Forest dynamics and agents that initiate and expand canopy gaps in *Picea–Abies* forests of Crawford Notch, New Hampshire, USA

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Summary

1 Data from elevations ranging from mixed hardwood-conifer forest at 600 m to subalpine *Abies balsamea* forest at 1120 m indicate that canopy gaps are not static but expand over time due to mortality of trees at the gap margin and coalescence of gaps. Gap expansion is more frequent than gap initiation. Ultimately such disturbance patches may become more extensive than is normally considered as typical of gap-phase disturbance, but the processes of development are the same.

2 Disturbance agents involved in gap initiation tend to differ from those involved in gap expansion. Spruce beetle, dwarf mistletoe and most root diseases predominate as agents of gap initiation, while windthrow/windsnap, chronic wind stress and Armillaria root disease are important agents of gap expansion.

3 Concepts of equilibrium gap-phase dynamics and a shifting-mosaic steady state do not fully account for the dynamics of these spruce-fir forests. A spruce beetle outbreak in the late 1970s/early 1980s killed most of a cohort of dominant, emergent *Picea rubens*. This epidemic initiated a long-term cycle of disturbance and release that is likely to be repeated in many years when a new cohort of *P. rubens* becomes sufficiently large to sustain another major bark beetle outbreak.

4 Episodic disturbance agents affect long-lived, dominant species at infrequent but regular intervals (up to hundreds of years) and operate at the landscape level. Gap-phase cycles appear to be nested within the long-term cycle. Over the long term, episodic disturbance drives such 'nested bicycle' dynamics.

5 Spatial and temporal distribution of disturbance results not only from stochastic events such as storms, but also from host specificity of agents of disturbance, their tendency to attack certain age classes of trees, local and regional contagion, and susceptibility of trees at the edge of disturbance patches.

Key-words: disturbance, gap dynamics, gap-phase processes, root disease, spruce beetle

Introduction

The theory of community and ecosystem dynamics has benefited greatly from understanding of the role of disturbance and, in particular, the concepts of gap or patch dynamics. Localized disturbance occurs occa-

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sionally at different points in a landscape, resulting in patches that are in different stages of response to disturbance (Watt 1947; Pickett & Thompson 1978; Bormann & Likens 1979; Pickett & White 1985). Runkle (1985b) concluded that the distribution of disturbance in space and time is more important than the average rate of disturbance. We should therefore expect spatial and temporal distribution of disturbance to be important determinants of forest dynamics.

Spatial distribution of disturbance is determined by factors that influence the size and location of distur-

bance events. If trees at the gap margin are more likely to die than random canopy trees, for instance, canopy gaps would expand. In southern Appalachian old-growth hardwoods, Runkle (1998) found that nearly half of the gaps expanded during a 14-year period. Most gaps in a subalpine conifer forest in British Columbia had multiple gapmakers with mortality events within gaps separated in time (Lertzman & Krebs 1991). In *Picea rubens-Abies balsamea* forests of the northern Appalachians, gap expansion is a prominent feature of the disturbance regime. Foster & Reiners (1986) showed that gaps coalesce into larger gaps at Crawford Notch, New Hampshire, and they suggested that such gap expansion was common in the forest. Multiple disturbance agents and asynchronous mortality were observed in almost half the gaps studied by Worrall & Harrington (1988) in the same forest. In similar forests on Camels Hump, Vermont, gaps expanded downwind at a rate of about 1 m year^{-1} (Perkins *et al*. 1992).

Temporal distribution of disturbance may be an even more critical factor than spatial distribution. At one extreme, continual, low-intensity disturbance may result in a forest at equilibrium, with proportions of the landscape at various stages and pathways of development remaining constant through time. This reflects the shifting-mosaic steady state of Bormann & Likens (1979). At the other extreme, infrequent but widespread and catastrophic disturbances such as stand-replacing fires or extreme wind events can clearly affect an entire landscape for hundreds of years afterwards. Indeed, Dale *et al*. (1986) suggested that a single episode of heavy disturbance could cause very long-term, complex dynamics of stand composition and leaf area.

However, more subtle episodic disturbances can also create conditions of non-equilibrium. Disturbance in old-growth hemlock-hardwood forests of upper Michigan (USA) was significantly non-uniform over 130 years (Frelich 1986). Over a period of 120 years, tree-fall gaps in boreal *Picea* forests of Sweden were highly aggregated in time (Jonsson & Dynesius 1993). Conifer stands in the south-west of the USA experienced nine regional-scale outbreaks of western spruce budworm between 1690 and 1989 (Swetnam & Lynch 1993). Similarly, subalpine *Abies balsamea* forests in southern Quebec experienced outbreaks of eastern spruce budworm several times in a century, but only certain outbreaks caused extensive mortality, depending on the stage of stand development (Filion *et al*. 1998). In the northern Appalachians, episodes of disturbance early in the 20th century probably led to release of *Picea rubens* and a synchronous growth decline in the 1960s as the *P. rubens* matured (Reams & Deusen 1993).

These spatial and temporal dimensions of disturbance are largely determined by the agents of disturbance. Some agents may affect trees in patches or expanding centres of mortality, while others randomly affect individual trees. Similarly, some agents cause relatively constant rates of mortality while others are more episodic, depending on the agent's population dynamics,

predisposing abiotic stresses, or the species composition and age of the stand. However, very few studies of gap dynamics have identified the specific agents that cause the death of gapmaker trees.

This research examines the disturbance regime and expansion of canopy gaps in old-growth forests at Crawford Notch, New Hampshire, USA. Specific objectives were to (i) describe the abundance of canopy gaps and extensive disturbance; (ii) determine the relative extent to which disturbance occurs as gap expansion or gap initiation; (iii) determine the causes of canopy tree mortality and test the hypothesis that different mortality agents are involved in gap initiation and expansion; (iv) test the hypothesis that tree species differ in their frequency of occurrence as gap initiators or expanders; and (v) assess the long-term temporal variability of gap formation and expansion.

Materials and methods

STUDY SITE

The study was conducted in an extensive old-growth subalpine forest on a west-facing slope at Crawford Notch in the White Mountain National Forest, New Hampshire, USA. The study area, and its soils and vegetation, as well as aspects of the disturbance regime were described in previous publications (Foster & Reiners 1983, 1986; Worrall & Harrington 1988). Briefly, the lowermost portion of the forest (up to 700–760 m a.s.l.) is occupied by northern hardwood-spruce forests dominated by *Fagus grandifolia* (American beech), *Acer saccharum* (sugar maple), *Betula alleghaniensis* (yellow birch) and *Picea rubens* (red spruce, hereafter referred to as *Picea*). The middle elevations are spruce-fir forest dominated by *Picea*, *Abies balsamea* (balsam fir, hereafter referred to as *Abies*) and, in the lower portions of the zone, *B. alleghaniensis*. The trees tend to be smaller, with *Picea* becoming less frequent above 900 m, and, at about 1100 m, the forest becomes nearly pure *Abies*, except for occasional patches of *Betula cordifolia* (mountain paper birch). For trees, nomenclature follows Gleason & Cronquist (1991), except for *Betula cordifolia*, which follows Brittain & Grant (1967).

TRANSECTS

Transects were established and sampling conducted in 1991 at 600, 640, 720, 800, 880, 960, 1040 and 1120 m elevation, running along the contour from the Webster-Jackson Trail until a total of about 32 gap and non-gap plots (see below) had been established. Transect lengths at the respective elevations were 430, 470, 600, 530, 530, 415, 364 and 353 m. When the transect encountered any change in stand conditions (gap, change in stand structure or composition, etc.) the location of the change was noted.

'Canopy' refers to the continuous crowns of the largest living trees; individual, emergent trees were not

considered part of the canopy. A gap was defined as an actual canopy opening of > 1 m diameter, but < 0.1 ha in area, formed by the death or mechanical failure of a canopy tree, with regeneration reaching less than half the height of the surrounding canopy. Canopy openings ≥ 0.1 ha were considered as extensive disturbance (Veblen 1992).

NON-GAP PLOTS

Segments of transects in areas of forest not meeting the definition of gap were classified as either continuous canopy or extensive disturbance. Circular plots of 7-m radius were established in these segments, with one plot in every 50-m subsegment of the transect in the same class (see below). Plots were centred along the subsegment where possible, providing this avoided boundaries with other classes. Within non-gap plots, the species, d.b.h. and crown class of each live stem ≥ 5 cm d.b.h. were recorded.

