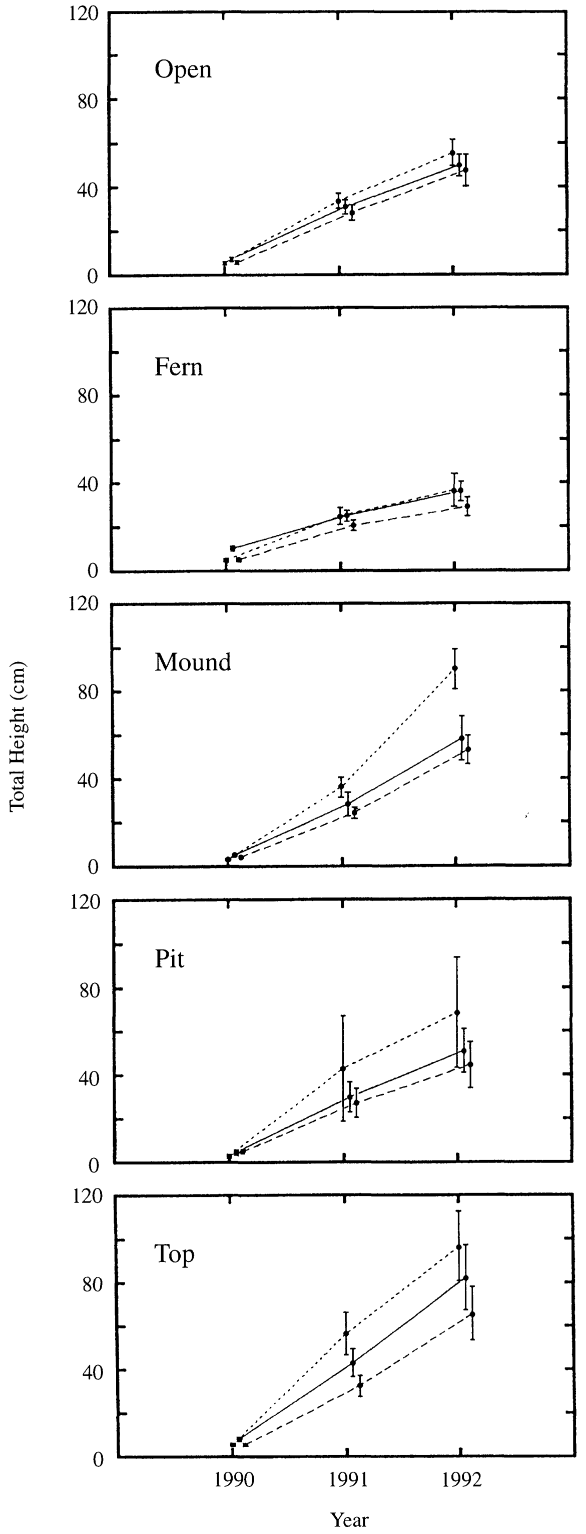

FIG. 6. Height growth of three birch species on experimental hurricane blowdown microsites. Mean values are connected by lines denoting white birch (- - -), black birch (———), and yellow birch (— — —). Vertical bars indicate ±1 SE. Lines and bars are offset slightly with order from left to right being white birch, black birch, and yellow birch. Values are mean height of main stem or dominant branch.

the eight sets of microsites, 18 were growing on mounds, 15 on top microsites, 5 on open sites, and 2 in pits (Fig. 8). Nineteen of these seediings were white birch, 14 were black birch, and 7 were yellow birch. The 9 tallest seedlings were all located on three of the eight sets of microsites (Fig. 8E, F, G).

To evaluate potential regeneration success of the largest experimental seedlings, we assumed that the tallest, fastest growing individuals on each set of microsites would have the greatest probability of reaching the canopy (Connell 1989). Because most mounds and pits selected for this study were created by the uprooting of large trees or clusters of several trees, we estimated that each set of microsites encompassed enough area to support two canopy trees. We then posited two scenarios, depending on rates of canopy closure by branch extension of surviving overstory trees (Hibbs 1982, Runkle 1982). If branch extension occurred slowly, we assumed that the two tallest and fastest growing birch seedlings on each set of microsites would reach the canopy. With rapid branch extension, we assumed that only one birch seedling on each set of microsites would reach the canopy.

