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Structure and spatial patterns of trees in old-growth northern hardwood and mixed forests of northern Maine

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Abstract

Stand structure including spatial patterns was studied in northern hardwood and mixed forest types in the 2000-ha old-growth Big Reed Forest Reserve in northern Maine using complete stem mapping, dendrochronology, and spatial analyses on ~ 0.5 ha plots. The inclusion of saplings, dead wood, age distributions, spatial pattern, and interactions provided some idea of underlying processes and temporal change. Structural characteristics were most comparable to spruce-northern hardwood forests of northern New England and New York, and most characteristics matched expected patterns for old-growth forests of the region.

Results indicated smaller maximum-tree sizes, lower basal areas (26–34 m^2/ha) and downed-wood volumes (29–64 m^3/ha), higher densities (475–649 stems/ha), but similar species longevities compared to other mesic old-growth forests further south and in the Lake States. The stands were dominated by very shade-tolerant tree species, including *Fagus grandifolia* Ehrh., *Acer saccharum* Marsh., *Picea rubens* Sarg. and *Abies balsamea* (L.) Mill, with each species found in many crown positions and age and size classes. The sapling layer was dominated by *Fagus grandifolia* followed by *Picea rubens*. Most species had reverse-J shaped diameter distributions, but age distributions were indicative of synchronous, episodic recruitment. In most plots, *Acer saccharum* diameter distributions were skewed towards the mid-larger size classes. Lack of young and small *Acer saccharum* stems suggested change in forest composition towards *Fagus grandifolia* dominance. Most species formed small-scale clusters ($\leqslant 15$ m) perhaps in response to small gap disturbances. Snags were the dominant dead wood type and were randomly to regularly distributed in most plots. Logfall directions were unrelated to hurricane paths. Recent small-scale disturbance events and topographic position appear to be important in explaining current structure and dynamics of the hardwood and mixed forests of Big Reed Forest Reserve in northern Maine. The continued effects of beech bark disease had a greater effect on hardwood plots, whereas a recent spruce budworm outbreak had a greater effect on plots with higher conifer density.

The dominance of very shade tolerant tree species in small-scale clusters, and randomly distributed snags rather than clustered uproots were indicative of the prevalence of small scale gap disturbance regimes in the hardwood and mixed forests of Big Reed Forest Reserve in northern Maine. Varying topographic position may allow for slight changes in disturbance regime leading to consequent variation in structure and dynamics. H1, a more open plot on upper exposed slopes, had distinctly different characteristics such as lower live and dead tree and sapling densities than the other plots, but more uprooted trees and *Acer saccharum* saplings. Such small scale gap disturbance regimes operating on an episodic basis, and effects of slight variations in this regime on stand composition and structure have significant implications for silvicultural interventions and management of these forest types.

Introduction

The few remaining old-growth forests in the northeastern United States are considered repositories of valuable information regarding the potential nature of pre-settlement forests in the region, as well as examples of how present-day forests might look in the absence of significant human manipulation. A general conceptual definition of old-growth includes relatively old age of the forest and minimal direct human disturbance (Hunter 1989), at least during and since the European settlement period. Details about natural species composition, disturbance history, forest structure, and function have all been unearthed by studying the remaining stands (e.g., Cline and Spurr (1942); Bormann and Buell (1964); Leak (1973, 1974); Henry and Swan (1974); Martin (1977); Foster (1988); Moesswilde's (1995)). Dendroecological studies in old-growth forests have also been used to identify long-term trends and changes in climate, natural disturbance, and vegetation (Conkey 1986, 1988; Hornbeck et al. 1986; Foster 1988; Cook and Cole 1991). Old-growth forests also serve as a baseline for monitoring the effects of long-term changes in climate and atmospheric deposition patterns.

Old-growth forests in Maine remain little studied (other than Davis (1966); Conkey (1988); Moesswilde's (1995); Hagan and Grove (1996)). The Acadian forest type represents a unique mix of species, being in the transition zone between boreal conifers and temperate northern hardwoods (Nichols 1935). Extrapolation from other northeastern U.S. sites may not be wholly valid due to the presence of regional differences. In this paper, we characterize tree composition, structure, and spatial patterns of northern hardwood and mixed forests of the Big Reed Forest Reserve in northern Maine, and compare their characteristics to those of other old-growth forests in the Northeast.

