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GAP DYNAMICS FOLLOWING FOREST DECLINE: A CASE STUDY OF RED SPRUCE FORESTS

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Abstract. Forest decline is perceived as a threat to forest health in many regions of the world. The decline of red spruce in the mountains of the northeastern United States is one well-known example. We evaluated the impact of spruce decline by considering its effect on the prevailing gap dynamics. We compared plant composition, height growth, and indices of resource availability in gaps to the forest as a whole in four old-growth stands.

In our study, there were no appreciable compositional differences between gaps and the forest as a whole. However, the relative height growth rate of saplings and seedlings was greater in gaps and was significantly different in three of the four old-growth communities studied. There were also significant differences in the response of species to gaps; birches grew faster than balsam fir which grew faster than spruce.

The initial stage of vegetation recovery in the spruce–fir forest was dominated by advance regeneration of balsam fir. Much of the recovery in the hardwood–conifer transition zone will depend on the response of spruce, and therefore the closure rate of gaps will be constrained by the slow growth of spruce advance regeneration. In both forest types, the shortage of mineral soil seedbed restricted birch establishment and limited its role in vegetation recovery.

Throughout the subalpine community, a large fraction of the potential radiation reached the understory regardless of canopy status (means ranged from 19% to 32% of potential radiation). In fact, gaps received less light on average than random points in the understory. Judging from indices of fine root growth, belowground resources were enriched in gaps relative to the forest as a whole. The lack of quantitative light gaps and the higher fine-root density in gaps suggest that the observed response of the trees resulted from changes in belowground resources or qualitative changes in the light regime.

The phenomenology of gap formation influenced the gap environment and consequently the course and rate of recovery. Many red spruce trees died standing. These standing dead trees continued to intercept an important fraction of available light. Damage to understory plants and disruption of the forest floor were minimal. These aspects of the gap regime favored recovery via upgrowth of advance regeneration rather than the establishment and growth of seedlings. General recommendations when evaluating other instances of decline include: (1) assess the impact of decline relative to the existing disturbance regime; (2) consider the influence of the phenomenology of decline on the recovery process; (3) recognize that vegetation recovery also depends on the inherent community organization of the affected forests.

Key words: belowground gaps; disturbance dynamics; forest recovery; gap dynamics; gap light index; null gaps; old-growth subalpine forests; Picea rubens; *red spruce; spruce decline; spruce–fir forest; understory light.*

INTRODUCTION

Forests throughout the world are experiencing worrisome increases in tree morbidity and mortality (Schulze et al. 1989, Manion and Lachance 1992, Huettl and Mueller-Dombois 1993, Landmann and Bonneau 1995). Some cases involve exotic forest pests or exploitative land use practices. In many others, the interaction of specifically ordered physical and biological factors produce the observed mortality, a phenomenon called forest decline (Manion 1991). Despite common usage, forest decline refers to a population decline since in most instances only individuals of a particular tree species are affected (Skelly 1992). Atmospheric pollution often is implicated as a contributor to forest decline. The perceived threat to regional forest health has concentrated national and international research efforts on a search for causes. The consequences of decline for specific forest communities has received much less attention.

This research describes how four forest stands in the mountains of the northeastern United States respond to the decline of red spruce trees (*Picea rubens* Sarg.). Red spruce decline is one of the most intensively stud-

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ied examples of forest decline (Eagar and Adams 1992), yet results to date provide little guidance to managers trying to cope with a complex ecological phenomenon. We conducted a detailed case study of red spruce decline with the hope of distilling some general insights to help evaluate the effects of declines on forest communities.

Red spruce is a common tree in the upland forests in the northeastern United States. It occurs across a biome transition from eastern deciduous forest to conifer forest (Bormann et al. 1970). Beginning in the mid-1960s, many overstory red spruce trees in the region have died standing. A distinguishing characteristic of spruce decline was the progressive loss of foliage beginning at the branch tips and moving downward and inward over time. By the 1980s, as many as half the standing spruce trees were dead in some high elevation stands (Siccama et al. 1982, Scott et al. 1984, Battles et al. 1992). Presently, the radial growth rates of mature spruce in several Northeastern forests have returned to predecline levels (Battles 1994, Reams and Van Duesen 1995), indicating that the decline may be over.

Our fundamental premise was that spruce decline must be understood in the context of the general disturbance dynamics of these forests (sensu Mueller-Dombois 1991). In the subalpine forest, stand-initiating disturbances like fires or hurricanes are infrequent compared to the longevity of the dominant trees (Fahey and Reiners 1981, White and Cogbill 1992). Generally, canopy turnover occurs via tree by tree replacement in fine scale forest gaps. Interrupting the relatively quiescent background dynamics are pulses of mortality localized in space (e.g., landslides and insect outbreaks, Battles et al. 1995) or episodic in time (e.g., drought and major windstorms, Battles and Fahey 1996). Spruce decline is an example of a periodic noncatastrophic increase in tree mortality that causes a quantitative but not qualitative shift in the disturbance regime. Even in the aftermath of spruce decline, gap processes are still the principal mechanisms of canopy replacement in the subalpine forest (Battles and Fahey 1996).

This study documents gap dynamics immediately following an episode of forest decline. First we evaluated the null hypothesis that gaps do not represent enhanced opportunities for canopy recruitment. Our second objective was to describe the initial stages of vegetation recovery in the red spruce forests. Specifically, we asked: (1) What characteristics of the decline influence resource availability and thus vegetation recovery? (2) How might the response to disturbance differ between location and forest type? (3) What lessons about red spruce forests and their decline can be generalized to other forests and other declines?

METHODS

Site descriptions

Research was conducted in the Baldwin Basin (Baldwin) on the northwest slope of Whiteface Mountain, New York (44°22′ N, 73°54′ W) and in the Bowl Research Natural Area (Bowl), New Hampshire (43°56′ N, 71°24′ W). Baldwin and the Bowl are old-growth subalpine forests with no historical or ecological evidence of logging or fires (Woods and Cogbill 1994, Gemborys 1996). At lower elevations in the northern hardwood forest, sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.) and yellow birch (*Betula alleghaniensis* Britton) are the most prevalent canopy trees; at the higher elevations in the spruce–fir forest, red spruce, balsam fir (*Abies balsamea* (L.) Mill.), and mountain paper birch (*Betula papyrifera* Marsh. var *cordifolia* Regel) dominate the forest. Between the northern hardwood and spruce–fir forest, a transition zone exists in which red spruce and the northern hardwood species are the most important trees.

The sites in this study reflected the regional vegetation gradient (Bormann et al. 1970, Cogbill and White 1991). Mean basal area in the spruce–fir zone was 32.2 m^2/ha at Baldwin and 23.6 m^2/ha at the Bowl. At both sites, balsam fir accounted for ~50% of the basal area; spruce and paper birch each accounted for ~20% of the basal area. Inventories conducted before the onset of decline had conifer dominance in the spruce–fir zone more equally split between spruce and fir (Battles et al. 1992, Leak and Graber 1974). Approximately 50% of the adult spruce trees were dead at the study sites by the early 1990s (Battles and Fahey 1996). Mean basal area was lower in the transition zone. At Baldwin, total tree basal area was 16.9 m^2/ha; at the Bowl it was 20.0 m^2/ha. Yellow birch and red spruce were two important species in the transition zone at both sites. Hobble bush (*Viburnum alnifolium* Marsh.) was an abundant shrub in the transition zone. The major difference in tree composition between the two sites was that beech was more abundant at the Bowl than at Baldwin (Battles and Fahey 1996).

Canopy structure and environmental characteristics of the sites varied but the magnitude of variation was typical for the northeastern subalpine forest. Furthermore, gap fractions observed in the specific research areas were representative of the overall level of disturbance in these forests (Table 1, Battles and Fahey 1996). Nomenclature follows Britton and Brown (1970).