GAP PLOTS

Each gap was considered to be a plot bounded by the line connecting the stems of the gap margin trees. Gap margin trees were defined as trees at the margin of the gap, greater than half the height of the surrounding canopy and with crowns within a metre of adjacent margin trees.

Gaps were sketched in the field, indicating margin trees and gapmakers. Gapmakers were initially defined as any trees ≥ 10 cm d.b.h. that could be identified to species and which died, broke or uprooted to make the gap. Broken tops were noted for all living *Abies* and *Picea* trees at the gap margin. The maximum length of the gap and the maximum gap width perpendicular to the length were recorded.

For each gapmaker, species, d.b.h. and condition (uprooted, standing dead or snapped) were recorded. If snapped, an attempt was made to determine if the wood failure was splintery near the cambium (indicating that the sapwood was sound and probably alive when it snapped) or if the failure was brash (indicating that the tree snapped after it had died and there was considerable sapwood decay). Any evidence of circumstances that may have contributed to removal of the gapmaker from the canopy was recorded. For instance, evidence of activity by butt rot or root disease fungi, bark beetles, dwarf mistletoe or canker fungi when the tree was alive was noted, along with any evidence of an active host response to the insects or pathogens (Worrall & Harrington 1988). Decay that may have contributed to stem or root failure when the tree was alive, and which could not be attributed to a particular fungal species, was sampled and brought to the laboratory for isolation of causal fungi or microscopic identification. Basal area of each gapmaker was calculated from the measured d.b.h.

Time since death was also estimated for each gapmaker. Deterioration rates of trees vary greatly among regions, and even locally, depending on many factors, so criteria from other studies were not considered applicable. We counted annual tube layers in perennial basidiomes (fruiting bodies) of saprobic fungi on dead trees, and added an appropriate number of years to account for the time between death and first year of fruiting (Spaulding 1937). Although most trees did not have such basidiomes, we used those that did to calibrate our estimates based on criteria that were always present: the criteria used were leaf colour and retention, retention of fine twigs and branches, breakage of the bole (when it occurred post-mortem), bark tightness and retention and stage of decay of the sapwood. Because the oldest basidiomes were about 15 years, we set that as the maximum estimable time since death, and older mortality was recorded as > 15 years.

GAP INITIATION AND EXPANSION

For analyses of gap initiation vs. expansion, gapmakers were restricted to those large enough to cause a gap with a substantial impact on neighbouring canopy trees. To establish this size threshold, we used the median d.b.h. of the live codominant and dominant canopy trees at that elevation, minus the median absolute deviation (a measure of variability that gives relatively little weight to outliers). Thus, for comparison of initiators and expanders, gapmakers were considered only if they were larger than or equal to 20.1, 16.4, 16.5, 18.5, 17.8, 15.1, 12.8 and 12.4 cm d.b.h. at 600, 640, 720, 800, 880, 960, 1040 and 1120 m elevation, respectively. These are hereafter referred to as 'large gapmakers'. In three exceptional gaps, no gapmakers met that threshold, and we included the largest gapmaker in this analysis.

Based on the year of death estimated in the field, the gapmaker that died earliest in each gap was considered a 'gap initiator'. Adjacent trees that died later were considered 'gap expanders'. Additional trees in the gap were considered initiators of other gap foci if they died earlier than surrounding trees (i.e. the distance between the intervening trees of more recent mortality was shorter than the distance between the older initiator trees). When trees in a cluster had the same estimated time since death and were otherwise qualified as initiators, the cluster was considered as one focus and the gapmakers were all considered initiators. To calculate the density of gap initiators and expanders, the total number of trees recorded at a given elevation was used; area was based on the total gap area sampled, divided by the proportion of forest in gaps (by transect proportion method).

MORTALITY AGENTS

Root and butt rot diseases

Failure of live trees with root and butt rot in the White Mountains is generally through snapping within 0.5 m

above the soil line. Snapped *Picea* and *Abies* trees in these forests are almost invariably butt-rotted (Rizzo & Harrington 1988b). Root- and butt-rot fungi were identified on the basis of macro- and micromorphology of decay and associated mycelium, hosts, part of the tree infected and, in some cases, by isolation and identification of fungal cultures. Isolations of wood decay fungi were conducted by plating pieces of decayed wood or fungal tissues on a selective medium, followed by maintenance of pure cultures on malt extract agar (Worrall 1991). Cultures were identified by microscopic observation using published descriptions (Nobles 1964; Stalpers 1978) supplemented by comparisons to known reference cultures (Rizzo & Harrington 1988b).

Because they behaved similarly in terms of gap initiation vs. expansion, and because they tended to kill the trees through predisposition to snapping just above ground level, root and butt rots caused by the following pathogens were grouped for analysis: *Resinicium bicolor*, *Hyphodontia aspera* and *Oligoporus balsameus* on *Abies*, *Climacocystis borealis* and *Coniophora* sp. on *Picea*, *Scytinostroma galactinum* on *Abies* and *Picea*, *Ganoderma applanatum* on *Acer* spp. and *Fagus grandifolia*, *Hypoxylon* (*Ustulina*) *deustum* on *F. grandifolia* and *B. alleghaniensis*, and unidentified white- and brown-rot fungi on various hosts.

Armillaria root rot

Armillaria root disease was kept separate because it appeared to have different characteristics with regard to elevation and gap initiation vs. expansion. Moreover, in contrast to other root and butt rot fungi, *Armillaria ostoyae* may kill the cambium, thus killing trees directly (Harrington & Wingfield 1998). *Armillaria ostoyae* can grow through soil from root to root via root-like structures (rhizomorphs) and cause expanding canopy gaps, with each tree in the gap colonized by a single clone or genet of the fungus (Worrall 1997).

Stem decays

Stem decays in living trees, often called heartrots, typically lead to mortality by structural degradation of the wood, leading to snapping of the stem. Stem-decay fungi decay the heartwood and inner sapwood, but they vary in their capacity to kill sapwood. We looked for decay in the stems of all snapped gapmakers, and if the decay was extensive and appeared to have predisposed the stem to breakage while the tree was alive, then the species of fungus was identified by their fruiting bodies or decay characteristics (Eriksson *et al.* 1973; Hallenberg 1985; Gilbertson & Ryvarden 1986; Sinclair *et al*. 1987). The identified stem-decay fungi included *Phellinus* (*Porodaedalea*) *chrysoloma* on *Picea*, *Haematostereum sanguinolentum* on *Abies*, *Phellinus lundellii* and *Inonotus obliquus* on *B. alleghaniensis*, and *P. igniarius* on *B. alleghaniensis* and occasionally on *B.*

cordifolia. Because the biology of the stem decay fungi are similar and they behaved similarly in terms of gap initiation and expansion, stem decays by all pathogens were grouped for analysis.

Windsnap/windthrow

Windsnap was diagnosed when stems were snapped, resulting in tree death, and fracture surfaces indicated that the wood was predominantly sound at the time of failure. Windthrow was diagnosed when trees were uprooted and roots were intact or had evidence of mostly sound wood on fracture surfaces.

Chronic wind stress

Chronic wind stress is a common abiotic disease in higher elevation *Picea–Abies* forests of the northern Appalachians (Harrington 1986; Rizzo & Harrington 1988a; Worrall & Harrington 1988). In continuous canopies, the crowns may shelter each other from the wind, but mortality of neighbouring trees or crown shyness between adjacent trees (Putz *et al*. 1984) eventually exposes trees to wind. Once exposed, the root and crown damage that occurs is identical to that found on *Abies* growing in regeneration waves (Harrington 1986). Movements of the roots of wind-exposed *Picea* and *Abies* during windstorms correlate with root damage, loss of hydraulic conductivity and crown damage, all of which correlate with declines in growth rate (Rizzo & Harrington 1988a). Overstorey trees that have become exposed along the edges of canopy gaps may slow in growth rate and eventually die standing (Harrington *et al*. 1984; Harrington 1986).

Chronic wind stress was diagnosed on the basis of crown flagging (branches bent in the direction of the prevailing winds), crown dieback (death of branches or the top of the tree from the tips inward), small brooms (clusters of branches and twigs, usually due to branching below dead tips), broken tops on the gapmaker and the surrounding live trees and mechanical root damage typically found on wind-stressed trees (Harrington 1986; Rizzo & Harrington 1988a). Also taken into account were evidence of recent (prior to mortality) changes in exposure, wounded and abraded roots on nearby windthrown trees, and predisposing factors such as rooting in rocks or a canopy of hardwood trees on the windward side of the gapmaker, indicating exposure to winter winds and build-up of ice rime.

