

Etiology of canopy gaps in spruce-fir forests at Crawford Notch, New Hampshire

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Natural disturbance agents causing formation of canopy gaps were identified and quantified at five elevations (640, 765, 885, 1005, and 1130 m) in an old-growth spruce-fir forest. Actual and expanded gaps were measured to the inner edge of the crown or to the bole, respectively, of the live canopy trees at the gap margin. The percentage of forest canopy in gaps was lowest (6% for actual and 40% for expanded gap areas) at 1005 m elevation, near the upper limit of the spruce-fir phase, and highest (33% actual and 77% expanded) where the spruce-fir phase meets the mixed hardwood-conifer forest type at 765 m elevation. Mean gap size was smallest at the higher elevations. Expanded gap area was apportioned to tree species and disturbance agents according to basal area of affected trees in each gap. Twenty-two identified agents were involved in gap-phase mortality, and their relative importance varied strongly with elevation. Biotic diseases accounted for 66% of gap area at the lowest elevation (640 m) and only 7 and 15%, respectively, at the highest elevations (1005 and 1130 m). Root and butt rots were the most important group of biotic diseases at all elevations; their primary effect was to predispose trees to breakage of the stem near ground level. In contrast to biotic disease agents, chronic wind stress increased greatly in relative importance with elevation, accounting for 72% of gap area at 1130 m. The spruce beetle was an important disturbance agent at 640 and 765 m, where large, over-mature red spruce trees had dominated the stand. Gap etiology appeared to be rarely restricted in time to a single event, and was often complex, with multiple agents occurring in the same gap and on the same tree.

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Les agents perturbateurs naturels menant à la formation de trouées dans le couvert foliacé ont été identifiés et quantifiés à cinq altitudes (640, 765, 885, 1005 et 1130 m) dans une forêt d'épinette et de sapin de première venue. Les trouées actuelles et celles ayant pris de l'expansion ont été mesurées jusqu'en bordure des cimes ou des troncs, respectivement, des arbres vivants localisés en bordure des trouées. La proportion du couvert foliacé dans les trouées était plus faible (6% pour les trouées actuelles et 40% pour celles en expansion) à 1005 m, à proximité de la limite supérieure de la forêt d'épinette-sapin et plus forte (33% pour les trouées actuelles et 77% pour celles en expansion) là où la forêt d'épinette-sapin rejoint la forêt mixte de conifères et de feuillus à l'altitude de 765 m. La dimension moyenne des trouées était moindre aux plus hautes altitudes. L'expansion des trouées était attribuée à l'essence et aux agents perturbateurs, d'après la surface terrière des arbres affectés dans chaque trouée. On a identifié 22 agents responsables de la mortalité des arbres dans les trouées, et leur importance relative variait fortement avec l'altitude. Les maladies biotiques expliquaient 66% de la surface des trouées aux basses altitudes (640 m) et seulement 7 et 15%, respectivement, aux hautes altitudes (1005 et 1130 m). Les caries de racines et du pied formaient le plus important groupe de maladies biotiques, quelle que fut l'altitude; leur principal effet était de prédisposer les arbres aux bris de tronc à proximité du sol. Contrairement aux maladies biotiques, le stress chronique à l'action du vent augmentait considérablement en importance relative avec l'altitude, expliquant 72% de la surface des trouées à 1130 m. Le Charençon de l'épinette était un agent perturbateur important à 640 et 765 m, où des sujets surâgés d'Épinette rouge avaient dominé le peuplement. L'étiologie des trouées a semblé rarement restreinte dans le temps par un seul événement et a paru souvent complexe, de multiples agents se trouvant souvent dans la même trouée et sur le même arbre.

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Introduction

Natural disturbance plays an important role in the dynamics of old-growth forests (Pickett and White 1985). In many areas, small-scale disturbance (creating canopy gaps of <1 ha) is more important than large-scale, catastrophic disturbance (Foster and Reiners 1983; White et al. 1985). Such patch-phase processes of disturbance, followed by gap colonization, result in maintenance of species diversity, uneven-aged stands, and vegetation mosaics. The kind and abundance of disturbance agents control the amount, frequency, and pattern of disturbance, and may also influence subsequent gap dynamics. Although the importance of identifying specific disturbance agents has been recognized (Harmon et al. 1983; Pickett and White 1985), information

on the spectrum of etiological agents and their distribution in old-growth forests is lacking.