Two important ecological differences between the sites were the influence of mammalian herbivory and the progression of an insect disease complex. Moose (*Alces alces*) was the most prominent herbivore at the Bowl but was absent from Baldwin. Moose feed on all the common trees in the subalpine forest except red spruce. Balsam fir, in particular, makes up a large fraction of the winter moose diet (McLaren and Peterson 1994). Beech bark disease is the result of a sequential attack by the introduced beech scale, *Cryptococcus fagisuga* Lindinger and fungi from the *Nectria* genus (Sinclair et al. 1987). In the transition zone, beech trees

TABLE 1. Characteristics of the research areas and study gaps used in this study.

	Spruce–fir zone		Transition zone	
	Baldwin Basin	Bowl Natural Area	Baldwin Basin	Bowl Natural Area
Elevation range (m)	960–1010	938–990	740–793	775–843
Slope (%)	19	39	28	37
Aspect	NW–NE	NE–SE	NW–N	NE–SE
Gap fraction (%)				
Actual	8	21	29	11
Expanded	15	41	48	23
Potential PAR (mol/m^2)	6810	6642	6829	7712
Study gap size (m^2)				
Mean	161	106	222	174
Median	150	100	181	140
Range	51–575	37–255	86–510	47–599

Notes: Elevation range was determined by the study gaps at the highest and lowest elevation at each site. Gap fraction is the percentage of forest area under gaps in the research area (data from Battles and Fahey 1996). Actual gap consists of the area directly under the canopy opening; an expanded gap consists of the area delineated by the boles of the border trees and includes the actual gap. Potential PAR is the potential photosynthetically active radiation over the entire growing season, calculated from the equation: PAR = $I_0 \times \cos(Z_t)$ where I_0 is the solar constant and Z_t is the zenith angle of the sun at time t. Growing season in the spruce–fir zone was from 1 June to 15 September; in the transition zone it was from 25 May to 15 September. Potential PAR was corrected for slope and aspect. Size of the study gaps is expressed as expanded gap area; $n = 20$.

at both sites were infected but the disease was more advanced at Baldwin.

Research design

The complexity of canopy architecture in gap-dominated forests raises questions about the propriety of sampling schemes where comparisons are made between subjectively defined gaps and ‘‘non-gaps’’ (Lieberman et al. 1989). Such designs risk comparing extremes along a continuum of understory environments and invite the criticism of circular reasoning in which the observer defines different microenvironments in the forest and then proceeds to document the differences. To avoid these problems, gaps were compared not to the opposite situation of intact canopy but to the entire forest.

At Baldwin and at the Bowl, one reference grid (~0.5 ha) was randomly located in the spruce–fir zone and another in the transition zone for a total of four research areas. Each rectangular grid was oriented with the long axis parallel to the contour and consisted of either a 5 × 10 or 6 × 8 arrangement of equally spaced points. Around each grid, the 20 nearest canopy gaps were located. A gap was defined as an opening in the canopy caused by the recent death of at least one canopy tree. The minimum diameter at breast height (dbh; i.e., at a height of 1.37 m) of canopy-sized trees in these forests was 15 cm. The borders of the gap were defined by the boles of the trees with ≥10 cm dbh surrounding the opening. Following Runkle (1992), the area directly under the canopy opening is called the actual gap. The expanded gap consists of the area delineated by the boles of the border trees and includes the actual gap. In selecting the study gaps, small and extremely large gaps were excluded in order to represent most of the gaps in these forests (see *Results: Description of study gaps*).

The environmental and biological measurements taken in the gaps were also made in a 2 m radius plot centered on each reference point. Some of the plots in the reference grid (reference plots) were under gaps, some under an intact canopy, others somewhere in between. Together the reference plots represent a ‘‘null gap’’ (sensu Lieberman et al. 1989) and the null hypothesis was that gaps were no different from any other habitat in the forest.

Vegetation sampling in gaps

The species, dbh, and type of damage was recorded for the trees that caused the gap (gapmakers). If the gapmaker was a standing dead red spruce, increment cores were taken and evaluated in the field for signs of growth decline. In some cases, cores of the suppressed trees were extracted with the hope of documenting the time of gap formation from evidence of a recent release. Notes were made of other possible clues to the age of the gap (e.g., retention of foliage and fine twigs on gapmakers, age of seedlings growing on tip-up mounds). Thus a combination of evidence and intuition was used to reconstruct the history of the gaps.

In every study gap, the longest axis (A_{major}) and the longest perpendicular to the primary axis were measured (A_{minor}). Gap size was estimated as linear functions of A_{major} and A_{minor} from site-specific regression equations (Battles and Fahey 1996). These axes also served as sampling transects. All woody stems ≥1 m tall and within one meter on either side of the axes were counted, the species identified, and, for stems ≥2 cm diameter at breast height, the dbh was recorded. We used extension height growth to measure the relative growth rate of advanced regeneration. For each tree species present, we selected three individuals. Because advanced regeneration often occurs in even-aged and even-sized clumps, we measured only one representative individual from any one clump. If there were three or fewer individuals of any species in the gap, all individuals of that species were sampled. All measured trees were located under the canopy opening (i.e., in the actual gap). The total length of the apical stem or tallest lateral branch was recorded. Starting at the tip of the terminal bud, the length between terminal bud scars was measured. Annual increments were divided by the total shoot length of the previous year to get relative extension growth for that year (Marks 1975). For all tree species, terminal bud scars could be identified with confidence for the last three years of growth. The growth rate of hobble bush was estimated from sections of the stem cut near the base. The sections were sanded and annual ring widths measured with a sliding stage micrometer. Relative growth rate was expressed as the ratio of annual basal area increment divided by the total stem basal area of the previous year. To characterize tree seedling (individuals <1 m tall) and vascular herb composition, the entire gap was surveyed. From this survey, a list of the species present was compiled and species abundance was classified as either present, common, or dominant.

Light measurements

We took fisheye photographs of the canopy to evaluate differences in the light regime between gaps and the reference forest. We generally followed the protocols described in Rich (1989) for field acquisition of the photographs and subsequent conversion to digital images. Specifically, at each sample point, a black and white photograph was taken of the canopy with an extreme wide-angle lens (Canon 7.5 mm) that provided a 180° view of the canopy. Photographs were shot looking upward at 1.2 m above the ground. Understory vegetation taller than 1.2 m and within a 1 m radius of the sample point was pinned back to get an unobstructed view of the canopy. Pictures were taken near dawn and dusk to approximate uniform skylight conditions. Prints developed from the negatives were digitized using a flatbed scanner, cropped, and converted to a binary file with a resolution of 512×512 pixels. A threshold grey level was chosen that produced a digital image that best matched each print.

We analyzed the digital images using software provided by Canham (1988*b*) that computes a gap light index (GLI). The GLI software provides a robust estimate of long-term average light levels as well as precise information about the geometry of light penetration through the forest canopies (Canham et al. 1990, Battles 1999). Specifically, GLI estimates the percentage of incident photosynthetically active radiation (PAR) transmitted to a point in the understory during the growing season. Values range from 0% for a completely closed canopy to 100% for a completely open site. It includes the contribution of diffuse beam and direct beam radiation but does not account for radiation due to beam enrichment which can be an important fraction of the total radiation under some canopies (Canham et al. 1994). Incident PAR is calculated from standard equations of solar geometry and a site-specific atmospheric transmission coefficient (K_T). We computed the growing season K_T (Stoffel 1980) from five years (1985–1990) of daily solar flux data collected above the spruce–fir forest on Whiteface Mountain. Since the computed value of 0.47 was close to the regional average of K_T (Knapp et al. 1980), we used $K_T = 0.47$ in all GLI routines. Note that GLI is a theoretical estimate of PAR based on canopy architecture measured via fisheye photography and modeled inputs of above-canopy solar radiation.