Dwarf mistletoe

Eastern dwarf mistletoe, *Arceuthobium pusillum*, severely affects *P. rubens* and causes substantial mortality in old-growth stands on lower slopes (Hawksworth & Shigo 1980). Dwarf mistletoe was diagnosed and presumed to be severe enough to cause mortality when branches were severely contorted and swollen and mistletoe cankers were seen on the main bole.

Spruce beetle

Only one species of bark beetle, *Dendroctonus rufipennis*, commonly causes mortality of the tree species in these forests, where the beetle only attacks *P. rubens*. Spruce beetle was diagnosed when the characteristic galleries in the inner bark were dense and accompanied by resinosis, indicating that the beetles attacked the tree when the tree was still alive and capable of active response.

Other and multiple agents

A few agents were rarely encountered and were grouped under the category 'other' for analyses. A few trees were knocked over or snapped because another tree had fallen into them. Most canker diseases (where the pathogen causes necrosis of the inner bark and cambium) did not cause mortality, but beech bark disease (Sinclair *et al.* 1987) was occasionally found to cause death of *Fagus grandifolia* at low elevations.

Trees that died from unknown causes were excluded from most analyses of disturbance agents. Most gapmakers that had died from unknown causes died while still standing, and many had been dead for 15 or more years.

When multiple agents were involved in tree death, mortality was attributed to the proximate cause. For instance, mortality of spruce trees that had root disease or eastern dwarf mistletoe, but were attacked by spruce beetle while alive, was attributed to spruce beetle. Trees that had stem decay and then Armillaria root disease were attributed to Armillaria root disease.

Results

DISTURBED AREA

Disturbed area, calculated as the proportion of the transect in disturbed patches (gaps and extensive disturbance combined), was highest at middle and upper elevations and encompassed approximately half the forest area (Fig. 1). At those elevations, up to half of the disturbed area was extensive (in patches ≥ 0.1 ha). The proportion of the area in gaps as calculated by Runkle's (1985a) line-intersect method (taking gap areas into account) approximately corresponded with the transect proportion method.

GAP INITIATION VS. EXPANSION

Of the 161 gaps encountered, 100 had two or more gapmakers with disparate estimates of time since death, which was taken as evidence of gap expansion. In the 19 gaps that had 10 or more gapmakers, the standard deviation of estimated time since death ranged from 4.1 to 7.4 years (mean 5.8, SD 1.0), similar to the standard deviation of time since death of all gapmakers from all gaps (6.5). Thus, there was nearly as much variability in time since death among gapmakers in large individual gaps as there was among all gapmakers.
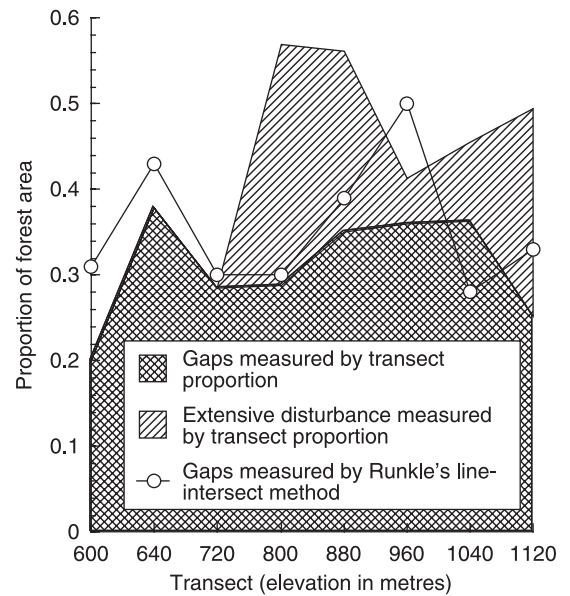
Fig. 1 Proportion of forest area in disturbance at each transect. Gaps are actual canopy openings $> 1\,\text{m}^2$ and < 0.1 ha. Extensive disturbances are openings ≥ 0.1 ha. In both cases they were quantified by measuring to the bole of marginal canopy trees (expanded openings). The two shaded areas are stacked. Gap area is calculated by two techniques.
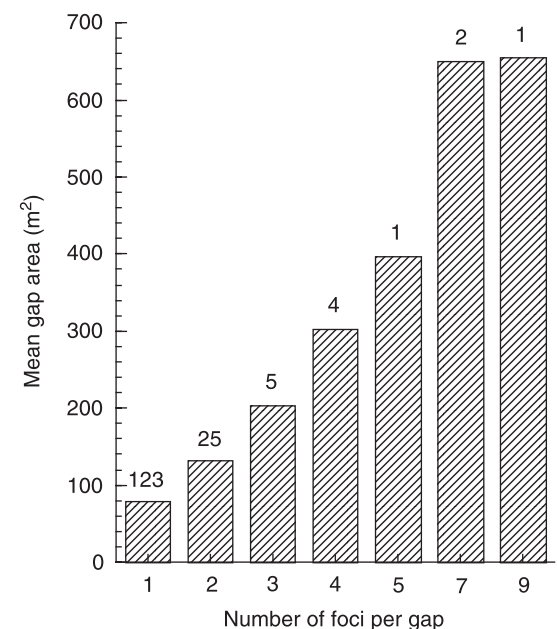

Fig. 2 Gap area increases with increasing number of gap foci. Value above each column is the number of gaps represented.

Within gaps, foci or subgaps were identified where two or more gapmakers independently initiated canopy openings. In gaps with multiple foci, initiators were separated by more recently killed gapmakers that expanded the foci, leading to coalescence of the subgaps. Multiple foci were found in 38 of the 161 gaps observed. Mean gap area increased with number of foci (Fig. 2). Sixteen plots were located in areas of extensive disturbance and these areas also had multiple foci and appeared to arise from coalescence of gaps.
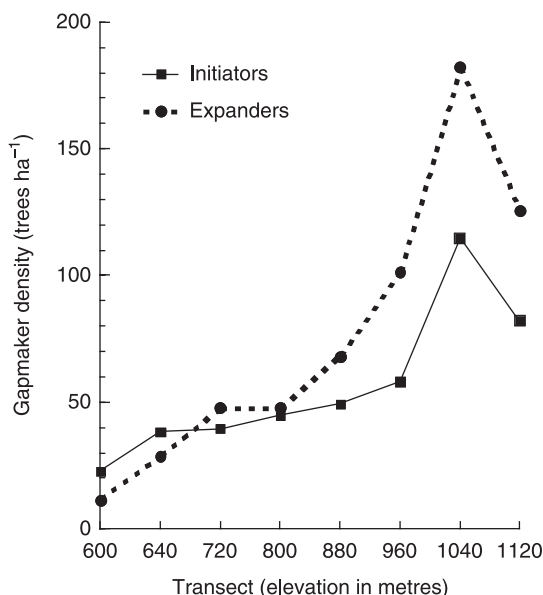
Fig. 3 Density of initiators and expanders vs. elevation, based on gap sampling.

Fig. 4 Numbers of trees (a) or basal area (b) as percentage of live canopy or disturbance mortality represented by each species. Live trees include all those from canopy plots. Dead trees include all mortality from gaps and areas of extensive disturbance. Tree species are: Pr = *Picea rubens*; Ab = *Abies balsamea*; Ba = *Betula alleghaniensis*; Bc = *B. cordifolia*; As = *Acer saccharum*; Fg = *Fagus grandifolia*; Ap = *Acer pensylvanicum* (striped maple). Other species (with expected values < 5 in chi-square analysis) are *Acer rubrum*, *A. spicatum*, *Tsuga canadensis* and *Prunus pensylvanica*. Overall chi-square value is 161, $P < 0.001$. Individual chi-square values (for tests of each species against all others combined) are given above the columns for each species. For individual tests, unadjusted critical chi-square value at $\alpha = 0.05$ is 3.84 (7.48 with Bonferroni adjustment).

Small gaps tended to be dominated by initiators, and larger gaps tended to have more expanders than initiators. However, the relationship between number of gapmakers in the gap and proportion of initiators among gapmakers was not linear ($y = 0.85 \times x^{-0.5}$, $r^2 = 0.63$, where x = no. of gapmakers and y = proportion that were initiators). As gaps exceeded about five gapmakers in size, they became dominated by the process of expansion. In gaps with 20 or more gapmakers, 80–90% of gapmakers were expanders.