Anthropogenic disturbance, in the form of air pollution, has been suggested as a cause of tree death in subalpine spruce-fir forests of northeastern North America (Johnson and Siccama 1983; Siccama et al. 1982; Vogelmann et al. 1985). Such suggestions cannot be assessed adequately without comprehensive knowledge of the natural disturbance regime upon which the anthropogenic disturbance may be superimposed. To address these problems, we initiated a study of disturbance agents in old-growth subalpine spruce-fir forests. Our objectives were to determine the importance of the various natural disturbance agents and evaluate variation in the disturbance regime with elevation.

Materials and methods

Study site

Foster and Reiners (1983) recently described the vegetation and disturbance patterns in the old-growth forests that we surveyed at Crawford Notch, White Mountain National Forest, New Hampshire. The relative importance values they calculated for the major tree species along an elevational gradient are shown in Fig. 1. The slope extends from 600 to 1300 m in elevation. Mixed hardwood-conifer forest covers the lower slope, subalpine spruce-fir forest extends from approximately 760 to 1100 m, and almost pure balsam fir (*Abies balsamea* (L.) Mill.) stands cover the upper slope. Tree density (live and dead) generally increases with elevation, but basal area is maximal at 890 m, where large red spruce (*Picea rubens* Sarg.) dominate (Foster and Reiners 1983).

Underlain by a gray gneiss, the surficial cover of the site ranges from glacial till at lower elevations to paleofelsenmeer or no surficial cover at higher elevations (Henderson et al. 1977). Soils derived from glacial till are Cryorthods or Cryohumods; those at higher elevations are organic mats resting directly on bedrock or boulders (Borofolists) (Pilgrim and Peterson 1979; Reiners and Lang 1979). The average slope is 24% and west facing.

Sampling procedure

Five transects were established at ~120 m intervals. Elevations of the transects were 640, 765, 885, 1005, and 1130 m, and transect lengths were 450, 240, 270, 270, and 180 m, respectively. The 765 and 1005 m transects were completed in 1986 and the others in 1987. Each transect began at the Webster-Jackson foot trail and headed north along the contour, continuing until approximately 20 gaps were encountered. Gaps were recognized as openings in the canopy that resulted from death, uprooting, or snapping of one or more trees, and in which regeneration was less than half the average height of the living canopy trees at the gap margin. An actual gap is the projection of the canopy edge on the forest floor. An expanded gap is the area circumscribed by the boles of the live canopy trees whose foliage borders the actual gap (Runkle 1985a). All expanded gaps intersected by the transect were included in the sample. Intersection length, the longest dimension of the gap, and the longest perpendicular to that length were recorded for both the actual gap and the expanded gap. Gapmakers were defined as dead or downed canopy-sized trees within the gap. In accordance with the minimum DBH (diameter at 1.4 m height) of canopy-sized trees at the respective elevations, trees of ≥ 15 cm DBH were considered gapmakers except at the highest elevation, where trees of ≥ 8 cm DBH were considered. Because reliable diagnosis was generally not possible with trees that had been dead too long for species identification, and because gaps with such old mortality generally had more recent mortality as well, gapmakers that could not be identified to species were not considered. Species, DBH, "posture" (i.e., standing dead, snapped, or uprooted), and stage of deterioration (condition of needles, twigs, branches, bark, and wood) were recorded for each gapmaker.

Etymology

Gapmakers were examined for evidence of diseases, insects, stress agents, etc. Diagnoses required consideration of a number of biotic and abiotic mortality agents (Boyce 1961; Hepting 1971; USDA Forest Service 1985; Sinclair et al. 1987).

Diseases involving wood decay were common and required some degree of dissection, including major roots. Even long after tree death, decay that occurred postmortem could generally be distinguished from decay that occurred in the living tree. Root, butt, and stem decay fungi generally decay the heartwood and inner sapwood to a much greater extent than outer sapwood. Sap rot occurring after death was usually at a very different stage of decay or was of a completely different type. Stems that had decayed saprophically were either evenly decayed across the stem or, more likely, the outer wood was at a more advanced stage of decay than the inner growth rings. Evidence of host response (e.g., callusing,