We randomly re-analyzed 5% of the photos to calculate precision error in GLIs. The two major sources of imprecision were: (1) variation in the quality of the prints, and (2) subjectivity in the selection of the threshold for digitizing photos. The precision error associated with the measurement of GLI ±5% of the mean.

Measurement of root growth response and seedbed

In situ screens were used to assess the belowground response to disturbance (Fahey and Hughes 1994). This technique involved peeling back the Oi and Oe layers in the forest floor and placing a 10 cm square nylon-coated fiberglass mesh screen (hole size = 4 mm^2) on top of the Oa layer. The forest floor layers were then replaced. A year later, the Oi and Oe were carefully removed and the number of fine tree roots intersecting the screen was counted. The number of intersections per screen was considered a measure of fine root growth (RGI = root growth index). This method caused little to no disturbance to the rhizosphere. Every sample consisted of three screens arranged in the pattern of an equilateral triangle (approximate length of a side = 50 cm). Two of the three screens in every set were selected randomly and read. If a screen was disturbed in any way, the third ‘‘spare’’ screen was used. The RGI result for each set of screens was the average of the two screens.

Line intersect sampling was used to quantity the extent and nature of the seedbed in gaps. Again the major and minor axes served as sample transects. The length of the transects in the following categories was recorded: intact forest floor, dead wood, exposed mineral soil, and other (e.g., rocks, exposed roots, and upright stems).

Sampling in reference grids

Each point sampled in the reference grids served as center of a circular plot with a 2 m radius. All woody stems ≥ 1 m tall in the plot were counted and dbh was recorded for trees ≥ 2 cm dbh. All the vascular species present in the herb stratum (plants <1 m tall) and their abundance were recorded. For all tree species in the plot, two representative individuals were sampled for relative extension growth. Relative basal area increment of hobble bush was also assessed in the plots. To measure light, fisheye photographs of the canopy were taken directly over the center point. To measure fine root growth, three root screens were placed around the point in the pattern of an equilateral triangle (approximate length of a side = 50 cm). The triangle was centered at the point. The cover of each seedbed type in the plot was visually estimated.

Analysis, spatial patterns, and sampling decisions

The focus of this research was the influence of canopy disturbances on vegetation recovery and resource availability. Therefore the experimental unit was a forest patch with the comparison being null gap versus gap. Given the inherent differences in environmental and vegetational characteristics (Table 1), the expectation was that plant response would necessarily vary among the sites and that there would be significant site by forest type interaction. However, with only two replicates in each forest type, there were not enough degrees of freedom to evaluate the interaction term. Since the main objective was to determine the gap effect, statistical investigations were limited to within-site comparisons.

To test properly the gap effect, we documented spatial patterns in resource availability. There was significant positive autocorrelation in GLIs at a 10 m distance for both reference grids at Baldwin (Battles 1999). Therefore, for analyses requiring independent samples of GLIs, we only included every other point (20 m × 10 m spacing) from the Baldwin reference grids to create a minimum distance between points (14.1 m) greater than the measured spatial autocorrelation (Clark et al. 1996). At the Bowl, we only measured every other point (20 m × 10 m spacing). The spatial autocorrelation in light values lends statistical support to a practical decision to measure root growth, species composition, and extension growth at only half the reference points. We also checked for within-gap patterns in GLI and RGI. There were no differences between GLI at the center of gaps and the north edge of gaps (Battles 1994). Nor were there any significant differences among RGI from center, intermediate, and edge locations in gaps (Battles 1994). Based on these patterns, we choose to use GLIs and RGIs from the gap center to compare resource availability in gaps and in the reference plots.

Most field measurements were made in 1990 and 1991 with some additional field work in 1992. The goal was to sample 20 study gaps and a similar number of references points in each forest. The major exception was that GLI and RGI were measured only in the 10 nearest gaps to the reference plots at Baldwin.

Differences in mean GLI and mean RGI between gaps and reference points were tested with two-sample t tests. The understory vegetation was divided into four classes for analysis: tree saplings (trees $\geq$1 m tall and $<$2 cm dbh), tree seedlings (trees $<$1 m tall), shrubs (only hobble bush), and vascular herbs. The principal metrics used to quantify the vegetation response were relative height growth of tree saplings and seedlings and, in the case of hobble bush, relative basal area increment. Significant differences in relative growth among species and between plants in gaps and in reference plots were evaluated with general linear models. The relative growth data were transformed with the arcsine square-root function to meet parametric assumptions (Sokal and Rohlf 1995). In the case of seedling growth, the transformed data still did not meet the assumption of normality. Therefore nonparametric Mann-Whitney U tests were used to test for differences in median growth rates of seedlings.

Plant compositional differences between the reference plots and gaps were quantified using two indices of community similarity. For saplings, Sørensen's percent similarity was used; for the herb community, Sørensen's coefficient of community was used (van Tongeren 1995). Percent similarity incorporates information about species presence or absence and relative abundance to estimate the similarity of species composition between two samples. Values range from 0 for samples with no species in common to 1 for samples with identical composition. The coefficient of community is a measure of similarity based only on information about species presence or absence. It, too, ranges from 0 for samples with no species in common to 1 for samples where all species are in common.

RESULTS

Description of study gaps

Expanded gap area of the study gaps ranged from 37 m^2 to 599 m^2 (Table 1). For the northeastern subalpine forest, gaps in this size range account for 80% of the land area in gaps (Table 1, Battles and Fahey 1996). The typical study gap had three gapmakers. Often, at least one was a spruce tree that showed a marked reduction in radial growth during the last decade of its life: a characteristic sign of spruce decline (Siccama et al. 1982). The gradual death of a spruce tended to mask the release response of subcanopy trees. Rather than a sharp increase in growth, a slow increase over several years was frequently observed. No study gap was without signs of gradual or sudden release in the last ten years. In 68 of the gaps, there was evidence that a canopy tree had died within the last five years.

In the spruce–fir zone, $>$90% of the gapmakers were red spruce and balsam fir. In the transition zone, spruce was the most abundant gapmaker, with fir, yellow birch and striped maple (*Acer pensylvanicum* L.) trees also notable contributors to the gap area. Trees that died standing were the majority of gapmakers at every site.

Vegetation response to gaps

Tree saplings.—Although the sapling community in the spruce–fir zone at Baldwin was the most dissimilar

TABLE 2. Comparison of the density, frequency, height, and mean relative extension growth of saplings (trees ≥1 m tall and <2 cm dbh) in reference plots (REF) and in gaps (GAP) for two old-growth spruce–fir forests in the mountains of the northeastern United States.

	Density (stems/ha)		Frequency (%)		Height (m)		1991 growth (%)		1990 growth (%)	
Species†	REF	GAP	REF	GAP	REF (*n*)	GAP (*n*)	REF (*n*)	GAP (*n*)	REF	GAP
Baldwin (PS = 67%)										
Red spruce	605	443	44	55	1.5 (10)	1.7 (9)	2.3 (9)	6.0 (6)	2.9	8.1
Balsam fir	1909	3650	52	85	1.6 (15)	1.8 (17)	2.8 (12)	8.1 (9)	3.9	9.2
Paper birch	32	434	4	35	2.8 (1)	1.8 (10)	6.0 (1)	13 (5)	5.9	14
Bowl (PS = 75%)										
Red spruce	1942	2412	64	80	1.5 (19)	1.6 (40)	7.5 (14)	9.2 (15)	6.4	10
Balsam fir	3629	3416	64	85	1.9 (20)	1.5 (36)	9.4 (15)	11 (18)	7.9	10
Paper birch	3119	344	52	55	1.4 (13)	1.3 (24)	11 (18)	19 (13)	15	20
Yellow birch	286	100	16	15	1.4 (5)	2.2 (6)	17 (4)	16 (3)	39	32
Striped maple	32	56	4	25	1.2 (1)	1.4 (7)	68 (1)	36 (6)	1.9	15
Mountain ash	191	38	20	8	1.4 (3)	1.8 (8)	19 (3)	16 (4)	21	19

Notes: In the ''Height'' columns, *n* is the number of saplings sampled; in the ''1991 growth'' column, *n* is the number of plots or gaps used in the 1991 and 1990 growth analyses. Statistical results for relative growth are based on transformed data. The means reported are the backtransformed values. PS = percent similarity in sapling composition. At the Baldwin site, differences between reference plots (REF) and gaps (GAP) were not significant for density and height but were significant at the $P \leq 0.001$ level for 1990 growth and 1991 growth. At the Bowl site, differences between REF and GAP were not significant for any of the parameters compared.