If the probability of mortality is augmented by proximity to a gap, gap margin trees should have a higher mortality rate than trees in a closed canopy. Although we cannot compare rates from sampling at a single point in time, we can compare density of expanders (former gap margin trees that have died) with density of initiators. The density of expanders in the forest as a whole was 68.4 ha⁻¹ while that of initiators was 51.3 ha⁻¹, suggesting that gap expansion occurred more frequently than initiation. The difference was mostly at 880 m and above (Fig. 3).

TREE SPECIES IN INTACT CANOPY VS. DISTURBANCE MORTALITY

The tree species composition varied significantly between the live canopy and the dead trees in gaps and extensive disturbance plots (Fig. 4a, $P < 0.001$). *Picea* formed a strongly disproportionate proportion of the mortality in gaps and extensive disturbance areas, where it formed nearly 50% of the basal area of dead trees compared with less than 20% of the basal area of the live canopy (Fig. 4b). *Abies* basal area was about equally represented in live canopy and mortality. Hardwood species generally comprised a greater proportion of the live canopy than they did mortality.
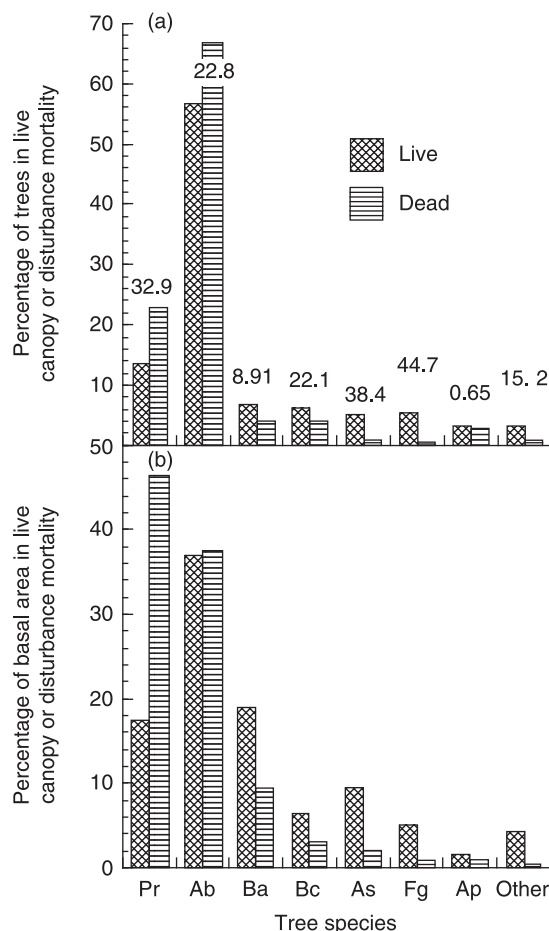
TREE SPECIES AS INITIATORS VS. EXPANDERS

Chi-square analyses showed highly significant variation among tree species occurring as initiators vs. expanders ($P < 0.001$, Fig. 5). *Picea*, *Betula cordifolia* and, to a lesser extent, *B. alleghaniensis* gapmakers were involved in initiation more than expected, with *Picea* accounting for over 50% of initiator basal area. *Abies* was very strongly associated with gap expansion.

DISTURBANCE AGENTS

Chronic wind stress and windsnap were the most commonly identified mortality agents, especially at upper elevations (Table 1). Biotic mortality agents were more
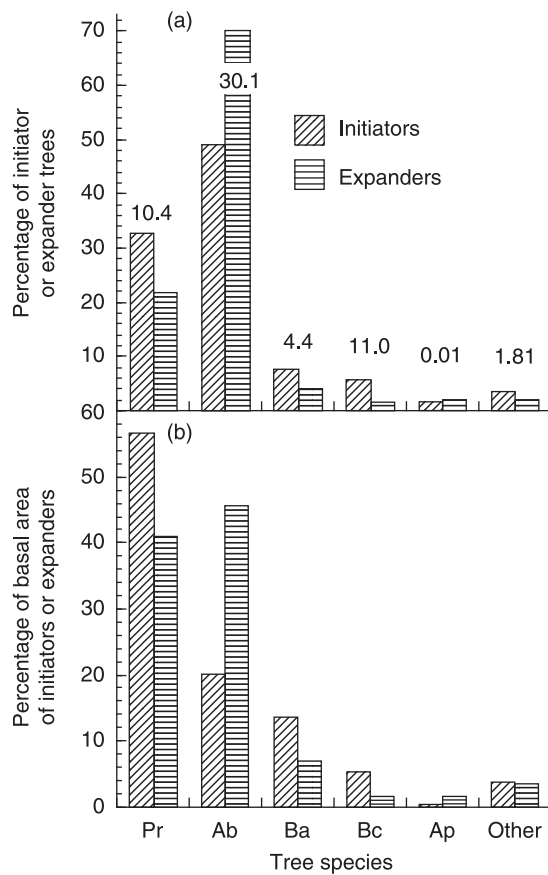
Fig. 5 Numbers of trees (a) and basal area (b) as percentage of initiators or expanders in each species. Based on large gapmakers. Tree species as listed in Fig. 4. Overall chi-square value in 36.04, $P < 0.001$. Individual chi-square values (for tests of each species against all others combined) are given above the columns for each species. For individual tests, unadjusted critical chi-square value at $\alpha = 0.05$ is 3.84 (6.96 with Bonferroni adjustment).

Fig. 6 Numbers of trees (a) and basal area (b) as percentage of initiators and expanders killed by each agent. Based on large gapmakers. R&BR = root and butt rots other than Armillaria; SB = spruce beetle; SR = stem rots; AO = Armillaria root and butt rot; WT&WS = windthrow and windsnap; CW = chronic wind stress. Overall chi-square value is 20.6, $P < 0.001$. Individual chi-square values (for tests of each agent against all others combined) are given above the columns for each agent. For individual tests, unadjusted critical chi-square value at $\alpha = 0.05$ is 3.84 (7.24 with Bonferroni adjustment).

important at low and mid-elevation transects. Root and butt rots and Armillaria root disease were the most frequent biotic mortality agents, followed closely by spruce beetle.

Sizes of live trees and those killed by different mortality agents varied substantially, but such differences were particularly pronounced in *Picea* (Table 2). Live *Picea* averaged 22.7 cm d.b.h., but *Picea* killed by mistletoe in gaps and extensive disturbance averaged 42.3 cm and those killed by spruce beetle averaged 47.2 cm. The differences were even more striking within an elevation range, such as at 600 and 640 m, where the average size of living, mistletoe-killed and spruce beetle-killed *Picea* was 26.1, 53.5 and 53.8 cm d.b.h., respectively.

Trees killed by all agents except chronic wind stress and tree fall were significantly larger than living canopy trees (Table 2). Most of the trees killed by chronic wind stress were *Abies* at relatively high elevations, which tended to be the smallest trees in the study. Even with *Abies*, however, the average size of trees killed by all agents was greater than that of the living trees.
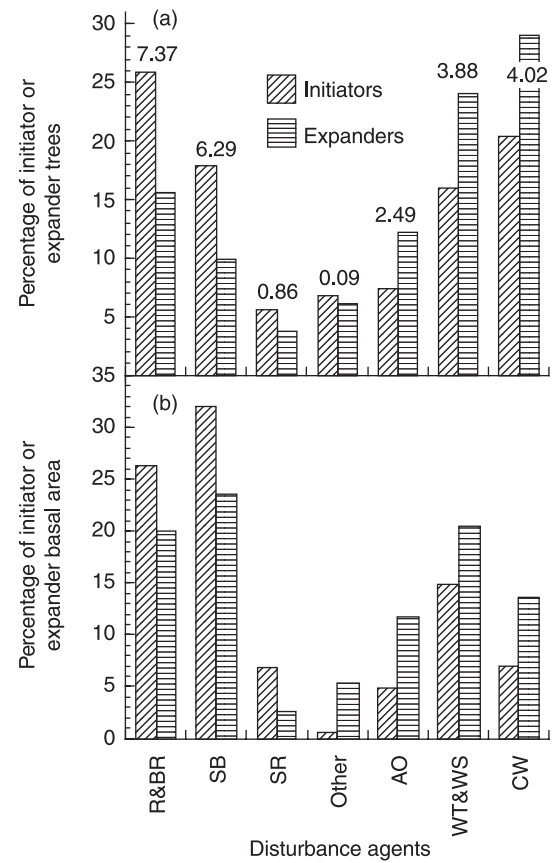
DISTURBANCE AGENTS AND GAP INITIATION VS. EXPANSION

Some agents were more commonly associated with gap initiation than expansion (Fig. 6a). Chi-square analysis showed significant variation among agents in proportions of initiators vs. expanders killed ($P < 0.001$). Spruce beetle and root and butt rots other than that caused by *Armillaria ostoyae* were more likely to initiate than expand gaps. *Armillaria ostoyae* and wind-related agents, in contrast, expanded gaps more than they initiated them; chronic wind stress and windthrow/ windsnap were most strongly associated with expansion. When the basal area of gapmakers was considered, the same trends were evident (Fig. 6b). Of 33 gap plots in which only a single gapmaker was found, eight were initiated by root and butt rots, five by spruce beetle, four by Armillaria root disease, three by stem decays and three by windthrow/windsnap.

