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RESOURCE CONGRUENCE AND FOREST REGENERATION FOLLOWING AN EXPERIMENTAL HURRICANE BLOWDOWN

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Abstract. Catastrophic uprooting of forest canopy trees creates mounds, pits, and other microsites that provide opportunities for regeneration of particular species. We measured environmental factors on five types of microsites created by simulated blowdown of a mixed deciduous forest in central New England, United States. We then estimated spatial variation in resource levels and quantified congruence among different resources at each site. Effects of simulated blowdown on light levels and CO_2 concentrations were more pronounced after three years than effects on nitrogen availability and other soil resources. Spatial heterogeneity in light levels and net nitrification rates was greater in the blowdown, but heterogeneities of soil organic matter concentration and net mineralization rates were greater in the undisturbed forest. Availability of nitrate, a limiting resource in most New England forests, was low on mounds and in pits, but high on the vertical portion of forest floor resulting from uprooting of canopy trees. At a spatial scale relevant to seedlings, resource congruence was greater in the undisturbed forest than in the experimental blowdown, primarily because of the effects of blowdown on light levels. Congruence in the blowdown increased with an increase in spatial scale, but congruence in the undisturbed forest was similar at both spatial scales. Seedling growth of two birch species was correlated with light levels and with congruence among soil resources. This study shows that immediate disturbance effects on microtopography and light levels determine recruitment patterns of colonizing species, with changes in soil resource levels influencing later community development. Furthermore, some species appear to respond to resource congruence, which may provide an additional dimension to the regeneration niche.

Key words: CO_2 concentration; disturbance; microsite environment; mound-and-pit microrelief; N mineralization; nitrification; photon flux density; recruitment; resource congruence; simulated hurricane blowdown; soil organic matter; soil water.

INTRODUCTION

Disturbance is thought to promote species diversity in natural systems by creating patchiness or heterogeneity in the environment (Connell 1978, Sousa 1979, Denslow 1985). According to this view, different types of patches provide opportunities for species with different regeneration requirements to become established in the community (Grubb 1977, Chesson and Warner 1981, Bazzaz 1983, Schmida and Ellner 1984). Less emphasis has been placed on two other potentially important consequences of disturbance. Disturbances may affect both the overall levels of resource availability on a site and the congruence, or balance, among levels of different resources (Bazzaz 1996).

Disturbance events may profoundly alter overall resource levels in natural communities. Disturbances that remove dominant vegetation, for example, dramatically increase light levels near the soil surface, which promotes rapid colonization by shade-intolerant species (Bazzaz 1979, Poulson and Platt 1989). Conversely, disturbances that produce a flush of nutrients to the soil without increasing light levels favor shade-tolerant plants (Denslow 1980, Canham 1989, Whitmore 1989, Bazzaz 1991). When assessing the impact of disturbance on species coexistence and diversity, we must consider the consequences of the disturbance event on overall resource levels.

Disturbance events that alter resource levels and create a patchy distribution of resources across a landscape may also change the congruence among resources. Congruence is a concept that has received little attention, but may be important for autotrophic organisms. Plants, for example, require adequate levels of CO_2, water, nutrients, light, and radiant energy for photosynthesis. Therefore, some degree of congruence among these physical resources is probably necessary for normal plant growth and development (Chapin et al. 1987). Minor deficiency of one resource may increase plant sensitivity to deficiencies of other resources and increase susceptibility to attack by insects and pathogens (Osmond et al. 1987, Waring 1987, Mooney et al. 1991).

Resource congruence is related to the concept of the ecological niche. In many animal species, niche differentiation occurs primarily through selection of dif-

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ferent resources, which are often in the form of specific food items. If different plant species require similar quantities of abiotic resources, it might seem that the potential for niche differentiation would be limited. However, plant species that require the same basic resources may differ substantially in the mode and timing of resource uptake (Whittaker 1972, Tilman 1982). Niche differences among plant species are also defined by subtle differences in physical regeneration requirements (Grubb 1977) and by interactions with pollinators, seed dispersers, herbivores, pathogens, and fungal or microbial symbionts (Bazzaz 1987). Therefore, plant species need not differ in abiotic resource requirements to occupy different ecological niches.

In the forests of southern New England, hurricanes and other catastrophic windstorms are important disturbance agents (Foster and Boose 1992). Many of today's forests in the region originated after past hurricanes, and several tree species in these forests apparently depend on specific microsites created by hurricanes for successful regeneration (Hutnik 1952, Henry and Swan 1974). Hurricane blowdowns of forest canopy trees create a patchwork of resource fluxes at the forest floor (Bazzaz 1983, Chazdon and Fetcher 1984, Brokaw 1985, Poulson and Platt 1989). Blowdowns affect not only climatic factors such as light levels and carbon dioxide concentrations, but also soil resources such as water and nutrient availability.

Uprooting of canopy trees increases the intensity and duration of direct-beam solar radiation and changes the spectral distribution of light reaching the forest floor (Geiger 1965, Holmes and Smith 1975, Chazdon and Fetcher 1984). Because of the patchy distribution of uprooted trees and surviving residual vegetation, light levels following catastrophic blowdown are likely to be spatially and temporally heterogeneous (Denslow 1980, Fetcher et al. 1984, Brokaw 1985, Schaetzl et al. 1989*a*, *b*, Fernandez and Fetcher 1991). Catastrophic windthrow may also influence carbon dioxide concentrations near the forest floor. After canopy removal, enhanced respiratory activity of soil microorganisms and increased uptake of CO_2 by understory vegetation may create a steeper CO_2 gradient near the soil surface (Schlesinger 1977, Garrett et al. 1978). On the other hand, increased winds may mix surface air more effectively, thereby reducing CO_2 levels near the forest floor (Bazzaz and Williams 1991). The presence of exposed mineral soil may also affect CO_2 fluxes. For example, CO_2 efflux from the surface of tip-up mounds and pits may be lower than efflux from the undisturbed forest floor (Edwards and Sollins 1973, Bazzaz 1990, Wofsy et al. 1993).

The uprooting of canopy trees affects soil properties through the creation of mound-and-pit microrelief (Goodlett 1954, Beatty and Stone 1986, Schaetzl et al. 1990). Mounds are characterized by extremes in soil conditions. Soils are dry during much of the growing season and low in organic matter, cation exchange capacity, and nutrient levels (Beatty 1984, Vitousek and Denslow 1986, Peterson et al. 1990). Resource availability in pits may depend on the length of time since the uprooting event occurred, and on physiographic position and other large-scale features of the disturbed site (Beatty and Stone 1986, Peterson and Pickett 1990). Recently created pits are generally drier than adjacent intact soils (Peterson et al. 1990) and lower in organic matter and available nitrogen and phosphorus (Vitousek and Denslow 1986). Old pits, conversely, may have more soil moisture and greater nutrient availability than adjacent soils (Beatty 1984).

Previous research has therefore demonstrated that climatic factors and soil resources are altered on tip-up mounds and pits created by windthrown canopy trees. However, mounds and pits generally cover $<10\%$ of a windthrown site (Henry and Swan 1974, Webb 1988, Schoonmaker 1992). Most of the soil surface remains relatively undisturbed following hurricane blowdown. Residual trees, patches of understory vegetation, and downed boles and crowns create heterogeneous conditions across this undisturbed soil surface, suggesting the presence of other microsites in addition to mounds and pits (Fernandez and Fetcher 1991). Such microsites, which may play an important role in forest regeneration, have seldom been studied.