† Species differences in the relative extension growth were significant both years at Baldwin and the Bowl.

between reference plots and gaps in terms of composition (percent similarity = 67), there was no significant difference in sapling density (trees ≥1 m tall and <2 cm dbh, Table 2). Saplings of all species were more frequent in gaps. Balsam fir was by far the most abundant sapling species with 1909 stems/ha in the reference plots and 3650 stems/ha in the gaps. Spruce was common; paper birch was common only in gaps. Mountain maple (*Acer spicatum* Lam.) and mountain ash (*Sorbus americana* Marsh.), both understory tree species, were present only in gaps. The height of the sampled plants was the same but relative extension growth was significantly greater in gaps both years (Table 2). Spruce and fir grew two to three times faster in gaps. Differences in growth rates among species were significant ($P < 0.001$). In gaps, paper birch had the greatest relative growth rate (13–14%), followed by fir (8–9%), then spruce (6–8%).

In the spruce–fir zone at the Bowl, overall sapling density and frequency were greater than at Baldwin (Table 2). In addition, saplings were 44% more abundant in Bowl reference plots than gaps. Much of this difference was due to the high density of birch encountered in three of the 25 reference plots. These three plots were located in a birch thicket and had a mean density of >18,000 stems/ha. The frequency of spruce, fir, and striped maple was substantially greater in gaps. While fir was again the most abundant sapling species, there was a more even mix of canopy species. The mean height of the sampled plants was similar in gaps and reference plots (Table 2). Extension growth was generally greater in the gaps but the increase was not significant. When only canopy species were considered (i.e., spruce, fir, paper birch, and yellow birch), relative extension growth was marginally higher in 1991 ($P = 0.09$). Growth rate differences among species ($P < 0.001$) followed the same pattern observed at Baldwin: the birches grew from 50% to >200% faster than fir or spruce. The growth of striped maple and mountain ash was highly variable, but they generally grew at least as fast as the birches in gaps.

In the transition zone at Baldwin, sapling composition (percent similarity = 83) and density were similar between reference plots and gaps (Table 3). Spruce and striped maple were the most abundant species with densities >1400 stems/ha. Spruce saplings were found in every gap. For both years, there was significantly greater height growth for trees in gaps (Table 3). The two fastest growing species in gaps were yellow birch and striped maple. Spruce was again the slowest growing species.

In the transition zone at the Bowl, sapling density was greater in the reference plots but the difference was not statistically significant (Table 3). Spruce, yellow birch, and mountain maple accounted for 70% of the saplings present. Relative height growth was significantly greater in gaps for 1990 but not in 1991 (Table 3). Yellow birch and the two understory trees, mountain maple and striped maple, had the greatest relative height growth in gaps (15–23% per year). Balsam fir and beech grew more slowly (11–14% per year); spruce increased in height ~6% per year. In contrast to the Baldwin site, where sugar maple grew >15% per year, it grew little in gaps at the Bowl (<4% per year).

Shrubs.—Hobble bush was the only common shrub species encountered at either location. Gap specialists such as *Rubus* spp. and *Sambucus racemosa* L. were rare. Hobble bush was much more abundant in the transition zone (2734 stems/ha) than in the spruce–fir forest

TABLE 3. Comparison of the density, frequency, height, and mean relative extension growth of saplings (trees ≥1 m tall and <2 cm dbh) in reference plots (REF) and in gaps (GAP) for two old-growth transition zone forests in the mountains of the northeastern United States.

	Density (stems/ha)		Frequency (%)		Height (m)		1991 growth (%)		1990 growth (%)	
Species†	REF	GAP	REF	GAP	REF (*n*)	GAP (*n*)	REF (*n*)	GAP (*n*)	REF	GAP
Baldwin (PS = 83%)										
Red spruce	1458	1759	62	100	1.8 (28)	1.7 (21)	5.2 (18)	10 (10)	8.8	14
Balsam fir	398	478	21	80	1.4 (8)	1.8 (16)	12 (5)	13 (8)	14	17
Yellow birch	332	20	25	5	1.4 (5)	1.6 (9)	19 (4)	22 (6)	31	34
Sugar maple	497	218	21	20	2.4 (7)	2.4 (5)	5.4 (5)	15 (3)	3.8	23
Striped maple	2586	1790	75	80	1.9 (21)	2.0 (20)	14 (13)	21 (9)	17	24
Mountain maple	365	335	12	30	2.0 (5)	2.1 (14)	5.9 (3)	13 (9)	4.9	16
Beech	99	96	12	40	1.9 (3)	1.6 (3)	22 (3)	11 (2)	20	20
Bowl (PS = 78%)										
Red spruce	1210	656	64	80	1.7 (24)	2.1 (50)	4.7 (18)	6.3 (17)	5.4	7.3
Balsam fir	96	138	12	45	1.8 (3)	1.9 (6)	8.0 (3)	11 (4)	5.9	14
Yellow birch	1114	914	56	70	2.2 (16)	1.9 (34)	11 (12)	15 (14)	19	23
Sugar maple	32	69	4	10	1.5 (1)	3.3 (5)	7.4 (1)	3.7 (2)	14	4.0
Striped maple	668	612	24	65	2.0 (10)	2.5 (42)	12 (6)	15 (15)	21	21
Mountain maple	1655	763	52	65	1.9 (18)	2.1 (24)	12 (13)	15 (9)	13	22
Beech	382	491	20	35	2.0 (7)	2.9 (13)	16 (5)	13 (6)	8.4	12

Notes: In the ''Height'' columns, *n* is the number of saplings sampled; in the ''1991 growth'' column, *n* is the number of plots or gaps used in the 1991 and 1990 growth analyses. Statistical results for relative growth are based on transformed data. The means reported are the backtransformed values. PS = percent similarity in sapling composition. At the Baldwin site, differences between reference plots (REF) and gaps (GAP) were not significant for density or height but were significant at the $P \leq 0.001$ level for 1991 growth and at the $P \leq 0.01$ level for 1990 growth. At the Bowl site, differences between REF and GAP were not significant for density but were significant for height at the $P \leq 0.01$ level, for 1990 growth at the $P \leq 0.05$ level, and for 1991 growth at the $P \leq 0.1$ level.

† Species differences in the relative extension growth were significant both years at Baldwin and the Bowl.

(318 stems/ha). It was also larger and much more dense at the Bowl than at Baldwin. In the transition zone at the Bowl, hobble bush density was >4000 stems/ha in the reference plot (compared to 637 stems/ha at Baldwin), making it the most numerous woody plant in that research area. There were no significant differences in density and size of hobble bush between reference plots and gaps for any forest. Also, there was no consistent pattern in relative basal area increment between reference plots and gaps. For example, hobble bush grew significantly faster in gaps in the spruce–fir forest at the Bowl ($P = 0.04$) but in the transition at the Bowl, they grew faster in the reference plot ($P = 0.02$). Wherever hobble bush was encountered, it averaged >20% per year increase in relative basal area during 1991 and 1990.