If extensive disturbances in these forests primarily develop by gap expansion and coalescence, the same agents should be involved in the mortality in extensive

Table 1 Number of trees killed at each elevation by abiotic and biotic agents in gaps and extensive disturbance plots

Agent	Total gapmakers	Transect (elevation in metres)							
		600	640	720	800	880	960	1040	1120
Chronic wind stress	206	0	0	3	2	16	9	75	101
Windthrow/windsnap	155[a]	6	6	6	21	32	42	14	28
Root & butt rots	131	11	16	10	25	13	37	9	10
Armillaria	74[b]	3	10	5	6	27	20	2	1
Spruce beetle	63[c]	1	4	26	10	15	4	3	0
Stem rots	26	2	3	0	3	4	6	2	6
Tree fall	20	0	3	4	5	3	4	0	1
Mistletoe	10	1	2	1	1	5	0	0	0
Other	7[d]	0	0	0	0	0	2	5	0
Beech bark disease	6	2	4	0	0	0	0	0	0
Unknown	396	20	18	44	68	75	51	71	49
Total	1094	46	66	99	141	190	175	181	196

[a]Thirty-eight were windsnapped; 117 were windthrown.
[b]Six of the Armillaria-killed trees also had stem decay.
[c]Fifteen of the trees killed by spruce beetle also had dwarf mistletoe; 12 also had Armillaria root disease.
[d]Five trees had animal damage; two had lightning strikes.

Table 2 Mean size of gapmaker trees (d.b.h., cm) according to species and disturbance agent and of trees in live canopy[a]

	Ba[b]	Pr	As	Bc	Other	Fg	Ab	Ap	Mean	
Spruce beetle		47.2							47.2	a[c]
Mistletoe		42.3							42.3	a, b
Other		61.6					30.8		39.6	b, c
Beech bark disease						32.0			32.0	c, d
Root & butt rots	46.1	38.0	44.1	35.5			20.9	15.1	27.6	d
Stem rots	38.5	24.0		26.8			22.6	10.4	26.1	d, e
Windthrow/windsnap	21.1	29.5		34.6	28.0		23.2	16.5	24.9	e
Armillaria	45.3	25.1			19.3		21.4	17.0	23.3	e, f
Unknown	39.4	32.8	32.0	30.1	13.4		18.5	15.6	22.6	f
Chronic wind stress	33.0	23.7		15.8			17.4		17.8	g
Tree fall	15.6	16.6					17.5	14.0	16.8	g
Live canopy	32.0	22.7	26.5	20.2	22.2	19.6	16.6	15.1	19.5	g
Mean	34.5	30.9	28.4	22.9	21.3	20.7	18.1	15.5		
	a[c]	b	c	d	d	d	e	f		

[a]Mortality in intact canopy plots is not included.
[b]Abbreviations for tree species as in Fig. 4.
[c]The overall means of columns or rows not ended with letters in common were significantly different according to Fisher's protected least significant difference ($\alpha = 0.05$).

disturbance plots as in gap plots. Extensive disturbance occurred at and above 800 m, but at these elevations overall chi-square analysis showed significant variation among agents in occurrence in gaps vs. extensive disturbance ($P = 0.0103$). However, most of the variation was due to Armillaria root disease, which was more common in gaps than in extensive disturbance plots (it was rare above 960 m, Table 1, where extensive disturbance was common, Fig. 1), whereas other agents did not differ in incidence between extensive disturbance and gap plots.

The role of wind in gap expansion was further assessed by observing its effects on gap margin trees. At middle and upper elevations, margin trees often showed extensive damage from wind. *Betula* spp. often had broken branches and conifers had evidence of snapped tops leading to loss of substantial portions of the crown (Fig. 7). In some cases repeated episodes of top breakage and regrowth led to formation of candelabra tops. Although our data on this point are not complete, at least 25% (154 of 619) of *Abies* and 19% (43 of 231) of living *Picea* margin trees had tops snapped one or more times.

As another approach to understanding sequences of agents in disturbance patches, time since death was ranked among gapmakers within each gap with 10 or more gapmakers and within each extensive disturbance plot (Table 3). Kruskal–Wallis one-way analysis of variance showed significant variation among agents ($P < 0.001$). Windthrow and windsnap, Armillaria root disease, and chronic wind stress occurred significantly later during gap development than other root and

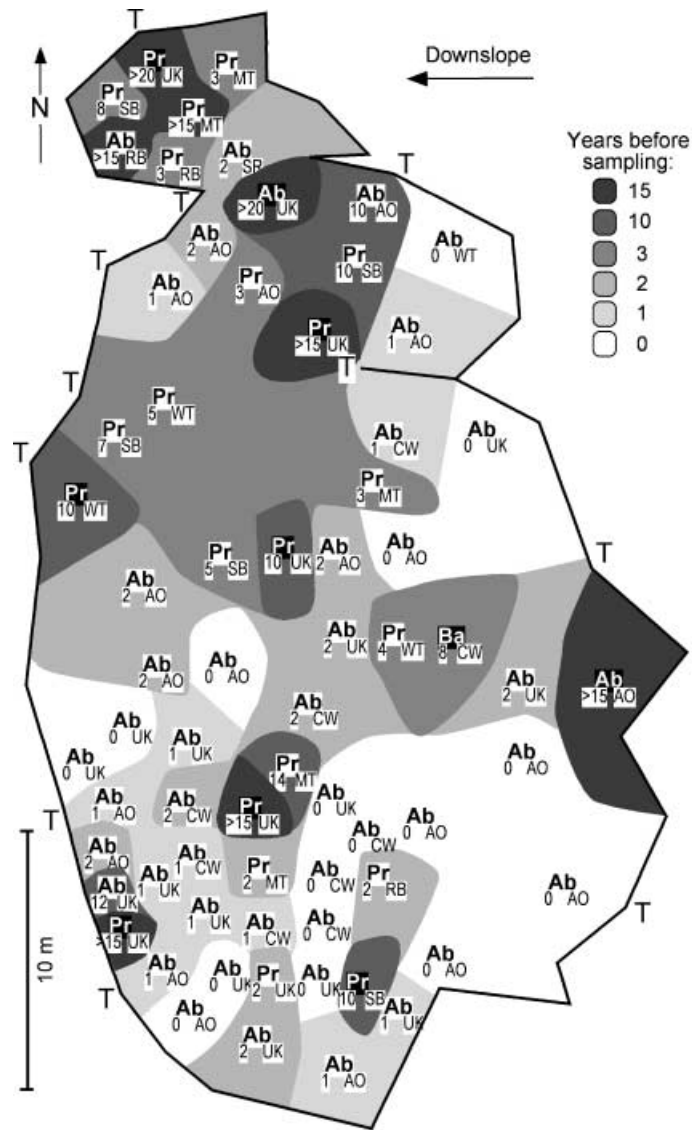**Fig. 7** Gap plot 1 at 880 m. Bold letters refer to gapmakers: Ab = *Abies balsamea*; Pr = *Picea rubens*; Ba = *Betula alleghaniensis*. Gapmakers in white text on black are initiators, others are expanders. Shading indicates sequence of gap expansion. Numbers at lower left refer to estimated time since death; letters at lower right indicate disturbance agent: Ao = root disease caused by *Armillaria ostoyae*; SR = stem rot; MT = mistletoe; RB = other root and butt rot; SB = spruce beetle; WT = windthrow or windsnap. Inflections of the gap outline indicate gap margin trees; 'T' indicates that that margin tree had had the top blown off at least once.

butt rots and spruce beetle (Table 3). The number of gapmakers killed by other agents was too low (seven or fewer) to make robust statistical comparisons of their rankings.