This paper reports the effects of an experimental hurricane treatment on resource availability, heterogeneity, and congruence (sensu Bazzaz 1996) three years after the disturbance. We simulated hurricane damage by pulling down selected canopy trees, identified five types of microsites created by the disturbance, and then measured six environmental factors on these microsites. The study was designed to address the following questions:

1. Are average levels of key resources altered on the disturbed site three years after the simulated blowdown? It is well known that light levels increase immediately following blowdown. However, light availability at the forest floor may decline again as residual herbaceous and woody vegetation proliferates. We predicted that light levels would still be significantly higher on the disturbed site than in the forest understory. We also predicted that CO_2 concentrations would be lower on the disturbed site, but that average soil resource levels would not be significantly altered.

2. Is resource heterogeneity increased or decreased following the disturbance? We predicted that heterogeneity of all six resources that we measured would increase on the simulated blowdown site, because of the combined effects of downed boles and crowns, tip-up mounds and pits, and residual trees and understory vegetation.

3. How do the five blowdown microsites that we identified differ in resource availability? We predicted that light levels would be highest on mounds and open sites, that CO_2 concentrations and soil resource levels would be lowest on mounds and in pits, and that fern

microsites would be similar to the undisturbed forest understory in resource availability.

4. Is the congruence among light, soil water, organic matter, and nitrogen mineralization and nitrification rates altered by the simulated blowdown? We predicted that congruence among soil resources would be greater than congruence among light and soil resources, and that congruence at the sapling scale would be greater than congruence at the smaller seedling scale. We also predicted that congruence among light and soil resources would be reduced on the disturbed site, but that congruence among the soil resources would not be affected by the disturbance.

5. Are resource levels and congruence positively related to growth of birch seedlings planted on the five types of microsites? We predicted that growth of the shade-intolerant white birch (*Betula papyrifera* Marsh.) would be most strongly related to light levels on the disturbed site, but that growth of the more shade-tolerant yellow birch (*Betula alleghaniensis* Britton) would be most strongly related to resource congruence.

METHODS

Study sites

The Harvard Forest occupies 1200 ha in the Central Uplands physiographic region in central Massachusetts, United States. The area is characterized by ridges and valleys ranging in elevation from 180 m to 420 m a.s.l. Soils are thin, acidic, sandy loams derived from glacial till overlying a bedrock of granodiorite, gneiss, and schist. Soils are locally variable in drainage, texture, and structure. The regional climate is cool temperate, with mean temperatures of 20°C in summer and −4°C in winter. Local relief influences maximum and minimum temperatures and length of the frost-free season, which averages five months (Spurr 1957). The mean annual precipitation of 105 cm is evenly distributed throughout the year, with an average snowfall of 150 cm (unpublished Harvard Forest archives).

The Harvard Forest is in the Transition Hardwoods–White Pine–Hemlock forest region, which is characterized by a diverse assemblage of species representing both the northern and southern hardwood forests (Spurr 1956, Westveld 1956). The forest has been severely damaged by four hurricanes since 1635, most recently in 1938 (Foster and Boose 1992). Much of the present structure and composition of the forest is probably attributable to effects of past hurricanes (Henry and Swan 1974, Oliver and Stephens 1977). Other major components of the historical disturbance regime are periodic disease and insect epidemics, timber harvesting, and clearing of the land for cultivation (Raup and Carlson 1941, Oliver and Stephens 1977, Foster 1992).

This study was conducted in the Prospect Hill tract of the Harvard Forest in a 60-yr-old stand dominated by *Quercus rubra* L. and *Acer rubrum* L. Other canopy species include *Betula papyrifera* Marsh., *Betula alleghaniensis* Britton, and *Pinus strobus* L. The Prospect Hill study site is on a gentle, east-facing slope at an elevation of 360 m a.s.l. This site was probably cleared for agriculture as early as 1780 and subsequently abandoned in the early 1900s (Raup and Carlson 1941, Foster 1992). The existing stand developed following abandonment, with minor damage during the 1938 hurricane.

In September 1989, a 0.25-ha experimental hurricane blowdown was created by pulling down selected canopy trees. In similar hardwood forests exposed to full wind in 1938, >80% of hardwood trees and nearly all white pine trees in the forest canopy were damaged (Foster 1988). To approximate such severe damage, we marked a subset of canopy trees in the experimental area to be pulled down. Trees were pulled over by fastening a cable around the bole at a height of 3–5 m and applying force until the roots failed or the bole snapped. Force was applied by a winch operated from a logging skidder located 100 m northwest of the experimental site. Trees nearest the skidder were pulled first, and more distant trees were then winched onto previously uprooted or snapped trees. Force was applied only until trees came to rest against the forest floor or other standing or uprooted trees. Trees were pulled down in a northwesterly direction to simulate effects of historical storms in the region (Foster and Boose 1992).

Experimental design

We identified five types of forest floor microsites that were created by the simulated blowdown treatment: tip-up mounds; pits; north-facing vertical forest floor surfaces referred to as top sites; level and unshaded portions of the forest floor referred to as open sites; and level portions of the forest floor covered by ferns or other dense herbaceous vegetation, which are called fern sites (Fig. 1). We selected eight replicate sets of these five microsites as our experimental units on the simulated blowdown site. We then subsampled by measuring environmental factors at five random points on each of the microsites. Therefore, we had a total of 200 sample points on the simulated blowdown site (8 sets of microsites × 5 microsites per set × 5 points per microsite).

We also measured the same environmental factors at five random locations on each of eight 1-m^2 plots in the adjacent undisturbed forest understory. These eight understory plots were randomly located within a 0.25-ha area to approximate the spatial arrangement of experimental units in the blowdown. Environmental factors measured on both the blowdown and understory sites were photon flux density (PFD), CO_2 concentration, percent soil water by mass, percent soil organic matter, net N mineralization rate, and net nitrification rate.

Seedlings of three birch species were planted on 120 of the 200 environmental sample points in the exper-

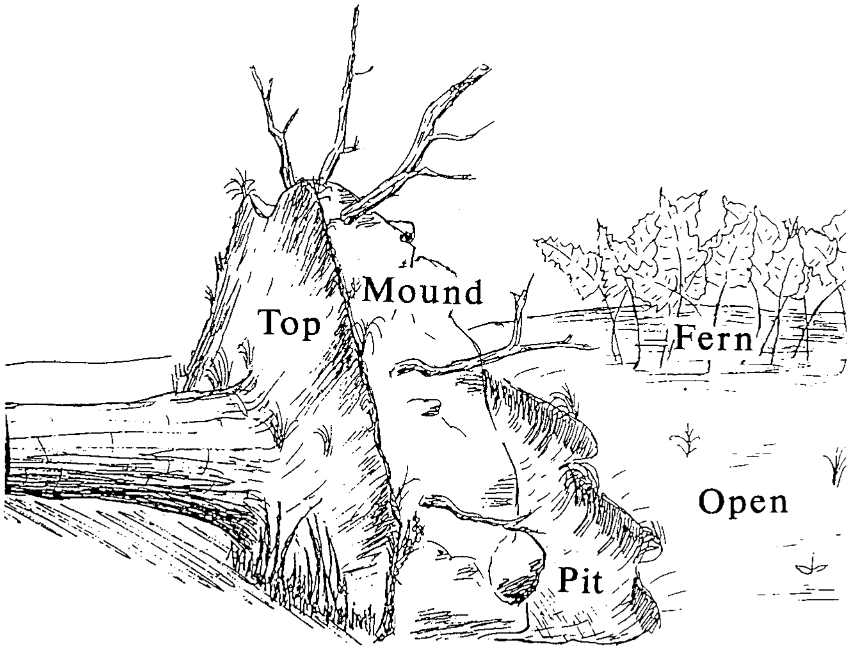

FIG. 1. Five microsites created by the experimental blowdown treatment.

imental blowdown. Seedlings of white birch, black birch, and yellow birch were germinated in June 1990, and 120 seedlings of each species were transplanted 2 mo later to the experimental blowdown (Carlton and Bazzaz 1998). We planted 40 seedlings of each species in locations at which environmental measurements were made. All growth data in this paper are reported from that subset of birch seedlings.