Tree seedlings and herbs.—Seedlings (trees <1 m tall) of adult species present in the surrounding forest were common in reference plots and gaps, but seedlings were more abundant and frequent in gaps. The distribution of seedlings was very heterogeneous. Decaying wood was a preferred substrate for one- and two-year-old seedlings of all species. Birch seedlings were the only tree species typically found growing on exposed mineral soil. In the spruce–fir zone, fir seedlings were more numerous than spruce but spruce seedlings were present in >80% of gaps.

Overall median extension growth of seedlings was always larger in gaps and the difference was significant in several cases (Table 4) but there was extreme variation in growth rates. For example, in the spruce–fir zone at Baldwin mean 1991 relative growth for seedlings in gaps ranged from a low of 10% (red spruce) to a high of 74% (yellow birch). Growth rate differ-

TABLE 4. Comparison of median relative extension growth of seedlings (trees <1 m tall) and herb layer composition (seedlings and herbaceous vascular plants) in reference plots (REF) and in gaps (GAP).

	1991 seedling growth (%)			1990 seedling growth (%)			Species richness		Coefficient of community
Site: forest type	REF	GAP	*P*	REF	GAP	*P*	REF (*n*)	GAP (*n*)	
Baldwin: Spruce–fir	13	19	0.05	14	24	0.001	21 (25)	27 (20)	79
Bowl: Spruce–fir	17	19	0.4	17	24	0.07	24 (25)	25 (20)	78
Baldwin: Transition	19	20	0.2	26	27	0.8	36 (24)	36 (20)	92
Bowl: Transition	19	27	0.08	24	39	0.02	26 (25)	31 (20)	84

Notes: Sites are two old-growth forests in the mountains of the northeastern United States. Species differences in relative extension growth were significant in all cases. *P* values reported for 1991 and 1990 seedling growth are the results from Mann-Whitney *U* tests on the REF vs. GAP comparison. Grasses and sedges were not identified to species.

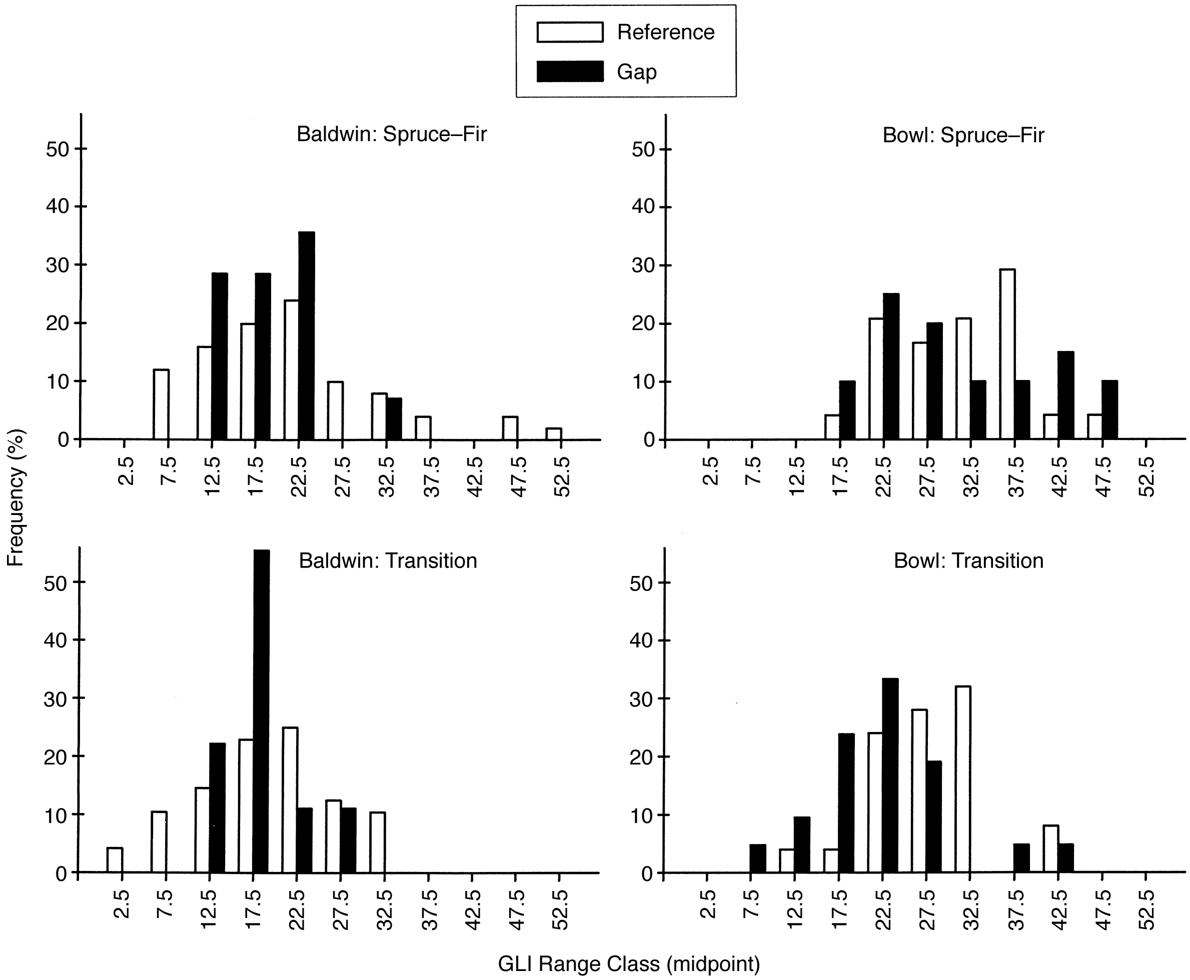

FIG. 1. Frequency distribution of GLI in gaps and the reference grids for four old-growth, subalpine forests in the northeastern United States.

ences among species followed the same pattern observed for saplings: balsam fir seedlings grew faster than spruce, and the fastest growth recorded was in the birches and understory tree species.

There were only minor differences in species composition of seedlings and vascular herbs between reference plots and gaps. The coefficient of community was 78% or greater at all four sites (Table 4). Species characteristically intolerant of shade such as *Prunus pennsylvanica* L. and *Fragaria virginiana* Mill. tended to be more frequently encountered in gaps, but the herb layer in both habitats was dominated by three common plants: spinulose woodfern (*Dryopteris spinulosa* Watt.), wood sorrel (*Oxalis montana* Raf.), and shining clubmoss (*Lycopodium lucidulum* Michx.). Overall, herb cover was greater in gaps and species richness was higher in the transition zone (Table 4).

Light, root growth, and seedbed comparisons

At Baldwin, the frequency distribution of GLI in the reference grid and gaps was unimodal and continuous (Fig. 1). In both the spruce–fir and transition forest, the range of understory light values was greatest in the reference grid. The frequency distribution of GLI in the transition forest at the Bowl was also unimodal but there was not such a discrepancy in the range of understory light availability in the reference grid compared to gaps. In contrast to the other sites, the distribution of GLI in spruce–fir forest at the Bowl was bimodal. Interestingly, this bimodality was apparent in the reference grid and gaps (Fig. 1).

The mean GLI ranged from a low of 16% under gaps in the transition zone at Baldwin to a high of 32% in the spruce–fir reference grid at the Bowl. At every site, the mean and median GLI were higher in the reference grid than in the gaps; these differences were significant in the spruce–fir zone at Baldwin and the transition zone at the Bowl (Table 5). The points in the understory with the greatest transmission of PAR were in the reference grids.

The mean RGI (mean fine root intersections/screen) was higher in gaps than in the reference plots (Table

TABLE 5. A comparison of mean understory light availability and mean fine root growth in reference plots (REF) and in gaps (GAP) for two old-growth forests in the mountains of the northeastern United States.