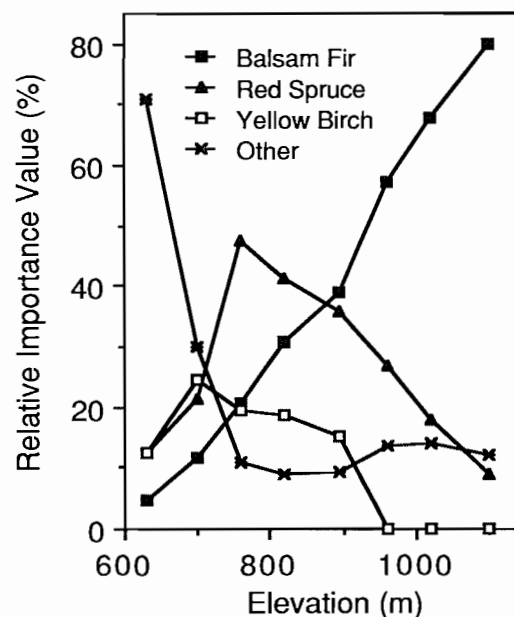


FIG. 1. Relative importance values of tree species versus elevation at Crawford Notch. Data are from Foster and Reiners (1983), whose data for 700 m total 88% rather than 100%.

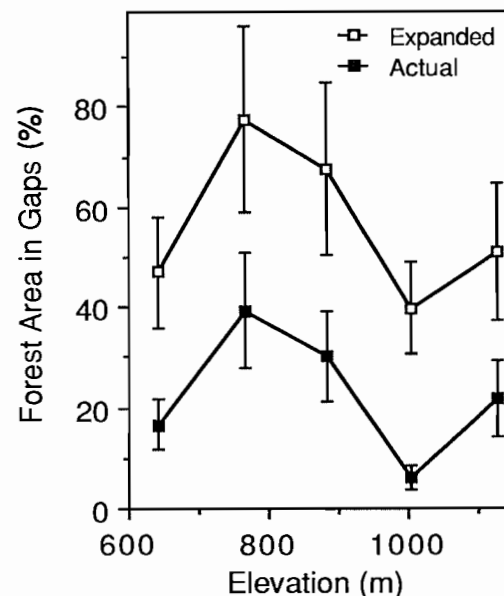


FIG. 2. Percentage of forest area occupied by actual and expanded gaps at five elevations. Vertical bars represent standard error.

resinosis) (Tippett and Shigo 1981; Worrall and Harrington 1988) associated with wood infected by a pathogenic fungus indicated that infection occurred while the tree was still alive and capable of active resistance.

The mode of falling, together with spatial distribution of decay, was critical to diagnosis. Windthrow was distinguished by the presence of an upended root ball or root plate. Roots or stems that broke in the absence of decay had splintered fracture surfaces that remained relatively intact where they were exposed to the atmosphere. In contrast, breakage that involved decay was brash, showed evidence of decay on the fracture surface, and was often somewhat eroded. Because snapping of intact stems just above the groundline was very rare in these forests (Rizzo 1986), snapping