For site-level comparison of the understory and blowdown, we selected five points from each of the eight sets of blowdown microsites to compare with the 40 understory data points on the eight 1-m^2 plots. Blowdown sample points for this comparison were determined by choosing the four points nearest a randomly selected initial point on each set of microsites. The probability of the initial point being located on a given microsite type was proportional to the areal representation of that microsite over the entire blowdown (open 45%, fern 43%, mound 3.9%, pit 4.4%, top 3.7%; D. R. Foster and A. L. Lezberg, *unpublished data*). On seven of the eight sets of blowdown microsites, the five sample points selected in this manner were located within an area of 1 m^2, corresponding to the size of sample plots in the undisturbed forest understory. Sample points on the eighth set of microsites were within an area of 2 m^2.

Data collection

Because the emphasis of this research was on detecting fine-scale spatial patterns, we conducted intensive spatial sampling of resource levels, rather than repeated sampling at fewer data points. Temporal patterns of resource availability are presented in Sipe (1990), Wayne and Bazzaz (1993), and Bazzaz and Wayne (1994). The six environmental factors were not measured at the same time during the growing season. Data were collected when differences among microsites in availability of a particular resource were likely to be most pronounced or when a given resource, such as soil water, was most likely to limit plant growth.

Photon flux density (PFD) was estimated with photosensitive paper sensors. Sensors consisted of 15 layers of Proprint sepia photosensitive paper enclosed in 2.5 × 3 cm cardboard jackets with a 0.6 cm diameter exposure hole (Friend 1961). Sensors were placed in 4 × 6 cm clear plastic zip-lock bags to protect them from moisture and were mounted horizontally on metal stakes 10 cm above the substrate. Sensors were deployed from 30 June to 8 July 1992 at each of the 200 sample points in the simulated blowdown and at each of the 40 points in the undisturbed forest understory. Paper sensors were calibrated against quantum sensors (Model LI-190SA, LI-COR, Lincoln, Nebraska, USA). The calibration equation was obtained by regressing the number of exposed sheets of sepia paper on cumulative PFD recorded by quantum sensors. Results reported in this paper were derived from the following equation:

$$\mathrm{PFD} = 4.496080 \times 10^{(0.443522S)} \qquad R^2 = 0.994 \quad (1)$$

where PFD is the estimated photon flux density in micromoles per square meter and S is the number of sheets of photosensitive paper exposed. Results are reported in moles per square meter per day.

Carbon dioxide concentrations 10 cm above the forest floor were sampled in mid-August 1992 using four portable infrared gas analyzers (Model LI-6250, LI-COR, Lincoln, Nebraska, USA). Data were collected at four points simultaneously from 0830 to 1630 on two consecutive days. At each of the 240 sample points, measurements were made at four times during the two days. During each sampling period, data were logged for 3 min and stored as the mean and range of 30 5-s samples. Microsite CO_2 values, therefore, represent mean diurnal concentrations based on four sets of data collected at different times of the day from each of the 240 sample points.

On 15 September 1992, following the longest dry period of the summer, we collected soil samples from the upper 10 cm of the soil horizon, excluding litter, at each of the 240 sample points. Samples were passed through a 2-mm mesh sieve to remove rocks and coarse roots, and the coarse fraction was weighed and discarded. The sieved soil was then divided into subsamples for determination of percent soil water by mass, percent soil organic matter, and N transformation rates. Percent soil water was obtained by drying a 1-g subsample of sieved soil at 105°C for 24 h, reweighing, and calculating the water lost as a percent of the oven-dry mass of the soil sample.

Soil organic matter concentration was estimated on the sieved samples used for determination of percent soil water by mass. Oven-dry samples were transferred to crucibles and combusted in a muffle furnace at 400°C for 24 h. Samples were then transferred to a glass dessicator, allowed to cool for 4 min, and reweighed. Organic matter concentration was estimated from the loss of mass on ignition as a percentage of the oven-dry soil mass (Davies 1974, Page et al. 1982).

Nitrogen transformation rates were determined by the aerobic laboratory incubation method (Hart et al. 1994). This method is appropriate when an index of differences in soil fertility among sites is desired (Binkley and Vitousek 1989). After removing 1-g subsamples for determination of soil water and organic matter concentrations, we divided the remaining sieved soil into 3-g and 10-g subsamples (or proportionally smaller subsamples when inadequate sieved soil was available). The 3-g samples were extracted immediately with 2 mol/L KCl in 100-mL glass jars, and the 10-g samples were extracted after incubating at 25°C for 28 d. All extracts were analyzed for ammonium and nitrate on a QuikChem AE Automated Ion Analyzer (Lachat Instruments, Milwaukee, Wisconsin, USA) using QuikChem Method 12-107-06-1-A for ammonium and Method 12-107-04-1-E for nitrate. Potential N mineralization rates were then calculated as the difference between concentrations of KCl-extractable NH_4^+ and NO_3^- before and after incubation. Potential nitrification rates were calculated similarly as the difference in extractable nitrate before and after the incubation period (Binkley and Hart 1989).

Statistical analysis

Resource data collected from the 240 sample points at the Prospect Hill site were analyzed by one-way ANOVA. We used fixed-effects models to test for differences among microsites, and separate random-effects nested models for each microsite to estimate components of variance within and between replicate microsites. We also used a random-effects model to estimate site-level variability at two spatial scales. Variation within sets of sample points (blowdown) or within 1-m^2 plots (understory) is referred to as small-scale or microsite-scale variation. Statistically, this is variation among sampling units within experimental units (Sokal and Rohlf 1981, Petersen 1985). Variation among sets of sample points or 1-m^2 plots (the experimental units) is referred to as the large-scale variance component of nested ANOVA models. Light, soil water, and organic matter data were log-transformed for ANOVA.

Homogeneity of variance among microsites was tested by merging absolute values of residuals with original grouping variables and conducting an ANOVA on the absolute residuals (Levene 1960). Significant microsite effects obtained by this test indicate unequal variances among microsites (Wilkinson 1990). In such cases, single-degree-of-freedom contrasts were used in lieu of ANOVA to test for differences among microsites (Milliken and Johnson 1984). For all variables, single-degree-of-freedom contrasts were also used to test for differences between understory sites and all blowdown microsites combined. For variables satisfying homogeneity-of-variance assumptions and showing significant microsite effects, we used Fisher's protected least significant difference (PFLSD) to compare means (Carmer and Swanson 1973, Petersen 1985). We conducted all statistical analyses with SYSTAT (Wilkinson 1990).

Quantification of congruence

Congruence among levels of PFD, soil water, organic matter, and net mineralization and nitrification rates was quantified at 38 of the 40 randomly selected sample points in the blowdown, and at 35 of the 40 sample points in the undisturbed forest understory. Across the experimental sites, levels of each of these five resources ranged from very low to nearly optimal for growth of species such as *Betula* that commonly colonize blowdown microsites (Wayne and Bazzaz 1993, Carlton and Bazzaz 1998). Because the range of CO_2 concentrations (351–388 μL/L) was much more restricted than the range of the other resources, CO_2 was not included in congruence calculations. Two of the 40 sample points in the blowdown and five of the 40 sample points in the forest understory were not used in congruence calculations because of missing data. To test for the relationship between congruence and seedling growth, congruence was also quantified at 90 points within the blowdown where birch seedlings were planted and survived throughout the experiment.