	Gap light index (%)			Root growth index (no./screen)		
Site: forest type	REF (*n*)	GAP (*n*)	*P*†	REF (*n*)	GAP (*n*)	*P*†
Baldwin: spruce–fir	22 (25)	16 (10)	0.03	14 (24)	24 (10)	0.003
Bowl: spruce–fir	32 (24)	30 (20)	0.64	13 (25)	14 (20)	0.68
Baldwin: transition	19 (24)	18 (9)	0.82	32 (24)	44 (10)	$<$0.001
Bowl: transition	28 (25)	22 (20)	0.01	24 (25)	37 (19)	0.023

† *P* value based on *t* test between REF and GAP.

5). There were 71% more fine roots in gaps in the spruce–fir zone at Baldwin; 38% more in the transition zone at Baldwin; and 54% more in the transition zone at the Bowl. At these sites, the gap effect on the RGI was significant ($P < 0.05$ in every case, Bonferroni corrected significance level for multiple comparisons: $P = 0.006$). However, the mean RGI in the spruce–fir zone at the Bowl was only slightly and insignificantly larger in gaps.

At all sites, >80% of the seedbed was intact forest floor (Table 6). There was generally more dead wood in the gaps than in the reference plots. In the spruce–fir zone at both locations, dead wood accounted for ~13–14% of the substrate in gaps. The percentage of seedbed that was exposed mineral soil varied greatly and ranged from 0.2% in transition zone gaps at the Bowl to 8% in the spruce–fir zone reference grid at Baldwin. At the Bowl, a relatively large fraction of the substrate in both forest types was either exposed bedrock or bedrock covered with a mat of moss (categorized as "other" in Table 6).

DISCUSSION

Gap dynamics and forest recovery

To place our results in a more general framework, we developed a conceptual model to describe the role of disturbance in these forest communities (Fig. 2). In the mountains of the northeastern United States, elevation is the principal environmental variable that organizes the spatial distribution of vegetation (Bormann et al. 1970, Siccama 1974, Cogbill and White 1991). Against this background of environmental gradients, the exact composition of the subalpine forest is shaped by species-specific responses to fine-scale disturbances. Canopy gaps create local disturbances where resource availability and substrate for plant reproduction are profoundly altered in comparison to the intact forest (Beatty and Stone 1986, Canham et al. 1990, Parsons et al. 1994*a*). Vegetation can reoccupy gaps by a combination of lateral extension of the crown and roots of plants surrounding the gap, growth of advance regeneration, and establishment and growth of seedlings/sprouts. The relative importance of each mode depends on the nature of the gap and the autecology of the species present (White et al. 1985*a*, Runkle 1990). An

TABLE 6. Seedbed distribution (%) in reference plots (REF) and gaps (GAP) for two old-growth forests in the mountains of the northeastern United States.

	Baldwin Basin		Bowl Natural Area	
Seedbed	REF	GAP	REF	GAP
Spruce–fir forest				
Forest floor	85	81	82	82
Dead wood	7	14	9	13
Mineral soil	8	4	1	3
Other	1	2	9	2
Transition forest				
Forest floor	98	90	92	91
Dead wood	2	8	3	3
Mineral soil	1	1	1	<1
Other	0	1	4	7

Note: The category of "other" includes bare and moss-covered rock.

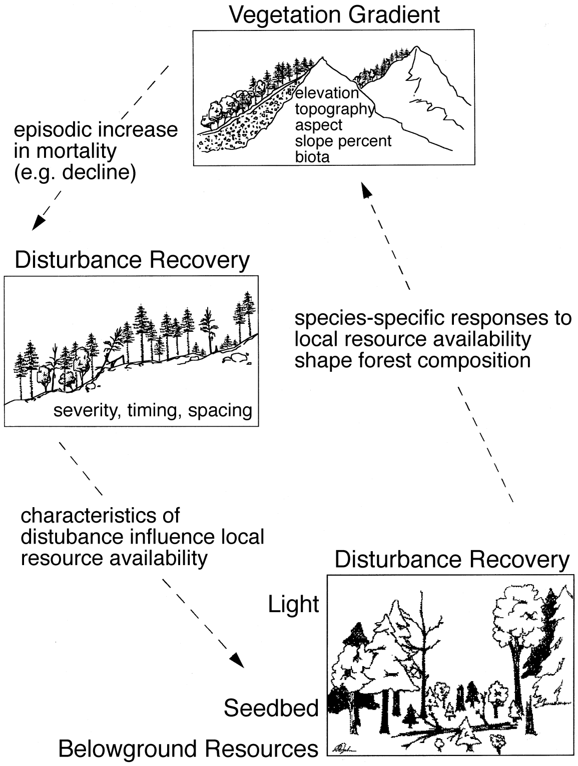

FIG. 2. A conceptual model summarizing our understanding of stand dynamics for forests in which fine-scale canopy disturbances predominate.

immediate corollary from this model is that a shift in the disturbance regime results in redistribution of resource availability that, in turn, could cause a shift in community composition (Harmon et al. 1983, Clark 1996).

A fundamental assumption of our gap model is that seedlings and saplings in gaps will outperform trees found in the intact forest. We tested this assumption by comparing growth rates in gaps to the forest as a whole (our null gap). Saplings and seedlings in gaps had greater relative extension growth than similar individuals in nearby reference plots in most cases (Tables 2–4). Based on these results, we rejected our null hypothesis. Gaps were distinct patches where woody plants grew better. For juvenile plants, growth rate is intrinsically linked with survival and fecundity (e.g., Pacala et al. 1995). Thus gaps directly influence key population processes that affect forest community dynamics.

We now describe the initial stages of vegetation recovery in the red spruce forests using Baldwin as an example. Next, we comment on site differences between Baldwin and the Bowl. Consistently, we direct our discussion to the general influence of gaps.

Spruce–fir forests.—At Baldwin, advance regeneration of balsam fir was dominating the vegetation response to decline. Canopy encroachment of trees bordering gaps is slow in the spruce–fir forest (White et al. 1985*b*, Perkins et al. 1992). Thus, closure of all but the smallest gaps occurs largely via the upgrowth of understory trees. Paper birch might be predicted to capture a significant fraction of the available canopy space based on its rapid growth (Table 2). However, a litter-free seedbed is essential for birch germination (Perala and Alm 1990). Spruce decline opened up the canopy, but >80% of the forest floor was left intact (Table 6). From a competitive perspective, birch success seemed restrained by the scarcity of suitable seedbed. In contrast, fir was by far the most abundant woody plant. Since it consistently outgrew spruce and vastly outnumbered birch (Table 2), fir was poised to fill many of the openings in the canopy.

Spruce will constitute a smaller fraction of the next generation of canopy trees at Baldwin. But spruce is a very shade-tolerant species that outlives fir by >100 yr (White and Cogbill 1992). Saplings and seedlings of spruce were common throughout the forest and growing well. Slow-growing competitors like spruce can survive several cycles of suppression and release prior to canopy recruitment (Canham 1988*a*, Wu et al. 1999). In 80 yr, when the fir that reached the canopy in the 1990s are dying, spruce will be well positioned to enlarge its representation in the canopy.

Transition forest.—Much of the recovery in the transition zone at Baldwin will depend on the response of spruce and therefore the rate of closure will be constrained by the slow growth of spruce advance regeneration. Red spruce and striped maple saplings were more dense in gaps than any other woody species but striped maple extension growth was faster than spruce (Table 3). Striped maple trees did capture many gaps but only temporarily. Canopy-sized striped maple trees were frequently observed to be dead or dying in the middle of openings (Battles and Fahey 1996). They were not overtopped by other trees. It is part of the life history of this understory tree to die after release and heavy reproduction (Hibbs and Fischer 1979). The consequence of this response was that some gaps, particularly those caused by declining spruce, were partially closed by rapid growth of suppressed striped maple trees only to be reopened by the senescence of the postreproductive adults. Striped maple response to gaps may slow the ultimate rate of gap closure by preventing a longer-lived but slower-growing species from initially capturing the gap.