We determined the seedlings most likely to succeed in each of these scenarios using three criteria to evaluate seedling potential. The most important criterion was absolute height above the forest floor, which depended on both seedling height and elevation of the seedling base. For seedlings within 5% of the same absolute height, we chose those with the greatest stem height. For seedlings within 5% of the same absolute height and stem height, we chose seedlings with the greatest 1991–1992 height growth increment. Assuming slow branch extension and canopy closure by surviving overstory trees, 10 white birch, 5 black birch, and 1 yellow birch would reach the canopy (Fig. 8; seedlings 1 and 2 in panels A, B, C, D, and F; seedlings 1 and 3 in E, G, and H). Ten of these 16 seedlings were located on mounds and the other six were on top microsites. With more rapid branch extension by overstory trees, five white birch, two black birch, and one yellow birch would reach the canopy (Fig. 8; seedling 1 in all panels except seedling 3 in H). Five of these seedlings were located on mounds and three were located on top microsites.

DISCUSSION

Seed rain onto the disturbed site

Seed rain of white birch was significantly greater in the blowdown than in the understory of the adjacent forest even though the density of canopy trees was much lower in the blowdown. Furthermore, seed rain of white birch was much more heterogeneous in the blowdown than in the forest understory. Black birch seed rain was somewhat lower and only slightly more heterogeneous in the blowdown than in the adjacent undisturbed forest. The reduction in black birch seed

TABLE 5. Summary of ANOVA results for total, linear, and quadratic contrasts describing height growth of three birch species over three growing seasons.

		Total		Linear		Quadratic	
Source	df	SS	*F*	SS	*F*	SS	*F*
Open							
Grand mean	1			126 361.3	181.264***	1 651.8	8.162**
Species	2	4 372.4	1.742	1 888.0	1.768	120.4	0.297
Error	59	72 778.1		30 964.8	11 939.5		
Fern							
Grand mean	1			32 899.8	89.494***	1 858.1	38.977***
Species	2	2 573.0	1.537	431.6	0.587	133.5	1.401
Error	44	36 831.4		16 175.3		2 097.5	
Mound							
Grand mean	1			210 861.3	179.986***	8 394.1	13.874**
Species	2	27 140.2	7.393**	18 229.6	9.841***	1 978.9	1.623‡
Error	49	89 936.4		45 382.8	29 876.5		
Pit							
Grand mean	1			27 646.2	31.517***	462.0	0.942
Species	2	1 910.2	0.830	363.0	0.403	321.9	1.144
Error	9	10 355.1		4 051.6		1 266.4	
Top							
Grand mean	1			230 625.0	87.853***	1.2	0.001
Species	2	20 455.6	1.804	11 344.1	2.640†	2 031.6	1.661
Error	37	215 497.4		99 754.5		35 377.5	

† $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

‡ Indicates that single-degree-of-freedom contrasts were used instead of the *F* test because of unequal variance among cells in the ANOVA. One or two outliers were deleted for some ANOVAs, reducing the error df.

rain in the blowdown closely paralleled the reduction in density of live canopy trees. Even in black birch, however, the decline in seed input on the disturbed site was not as pronounced as reported from clearcuts and other types of forest disturbance (Hughes and Fahey 1988).

There are several possible explanations for the observed patterns of birch seed dispersal on the blowdown site. First, some large canopy trees were left standing on the experimental site. Furthermore, trees surrounding the blowdown site may have dispersed preferentially into the gap created in the canopy. Trees at the edge of the blowdown may also have had greater access to light and other resources and therefore may have produced more seed than trees in a dense canopy. Lastly, many uprooted trees remained alive and reproductive during the course of the experiment. In fact, >75% of all uprooted trees were still alive after 1 yr and many were flowering, fruiting, and dispersing seed (D. R. Foster and A. L. Lezberg, *unpublished data*). Seeds dispersing from these crowns near the ground resulted in extremely heterogeneous seed input for white birch. Scattered residual canopy trees and surviving uprooted trees are probably characteristic of many sites damaged by catastrophic winds (Foster and Boose 1992). Results from this study suggest that such trees may provide a critically important source of seed during the initial revegetation phase.