Congruence was calculated for all combinations of four or more of the five resources and for all combinations of three or more of the four soil resources. Congruence was estimated from resource levels measured directly on different microsites, rather than levels scaled to some measure of growth of a particular plant species. This approach sacrifices a direct connection to plant performance, but has the advantage of being more general and easily understood. Effects of microsite environment on the survival and growth of the three birch species are described in greater detail in Carlton and Bazzaz (1998).

Resource levels were standardized by subtracting the minimum value from each raw value, dividing by the range of values, and multiplying by 100. Standardized levels of each resource were therefore scaled from 0 to 100. Congruence was then calculated in two ways. First, resource levels were ranked from low to high and ranks were used to calculate Kendall's coefficient of concordance, *W*, which was then converted to an estimate of chi-square for tests of significance (Zar 1996). Kendall's coefficient is a useful nonparametric measure of correlation among more than two variables. However, only one value of Kendall's *W* can be obtained for each sample, which means that tests of significant differences among samples are not possible.

To test for differences in congruence among samples, we derived a single variable to estimate congruence at each sample point. This derived variable, which we call congruence, *C*, is not used as a statistic, but rather as a data transformation. Congruence is essentially the inverse of dispersion. Therefore, to quantify congruence at each sample point, we began with a measure of dispersion among standardized levels of *r* resources, x_1 to x_r. A general formula for dispersion is given by

$$D_n = \Big(|x_1 - x_2|^{1/n} + |x_1 - x_3|^{1/n} + \ldots + |x_1 - x_r|^{1/n} + |x_2 - x_3|^{1/n} + |x_2 - x_4|^{1/n} + \ldots + |x_2 - x_r|^{1/n} + \ldots + |x_{r-1} - x_r|^{1/n}\Big)^n. \quad (2)$$

If $n = 1/2$, then $D_{1/2}$ is equal to *r* times the standard deviation of the population, x_1 to x_r (Zar 1996). The standard deviation, however, measures dispersion about a single mean value rather than dispersion among all data points. For example, given standardized levels of four resources, x_1, x_2, x_3, and x_4, the maximum value for $D_{1/2}$ is obtained when two resources have standardized levels of 0 and two resources have standardized levels of 100. However, maximum dispersion, for purposes of calculating congruence, should occur when no two resources have the same standardized value. In other words, we require a measure of dispersion, D_n, that is more sensitive to the differences between all individual values and less sensitive to differences between individual values and the mean. This occurs as *n* becomes greater than 1. If $n = 2$, for example, the maximum dispersion, $D_{2\max} = 1989$, occurs at standardized levels of 0, 18, 82, and 100 for four resources. With only three resources, the maximum dispersion for $n = 2$, $D_{2\max} = 583$, occurs at standardized levels of 0, 50, and 100. Therefore, D_2 appears to be a more appropriate measure of dispersion for use in quantifying congruence than is $D_{1/2}$.

TABLE 1. Calculations of congruence, C_n, among different combinations of four hypothetical resources, x_1 through x_4, using different values of *n* in the equation for C_n (see *Methods*). In this paper, congruence was calculated using $n = 2$.

Standardized resource levels				Congruence (C_n)				
x_1	x_2	x_3	x_4	$n = ½$	$n = 1$	$n = 2$	$n = 3$	$n = 4$
0	0	100	100	0.000	0.000	0.196	0.450	0.626
0	1	99	100	0.010	0.005	0.122	0.256	0.334
0	5	95	100	0.049	0.025	0.051	0.121	0.162
0	10	90	100	0.094	0.050	0.016	0.052	0.074
0	20	80	100	0.175	0.100	0.001	0.002	0.005
0	25	75	100	0.209	0.125	0.009	0.001	0.000
0	33	67	100	0.253	0.165	0.040	0.026	0.021
0	50	50	100	0.293	0.250	0.263	0.371	0.471
0	0	0	100	0.134	0.250	0.548	0.768	0.882
10	10	10	90	0.307	0.400	0.638	0.814	0.905
10	10	90	90	0.200	0.200	0.356	0.559	0.701
20	20	80	80	0.400	0.400	0.517	0.668	0.776
30	30	70	70	0.600	0.600	0.678	0.778	0.851
40	40	60	60	0.800	0.800	0.839	0.888	0.925
45	45	55	55	0.900	0.900	0.920	0.944	0.963
49	49	51	51	0.980	0.980	0.984	0.989	0.993
50	50	50	50	1.000	1.000	1.000	1.000	1.000
100	100	100	100	1.000	1.000	1.000	1.000	1.000

At $n = 3$, the maximum dispersion for four resources, $D_{3\max} = 11\,113$, occurs at standardized levels of 0, 23, 77, and 100; the maximum dispersion for three resources, $D_{3\max} = 1661$, occurs at standardized levels of 0, 50, and 100. When $n > 2$, however, D_n becomes increasingly sensitive to minor changes in standardized resource levels near 0 and 100. For example, $D_3 = 6112$ (55.0% of $D_{3\max}$) for four resources with standardized levels of 0, 0, 100, 100, whereas $D_3 = 8270$ (74.4% of $D_{3\max}$) for four resources with standardized levels of 0, 1, 99, and 100. By comparison, $D_2 = 1600$ (80.4% of $D_{2\max}$) for 0, 0, 100, 100, and $D_2 = 1747$ (87.8% of $D_{2\max}$) for 0, 1, 99, 100. In this paper, therefore, we use D_2 as the measure of dispersion to calculate congruence, and we quantify congruence as

$$C = 1 - D_2/D_{2\max}. \quad (3)$$

Congruence of all resources at a given point, *C*, is therefore scaled from 0 (completely incongruent) to 1 (perfectly congruent). Values of congruence at different combinations of resources and at different values of *n* are illustrated in Table 1.

Site-level estimates of small-scale resource congruence were derived by calculating the median congruence of the 38 sample points in the simulated blowdown

TABLE 2. Mean resource levels and variability in the Prospect Hill experimental hurricane blowdown (BD) and in the adjacent forest understory (US). Added large-scale variance is the variance among eight replicate sets of microsites on each site, expressed as the component and percentage of total variance.

					Added large-scale variance			
	Mean		CV		Component		Percentage	
Resource†	BD	US	BD	US	BD	US	BD	US
PFD	9.95	3.46***	1.20	0.63***	46.1**	1.6**	31.7	32.5
CO_2	358.8	376.4***	0.03	0.03	48.9*	24.5*	31.2	23.9
SW	43.88	47.21	0.42	0.64	241***	775***	65.0	83.3
SOM	14.17	18.57	0.51	0.87***	25***	138***	44.7	50.5
N	9.44	11.15	1.21	1.48*	27.4	96.4**	20.7	35.2
NO_3	1.50	0.67	1.83	1.41***	0.70	0.31**	9.2	34.7

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ for significance of differences between BD and US in mean values and small-scale variance (CV) and for significant large-scale variance components (Component columns).