Sugar maple and beech were common in transition forest gaps (Table 3). Both species rely on gaps for recruitment into the canopy (Canham 1988*a*). Neither seemed to be aggressively filling available canopy space. The relative shoot growth rates of sugar maple and beech saplings in transition zone gaps were much lower than rates observed in gaps in old-growth northern hardwood forests in upstate New York (Table 3, Canham 1988*a*). When present, fir saplings were growing as well as they were in the spruce–fir forest but they were much less abundant in the transition zone (Table 2, Table 3). This lack of a vigorous response to gaps may be due to the fact that all three species approach the limits of their respective elevational ranges in the transition zone. Sugar maple and beech hit their upper boundary and fir its lower boundary (Bormann et al. 1970). Again, birch response seemed to be restricted by a shortage of appropriate seedbed (Table 6). Sapling density and frequency of yellow birch were particularly low in gaps at Baldwin (Table 3).

Summary.—In the subalpine forests at Baldwin and the Bowl, advance regeneration was abundant and there were only small floristic differences between gaps and the forest as a whole. The majority of gaps were formed by standing dead trees that neither destroyed advance regeneration nor disrupted the soil surface. Barring future pulses of differential species mortality, the individuals that will capture these gaps are most likely those that are already present as seedlings or saplings (fir in the spruce–fir forest; striped maple and spruce in the transition zone). In this sense, gaps act on patterns already established in the understory (Brokaw and Scheiner 1989). However in terms of maintaining populations, the minority of gaps that did alter the seedbed present critical colonization opportunities for paper and yellow birch (Perala and Alm 1990, Houle 1992).

Resource availability

In the northeastern subalpine forest, the lower light levels and the higher fine root densities found in gaps suggest that the observed increases in plant growth

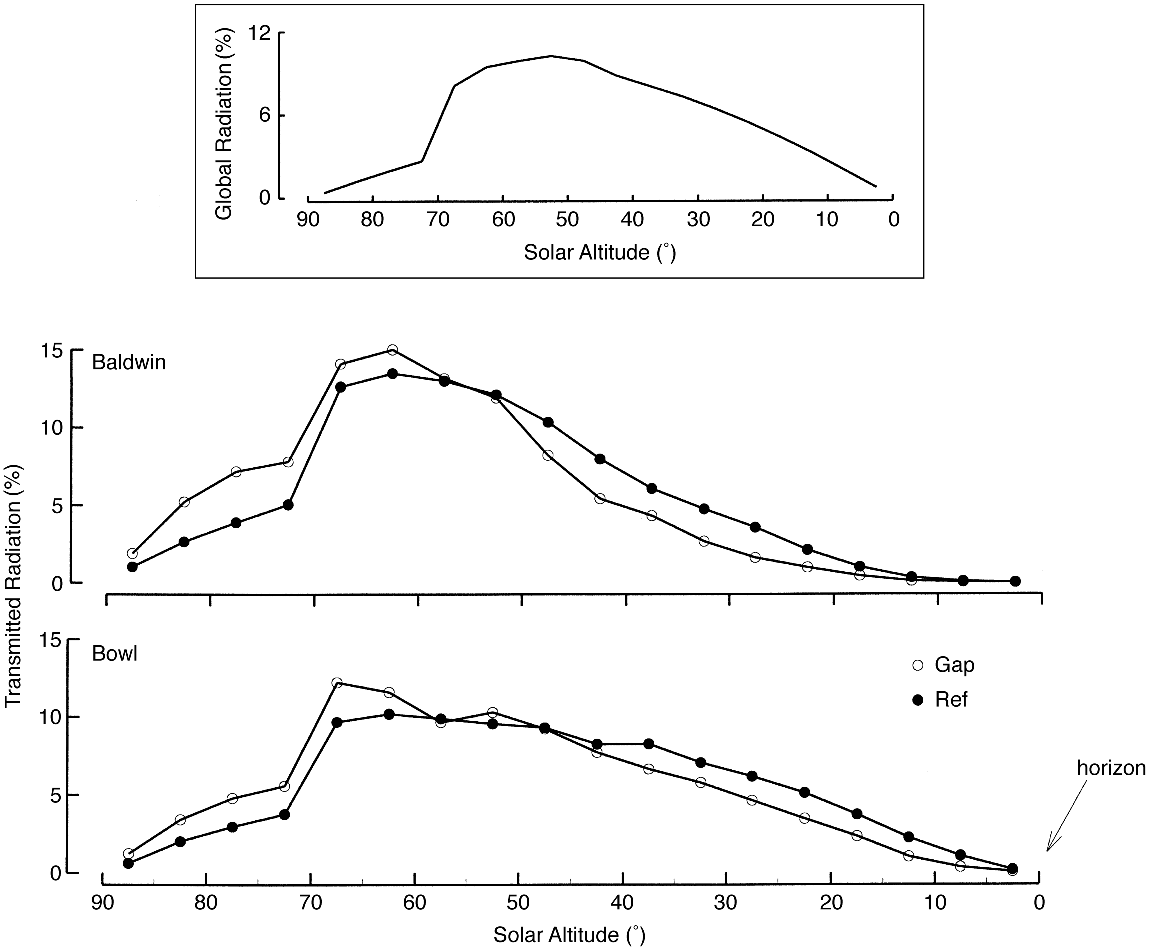

FIG. 3. Angular distribution of transmitted radiation during the growing season for points in the reference grid (REF) and for the points under the center of gaps (GAP). Distributions are shown for the spruce–fir forest at the Baldwin Basin and the Bowl Natural Area. The angular distribution of global radiation (incident radiation reaching the top of the canopy) is shown for a site at 44° N latitude (top). Solar altitude (also called solar height) is the angle formed between the horizon, an observer, and the center of the sun. If the sun is directly overhead, the solar altitude = 90°; if the sun is bisected by the horizon, the solar altitude = 0°.

were related to changes in belowground resources. Considering that >19% of the above-canopy light reached the understory regardless of gap status (Table 5), the understory of these postdecline, subalpine forests was well lit compared to other temperate forests (Canham et al. 1990, Battles 1999). These estimated light levels approach the light saturation point for shade-tolerant trees and thus could be high enough to shift the primary constraint on growth to soil resource availability (e.g., Ellsworth and Reich 1992, Canham et al. 1996). Unlike the gap light index (GLI), the root growth index (RGI) did correspond to the plant growth response. When RGI was significantly larger in gaps (three out of four sites), the relative growth rate of saplings was greater in gaps than in the reference plot. The counter example supports this conclusion as well: Where there was no increase in the fine root index in gaps (Bowl: spruce–fir), there were only marginal increases in shoot growth (Table 5, Table 2). As noted by Publicover and Vogt (1991), the effect of gaps on belowground processes may be more important in situations where growth is limited by nutrients or moisture rather than light.

Our conclusion that canopy openings do not result in light gaps is admittedly a counterintuitive finding. Nonetheless, gaps were identifiable patches ecologically distinct from the forest as whole. By design, tree basal area in gaps was seven to ten times less than in the adjacent reference plots (Battles 1994). Furthermore, the canopy above gap centers was more open and gaps received significantly more light from the upper third of the sky hemisphere (Fig. 3, solar altitude 90° to 60°). Our decision to exclude very large gaps did introduce a bias (e.g., see Fig.1, Baldwin: spruce–fir). However, if we adjust for this bias by using trimmed means (smallest and largest 5% of the values excluded) to compare the light regime in gaps to reference plots, we get the same result.