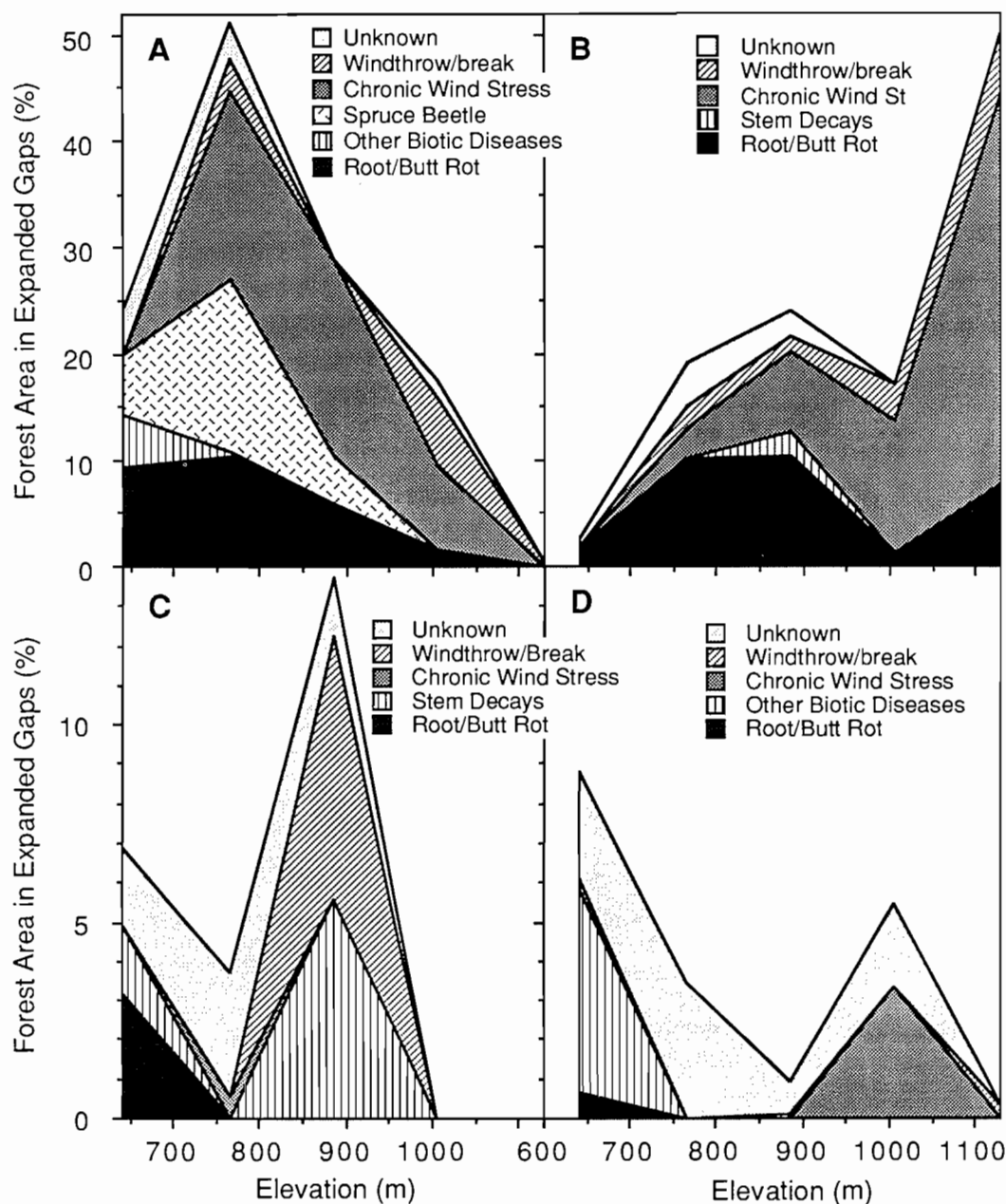


FIG. 3. Percentage of forest area occupied by expanded gaps caused by mortality of red spruce (A), balsam fir (B), yellow birch (C), and other hardwoods (D). Gap area is apportioned to disturbance agents for each tree species on the basis of the basal area of gapmakers. Note that the graphs have different scales for the y-axis.

at this height, together with the presence of a hollowed-out butt section, was used to diagnose the mortality as butt rot.

Fruiting bodies of decay fungi were only occasionally present, so diagnosis relied on isolation of the decay agent in pure culture. Samples of root and butt rot or stem heart rot were bagged and taken to the laboratory. Microscopic examination of the decay was used to identify certain distinctive fungi, but isolations were required to identify most causes of decay. Isolation and identification procedures were outlined by Rizzo and Harrington (1988a).

Root and butt rot was considered a primary agent if the tree snapped at the hollow butt or if, as happened occasionally, it died standing and had extensive decay of the sapwood in the major lateral roots and lower bole. Infections by *Armillaria* spp. (primarily *A. ostoyae* (Romagn.) Herink (= *A. obscura*)) were grouped with root and butt rots, but *Armillaria* caused mortality primarily through cambial necrosis rather than through the effects of advanced internal decay. Death was attributed to *Armillaria* spp.

if the fungus had colonized the root collar extensively and portions of the cambium were still alive, or if there was evidence of active host response against the fungus before tree death (Tippett and Shigo 1981).

Dead and nearby living canopy trees were inspected for evidence of chronic wind stress, particularly where contributing site conditions were evident (high elevation, exposure, shallow stony soil) (Harrington 1986a; Marchand et al. 1986; Rizzo and Harrington 1988b). Symptoms include characteristic small, terminal witches' brooms, crown shyness, wind flagging of emergent crowns, twig and branch dieback beginning at the tips, and root wounding with accompanying callusing and xylem discoloration (Rizzo and Harrington 1988b). Crown flagging in the absence of other symptoms was considered an adaptation to wind exposure rather than an indication of stress.