† Resources are mean photon flux density in $mol \cdot m^{-2} \cdot d^{-1}$ (PFD), carbon dioxide concentration in μL/L (CO_2), percent soil water by mass (SW), percent soil organic matter (SOM), potential net nitrogen mineralization rate in μg N/g soil (N), and potential net nitrification rate in μg NO_3/g soil (NO_3).

and of the 35 points in the undisturbed forest. We quantified congruence at a larger spatial scale using median resource levels. Within each of the eight sets of blowdown microsites, we calculated median resource levels among the five sample points selected as described in *Experimental design.* We also calculated median resource levels among the five sample points within each of the eight 1-m^2 plots in the undisturbed forest. Estimates of large-scale congruence were then derived by calculating the median congruence among the eight sets of median resource values in the blowdown and understory sites. The small and large spatial scales represent resource availability relevant to 1st-yr seedlings and larger saplings, respectively. Estimates of congruence among points occupied by birch seedlings were calculated in the same manner as estimates of small-scale congruence.

Because congruence values for several combinations of resources were not normally distributed and could not be transformed to approximate a normal distribution, we used nonparametric measures of central tendency and nonparametric tests of significant differences between blowdown and understory sites and between sites occupied by different birch species. We also calculated Spearman rank correlation coefficients to test the hypothesis that resource congruence and 1st-yr seedling growth rates were positively correlated.

RESULTS

Resource availability and heterogeneity

Three years after the simulated blowdown, midsummer light levels (PFD) at 40 locations on the disturbed site were still three times higher than levels in the adjacent undisturbed forest understory (Table 2). Conversely, ambient carbon dioxide concentrations 10 cm above the forest floor (CO_2) were significantly lower in the blowdown than in the undisturbed forest understory. Soil resource levels, however, did not differ significantly between the blowdown and understory sites. Percent soil water by mass (SW) was very similar on both sites, and percent soil organic matter (SOM) was only slightly higher in the undisturbed forest (Table 2). Net nitrogen mineralization rates (N) were slightly, but not significantly, higher in the understory, whereas net nitrification rates (NO_3) tended to be higher in the blowdown (Table 2).

Light levels at the forest floor were much more heterogeneous on the blowdown site than in the undisturbed forest (Table 2, CV). On both sites, large-scale (also called sapling-scale) variance accounted for ~32% of the total variability (Table 2, Percentage columns). Spatial heterogeneity in CO_2 concentrations was very low (CV = 3%) on both sites. Soil water concentration was slightly more heterogeneous in the understory than on the disturbed site, but the differences were not significant (Table 2). Most of the variability in soil water occurred among microsites at the sapling scale, particularly in the forest understory. Heterogeneity in soil organic matter concentration was significantly greater in the undisturbed forest than on the blowdown site (Table 2). Nitrogen transformation rates were extremely heterogeneous, with most variability occurring at the small scale, particularly in the blowdown. Mineralization rates were significantly more variable in the understory, but nitrification rates were more variable in the blowdown (Table 2).

Effects of microsites on resources

Midsummer photon flux density (PFD) was significantly greater on open and mound microsites than on all other microsites except pits ($P < 0.001$ for all tests; Fisher's Protected LSD) (Fig. 2). Photon flux density on mounds, open sites, and pits was higher than in the undisturbed forest understory, but PFD was greater in the understory than on fern and top microsites ($P < 0.001$ for all FPLSD tests). Variability was somewhat greater on all blowdown microsites than in the understory (Table 3). Large-scale variability among replicate microsites accounted for 30% to 45% of the variance

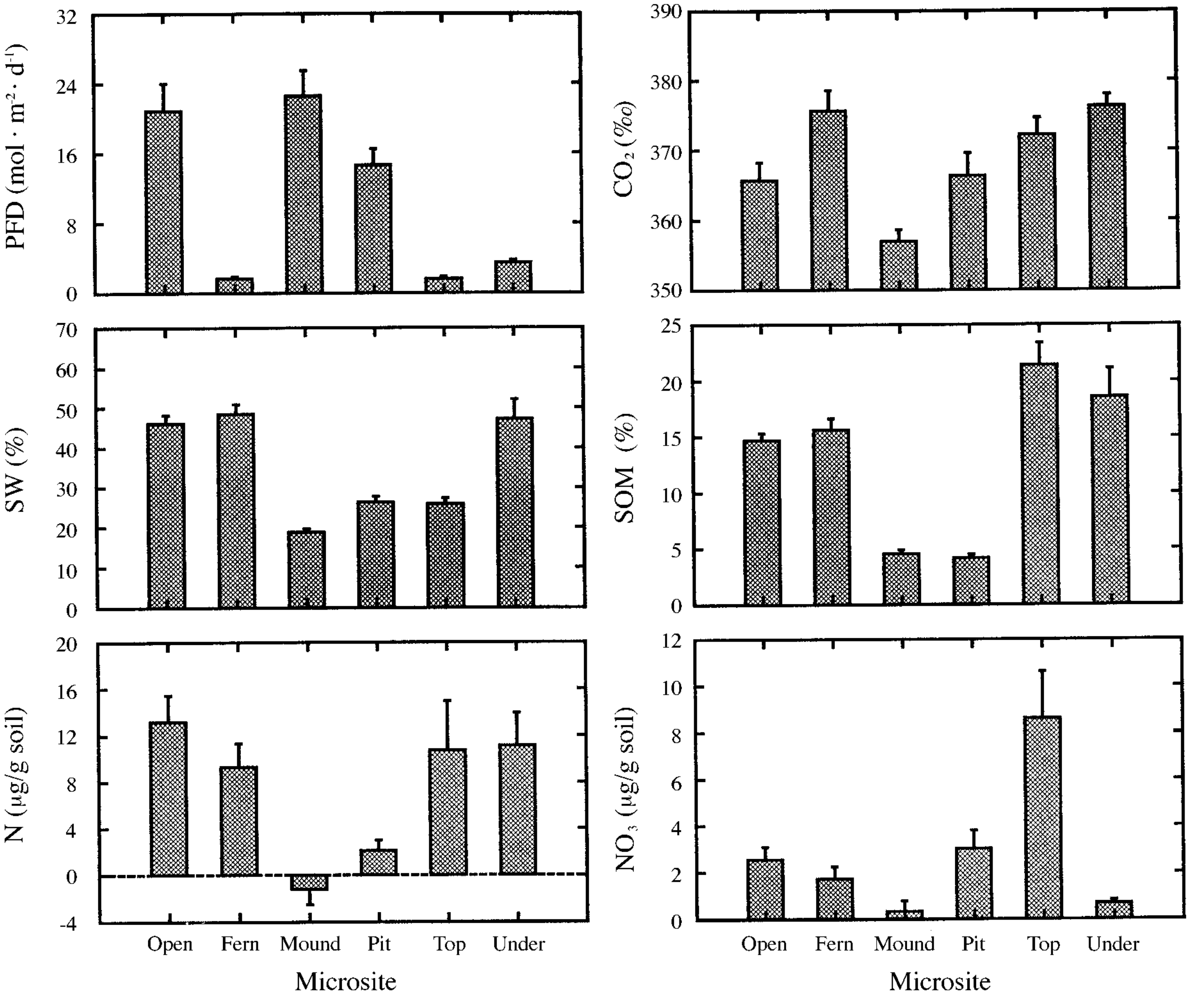

FIG. 2. Levels of six resources on the experimental blowdown microsites and in the adjacent forest understory (Under). Resources are mean daily photon flux density (PFD) from 30 June to 8 July 1992; carbon dioxide concentration (CO_2), by volume, in mid-August 1992; percent soil water by mass (SW); percent soil organic matter (SOM); potential net nitrogen mineralization rate (N); and potential net nitrification rate (NO_3). All soil data are from samples collected on 15 September 1992. Error bars indicate +1 SE.

on open, mound, pit, and understory sites, but almost none of the variance under ferns and on top microsites.