Other potential explanations for the lack of a gap effect on light include the intrinsic canopy architecture of the subalpine forest which produces few dark spots in the understory. The lowest GLI recorded above a reference point was 4% despite some of these points being under an intact canopy. Even undisturbed patches in the canopy are rather porous (Miller et al. 1993) presumably due to chronic physical abrasion from neighboring crowns swaying and banging in the wind (i.e., crown shyness). Another contributor was the angular distribution of light in these high latitude forests. At 44° N latitude, 76% of the radiation originates at solar altitudes $<60°$. So while gaps received more overhead light, a disproportionate share of the light came from lower angles and a smaller fraction of the low-angle light reached gap centers (Fig. 3). Finally, the prevalence of standing dead trees reduced the light availability in gaps. To estimate the magnitude of the reduction, one dead tree was removed from the digital image of two multi-tree gaps. Depending on the size and position of the tree, one standing dead tree can block 10% of the transmitted radiation during a growing season.

We interpreted the higher RGI in gaps as an indication of increased belowground resource availability with the concomitant plant response being a proliferation of fine root growth. This tentative interpretation should be considered in light of the recent observations about root growth responses to disturbance or changes in soil resource availability. First, belowground root gaps corresponding to canopy gaps have been detected in some forests (Sanford 1990, Wilczynski and Pickett 1993). However, the attendant decrease in fine root biomass in gaps was documented for two years or less after overstory removal. In contrast, five years after creating experimental gaps in a subalpine lodgepole pine forest in Wyoming, Parsons et al. (1994*b*) observed higher root growth in 50 m^2 gaps, corresponding to increased NO_3-N concentrations (Parsons et al. 1994*a*), than in smaller gaps or undisturbed forest. Second, although the prominent tree response to increased soil resource availability is a reduction in C allocation to roots (St. John et al. 1983, Yanai et al. 1995), this response is scale dependent. That is, under a regime of low nutrient availability plants will allocate more C to roots in fertile microsites (Pregitzer et al. 1993, Fahey and Hughes 1994). Thus if belowground resource allocation associated with a gap represents a substantially enriched site relative to the forest soil as a whole, the RGI will distinguish gaps from the rest of the forest.

Both of our measures of resource availability are indices. We believe that these indices provide robust, relative comparisons of resource availability, but recognize their limitations. As noted above, the GLI does not account for the contribution of reflected light. Also, plants could be responding to other differences in the light regime such as the angular distribution of light, its spectral composition, or patterns in its temporal availability (Canham et al. 1990, Endler 1993, Wayne and Bazzaz 1993). A difficulty in interpreting RGI results is the unknown origin of the fine roots intersecting the screen. We assumed that the larger RGI observed in gaps was an indication that saplings and seedlings in gaps had greater access to nutrients and/or water, but both canopy-sized border trees and understory gap trees contributed to the root index. Certainly we need to confirm our results by comparing tree growth to direct measures of light, water, and nutrient supply.

Differences between sites and forest types

Moose were present in the Bowl but were absent from the Baldwin site. Feeding preferences and physical disturbance by moose can affect conifer abundance (McInnes et al. 1992). In the spruce–fir forest at the Bowl, 12% of the fir trees sampled had signs of herbivore damage, much of it consistent with patterns of moose browse (as described in McLaren and Peterson 1994). In contrast, none of the spruce trees sampled had any observable herbivore damage. Overall herbivore damage at Baldwin was much less; only 4% of conifer saplings had signs of browse and there was no difference in damage between spruce and fir. By several measures (e.g., relative density, mean sapling height, relative height growth), the competitive status of red spruce was improved relative to balsam fir at the Bowl. For the birches, the incidence of herbivory was generally much higher. We noted signs of herbivore damage on 20–30% of the birch stems sampled, but there were only minor differences between sites and forest types.

In the transition zone forest at Baldwin, one third of the living beech trees and one half of the standing dead beech trees had signs of beech bark disease, and beech contribution to gap area exceeded its relative basal area (Battles and Fahey 1996). At the Bowl, there was evidence of the disease in $>75\%$ of the living beech trees but the extent of injury was typically less severe and beech death less prominent compared to Baldwin (Battles and Fahey 1996). Nevertheless, many of these symptomatic beech trees at the Bowl are expected to die within the decade (Sinclair et al. 1987). Because of the potential for beech to proliferate via root sprouting from moribund, mature stems (Jones and Raynal 1986), sprout thickets may come to dominate the advance regeneration in beech gaps at both sites.

The impact of spruce decline, and the role of disturbance in general, differed between the two forest communities. The increase in canopy disturbance associated with the decline reduced the current adult population of red spruce trees, and fir trees seemed to be dominating the initial stages of recovery in the spruce–fir forest. In contrast, spruce trees were controlling recovery in the gaps in the transition zone. An abundance of spruce is characteristic of the transition forest throughout the mountains of the northeastern United States (Cogbill and White 1991). It is worth noting that a shade-tolerant, long-lived, slow-growing species like red spruce reaches its greatest dominance in an ecotone between two more homogeneous forest communities (Siccama 1974). Perhaps the lack of competition from other canopy species (i.e., fir and northern hardwoods) allows spruce to flourish. In some respects these transition zone spruce trees may act as a source of colonists for depleted red spruce populations in the adjacent spruce–fir forest. However such a buffer against an episodic increase in spruce mortality presupposes the maintenance of large expanses of intact old-growth forest. Many of the transition zone spruce trees were removed for timber in the 19th century (White and Cogbill 1992), thus making second-growth subalpine forest communities potentially more vulnerable to sustained population declines.

Lessons from red spruce decline

We built a conceptual model to help evaluate the impact of episodic increases in tree mortality and then applied it to the particular case of spruce decline. This framework may provide a helpful guide to managers trying to gauge the potential impact of forest decline and similar disturbance phenomena. From our experience with red spruce decline, we offer three specific recommendations.

First, the impact of decline should be assessed relative to the existing disturbance regime. The death of mature trees is a major event in forest communities. The disturbance caused by dying canopy trees is such a fundamental process that the life histories of forest plants reflect the typical timing and patterning of canopy mortality (White et al. 1985*a*, Canham 1988*a*, Runkle 1990, Clark 1996). Although spruce decline effected a disturbance similar to the existing regime, novel biotic or abiotic stresses can create atypical disturbances that potentially overwhelm the normal resiliency of forest communities (Klein and Perkins 1988, Liebhold et al. 1995, Foster et al. 1998).

Second, the phenomenology of the decline disturbance profoundly influences the course and rate of recovery. As discussed above, the progressive deterioration of red spruce ending with a standing dead bole played a fundamental role in shaping the recovery. Many trees died gradually rather than suddenly. Environmental conditions and resource availability are likely to differ in gradually forming gaps compared to sudden gaps (Krasny and Whitmore 1992).

Third, vegetation recovery also depends on the inherent community organization of the forests involved. Peterson and Pickett (1995) discuss the dependence of recovery from a disturbance on multiple ecological contingencies. Specific contingencies in these red spruce forests included the grazing preference of moose at the Bowl and the progression of beech bark disease in the transition zone forests. Such features of the community modify plant performance and, in part, determine which species capture the available resources.

Although forest decline may not be atypical for certain forest communities, declines can be caused, initiated or exacerbated by human activity (Manion 1991, Eager and Adams 1992). With the expanding sphere of anthropogenic influence on forested landscapes, such declines are likely to be more common in the future (Woodwell 1990, Huettl and Mueller-Dombois 1993, Foster et al. 1998). Therefore it is important for practical and theoretical reasons to understand how forests respond to and recover from such a decline. However, the diversity of forests affected, coupled with the complexity of the decline phenomenon and the scarcity of long-term information about forest health, contribute to the uncertainty surrounding decline disturbances. In the face of this acknowledged uncertainty, we offer managers a detailed case study, an approach to help evaluate the consequences of a potentially novel disturbance, and a pledge to continue to collect the necessary long-term data to help build a more certain model of forest community dynamics.

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