Stem swellings with cankers and resin streaming, and large systemic witches' brooms were indicative of dwarf mistletoe

(*Arceuthobium pusillum* Peck) infection on red spruce (Hawksworth and Shigo 1980). Dwarf mistletoe was considered a primary agent only when severe bole infections were present. Spruce beetle (*Dendroctonus rufipennis* Kirby), recognized by the presence of boring dust and (or) pitch tubes together with the characteristic galleries, was considered primary when dense galleries under the bark on the lower bole indicated mass attack (USDA Forest Service 1985). Trees killed by other agents may later be attacked by bark beetles, in which case the attacks would be more sparse and there would be little resinosis around the galleries.

Analysis

The fraction of land area in gaps was determined by Runkle's (1985a) method 4, a line-intersect method based on the areas of gaps intersected. Data are presented primarily in terms of expanded rather than actual gaps, for the following reasons: (i) the expanded gap is a realistic measure of area affected by the opening and is compatible with existing forestry literature (Runkle 1982); (ii) an estimate based on all expanded gaps that intersect the transect includes a larger sample and is thus more accurate than one based only on actual gaps; and (iii) field measurement at the base of the stem is much more accurate than measurement of the projection of the canopy edge at the ground surface.

The fraction of forest area in gaps at each elevation was apportioned to each disturbance agent and tree species, using a modification of Runkle's (1985a) line-intersect equation:

$$F_c = \frac{1}{L} \sum_{j=1}^n \left(\frac{(\pi \cdot A_j)^{1/2}}{2} \times \frac{BA_{cj}}{BAG_j} \right)$$

where F_c = fraction of forest area in gaps attributable to tree species or disturbance agent c , L = transect length, A_j = area of the j th gap, BA_{cj} = total basal area of all gapmakers in category c in the j th gap, and BAG_j = total basal area of all gapmakers in the j th gap.

Results

The elevations with the greatest area in canopy gaps were those in the lower spruce-fir zone (at 765 and 885 m), where 77 and 68%, respectively, of forest area was in expanded gaps (Fig. 2). The lowest level of gap area was in the upper spruce-fir zone, where 40% of the forest area was affected. Portions of the transects at two elevations (8% at 765 m and 13% at 1005 m) fell in nonforested areas such as rock outcrops or streams and were subtracted from the transects before calculations were made.

In total, 298 gapmakers were studied in 94 gaps. Twenty-seven gaps had one gapmaker, 31 gaps had two, and 13 gaps had three. Six gaps had more than 10 gapmakers, and 15 was the maximum number encountered in one gap. Mean expanded gap sizes at the five elevations, from lowest to highest, were 145, 118, 150, 43, and 45 m².

Over half the gap area at the lowest elevations was associated with red spruce mortality (Fig. 3). Red spruce and balsam fir both accounted for large portions of gap area at 885 and 1005 m, and fir was practically the only gapmaker at the highest elevation, in the fir phase of the subalpine zone (Fig. 3).

The relative importance of the various disturbance agents varied greatly with elevation (Fig. 4). Biotic diseases (root and butt rots, stem decays, cankers, and dwarf mistletoe) accounted for 66% of the gap area at the lowest elevation, but only 7 and 15% at the two highest elevations. Chronic wind stress and windthrow or windbreak increased strongly with elevation, accounting for almost 85% of the gap area at 1130 m. The spruce beetle was a major agent at lower elevations, where large, overmature red spruce were present.