Carbon dioxide concentrations were lowest on mounds ($P < 0.012$ for all FPLSD tests) and higher on understory plots and fern microsites than on open sites and in pits ($P < 0.01$ for all FPLSD tests) (Fig. 2). Variability was extremely low on all blowdown microsites and in the forest understory (Table 3). Most variation was small-scale, occurring within, rather than between, replicate microsites.

Percent soil water by mass (SW) was highest on fern, open, and understory sites, intermediate on pit and top sites, and lowest on mounds (Fig. 2). Differences were highly significant ($F = 64.67$, $P < 0.001$ for all single-degree-of-freedom contrasts). Variability (CV) was greater in the understory than on any blowdown microsites (Table 3). On all microsites except ferns, large-scale variation among replicate sets of microsites was much more important than variation within microsites.

Top sites were higher in soil organic matter (SOM) than all other blowdown microsites ($P < 0.024$ for all single-degree-of-freedom contrasts), and the newly exposed soils of mounds and pits were lowest ($P < 0.001$ for all contrasts against other microsites) (Fig. 2). Variability in organic matter concentration was greatest in the understory and least on open sites (Table 3). Most variability on mounds was among replicate microsites (large-scale), but small-scale and large-scale variability were both important on other microsites.

Patterns of potential nitrogen mineralization rates were similar to those of soil organic matter, but small-scale variability within microsites was much greater (Fig. 2). Mounds and pits were lower than all other sites in net mineralization rates ($P < 0.035$ for all sin-

TABLE 3. Variability of resource levels on Prospect Hill blowdown miscrosites and in the undisturbed forest understory. The three values in each entry, from top to bottom, are: coefficient of variation, component of variance among replicate microsites, and component of variance within replicate microsites. Resources are as in Table 2.

Resource	Open	Fern	Mound	Pit	Top	Understory
	0.91	0.86	0.79	0.79	0.98	0.63
PFD ($mol \cdot m^{-2} \cdot d^{-1}$)	103.0*	0.1	151.8***	59.2***	0.0	1.6**
	256.5	2.0	178.1	76.7	2.7	3.3
	0.04	0.05	0.03	0.05	0.04	0.03
CO_2 (ppm)	17.2	0.0	1.5	146.2*	0.0	32.1**
	245.4	331.3	112.6	260.0	253.2	71.0
	0.27	0.31	0.29	0.34	0.40	0.64
SW (%)	112.8***	134.3***	22.2***	66.4***	89.6***	775.0***
	54.5	109.6	9.9	21.0	25.9	155.0
SOM (%)	0.29	0.39	0.49	0.56	0.58	0.87
	6.3**	18.9***	4.3***	3.7***	73.7***	138.0***
	12.0	19.7	0.8	2.0	89.3	135.0
N (μg/g soil)	1.07	1.34	6.50	2.65	2.50	1.48
	67.6**	4.4	7.4	8.7*	0.0	96.4**
	134.5	151.4	57.6	22.9	745.0	177.5
	1.34	1.91	8.49	1.63	1.47	1.41
NO_3 (μg/g soil)	1.7	0.0	2.0*	4.8	70.6***	0.3**
	10.1	11.5	6.3	20.1	96.0	0.6

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ (significance levels of the added among-microsite variance component).

gle-degree-of-freedom contrasts). Mean rates on mounds, in fact, were slightly negative, signifying net immobilization. However, variability within mound samples was very high relative to mean rates (Table 3). Most variation was small-scale, particularly on top, fern, and mound microsites.

Patterns of nitrification were much different than mineralization patterns (Fig. 2). Net nitrification was much greater on top microsites than all other sites ($P < 0.001$ for all single-degree-of-freedom contrasts) and higher in pits than in the understory ($P = 0.004$) or on mounds ($P = 0.003$). As with mineralization rates, net nitrification was extremely variable, particularly on mounds (Table 3). Variability in nitrification rates was primarily small-scale, occurring within replicate microsites.

TABLE 4. Kendall's coefficient of concordance among different combinations of resources at the Prospect Hill experimental blowdown (BD) and in the adjacent forest understory (US), with significance of chi-square tests indicated by asterisks.

	Small-scale‡		Large-scale§	
Resources†	BD	US	BD	US
W–O–M	0.768***	0.826***	0.852***	0.915***
W–O–N	0.673***	0.320	0.873***	0.302*
W–M–N	0.670***	0.343	0.868***	0.249
O–M–N	0.679***	0.327	0.868***	0.249
W–O–M–N	0.660***	0.386*	0.848***	0.357*
L–W–O–M	0.318	0.519**	0.304*	0.539***
L–W–O–N	0.267	0.228	0.313*	0.253+
L–W–M–N	0.288	0.288	0.366*	0.220
L–O–M–N	0.292	0.266	0.357*	0.220
L–W–O–M–N	0.323*	0.293*	0.400**	0.272*

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

† Resources and codes are photon flux density (L), percent soil water by mass (W), percent soil organic matter (O), net mineralization rate (M), and net nitrification rate (N).

‡ Small-scale concordance values were calculated from 38 sample points in the blowdown and 35 sample points in the understory.

§ Large-scale concordance values were calculated from eight 1-m^2 plots in the blowdown and in the forest understory. Critical values of the Friedman chi-square distribution were used for large-scale tests (Zar 1996).

Resource congruence

Kendall's coefficient of concordance was greater for all combinations of soil resources without light than for combinations of soil resources and light (Table 4). Concordance among all soil resource combinations was greater at the sapling (large) scale than the seedling (small) scale in the blowdown, but not in the understory. In the blowdown, concordance among light and various combinations of soil resources was also generally higher at the sapling scale than the seedling scale, but this was not the case in the understory (Table 4). For most combinations of soil resources, concordance was much greater on the blowdown site than in the forest understory at both spatial scales. However, concordance among soil water, organic matter, and mineralization rate (W–O–M) was very high in the understory as well as the blowdown. At the sapling scale, concordance among light and most combinations of soil resources was greater in the blowdown than the understory. However, concordance among light, soil water, organic matter, and mineralization rates (L–W–O–M) was highly significant in the understory at both spatial scales (Table 4).

Congruence among levels of the different resources varied greatly across the 73 sample points, ranging from 0.259 to 0.907 in the blowdown, and from 0.129 to 0.905 in the understory. Patterns of median congruence were generally similar to concordance results. In

TABLE 5. Congruence in levels of different combinations of resources at the Prospect Hill experimental blowdown (BD) and in the adjacent forest understory (US). Congruence was calculated from standardized resource levels using the equations and procedures described in *Methods.* The significance of Mann-Whitney *U* tests is indicated by asterisks.

	Small-scale‡		Large-scale§	
Resources†	BD	US	BD	US
W–O–M	0.865	0.860	0.928+	0.847
W–O–N	0.839	0.808	0.917*	0.824
W–M–N	0.829*	0.767	0.903*	0.774
O–M–N	0.813+	0.780	0.898*	0.763
W–O–M–N	0.806	0.774	0.897*	0.770
L–W–O–M	0.680	0.817*	0.745	0.824
L–W–O–N	0.661	0.765+	0.751	0.742
L–W–M–N	0.671	0.747	0.798	0.762
L–O–M–N	0.599	0.726+	0.731	0.742
L–W–O–M–N	0.623	0.728	0.764	0.752

+ $P < 0.10$, * $P < 0.05$.

† Resources and codes are as in Table 4.

‡ Small-scale congruence values are the medians of 38 and 35 individual congruence calculations in the blowdown and understory, respectively.