A plot at 880 m illustrates the complexity of gap development in a large gap (Fig. 7). This was the largest gap sampled (870 m^2), near our upper area limit for gap sampling (disturbances > 1000 m^2 were considered extensive). At 15 years before sampling, six separate gaps existed, initiated by dwarf mistletoe, Armillaria root disease, other root and butt rots, and unknown causes. By 10 years before sampling, two gaps had coalesced, three more had been initiated (by spruce beetle, windthrow and unknown causes) and two others had expanded. The process of gap expansion and coalescence continued, primarily due to Armillaria root disease,

windthrow, chronic wind stress and other causes, resulting in the single large gap shown.

CHRONOLOGY OF SPRUCE BEETLE DISTURBANCE

In terms of basal area, *Picea* was the most important species killed in gap and disturbance areas (Fig. 4). This was particularly evident for trees killed 10 or more years prior to sampling (before 1982), during which time the basal area of the killed *Picea* trees was greater than that of all other killed trees combined (Fig. 8). In contrast, *Picea* comprised less than 50% of the basal area of mortality in the period 1982–91.

Much of the *Picea* mortality was apparently associated with a spruce beetle epidemic (Fig. 8). Within the

Table 3 Differences among disturbance agents in median, ranked time since death in gaps and extensive disturbances with ≥ 10 gapmakers (total of 29 plots)

Disturbance agent[a]	n	Median rank[b]			
Spruce beetle	9	0.181	a		
Other root and butt rots	38	0.286	a	b	
Mistletoe	5	0.330	a	b	c
Other	6	0.425		b	c
Chronic wind stress	114	0.456			c
Stem rots	7	0.500	a	b	c
Windthrow/windsnap	77	0.650			c
Tree fall	4	0.651	a	b	c
Armillaria	28	0.670			c.

[a]Gapmakers with unknown disturbance agents were removed prior to plot selection and analysis.
[b]Low values indicate older mortality (relatively early in gap development) and vice-versa. Medians without letters in common were significantly different according to Bonferroni-adjusted Mann–Whitney U-tests (α = 0.05).
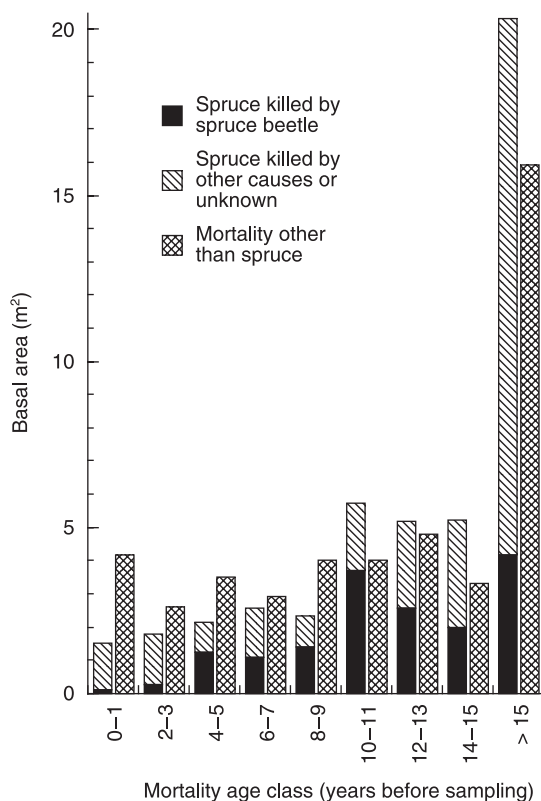

Fig. 8 Chronology of mortality of spruce due to spruce beetle, of spruce due to other causes, and of other species. Mortality is included from plots in gaps, extensive disturbance, and canopy.

period during which we could develop an absolute chronology of mortality by the spruce beetle, a major peak of activity appeared about 10–11 years before sampling, or about 1980 (Fig. 8). The sampled trees that died more than 15 years before sampling may have died over the previous decade or more and average annual mortality was therefore probably low. It seems likely that the outbreak began more than 15 years before

sampling, peaked near 10 years before sampling, and collapsed 3 years before sampling.

Discussion

GAP INITIATION

Agents that played a more significant role in initiation than in expansion of gaps included spruce beetle, root and butt rots (other than Armillaria root disease), and dwarf mistletoe. Overall, spruce beetle was the most important agent in initiating canopy gaps and it tended to kill the largest, and probably oldest, *Picea* trees. Root- and butt-rot fungi were also important in initiating gaps. These fungi, unlike *Armillaria ostoyae*, tended to kill trees scattered throughout the canopy. Root and butt rot diseases were important on *Picea*, but especially so on *Abies*.

Eastern dwarf mistletoe may be underestimated as a contributor to gap initiation, because it was difficult to discern if the infections caused mortality. After many decades this obligate parasite can cause witches' brooms, stem deformation, growth loss and mortality of *Picea* in the north-eastern USA (Hawksworth & Shigo 1980). Thus, symptoms of mistletoe infection are prominent on the oldest *Picea* trees, the same trees most susceptible to spruce beetle. For every two gapmakers attributed to mistletoe, there were three more that were obviously infected by mistletoe but killed by spruce beetle.

Although stem decays are important mortality agents in some old-growth forests (Hennon 1995; Lewis & Lindgren 1999), they were relatively unimportant at Crawford Notch, particularly in conifers. As hardwood species continue to increase in importance in the canopy and as their branches become increasingly wounded by wind and ice, we predict that stem decays will become more important mortality agents.

GAP EXPANSION AND EXTENSIVE DISTURBANCE

We had considered that larger patches of disturbance (> 0.1 ha) may represent 'catastrophic disturbance' that is qualitatively different from gap-phase disturbance and caused by different agents (White 1979; Peet 1992). However, at the elevations where extensive disturbance occurred (800 m and above), mortality in extensive disturbance plots was caused by the same agents as caused mortality in gap plots. Extensive disturbances in this forest appear to arise by expansion and coalescence of smaller canopy gaps. At Crawford Notch, particularly at higher elevations, the causes of gap expansion play a major role in forest dynamics.

Wind was a major cause of gap expansion, particularly at the middle and upper elevations of our study. Mortality due to wind can result from chronic wind stress, windthrow or windsnap. Chronic wind stress is a less organized manifestation of the same phenomenon that leads to fir waves at higher elevations in the White

Mountains and Adirondack Mountains of the USA and in the Yatsugatake Mountains of Japan, where winter winds are very strong and directional (Iwaki & Totsuka 1959; Sprugel 1976). An increase in wind exposure leads to crown damage from rime ice and associated wind, and to root damage from root movement and underlying rocks. Growth slows and, ultimately, death may result (Harrington 1986; Marchand *et al.* 1986; Rizzo & Harrington 1988a). Although chronic wind stress was very important in expanding canopy gaps, none of the 33 single-tree gaps we encountered was caused by chronic wind stress.

Windthrow and windsnap in the absence of substantial decay are more obvious results of wind, but such mortality tended to expand gaps rather than cause large disturbance patches. It might at first seem surprising that, although wind is a very important agent of disturbance, evidence of large, catastrophic blowdown was not observed. Such blowdowns occur when exceptionally severe episodes of wind occur in areas where they do not usually occur. At Crawford Notch, in contrast, winter winds tend to be sustained and from a consistent direction. Crown shaping and pruning, and root growth, lead to wind-tolerant trees and extensive blowdowns are rare in the absence of hurricanes. When exposure is suddenly increased, however, some form of wind damage may develop, leading to mortality. Thus, wind is a chronic rather than a catastrophic phenomenon in these forests (Harrington 1986).

Further evidence of the complex consequences of wind in this system is the broken branches on hardwoods and the snapped tops on conifers, particularly on gap margin trees. *Abies* was particularly impacted by such snapping, contributing to its importance as a gap expander. In addition to reducing the crowns of these trees, and possibly killing them directly, the broken branches and stems serve as infection courts for stem-decay fungi that contribute to later mortality. Crown dieback of exposed hardwood tree species at mid- to upper elevations was particularly evident.

Armillaria ostoyae is also a common cause of gap expansion, especially at low and middle elevations. Establishment of new infections by long-distance dispersal is rare (Worrall 1994), so it may be expected that the disease causes more gap expansion than initiation. Using resources from previously colonized root systems, the pathogen spreads readily to neighbouring trees, either via root contacts or by growth through soil in the form of rhizomorphs. Thus, expanding centres of mortality may occur. The pathogen may have developed in root systems of the large spruce trees killed by the spruce beetle in the late 1970s, using these dead trees as a food base from which to attack adjacent saplings or weakened larger trees (Wargo & Harrington 1991).