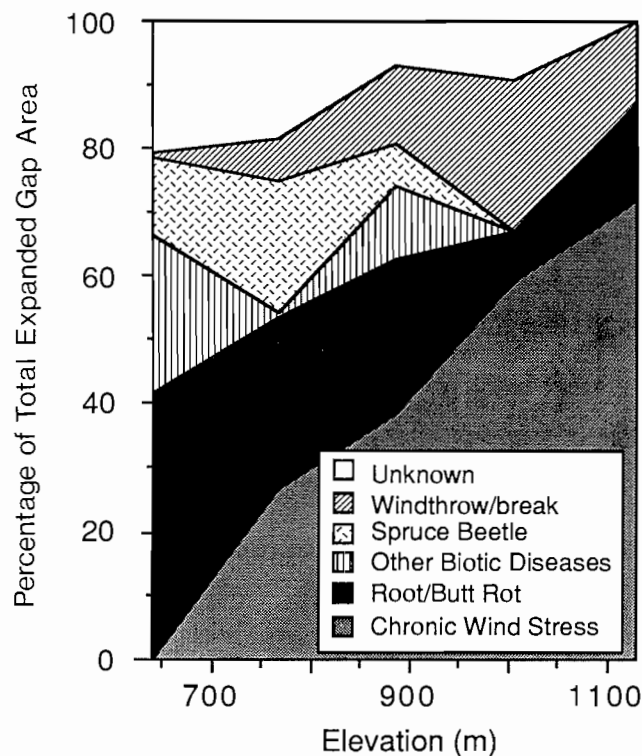


FIG. 4. Relative contribution of disturbance agents to expanded gap area at five elevations.

Gap area in the "unknown" category was largest at the lowest elevation (Table 1) and was associated primarily with hardwood gapmakers (Fig. 4).

Nineteen different biotic disease agents were identified as causes of canopy gaps (Table 1). At all elevations, root and butt rot fungi were by far the most important in terms of contribution to gap area. Of 14 isolates of *Armillaria* spp. obtained from gapmakers, all but 3 (all from *Acer* spp.) were identified as *A. ostoyae* on the basis of compatibility testing in diploid-haploid pairings (Harrington 1986b). *Armillaria* spp. were the major root and butt rot pathogens at the lowest elevation, but they were less common at 765 and 885 m and were not found at higher elevations. Most other root pathogens were also found more commonly at low than at high elevations (Table 1). Several other biotic diseases, such as dwarf mistletoe, beech bark disease, and stem decays, were most important at 640 m.

The disturbance regimes of the major tree species showed different elevational patterns, both in forest area involved and in relative contribution by disturbance agents (Fig. 3). For instance, at 765 m, where red spruce accounted for more gap area than at any other elevation, 34% of the gap area involving red spruce was due to chronic wind stress, and an almost equal portion was due to the spruce beetle (Fig. 3A). In contrast, balsam fir is not attacked by the spruce beetle, and at 765 m, only 13% of the gap area associated with balsam fir was due to chronic wind stress. Most balsam fir gap area at that elevation was due to root and butt rot, with windthrow and unidentified agents also contributing. Yellow birch (*Betula alleghaniensis* Britton) was most important as a gapmaker at 885 m, near the upper limit of its elevational distribution (Fig. 3C). Windthrow and stem decays were more prominent causes of yellow birch mortality at that elevation than at lower elevations, and more prominent for

TABLE 1. Percentage of total expanded gap area associated with each disturbance agent at the five elevations and the host species on which the agent was usually found

	640 m	765 m	885 m	1005 m	1130 m	Host
Root and butt rots						
<i>Armillaria</i> spp.	15.1	2.3	5.0	0.0	0.0	Ab, Ap, Ba, Pr
<i>Coniophora</i> spp.	4.6	0.0	0.0	0.0	1.9	Pr
<i>Climacocystis borealis</i>	7.6	0.0	1.2	0.0	0.0	Pr
<i>Resinicium bicolor</i>	0.0	0.4	0.0	0.0	0.0	Ab
<i>Resinicium</i> sp.	0.0	4.8	1.4	0.0	6.9	Ab
<i>Scytinostroma galactinum</i>	8.0	10.4	3.7	0.0	0.0	Ab, Pr
<i>Serpula himantoides</i>	0.0	0.0	3.7	0.0	0.0	Pr
<i>Oligoporus balsameus</i>	0.0	0.0	0.7	0.0	0.0	Ab
<i>Ustulina</i> sp.	4.0	0.0	0.0	0.0	0.0	As
<i>Xeromphalina campanella</i>	0.0	0.0	0.0	0.0	0.6	Ab
Unidentified butt rots	2.0	8.6	8.3	7.4	5.6	Ab, Ap, As, Pr
Total	41.3	26.5	24.0	7.4	15.0	
Stem decays						
<i>Cystostereum murraini</i>	3.7	0.0	0.0	0.0	0.0	Ba
<i>Haematostereum sanguinolentum</i>	0.0	0.0	3.0	0.0	0.0	Ab
<i>Inonotus obliquus</i>	0.0	0.0	0.7	0.0	0.0	Ba
<i>Oxyporus populinus</i>	0.3	0.0	0.0	0.0	0.0	Ap
<i>Phellinus igniarius</i>	1.1	0.0	0.0	0.0	0.0	Ap
<i>Phellinus lundellii</i>	0.0	0.0	5.6	0.0	0.0	Ba
<i>Phellinus pini</i>	0.0	0.5	0.0	0.0	0.0	Pr
Unidentified canker rot	0.0	0.0	2.0	0.0	0.0	Ba
Unidentified stem rot	0.0	0.0	0.3	0.0	0.4	Ab
Total	5.1	0.5	11.6	0.0	0.4	
Beech bark disease	9.7	0.0	0.0	0.0	0.0	Fg
Dwarf mistletoe	10.3	0.0	0.0	0.0	0.0	Pr
Spruce beetle	12.1	21.1	6.5	0.0	0.0	Pr
Chronic wind stress	0.0	27.0	38.7	59.4	71.8	Ab, Pr
Windthrow or windbreak	0.6	6.6	12.2	24.0	12.9	Ab, Ap, Ba, Bc, Pr
Unknown	20.8	18.3	7.0	9.3	0.0	