Mixed (26–75% conifer composition) and northern hardwood (>75% hardwood composition) forests are among the less studied forest types in Maine, though they comprise 30% of the state's timberland area (Powell and Dickson 1984) and are gaining in importance in the state's economy with the recent decline of the spruce-fir resource (Seymour and Lemin 1989). Studies by Davis (1966); Conkey (1988); Moesswilde's (1995) were all in the old-growth spruce-fir type. The interaction of *Abies balsamea*, *Picea rubens*, and northern hardwood species (e.g., *Acer saccharum*, *Fagus grandifolia*) in mixed forests is of particular interest given its uniqueness to the region, the number of shade-tolerant species that coexist within, and the potential effects of expected future climate change (Manabe and Wetherald 1980) on the relative competitive abilities of species in these forests.

Old-growth forests in Maine for the most part consist of small tracts (2–20 ha each) of single forest types (Maine Critical Areas Program 1983). These small tracts often may be atypical, having escaped the axe because of poor site productivity or inaccessibility. The biggest continuous tract of old-growth forest in this state is the ~2000 ha Big Reed Forest Reserve in northern Maine. Such a large area of old-growth forest increases the likelihood that it is representative of the natural landscape. The Reserve has a mix of stand types (including cedar swamps, spruce-fir flats, mixed forests, and hardwood forests) reflecting the range in elevations and soil drainage (Kasmer 1985; Widoff 1985). Cogbill (1985) suggests that there has not been much compositional change in the Reserve area since the time of the pre-settlement surveys in 1840.

Characterization of the composition, structure, and spatial patterns of these old-growth forests can be used to design conservation or management strategies for similar forest types. Further, there is increasing public demand that forests should be managed to look as "natural" as possible, and knowledge of old-growth characteristics in the region could help direct efforts in this regard. One important characteristic quantified in this paper is dead wood, about which relatively little is known in northeastern forests, especially in old-growth forests (Gore and Patterson 1985; Hagan and Grove 1996). Dead wood plays an important role in nutrient cycling (Harmon et al. 1986), provides micro-habitats for numerous species of flora and fauna (Maser et al. 1979; McClelland et al. 1979), and can influence the disturbance regime (especially fire and insect outbreaks) (Romme 1982). Also, adding in the dead tree component indicates changes in stand composition and structure over the recent past.

Most studies in the past have been descriptive of average stand structure, but there is increasing recognition that trees or plants are units that have distinct spatial locations that arise out of, and lead to, certain interactions, dynamics, and future development of the stand (Reed and Burkhart 1985; Penttinen et al. 1992; Moeur 1993). In this paper, besides the general average structural descriptors, we also deal with spatial patterning as an element of structure and to obtain some understanding of the possible underlying processes responsible for the structure. Most studies of spatial pattern are still based on quadrat counts (as in Daniels and Klinka (1996)) or samples taken at fixed intervals (Frelich and Graumlich 1994; Parshall 1995), both of which are limited in accuracy and confounded by problems of actual scale of vegetation pattern (Cressie 1993). In this paper, powerful point-based techniques (Diggle 1983) were used to detect spatial pattern in live and dead trees at multiple scales, based on actual locations of all trees.

Our objectives in this paper are to: 1) describe stand structure (tree species, size and age distributions, canopy structure and dead wood) of northern hardwood and mixed forest types in the Big Reed Forest Reserve, and 2) describe the spatial patterns and interactions of trees at multiple scales.

Study area

The ∼2000 ha Big Reed Forest Reserve is located in Township 8, ranges 10 and 11 W.E.L.S. in northern Piscataquis County, Maine (Figure 1), at latitude 46 ° 21′ and longitude 69 ° 3′. The area has been privately owned since 1844, and bears minimal evidence of timber harvesting in both historical records and field observations (Young 1982; Cogbill 1985; Kasmer 1985; Widoff 1985; Moesswilde's 1995). Ownership was transferred to The Nature Conservancy in 1984. (Cogbill 1985) suggests that the limited harvesting may have been due to the rugged nature of the site, its distance from suitable streams for transporting wood, perhaps a low merchantable volume in pine or spruce, and protection from recent logging by its owners. All of the area around the Reserve has been and is being intensively harvested to the present day (Young (1982); Cogbill (1985), and personal observation).

In Millinocket, Maine (the nearest weather station – see Figure 1), precipitation is relatively evenly distributed throughout the year; mean annual precipitation averages 106 cm and ranges from 79 to 150 cm (Baron et al. 1980). Mean annual temperatures average 5.3 °C and range from 3.7 to 7.5 °C, whereas mean monthly temperatures for January average −10.0 °C and range from −15.4 to −4.2 °C; for July they average 19.8 °C and range from 17.1 to 22.5 °C.