Seed dispersal on mounds and pits

Effects of mound-and-pit microtopography on birch seed dispersal differed on the two replicate mound–pit complexes. Many experimentally released yellow birch seeds dispersed onto the large mound, which had a broad, relatively flat surface. However, seeds tended to disperse away from the small mound and collect in the associated pit. Less than 2% of seeds dispersed onto the top microsite of either mound–pit complex. Yellow birch seed was less equitably dispersed across microsites than red maple but more equitably dispersed than acorns of red oak, which tended to roll into the pits. Mounds are known to provide favorable conditions for germination and growth of birch species (Henry and Swan 1974, Houle 1992). Results of the seed dispersal experiments suggest that regeneration of these species on top microsites and some mounds may have been limited by lack of seed dispersal onto the microsites. Conversely, seed dispersal was not likely to limit reproduction on open, fern, or pit microsites. Inferences regarding seed dispersal were limited by the fact that only two mound–pit complexes were sampled and experimental dispersal was confined to periods with little or no wind. Seeds dispersed in stronger winds may exhibit more horizontal movement and may be more likely to lodge on top or root plate microsites.

Seedling germination and survival

Seedling recruitment was dominated by birch, particularly in 1992 when 95% of all new seedlings were birch. The majority of birch seedlings appeared on open sites, almost exclusively in places where litter and other materials had been removed to expose patches of organic soil (Carlton 1993). Germination and seed dispersal results suggest that any lack of birch regeneration on open microsites was probably attributable to poor seedling growth and survival rather than inadequate seed dispersal or germination. Approximately 15% of all new seedlings appeared on fern microsites, again primarily on exposed patches of organic soil, indicating that seed dispersal and germination were also adequate for regeneration to occur on these sites. Approximately 9% of all new seedlings appeared on top microsites and 6% in pits. Therefore, although lack of seed dispersal may have limited regeneration on some top microsites, as discussed in the preceding subsection, germination on these sites was quite good. Conversely, most pits received abundant seed but were apparently poor sites for successful germination, probably because of the accumulation of soil, leaf litter, and other materials (Facelli and Pickett 1991).

In 1991 only 7.3% of new seedlings were located on mounds. Poor germination on newly created mounds was probably due to both soil and light conditions. Newly exposed mineral subsoil horizons of mounds were very low in organic matter content and nitrogen availability (Carlton and Bazzaz 1998). Although most

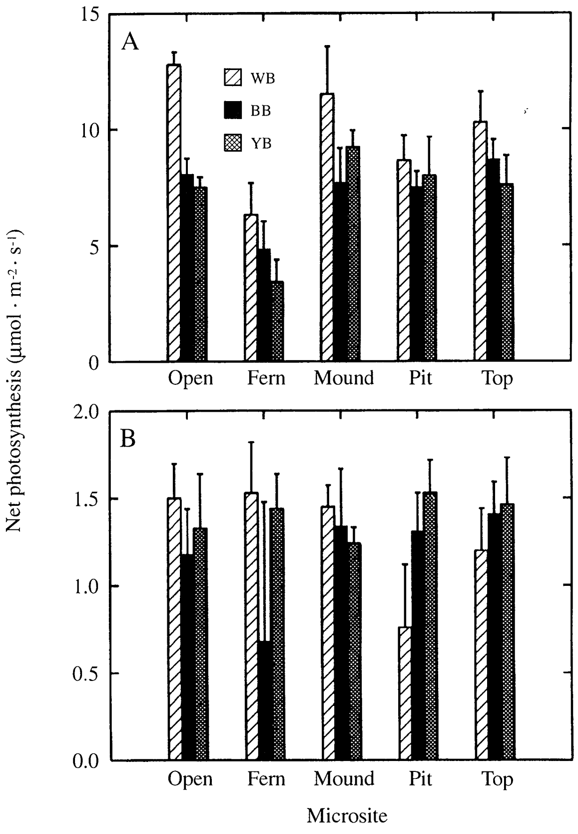

FIG. 7. Net photosynthetic rates of white birch (WB), black birch (BB), and yellow birch (YB) seedlings growing on microsites of experimental hurricane blowdown. Histogram bars denote means and 1 SE of net photosynthesis in (A) light-saturated and (B) light-limiting conditions. Measurements were made in early September 1992.