NOTE: Ab, *Abies balsamea*; Ap, *Acer pensylvanicum*; As, *Acer saccharum*; Ba, *Betula alleghaniensis*; Bc, *Betula cordifolia*; Fg, *Fagus grandifolia*; Pr, *Picea rubens*.

that species than for the other species (Fig. 3).

In 38 gaps, more than one primary mortality agent was diagnosed (on different trees). In gaps at the middle and upper elevations that were originally caused by windthrow or root disease (usually stem breakage of butt-rotted trees), sudden exposure of neighboring canopy trees appeared to lead to mortality as a result of chronic wind stress. Seventeen gaps had a combination of agents that included chronic wind stress with either root and butt rot or windthrow or windbreak. Particularly at lower elevations, combinations of apparently unrelated disturbance agents resulted in gaps of mixed etiology. Asynchronous mortality and gap expansion were also evident in some gaps with only one major disturbance agent, such as root pathogens.

Coincidence of several agents on a single tree was also common. For instance, trees killed by spruce beetle often had mistletoe or root and butt rot that may or may not have predisposed the tree to beetle attack. On the other hand, light spruce beetle attacks were often found on trees killed by other agents, in which case the beetle was considered secondary. *Armillaria* spp. were common secondary agents at lower elevations, where the fungus appeared to saprophytically colonize hosts killed by other agents such as spruce beetle. At most elevations, butt rot was present in some trees but was not advanced enough to be considered a primary mortality agent.

Discussion

Roughly half of the forest area at Crawford Notch was affected by gap-phase disturbance (measured as expanded gaps) in our study. Large-scale disturbance, such as landslides and wave-regeneration sequences, occupied another 15% of the forest area, according to an earlier study (Foster and Reiners 1983). Despite a region-wide correlation of red spruce mortality (based solely on standing-dead trees) with elevation (Johnson and Siccama 1983), we found no trend of increasing gap-phase disturbance with elevation. However, red spruce was not the only gapmaker species and not all gapmakers died standing.

Gapmakers and disturbance agents

As previously noted (Foster and Reiners 1983), red spruce was the dominant gapmaker at lower elevations, where there was an abundance of large red spruce trees. The conspicuous standing mortality of overstory red spruce is attributable in large degree to mass attacks by the spruce beetle. Once a prominent cause of spruce mortality (Hopkins 1901), *D. rufipennis* has been at low population levels throughout much of the range of red spruce. However, an outbreak apparently occurred in the Crawford Notch area around 1980–1982 (T. C. Harrington, personal observation). As with many bark beetles, large, overmature trees are most

susceptible to attack, and high beetle populations are needed to cause mass attacks that can kill otherwise healthy trees (USDA Forest Service 1985). Also important on red spruce at lower elevations were dwarf mistletoe and root and butt rot diseases.

Although a strict comparison is complicated by the fact that their values incorporate density and include all stems of ≥ 5 cm DBH, the relative importance values (RIV) of the tree species, as determined by Foster and Reiners (1983), generally followed the same elevational trends as the gap area caused by mortality of the respective species. At some elevations, however, species were more or less important as gapmakers than would be expected on the basis of their RIV.