§ Large-scale congruence values are the medians of eight congruence calculations each in the blowdown and understory.

the blowdown, congruence was greater for all combinations of soil resources without light than with light (Table 5). Including light did not reduce congruence substantially in the understory. In the blowdown, congruence among all combinations of soil resources, with or without light, was greater at the sapling scale than the seedling scale. In the understory, there was no consistent difference in congruence at the two spatial scales (Table 5). For most combinations of soil resources, large-scale congruence was significantly greater in the blowdown than in the forest understory. The same patterns were observed at the seedling scale, but there were few significant differences. Seedling-scale congruence among light and different combinations of soil resources was greater in the understory than in the blowdown. At the sapling scale, however, there were no consistent differences in congruence between the blowdown and the understory (Table 5).

Resource congruence also differed among the five types of microsites on the experimental blowdown. Pits had the highest concordance among the four soil resources ($W = 0.581$) and the highest concordance when light was included ($W = 0.488$). Pits also had the highest median congruence among light and the soil resources ($C = 0.789$). Median congruence among the four soil resources without light was highest on mounds ($C = 0.891$). Fern microsites had the lowest concordance among soil resources without light ($W = 0.303$) and when light was included ($W = 0.187$). Fern sites also had the lowest median congruence ($C = 0.608$) among the four soil resources. Top microsites had the lowest median congruence among light and the soil resources ($C = 0.475$).

Effects of resources on seedling growth

Overall, seedlings of the three birch species experienced very similar levels of resources and resource congruence. There were significant differences among species for only one of the 10 resource combinations for which congruence was calculated. Congruence among light, soil water, organic matter, and mineralization rate was significantly greater on sample points occupied by black birch ($C = 0.820$) than on points occupied by white birch ($C = 0.567$, $P < 0.01$) or yellow birch ($C = 0.600$, $P < 0.05$; multisample median test and Levy's multiple-comparison test, Zar 1996). All other mean resource levels and median resource congruence values were similar for the three species.

First-year growth of all three birch species was positively related to light levels on the blowdown sites. Diameter growth of black birch and diameter and height growth of white birch and yellow birch were correlated with photon flux density (Table 6). However, growth of the birch seedlings was not positively related to any of the other resources that we measured. The three species differed in their response to resource congruence. Both diameter and height growth of white birch seedlings were positively correlated with congruence among soil resources (Table 6). Diameter growth, but not height growth, of yellow birch was correlated with soil resource congruence. First-year growth of black birch seedlings was not strongly related to soil resource congruence. Congruence among light and different combinations of soil resources had no significant effect on 1st-yr growth of the three species of birch seedlings (Table 6).

DISCUSSION

Disturbance effects on resources

Results from comparisons of randomly located points in blowdown and understory sites supported several, but not all, of our predictions. As predicted, the two climatic factors that we measured were significantly altered by the disturbance treatment (Poulson and Platt 1989, Canham et al. 1990, Sipe 1990). Light levels were significantly higher and CO_2 concentrations were significantly lower on the blowdown site than in the undisturbed forest (Table 2). In contrast to the marked impact of our disturbance treatment on climatic factors, there was no significant site-scale effect on soil resource levels three years after the experimental blowdown was created. Net nitrification rates were much higher on top microsites than in the forest understory, but these microsites represented a very small proportion of the blowdown area. Nitrification rates on 40 randomly selected plots throughout the blowdown were not significantly higher than rates in the understory.

We predicted that heterogeneity of all six resources would be greater on the disturbed site than in the forest understory because of the influence of boles, crowns,

TABLE 6. Spearman rank correlation between resources (levels of individual resources and congruence) and growth of birch seedlings on experimental hurricane blowdown microsites. Sample sizes are 32, 31, and 27 for black, white, and yellow birch, respectively. Diameter and height refer to first-year growth in basal stem diameter (mm) and height (cm).

	Black birch		White birch		Yellow birch	
Resources†	Diameter	Height	Diameter	Height	Diameter	Height
L	0.439**	0.223	0.460**	0.448**	0.354*	0.335*
W	−0.127	−0.155	−0.468	−0.374	−0.387	−0.151
O	−0.066	−0.006	−0.320	−0.291	−0.300	−0.010
M	−0.009	0.053	−0.316	−0.378	−0.362	0.038
N	0.078	0.150	−0.527	−0.472	−0.242	−0.134
W–O–M	0.251+	0.154	0.307*	0.280+	0.239	−0.064
W–O–N	0.257+	0.241+	0.423**	0.384*	0.336*	0.085
W–M–N	0.217	0.156	0.438**	0.472**	0.465**	0.150
O–M–N	0.176	0.070	0.337*	0.274	0.402*	−0.025
W–O–M–N	0.250+	0.201	0.401*	0.396*	0.389*	0.060
L–W–O–M	−0.190	−0.071	−0.035	−0.039	−0.030	−0.353
L–W–O–N	−0.143	0.011	−0.030	−0.152	−0.048	−0.242
L–W–M–N	−0.180	−0.068	−0.004	−0.017	0.000	−0.247
L–O–M–N	−0.240	−0.086	−0.222	−0.172	−0.216	−0.306
L–W–O–M–N	−0.103	0.028	0.028	−0.018	0.041	−0.267

Notes: Sample sizes are 32, 31, and 27 seedlings for black, white, and yellow birch, respectively. Congruence calculations are as in Table 5.

+ $P < 0.10$, * $P < 0.05$, ** $P < 0.01$ for one-tailed significance of Spearman rank correlation coefficients.

† Resources and codes are as in Table 4.

and microtopography caused by uprooting (Beatty 1984, Vitousek and Denslow 1986, Schaetzl et al. 1989*a*, *b*, Peterson et al. 1990, Fernandez and Fetcher 1991). As predicted, light levels and nitrification rates were more variable in the blowdown. However, heterogeneity in CO_2 concentration and percent soil water was similar on both sites, and soil organic matter and N mineralization rates were more variable in the understory than in the blowdown. Soil water concentration varied primarily at the larger scale relevant to growth of saplings, whereas most variation in mineralization and nitrification rates occurred at the smaller seedling scale (Table 2).

These results suggest that edaphic effects of catastrophic blowdown develop more slowly than climatic effects throughout most of the disturbed site. This is not surprising. Changes in soil properties arise through secondary processes of decomposition and nutrient cycling operating on the patchy distribution of foliage and woody material and upturned soil profiles that result directly from the disturbance (Vitousek and Denslow 1986, Vogt et al. 1986). Previous studies of pit-and-mound microtopography have emphasized that the passage of time is essential for development of soil texture and structure (Stephens 1956, Schaetzl et al. 1990) and for the accumulation and decomposition of organic material in pits (Beatty and Sholes 1988, McClellan et al. 1990). If a disturbance event immediately and dramatically alters fluxes of light and other climatic factors, but initiates a process of gradual change in soil nutrient and water availability, we might expect relationships among resource levels to be affected. We addressed this question by quantifying microsite environments and resource congruence.

Microsite environments

Open microsites in this study received more direct-beam radiation than all other microsites except mounds. The light environment, however, was quite variable because of shading by downed boles and crowns and the influence of the surrounding forest (Canham et al. 1990, Sipe and Bazzaz 1994). Soil moisture, organic matter content, and N mineralization rates on our open microsites were slightly higher than those recorded adjacent to old mound–pit complexes in a forest dominated by *Acer saccharum* and *Fagus grandifolia* in eastern New York, United States (Beatty 1984, Beatty and Stone 1986). Because of their abundance and suitability for recruitment, open microsites are extremely important for successful regeneration of the forest community (Carlton 1993).