The topography of the Reserve is rugged with 62% of the landscape at 336–457 m above sea level, and 15% above 457 m (Maine Office of GIS; http://apollo.ogis.state.me.us/). Soils in the region are primarily Elliotsville-Monson and Telos-Monarda-Monson associations (Grisi 1985). The Big Reed landscape mosaic consists of mixed forests (46% of the area), conifers (36%), hardwoods (9%), and forested wetlands (6%) (Seven Islands Land Co. 1976). The spruce-fir type mostly occupies the poorly drained flats with some stands on steep mid-slopes. Mixed forests are mostly found on lower slopes, and some on the gentler or steeper sections of mid-upper slopes. Northern hardwoods occupy the well-drained, moderately steep mid-upper slopes. Forested wetlands are restricted to very poorly drained, low areas.

Sampling design and methods

Three (H1, H2, and H3) permanent 0.49 ha (70×70 m) sample plots were established in the northern hardwood type and two (M1 and M2) in the mixed forest type using information from 1992 aerial photographs, topographic and forest stand (Seven Islands Land Co. 1976) maps, and field checks. The exact locations were chosen at random within stands that were reasonably accessible around the Reserve (Figure 1). Cluster analysis supported plot classification into mixed and hardwood types (Chokkalingam 1998). The plots were subdivided into a grid of 49 subplots of 10×10 m each. Topographic and environmental characteristics (Table 1) were determined by averaging measurements across nine sample subplots systematically distributed over each plot. The two mixed plots (M1 and M2) were 351–381 m above sea level, on gentle slopes with NE-N-NW aspects (Figure 1). The hardwood plots were located within the largest, reasonably accessible stand of hardwoods in the Reserve. Two hardwood plots (H2 and H3) were 411–442 m above sea level, and plot H1 was at a higher elevation (442–503 m). All hardwood plots had S-SE aspects. H2 was located on the gentle terrain of a small hill, H1 and H3 on slightly steeper upper and lower slopes, respectively.

Within each plot, all trees (live and dead) $\geqslant 9.5$ cm diameter at 1.4 m height (d.b.h.) were tagged and mapped from subplot corners using a compass and measuring tape. For live trees, species, d.b.h., and crown class (dominant, codominant, intermediate, suppressed or gap) were recorded for each stem, and radial increment cores were taken at 1.4 m height above the ground. The term "crown class" is not being used in a strict silvicultural sense (Smith et al. 1997) where it applies to single-cohort monocultures, but its meaning with respect to crown position rela-