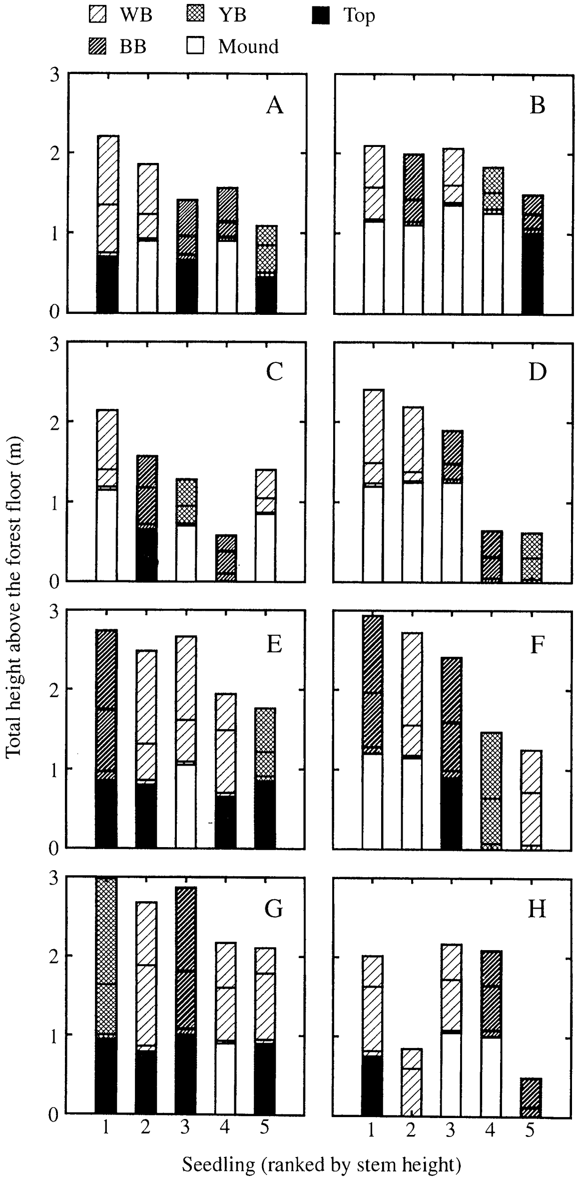

FIG. 8. Total height above the forest floor of the five tallest birch seedlings on each of the eight sets of experimental microsites. The lower part of each stacked histogram bar designates whether the seedling was growing on a mound or top microsite. The height of this part of the bar indicates the distance above the forest floor of the seedling base. The top part of each stacked histogram bar designates whether the seedling was a white birch (WB), black birch (BB), or yellow birch (YB). This part of the bar indicates the seedling height at the end of 1990 (lowest line), 1991 (second line), and 1992 (top of bar). All heights are in meters. Seedlings shown with no microsite bars in C, D, and F were growing on open sites where the seedling base was at the forest floor level. Seedlings 2 and 5 in panel H were growing in the pit with bases at −0.30 m and −0.35 m, respectively. Bars for these seedlings represent net height above the forest floor. The 1990 growth line is not visible for these seedlings, because they were still below the plane of the forest floor at that time.

birch species germinate readily on exposed soil, survival depends on adequate moisture and nutrient availability to support early root growth (Safford et al. 1990, Houle 1992). Excessive radiation may also have inhibited birch regeneration. During the 1991 growing season, most newly created mounds were subject to very high light levels. Tubbs (1969) found that yellow birch germination on well-drained soils was much better under shade than in high light conditions. Germination of both black birch and white birch is also enhanced by partial shade (Lamson 1990, Safford et al. 1990).