LONG-TERM DYNAMICS AND SPRUCE BEETLE

This study reports recent disturbance after a major outbreak of spruce beetle. The proportion of *Picea* as gapmakers far exceeded its proportion in the live canopy, particularly in terms of basal area. The rate of such disturbance is clearly not constant through time.

We use the term episodic disturbance for disturbance of large magnitude concentrated in time but not necessarily in space. Episodes of disturbance concentrated in large patches (Runkle 1985b) are often referred to as catastrophic disturbance. The disturbance that has affected the dominant *Picea* differs from a typical catastrophic disturbance in that it affects only one species in the forest, only the largest trees are killed, and it is not spatially aggregated.

Episodic disturbance affecting long-lived, dominant trees due to agents such as bark beetles may occur once every hundred or more years. However, the impacts may be long-term and complex, including altered forest structure and composition, with synchronous patterns of stand development across the landscape. In the southern Appalachians, high recruitment of *Picea*, apparently following extensive disturbance, occurred between 1790 and 1850. However, the incidence of small disturbances (resulting in periods of release of non-canopy *Picea* trees) did not show a decrease after 1850 (Wu *et al.* 1999). These patterns highlight the distinction between episodic disturbance and the more general forms of gap-phase disturbance. Based on reports of widespread *Picea* mortality over the last century and a half, and on dendrochronological evidence, Battles & Fahey (1996) concluded that periods of high *Picea* mortality and increases in gap fraction might be part of the long-term *Picea–Abies* disturbance regime in the northern Appalachians.

At Crawford Notch in 1991, *Picea* comprised nearly 50% of the dead basal area but less than 20% of the live canopy basal area. Large, dead *Picea* that emerged from the continuous canopy visually dominated the lower to middle elevations. Because *Picea* is a relatively slow-growing and long-lived species, these patterns strongly suggest a recent episode of elevated *Picea* mortality. Foster & Reiners (1986) recognized that there had been recent, increased mortality of large *Picea* in Crawford Notch and suggested that the forest was not in a steady state as a result. Worrall & Harrington (1988) provided evidence that the spruce beetle was primarily responsible for the observed mortality of the largest spruce at those elevations. Observations in 1983 (Harrington, personal observation) and the chronology of spruce beetle activity presented here indicate that the spruce beetle outbreak peaked about 1980. On a regional scale, the spruce beetle may also account for substantial portions of *Picea* mortality reported elsewhere in the north-eastern USA (Scott *et al.* 1984; Johnson *et al.* 1986).

When at low population levels, spruce beetle tends to reproduce in diseased and windthrown trees. When such habitat becomes abundant, populations may increase to a point where beetles overwhelm and kill healthy trees. Older, larger trees are the best habitat and produce the most successful brood of beetles, with

25 cm d.b.h. normally considered a minimum size of *Picea rubens* for successful beetle reproduction (Weiss *et al.* 1985). Vast, self-sustaining outbreaks may occur when a triggering event (such as a large blowdown) facilitates initial population rise and large trees are abundant to sustain the outbreak.

In the latter part of the 19th century, outbreaks of spruce beetle killed millions of trees in north-eastern USA (Hopkins 1901, 1909; Weiss *et al.* 1985). It is estimated that one-third to one-half of the merchantable spruce trees in the Adirondack Mountains of New York was killed in the 1880s (Johnson *et al.* 1986), and another major outbreak occurred in northern New England and eastern Canada in 1897–1901 (Hopkins 1909). Cutting of most stands of large spruce and subsequent fires near the turn of the century almost eliminated stands of large *Picea rubens* in the northern Appalachians, and outbreaks of the spruce beetle were smaller and less frequent in the 20th century (Weiss *et al.* 1985). As trees again reach large sizes, particularly in the few remaining old-growth stands such as Crawford Notch, however, spruce beetle outbreaks can still have significant ecological impact in initiating gaps and exposing other trees to Armillaria root disease and wind.

Our results suggest that forest disturbance regimes may be sufficiently complex that equilibrium or steady-state conditions in tree species abundances and forest structure are unlikely. At Crawford Notch, for example, nearly synchronous mortality of large *Picea* should be followed by increased regeneration of all tree species, especially *Betula* spp., though variation in gap size, expansion rate and seedbed will assure spatial heterogeneity of species composition in these forests. The regenerating stand will not be precisely even-aged because gap expansion may continue over several decades. Non-expanding, single-tree gaps should regenerate primarily *Picea* and *Abies*, mainly via release of advance regeneration (Runkle 1985b; White *et al.* 1985; Veblen 1986; Battles & Fahey 2000). Larger nonexpanding gaps, involving a few canopy trees, should allow the regeneration of mid-tolerant tree species such as *Betula alleghaniensis*, which cannot establish under a continuous canopy (Forcier 1975; McClure & Lee 1993). Slowly expanding gaps may favour a mix of the shade-tolerant and mid-tolerant species, but rapid gap expansion should enable shade-intolerant taxa such as *Betula cordifolia* and *Sorbus americana* (or *S. decora*) to join the mix, though the amount of birch may depend on seedbed availability (Battles & Fahey 2000).

Hardwoods that have been exposed by gap initiation and expansion will suffer crown damage due to wind and deteriorate as decay fungi invade broken branches and wounds. The canopy and subcanopy *Abies* that are released now will begin to die from root diseases, stem decays, windthrow and chronic wind stress as they reach 100 years of age. A similar pattern occurs in *Picea glauca* × *engelmannii-Abies lasiocarpa* forests of British Columbia (Lewis & Lindgren 1999). These smaller-scale disturbances may be tied to stand developmental conditions and susceptibility, but they are not tightly synchronized, as is the case with insect population outbreaks. In this way, gap-phase disturbance cycles are nested within the larger cycle of episodic disturbance in what might be termed a 'nested bicycle' system. Eventually a new cohort of *Picea*, already present in the understorey, will dominate, and as these *Picea* trees increase in size, the stage will be set for another large outbreak of spruce beetle.

Acknowledgements

References

Battles, J.J. & Fahey, T.J. (1996) Spruce decline as a disturbance event in the subalpine forests of the northeastern United States. *Canadian Journal of Forest Research*, **26**, 408–421.

Battles, J.J. & Fahey, T.J. (2000) Gap dynamics following forest decline: a case study of red spruce forests. *Ecological Applications*, **10**, 760–774.

Bormann, F.H. & Likens, G.E. (1979) *Pattern and Process in a Forested Ecosystem*, 2nd edn. Springer-Verlag, New York.

Brittain, W.H. & Grant, W.F. (1967) Observations on Canadian birch (*Betula*) collections at the Morgan Arboretum. V. *B. papyrifera* and *B. cordifolia* from eastern Canada. *Canadian Field-Naturalist*, **81**, 251–262.

Dale, V.H., Hemstrom, M. & Franklin, J. (1986) Modeling the long-term effects of disturbances on forest succession, Olympic Peninsula, Washington. *Canadian Journal of Forest Research*, **16**, 56–67.

Eriksson, J., Ryvarden, L. and other authors (varies by volume) (1973–88) *Corticiaceae of North Europe, Volumes 1–8*. Fungiflora, Oslo.

Filion, L., Payette, S., Delwaide, A. & Bhiry, N. (1998) Insect defoliation as major disturbance factors in the high-altitude balsam fir forest of Mount Mégantic, southern Quebec. *Canadian Journal of Forest Research*, **28**, 1832–1842.

Forcier, L.K. (1975) Reproductive strategies and the co-occurrence of climax tree species. *Science*, **189**, 808–811.

Foster, J.R. & Reiners, W.A. (1983) Vegetation patterns in a virgin sub-alpine forest at Crawford Notch, White Mountains, New Hampshire. *Bulletin of the Torrey Botanical Club*, **110**, 141–153.

Foster, J.R. & Reiners, W.A. (1986) Size distribution and expansion of canopy gaps in a northern Appalachian spruce-fir forest. *Vegetatio*, **68**, 109–114.

Frelich, L.E. (1986) *Natural disturbance frequencies in the hemlock-hardwood forests of the upper Great Lakes region*. PhD Dissertation, University of Wisconsin, Madison.

Gilbertson, R.L. & Ryvarden, L. (1986–87) *Polypores of North America, Volumes 1 & 2*. Fungiflora, Oslo.