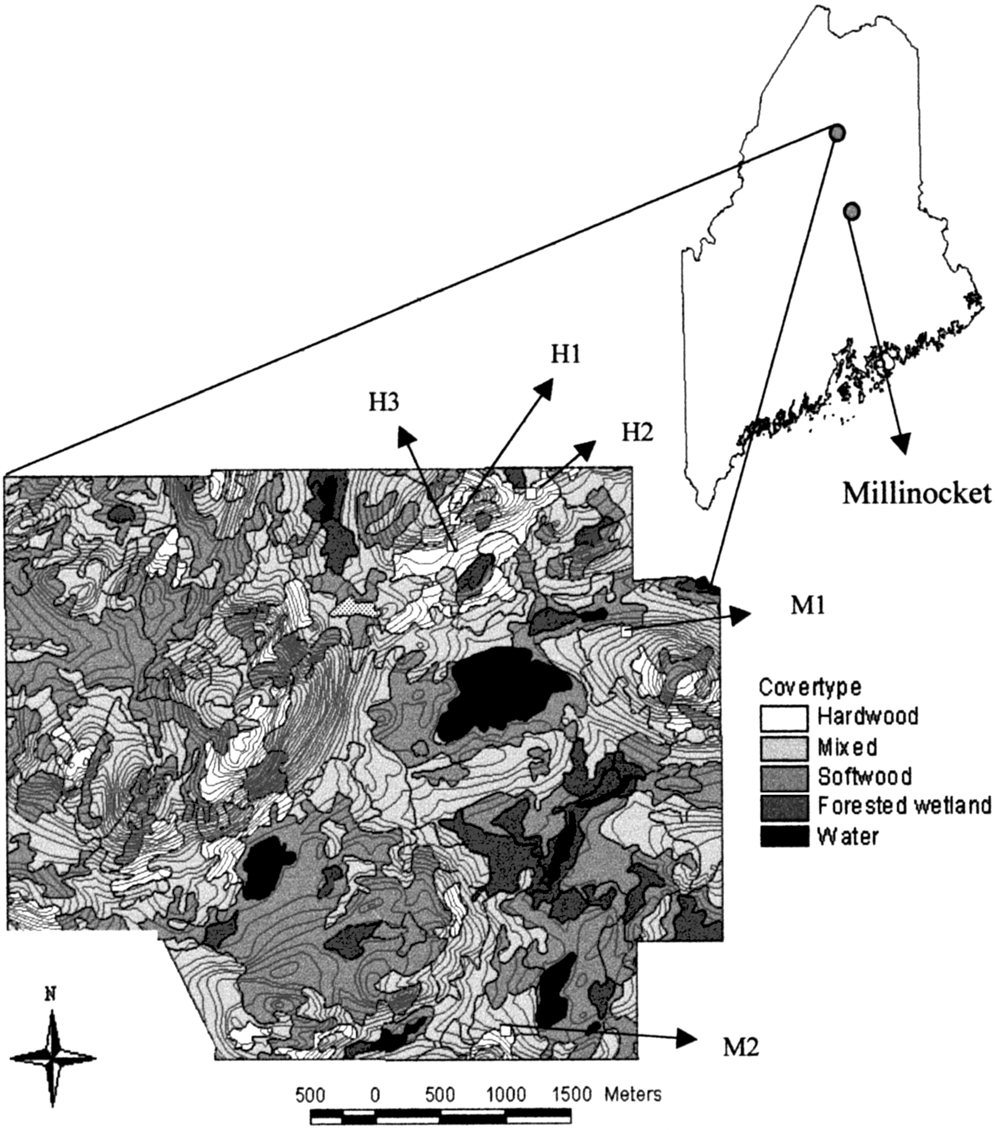

Figure 1. Big Reed Forest Reserve location, cover types, elevation contours, plot locations and nearest weather station in Millinocket, Maine.

tive to light availability is being retained. In these mixed multi-cohort stands, trees in the upper strata were classified as dominant, codominant, intermediate or suppressed. Trees in all lower strata were classified as suppressed (not receiving direct light from above) or gap (receiving direct light from above). Only dead trees that had some solid wood were tallied. For each dead tree, species, d.b.h. and type (uproot, snag or stump) was recorded. All downed logs >15 cm d.b.h. were mapped as to origin and orientation (direction of fall), and length, d.b.h., and species recorded. Within each 100 m^2 subplot, number of saplings (2.5–9.5 cm d.b.h.) were tallied by species.

All increment cores were sanded to a smooth polish and cross-dated by identifying and matching up marker years of slow radial growth recorded in most trees of a species (Schweingruber et al. 1990). Annual ring-widths were then measured using a Veimex measuring system to the nearest 0.01 mm and the raw ring-width series for each species and plot analyzed with the computerized cross-dating program "COFECHA" (Holmes 1983). Missing and absent rings were identified and corrected for on all cores as far as possible and age of each tree at 1.4 m height then determined. For cores that had missed the pith by <18 mm, pith locators were used to estimate the number

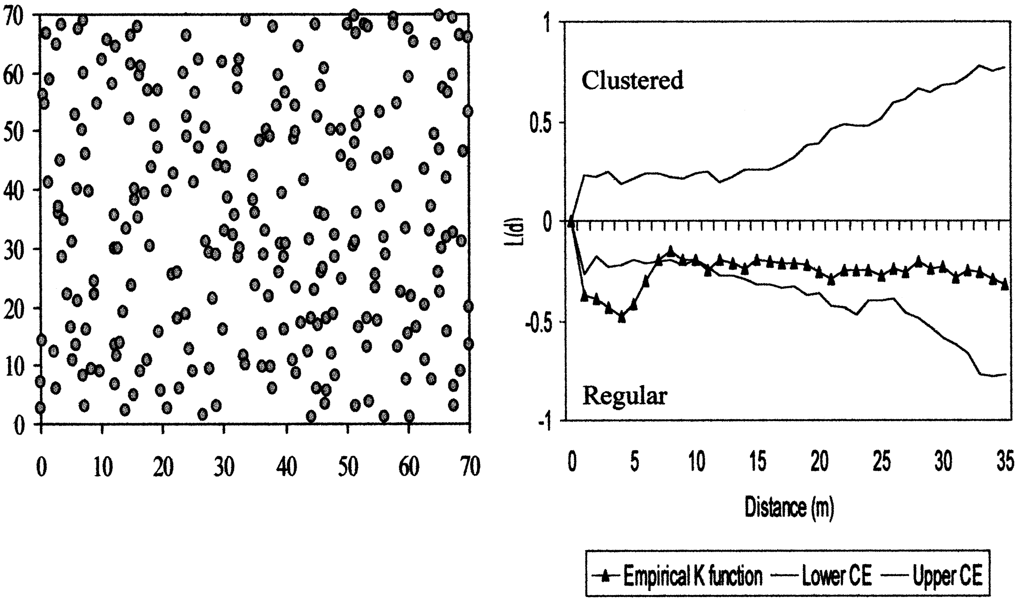

Figure 2. Distribution of live trees on plot M1 along with expected and empirical univariate K distributions and 95 % confidence envelopes.