In 1992 a much higher proportion (20.8%) of new seedlings germinated on mounds, indicating that these microsites had either become more favorable for germination or that seed dispersal onto mounds was greater the second summer following disturbance than the first. Because the blowdown treatment preceded the primary birch seed dispersal period in 1990, seeds probably dispersed onto the newly exposed mound surfaces during the first as well as the second winter following the disturbance. During the first winter, however, the unprotected mineral soil was very susceptible to frost heaving and erosion, and many birch seeds dispersing onto mounds were probably washed off during this period. By the second dispersal season, mound surfaces had stabilized somewhat, and vegetation and litter were available to trap seeds (Carlton 1993). Colonizing vegetation also reduced light intensities during the 1992 growing season and provided substrate for decomposition, which may have substantially improved conditions for germination (Houle 1992).

Survival of birch seedlings through the first growing season and winter was surprisingly high, particularly on open and mound microsites where two-thirds of all germinants survived. None of the seedlings in the forest understory survived, however, emphasizing the importance of disturbance events for regeneration of these species. Seedling survival was strongly associated with early growth rates on open and fern microsites. Birch seedlings that survived on these microsites had thicker and taller stems and greater leaf area than those that died the following winter or spring. The relationship between seedling size and future survival was much weaker on mound and top microsites.

The commonly observed association of birches with tip-up mounds does not imply that impoverished mineral soil horizons promote establishment and growth. Most seedlings observed on our experimentally created mounds were growing in the narrow band of organic-rich soil immediately beneath the uprooted forest floor layer. The vast majority of the mound surface appeared to be unsuitable for recruitment during the first growing season. Presumably, mineral subsoils were amended fairly rapidly as plant material and litter became available for decomposition. This suggests that mounds may provide an extended opportunity for recruitment from seed and a "safe site" that persists after others have been occupied. However, successful recruitment is probably limited to the first few years following the disturbance (Henry and Swan 1974).

Causes of seedling mortality

Most mortality of seedlings transplanted onto mound, pit, and open microsites occurred during the winter and was caused by extrinsic factors such as frost heaving, burial by soil and litter, and browsing (Fig. 5). Probability of death on these microsites was not strongly related to seedling size and was similar for all three species. Mortality rates were lowest on open sites, where browsing by snowshoe hares was the only important cause of death. Larger seedlings were preferred by hares, probably because of greater apparency or higher nutrient content (Crabtree 1992). Browsing damage increased during the second winter, particularly in yellow birch, and may have become a significant mortality factor in subsequent years. Although birches are preferred browse species for deer (Jordan and Rushmore 1969), there was no evidence of deer browsing and no sign of deer on either study site or in the adjacent undisturbed forest. During the first winter, frost heaving was very severe on mounds, probably because of the extended periods without snow cover, as suggested from other studies (Heidmann 1976). With snow cover adequate to prevent frost heaving, mortality on mounds would have been reduced by more than half. Frost heaving also contributed to the heavy mortality in pits during the first winter as seedlings were buried by loosened soil eroding from mounds. In the absence of frost heaving, browsing, and burial on these microsites, resource limitation would have become a much more important cause of mortality.

Most mortality under ferns and on top microsites occurred during the growing season and was due to resource limitation. Fern microsites were characterized by low light levels and low nitrate supply rates, whereas low light levels and low soil moisture were the main limitations on top sites (Carlton and Bazzaz 1998). Stem mass ratios for all three species were significantly greater on fern and top microsites than on all other sites. These birch species also allocated more to stems under low light conditions in controlled environments and in artificial canopy gaps (Walters et al. 1993*a*, Wayne and Bazzaz 1993). The three birch species differed in susceptibility to resource-related mortality, particularly on fern microsites, where the shade-intolerant white birch suffered heaviest mortality and yellow birch the least.

Growth, biomass, carbon allocation, and leaf-level physiology

Surviving seedlings of all three species grew best on top and mound microsites. Large seedlings on mounds had developed extensive root systems that appeared to be capable of drawing moisture and nutrients from top microsites. This may explain why foliar nitrogen levels in white birch seedlings were similar on the two microsites. Seedling survival and growth on top microsites depended primarily on vertical position. Most seedlings near the base of these north-facing microsites grew poorly or died, probably because of inadequate light. Seedlings planted higher above the forest floor, however, were generally able to survive long enough to extend above the mound. These seedlings were then able to take advantage of the high light levels and the high mineralization and nitrification potential of soils on this microsite (Carlton and Bazzaz 1998).