At some sites, major disturbance agents that affect primarily canopy-sized or mature trees may be of disproportionate importance to particularly susceptible species. For instance, gap area contributed by yellow birch, in contrast with its RIV, increased to a maximum at 885 m, near the upper limit of its elevational range. Windthrow or windbreak and stem decays were responsible for almost all that gap area. Broken branches and wounds associated with ice and wind damage can serve as infection courts for the stem rot fungi found in yellow birch (Lavallee and Lortie 1968). Thus, increasing wind speed and ice damage with increasing elevation may result in more stem decay, windthrow, and snapped stems in canopy-sized yellow birch at its highest elevations.

Another situation that might lead to the disproportionate importance of a species as a gapmaker is a recent increase (epidemic) of a host-specific disturbance. Of the agents identified on red spruce, the spruce beetle is a good candidate for this kind of change at lower elevations. Bark beetle populations fluctuate greatly with time, and much of the forest area at the lower elevations at Crawford Notch may now be at a successional stage conducive to an epidemic. Overmature trees are more susceptible than younger trees and, if windthrown, are ideal substrates for explosion of beetle populations (USDA Forest Service 1985).

On the other hand, gap area contributed by balsam fir at 1005 m was lower than would be expected by the trend of its RIV with elevation. The incidence of root and butt rot on fir was particularly low at this elevation, but the reason for this is unknown. Also, crown architecture and canopy structure of stands dominated by balsam fir may be particularly adapted to the severe winds found at upper elevations. A more detailed analysis of stand structure, conducted in concert with the study of disturbance, is needed to interpret patterns of disturbance and their relationships to forest structure and dynamics.

At lower elevations, root and butt rots were important factors, particularly affecting balsam fir. Balsam fir is very susceptible to root pathogens (Basham and Morawski 1964; Rizzo 1986; Rizzo and Harrington 1988a; Worrall and Harrington 1988). Thus, balsam fir may be relatively unimportant as a stand component on the lower slopes, partly because of the abundance of root pathogens there (Rizzo and Harrington 1988a).

Canopy turnover

The amount of gap-phase disturbance in Crawford Notch is high relative to the amount in other forests (Runkle 1985a, 1985b). To determine whether disturbance could occur continuously at this rate and allow the stand to maintain itself, the return interval of disturbance can be compared with

longevity of canopy trees. The return interval can be calculated as gap life-span (the average age at which gaps are no longer recognizable as such) divided by proportion of forest in actual gaps. Estimates of gap life-span are highly variable in other temperate forests (Runkle 1982) and could not be reliably determined at Crawford Notch (Foster and Reiners 1986). Long suppression periods for red spruce (D. C. LeBlanc, personal communication; Hornbeck et al. 1986) and the nonrandom distribution of disturbance in space further complicate such an analysis, tending to lengthen the expected longevity of canopy trees, based on return interval. Data needed to reliably evaluate such canopy dynamics include gap age distribution, age of regeneration at the time of disturbance, and an analysis of randomness of disturbance. A tentative analysis based on the data at hand suggests that the middle-elevation forests at Crawford Notch may not be in steady state, as Foster and Reiners (1986) have suggested. The recent spruce beetle epidemic argues against the assumption that the forest is in a steady state, and could account for a recent increase in disturbance.

Conclusions

The causal agents of mortality of both standing-dead and fallen trees could be identified in most cases. A wide variety of biotic and abiotic agents was responsible for canopy gap formation, and these agents varied greatly in relative importance with forest type and elevation. Gap etiology was complex and, as noted by Foster and Reiners (1986), was rarely restricted to a single event.

The activities of disturbance agents are regulated in part by dynamic processes such as stand maturation and succession, which may influence the disturbance regime through effects on species composition, tree vigor, and competition among canopy trees. Therefore, the disturbance regime we have documented should be regarded as representing only one point in time. In view of the variation encountered on one mountainside, it is also clear that the relative importance of these specific disturbance agents cannot be generalized to other forests.

The disturbance agents encountered in this study are known to be capable of causing tree death, and criteria were established to eliminate from consideration those agents in purely secondary roles, colonizing or affecting trees only during or after tree death. Thus, although the possibility cannot be ruled out that other agents such as pollutants may have stressed trees at Crawford Notch and rendered them more susceptible to natural disturbance agents, such a hypothesis is not necessary to explain most of the mortality that we observed. Further research on natural disturbance agents in spruce-fir forests is needed, both to determine how they influence stand composition and dynamics, and to evaluate the possible influence of exogenous factors, such as air pollutants, on these known, natural agents of disturbance.

Acknowledgements

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