Fern microsites occupied nearly half of the experimental blowdown site. Light levels were low and quite variable on these microsites. Carbon dioxide concentrations under ferns were similar to levels in the undisturbed forest understory and were higher than concentrations on all other blowdown microsites. Elevated CO_2 was probably due to reduced air movement beneath the fern canopy (Bazzaz and Williams 1991). Fern microsites were also similar to the forest understory in levels of most soil resources. Because of their abundance in central New England forests, fern microsites are important for recruitment of shade-tolerant species.

Experimentally created mounds were characterized by high light levels and low CO_2 concentrations. Levels of soil resources were similar to levels recorded on naturally occurring mounds (Beatty 1984, Beatty and

Stone 1986, Schaetzl et al. 1990). The experimental mounds were subject to early frosts in autumn and severe frost heaving during the winter (Carlton 1993). Suitability of mounds for regeneration depends on physiographic and climatic characteristics of the disturbed site (Peterson and Pickett 1990). In forests subject to periodic drought, moisture deficits on mounds would inhibit establishment. Similarly, on nutrient-limited sites, subsoil material of mounds may be too impoverished to support seedlings (Webb 1988). In more mesic conditions, however, mounds may be important for colonization of small-seeded species such as *Betula* that are unable to recruit through the thick litter layer on the undisturbed forest floor (Facelli and Pickett 1991).

As in other studies, our experimental pit microsites were characterized by mean light levels, CO_2 concentrations, soil water content, and nitrification rates adequate to support seedlings (Beatty 1984, Schaetzl et al. 1990). However, thick accumulation of leaf litter creates a physical barrier to seedling recruitment and establishment in pits (Beatty and Sholes 1988). Seasonal waterlogging also impedes regeneration in pits on many sites and may slow decomposition of heavy litter inputs (Beatty 1984, Beatty and Stone 1986, but see McClellan et al. 1990). In addition to leaf litter and waterlogging, erosion of soil from mounds into pits may severely inhibit establishment, particularly during the first year or two following disturbance (Carlton 1993).

Top microsites in this study were characterized by extremely variable light levels and by the highest nitrification rates of any microsite. Increases in nitrification are often linked to increased mineralization rates, which provide additional substrate for nitrifying bacteria (Aber et al. 1989), or to other factors affecting the microbial community (Paul and Clark 1989). High nitrification rates have also been observed in gaps within old-growth forests of upper Michigan (Mladenoff 1987) and on experimental plots at the Harvard Forest after tree roots were severed (R. Boone, *personal communication*). Uprooting and root severing may increase nitrification rates by reducing living root biomass and increasing organic material available for decomposition. Whatever the cause, increased nitrate availability in a nitrate-limited system such as the Harvard Forest may have important implications for tree regeneration (Chapin 1980, Marshner 1986, Crabtree and Bazzaz 1993).

Resource congruence

As predicted, congruence among soil resources without light was much greater than congruence among soil resources and light levels, particularly in the blowdown and at the smaller spatial scale. The differences were most pronounced using Kendall's coefficient of concordance to quantify congruence (Table 4). All of the soil resources that we measured depend on fundamental properties of the soil and are, therefore, somewhat interdependent. Light levels, on the other hand, do not generally depend on soil properties, but are strongly influenced by the physical structure of the community, which was substantially altered by the disturbance.

We had also predicted that congruence would be greater at the sapling scale than at the smaller seedling scale. On the blowdown site, both concordance and congruence were substantially greater at a scale relevant to saplings than at the seedling scale (Tables 4 and 5). This suggests that, if resource congruence is advantageous to plants, larger plants in the blowdown will benefit by being able to integrate their environment over a broader spatial scale. Such integration, however, may be less important for seedlings growing in the forest understory, where congruence was similar at both the seedling and sapling scales of measurement.

Lastly, we had predicted that congruence among soil resources should not be affected by the blowdown, but that congruence among light and soil resources should be reduced by the disturbance. Congruence among soil resources without light was actually greater in the blowdown, particularly at the sapling scale. When light was included, median congruence at the seedling scale was lower in the blowdown than in the understory, as predicted. At the sapling scale, median congruence was similar on both sites and Kendall's coefficient of concordance was greater in the blowdown than in the understory. Within the blowdown site, resource congruence was greatest in pits and lowest on fern microsites. These results suggest that the experimental blowdown reduced congruence between light and soil resources at a scale relevant to the growth of small seedlings, and that microsites differ not only in resource availability and heterogeneity, but also in resource congruence.

The last set of hypotheses concerned the effects of resource levels and resource congruence on seedling growth. As predicted, 1st-yr growth of the shade-intolerant white birch was strongly related to light levels. The relationship between light levels and seedling growth was not quite as strong in the other two species (Table 6). None of the species responded positively to levels of any of the other resources. We had predicted that yellow birch, the most shade-tolerant of the three species, would exhibit the strongest relationship between growth and resource congruence. Diameter growth of yellow birch was indeed strongly related to soil resource congruence, but height growth was not, perhaps because of variation due to etiolation in low light conditions and to browsing by snowshoe hares. The relationship between soil resource congruence and growth rate was actually strongest in white birch. Both diameter and height growth of this colonizing species were significantly correlated with soil resource congruence. Black birch, which is intermediate in shade tolerance and is often considered ecologically similar to yellow birch, exhibited little growth response to soil resource congruence. None of the three birch species responded positively to resource congruence when light was included, probably because of the relationship between light and growth.

Conclusions

Not all aspects of hurricane disturbance were simulated on our experimental blowdown site. Actual hurricanes, for example, are often accompanied by torrential rains (Foster 1988). Although we did not attempt to simulate rainfall on the blowdown site, we did receive fairly heavy rain immediately before initiating the treatment. A much more important limitation with our treatment was lack of wind. We feel confident that the uprooting and snapping of boles was simulated successfully, but other effects of wind were not adequately simulated by the pulldown treatment. For example, high winds may strip foliage from vegetation, with significant effects on photosynthesis, transpiration, and other physiological processes. This may be particularly important for saplings and seedlings, a potentially valuable pool of replacements for canopy trees destroyed by a storm. Hurricane-force winds may also disperse pollen or seeds much farther than normal, and may cause extensive loss of reproductive structures before they are mature. Successful regeneration of most disturbed sites, however, probably depends more on seed bank dynamics and the response of surviving individuals than on seed dispersal immediately preceding or during the disturbance event (Mladenoff 1990).

Results of this study suggest that hurricane blowdowns increase light levels immediately, but initiate a gradual change in availability of soil resources on many microsites. This has also been observed following some, but not all, natural disturbances (Silver et al. 1996). Microsites with high light levels, regardless of nutrient availability, may be colonized quickly by shade-intolerant pioneer species (Bazzaz 1983, Connell 1989, Schupp et al. 1989). Many of these species are able to maintain high photosynthetic capacity at relatively low leaf nitrogen concentration (Evans 1989). Gradual enrichment of soil fertility on microsites where light levels are too low to support colonizing species may be important for more shade-tolerant species. Thus, disturbance events such as hurricane blowdown may create patches with temporal patterns of resource availability that match the different requirements of colonizing and late-successional species.

The suitability of a particular microsite for germination may depend as much on the congruence among resources as on the absolute levels of those resources. In this paper, we presented two rather different measures of resource congruence and demonstrated that seedling growth of white birch and yellow birch is influenced by congruence. This suggests another possible dimension in the regeneration niche of Grubb (1977) and another means by which different plant species may coexist on the same set of abiotic resources.

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