On the productive top and mound sites, white birch attained twice the mean total biomass of black birch and three times the mean biomass of yellow birch. Growth of white birch was highly correlated with light-saturated net photosynthesis rates, whereas this relationship was much weaker in the other species. White birch also had the highest leaf nitrogen concentration, which probably contributed to the higher photosynthetic capacity of this species because most nitrogen in leaves is used in either the thylakoid membranes or the Calvin cycle (Evans 1989). These results suggest that white birch seedlings were better able than the other species to take advantage of high-light conditions on elevated mound and top microsites. Such physiological flexibility is characteristic of early successional plants (Bazzaz 1979, 1987) and has been documented in several birch species (Morse et al. 1993, Walters et al. 1993*a*).

Seedlings of all species were smallest on fern microsites, with fewer branches and fewer and smaller leaves than seedlings on other microsites. Most height extension in seedlings growing under ferns occurred from April through June, while fern fronds were still developing, whereas diameter growth was concentrated in late summer (Carlton 1993). During mid-summer, the most productive period on other microsites, seedlings grew very little in the deep shade cast by ferns. Black birch was most flexible in its foliar response to the low light levels under ferns, producing leaves with lower specific leaf mass, which resulted in significantly greater leaf area ratio and more efficient light capture for a given expenditure of carbon (Boardman 1977, Walters et al. 1993*a*). Black birch has also exhibited morphological flexibility in response to nitrate addition (Crabtree 1992) and to experimental light regimes in simulated canopy gaps (Wayne 1992).

Seedlings growing under ferns had acclimated to low light conditions and were limited in their photosynthetic response to saturating light levels (Fig. 7). However, they did not achieve higher net photosynthesis rates under low light conditions than seedlings from other microsites, as predicted by the trade-off model of photosynthetic performance (Bjorkman 1981, Pearcy et al. 1987). Seedlings on "high light" microsites probably experienced frequent periods of intermediate or low light and maintained a broader photosynthetic response to light than seedlings grown experimentally at uniform high light levels. Yellow birch seedlings growing on fern microsites were least responsive to high light conditions, as observed earlier by Logan (1970) and Wayne (1992).

The response of experimental seedlings to the extreme conditions on mound and fern microsites revealed differences in the ecology of the three species. White birch exhibited the greatest physiological flexibility in photosynthetic response to changing light levels but was least successful on shaded microsites. Black birch was not as flexible as white birch in photosynthetic response but altered leaf morphology to a greater extent than either of the other species. Allocation to maximize light capture in black birch was apparently achieved at the expense of allocation to roots, which was significantly lower in black birch than in yellow birch. Yellow birch exhibited neither the physiological flexibility of white birch nor the morphological flexibility of black birch and was least successful on mound and top microsites. Yellow birch seedlings, however, were better able to survive under the shade of ferns than seedlings of the other two species.

Predicting regeneration success

Investigation of seedling establishment in long-lived, sessile organisms such as trees is relatively easy. Extrapolation of results to predict ultimate regeneration success is much more difficult. It is not clear that dimensional growth, biomass accumulation, leaf area deployment, or other measures of seedling performance relate directly to successful ascension into the forest canopy. One potential problem arises because of changes that occur in both form and function during ontogeny. Seedlings differ from saplings and larger trees in the scale at which they perceive and respond to the environment (Harper et al. 1965). As their shoot and root systems develop, seedlings begin to integrate the environment and become less sensitive to small-scale fluctuations (Hartgerink and Bazzaz 1984). Basic resource requirements and intrinsic growth rate may also change as a plant grows (Parrish and Bazzaz 1985, Walters et al. 1993*b*). From these considerations, it is apparent that understanding a small seedling's response to the immediate environment may not allow us to predict the response of a much larger individual of the same species to its environment.

A second problem in extrapolating results from seedling studies rests in the potential incongruence between mean population response and the performance of individuals. Regeneration from seed on a disturbed forest site is literally a race against other seedlings, residual saplings, and lateral branch extension of surviving canopy trees (Hibbs 1982, Runkle 1985, 1990). Species achieving the most rapid growth on a particular site are most likely to succeed, and tall individuals of a given species are more likely to succeed than shorter individuals (Canham and Marks 1985, Connell 1989). This suggests that we should assess not only mean population responses but also the relative performance of the largest individuals of each species.