Gleason, H.A. & Cronquist, A. (1991) *Manual of Vascular Plants of the Northeastern United States and Adjacent Canada*, 2nd edn. The New York Botanical Garden, Bronx, New York.

Hallenberg, N. (1985) *The Lachnocladiaceae and Coniophoraceae of North Europe*. Fungiflora, Oslo.

Harrington, T.C. (1986) Growth decline of wind-exposed red spruce and balsam fir in the White Mountains. *Canadian Journal of Forest Research*, **16**, 232–238.

Harrington, T.C., Rizzo, D.M. & Marchand, P.J. (1984) Wind, rocks, root disease and mortality of subalpine red spruce and balsam fir. *Phytopathology*, **74**, 824 (Abstract).

Harrington, T.C. & Wingfield, M.J. (1998) Diseases and the ecology of indigenous and exotic pines. *Ecology and Biogeography of* Pinus (ed. D. Richardson), pp. 381–404. Cambridge University Press, Cambridge.

Hawksworth, F.G. & Shigo, A.L. (1980) Dwarf mistletoe on red spruce in the White Mountains of New Hampshire. *Plant Disease*, **64**, 880–882.

Hennon, P.E. (1995) Are heart rot fungi major factors of disturbance in gap-dynamic forests? *Northwest Science*, **69**, 284–293.

Hopkins, A.D. (1901) *Insect Enemies of the Spruce in the Northeast*. Bulletin 28. USDA Bureau of Entomology, Washington DC.

Hopkins, A.D. (1909) *Practical Information on the Scolytid Beetles of North American Forests. I. Bark Beetles of the Genus Dendroctonus*. Bulletin 83. USDA Bureau of Entomology, Washington DC.

Iwaki, H. & Totsuka, T. (1959) Ecological and physiological studies on the vegetation of Mt Shimagare. II. On the crescent-shaped 'dead-tree strips' in the Yatsugatake and Chichibu Mountains. *Botanical Magazine*, **72**, 255–260.

Johnson, A.H., Friedland, A.J. & Dushoff, J.G. (1986) Recent and historic red spruce mortality: evidence of climatic influence. *Water, Air and Soil Pollution*, **30**, 319–330.

Jonsson, B. & Dynesius, M. (1993) Uprooting in boreal spruce forests: long-term variation in disturbance rate. *Canadian Journal of Forest Research*, **23**, 2383–2388.

Lertzman, K. & Krebs, C. (1991) Gap-phase structure of a subalpine old-growth forest. *Canadian Journal of Forest Research*, **21**, 1730–1741.

Lewis, K.J. & Lindgren, B.S. (1999) Influence of decay fungi on species composition and size class structure in mature *Picea glauca × engelmannii* and *Abies lasiocarpa* in subboreal forests of central British Columbia. *Forest Ecology and Management*, **123**, 135–143.

Marchand, P.J., Goulet, F.L. & Harrington, T.C. (1986) Death by attrition: a hypothesis for wave mortality of subalpine *Abies balsamea*. *Canadian Journal of Forest Research*, **16**, 591–596.

McClure, J.W. & Lee, T.D. (1993) Small-scale disturbance in a northern hardwoods forest: effects on tree species abundance and distribution. *Canadian Journal of Forest Research*, **23**, 1347–1360.

Nobles, M.K. (1964) Identification of cultures of wood-inhabiting hymenomycetes. *Canadian Journal of Botany*, **43**, 1097–1139.

Peet, R.K. (1992) Community structure and ecosystem function. *Plant Succession* (eds D.C. Glenn-Lewin, R.K. Peet & T.T. Veblen), pp. 103–151. Chapman & Hall, London.

Perkins, T., Klein, R., Badger, G. & Easter, M. (1992) Spruce-fir decline and gap dynamics on Camels Hump, Vermont. *Canadian Journal of Forest Research*, **22**, 413–422.

Pickett, S.T.A. & Thompson, J.N. (1978) Patch dynamics and the design of nature reserves. *Biological Conservation*, **13**, 27–37.

Pickett, S.T.A. & White, P.S. (1985) *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, San Diego.

Putz, F.E., Parker, G.G. & Archibald, R.M. (1984) Mechanical abrasion and intercrown spacing. *American Midland Naturalist*, **112**, 24–28.

Reams, G.A. & Deusen, P.C.V. (1993) Synchronic large-scale disturbances and red spruce growth decline. *Canadian Journal of Forest Research*, **23**, 1361–1374.

Rizzo, D.M. & Harrington, T.C. (1988a) Root movement and root damage of red spruce and balsam fir on subalpine sites in the White Mountains, New Hampshire. *Canadian Journal of Forest Research*, **18**, 991–1001.

Rizzo, D.M. & Harrington, T.C. (1988b) Root and butt rot fungi on red spruce and balsam fir in the White Mountains. *Plant Disease*, **72**, 329–331.

Runkle, J.R. (1985a) Comparison of methods for determining fraction of land area in treefall gaps. *Forest Science*, **31**, 15–19.

Runkle, J.R. (1985b) Disturbance regimes in temperate forests. *The Ecology of Natural Disturbance and Patch Dynamics* (eds S.T.A. Pickett & P.S. White), pp. 17–34. Academic Press, London.

Runkle, J.R. (1998) Changes in southern Appalachian canopy tree gaps sampled thrice. *Ecology*, **79**, 1768–1780.

Scott, J.T., Siccama, T.G., Johnson, A.H. & Breisch, A.R. (1984) Decline of red spruce in the Adirondacks, New York. *Bulletin of the Torrey Botanical Club*, **111**, 438–444.

Sinclair, W.A., Lyon, H.H. & Johnson, W.T. (1987) *Diseases of Trees and Shrubs*. Cornell University Press, Ithaca, New York.

Spaulding, P. (1937) Estimating the length of time that trees have been dead in northern New England. *Journal of Forestry*, **35**, 393–395.

Sprugel, D.G. (1976) Dynamic structure of wave-generated *Abies balsamea* forests in the northeastern United States. *Journal of Ecology*, **64**, 889–911.

Stalpers, J.A. (1978) Identification of wood-inhabiting Aphyllophorales in pure culture. *Studies in Mycology*, **16**, 1–248.

Swetnam, T.W. & Lynch, A.M. (1993) Multicentury, regional-scale patterns of western spruce budworm outbreaks. *Ecological Monographs*, **63**, 399–424.

Veblen, T.T. (1986) Treefalls and the coexistence of conifers in subalpine forests of the central Rockies. *Ecology*, **67**, 644–649.

Veblen, T.T. (1992) Regeneration dynamics. *Plant Succession* (eds D.C. Glenn-Lewin, R.K. Peet & T.T. Veblen), pp. 103–151. Chapman & Hall, London.

Wargo, P.M. & Harrington, T.C. (1991) Host stress and susceptibility to *Armillaria*. Armillaria *Root Disease* (eds C.G. Shaw III & G. Kile), pp. 88–101. USDA Agriculture Handbook 691. Washington, DC.

Watt, A.S. (1947) Pattern and process in the plant community. *Journal of Ecology*, **35**, 1–22.

Weiss, M.J., McCreery, L.R., Millers, I., Miller-Weeks, M. & O'Brien, J.T. (1985) *Cooperative Survey of Red Spruce and Balsam Fir Decline and Mortality in New York, Vermont and New Hampshire, 1984*. NA-TP-11, USDA Forest Service, Northeastern Area. Broomall, Pennsylvania, USA.

White, P.S. (1979) Pattern, process and natural disturbance in vegetation. *Botanical Review*, **45**, 229–299.

White, P.W., MacKenzie, M.D. & Busing, R.T. (1985) Natural disturbance and gap phase dynamics in southern Appalachian spruce-fir forests. *Canadian Journal of Forest Research*, **15**, 233–240.

Worrall, J.J. (1991) Media for selective isolation of hymenomycetes. *Mycologia*, **83**, 296–302.

Worrall, J.J. (1994) Population structure of *Armillaria* species in several forest types. *Mycologia*, **86**, 401–407.

Worrall, J.J. (1997) Somatic incompatibility in basidiomycetes. *Mycologia*, **89**, 24–36.

Worrall, J.J. & Harrington, T.C. (1988) Etiology of canopy gaps in spruce-fir forests at Crawford Notch, New Hampshire. *Canadian Journal of Forest Research*, **18**, 1463–1469.

Wu, X., McCormick, J.F. & Busing, R.T. (1999) Growth patterns of *Picea rubens* prior to canopy recruitment. *Plant Ecology*, **140**, 245–253.