Many of the seedlings in this study had attained sapling stature (>1.4 m total height) before they were harvested, which enabled us to predict future performance with reasonable confidence. Of the 40 tallest seedlings, 19 were white birch, 14 were black birch, and 7 were yellow birch. Most of the tallest white birch were located on mounds, and the tallest black birch and yellow birch were all found on mound and top microsites. After three seasons' growth, these seedlings were nearly 2 m tall and reached nearly 3 m above the forest floor from their elevated position (Fig. 8). Clearly, elevation above the forest floor on mound and top microsites conferred an advantage on seedling growth.

On several experimental blocks, the tallest seedlings were in a strong competitive position relative to nearest residual saplings and surviving canopy trees. These seedlings had a high probability of reaching the canopy. Assuming different canopy closure rates by branch extension of surviving overstory trees made little difference in predicting species success in ascending to the canopy. White birch appeared most likely and yellow birch least likely to successfully regenerate on the disturbed site, assuming that all species began with equal numbers of germinants on each microsite type.

However, ultimate regeneration success also depends on the relative availability of the different microsites, on patterns of seed dispersal and germination on each microsite, and on resource requirements during growth to maturity. Although careful scrutiny of numerous forests in the eastern United States has revealed evidence of old mounds and pits on 14% to 50% of the forest floor (Stephens 1956, Armson and Fessendon 1973, Beatty 1984), mound–pit complexes resulting from a single catastrophic windstorm generally cover <10% of a disturbed site (Webb 1988, Schoonmaker 1992). On the Tom Swamp experimental blowdown site at Harvard Forest, mounds covered 3.9% and pits 4.4% of the forest floor (D. R. Foster and A. L. Lezberg, *unpublished data*). In contrast, open sites accounted for ~40% of the disturbed area (Carlton 1993). Mound and top microsites, in addition to covering a small proportion of the disturbed site, are unfavorable sites for seed dispersal. Even seeds released immediately above mounds tended to disperse away onto open sites or into pits. Furthermore, few seeds landing on mounds germinated the first year following disturbance because of low soil moisture and organic matter content. These results suggest that open and fern microsites should be weighted more heavily than mound, pit, and top microsites in evaluating regeneration potential. Because the three birch species were more similar in performance on open sites than on mounds or tops, this would reduce the apparent superiority of white birch over the other two species.

Differences in resource requirements during growth to maturity may also have a profound impact on the competitive balance between white birch and the other two, more shade-tolerant, birch species. Seedlings of both yellow birch and black birch are able to survive in the forest understory and are fairly abundant on some sites (Erdmann 1990, Lamson 1990). Seedlings of white birch, by contrast, cannot survive under the canopy in New England forests and are only able to attain reproductive maturity by immediate and rapid growth (Safford 1983. Therefore, only the largest white birch seedlings in the most favorable locations are able to reach the canopy, whereas many yellow birch and black birch seedlings may ultimately be successful.

This distinction between white birch and the two more shade-tolerant species may have important ramifications. When a catastrophic windstorm occurs, yellow birch and black birch seedlings growing in the understory near larger trees may be carried upward onto top microsites that form as the canopy trees are uprooted. Seedlings on these newly created microsites typically respond to their horizontal orientation with a curvature of the stem that produces a characteristic basal crook. Such seedlings have a substantial advantage in the race toward the canopy. Therefore, this mode of regeneration may be important even in forests with occasional understory seedlings of the two species. Because white birch is only able to regenerate directly from seed and few birch seeds disperse onto the vertical surface of top microsites, white birch may have limited access to these extremely productive microsites.

Surveys of windthrown sites in the Harvard Forest have confirmed that most white birch trees growing on old uproots appear to have originated as seedlings from mounds, whereas many yellow birch trees exhibit the basal crook characteristic of seedlings growing on top microsites. These results suggest that white birch and yellow birch specialize on different microsites for regeneration, with black birch assuming an intermediate position. Tip-up mounds resulting from catastrophic windthrow may therefore provide two distinct regeneration niches (sensu Grubb 1977) for birch species in New England transition hardwood forests.

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