Table 1. Topographic and environmental characteristics of sample plots in old-growth stands of the Big Reed Forest Reserve. H1 to H3 – hardwood plots, M1 and M2 – mixed plots.

Plot	% Slope	Aspect	Elevation (m)	Organic depth (cm)	Litter depth (cm)	Slope position
H1	23.4±7.6*	SE	442–503	3.2±0.5	2.2±0.8	upper
H2	14.8±8.6	S-SE	411–442	8.0±4.3	5.9±2.4	mid-top
H3	32.7±10.4	SE-S	411–442	3.2±1.1	1.9±0.5	low-mid
M1	8.2±4.0	N-NW	351–381	3.8±1.9	1.6±0.5	mid-upper
M2	15.5±5.7	NE-N	351–381	4.8±2.4	2.2±0.6	low-upper

*Mean±Standard Deviation.

of missing years from ring curvature and growth rate (Applequist 1958).

Basal area and density were calculated separately for live and dead trees of each species on each plot. Density of live + dead trees of different species as compared to density of live trees alone were used as indicators of changes in stand composition in the recent past. Diameters of live and dead trees, and downed logs were grouped into 5-cm size classes for each species and for all species combined on each plot. Live trees were also grouped into 10-year age classes for each species and for all species combined on each plot. The overall diameter distributions for live trees, dead trees, and downed logs were compared among plots using chi-square contingency table analyses (Zar 1996). Standardized deviates were used to look for the source of significant differences from expected values. Similarly, distributions of age-class, crown-class, and dead wood type were compared among plots and among species using chi-square analyses.

Spearman's rank correlation analyses (most diameter and age data were not normally distributed) were performed to determine if there were any strong relations between tree diameter and age for the four most common species, *Fagus grandifolia*, *Acer saccharum*, *Picea rubens*, and *Abies balsamea* (SYSTAT 1997). The analyses were done only in plots where there were 20 or more cores dated to the pith for the species.

Number of logs in each of eight orientations (of 45 ° each) were summarized for each plot, and distributions of orientation of downed logs were compared among plots and against expected uniform distributions using chi-square contingency table analysis. Volume of downed wood was obtained for each species on each plot as $\Sigma 1/3^{*}\pi r^{2}h$, where r = radius at 1.4 m height, and h = log length.

Empirical univariate K distributions of trees (live, dead, individual species, and dead wood type) were obtained using the Ripley's K Analysis program (Moeur 1995), and used to look for spatial dependence between points of the same type (e.g., one species) over a continuous range of spatial scales from 0 to 35 m. The K(d) distribution is the cumulative distribution function of the distance from all trees on a plot to all other trees (Ripley 1981), weighted to correct for boundary effects, and represents the expected number of trees within distance d of a tree. The reported value is L(d) which is a square root transformation that linearizes K(d), stabilizes its variance, and has an expected value approximately zero under the Poisson assumption. The model null hypothesis was that of complete spatial randomness of point locations. The empirical univariate K functions ($\check{L}(d)$) computed from the data were tested using 95% confidence envelopes obtained from 100 Monte Carlo simulations of a Poisson process. Significant departures of observed pattern from spatial randomness at a particular scale was indicated when $\check{L}(d)$ fell outside the envelopes, towards clustering if above the envelope, and towards regularity if below.

The bivariate K function was used to look for significant interactions between different species (Moeur 1993). The model null hypothesis was that of complete spatial independence between the two populations. The empirical bivariate K functions ($\check{L}_{12}(d)$) computed from the data were tested using 95% confidence envelopes obtained from 100 simulations under H_0. In the bivariate case, the Monte Carlo sequence preserves the background spatial patterns of the two species. The focus population is held constant, fixed in original locations. The second population is held constant in relative spatial distribution, but shifted randomly around the focus population in each Monte Carlo iteration. If $\check{L}_{12}(d)$ fell below the confidence envelope, there was significant spatial repulsion between the two populations and if above, there was significant spatial attraction at that scale.

Results

Density, dominance and species composition

Tree density ranged from 475–649 stems/ha, basal area from 26–34 m^2/ha, and sapling density from 763–1314 stems/ha (Table 2). Mixed plot M2 had the highest density and basal area of live trees and also low basal area and density of dead trees. Plots M1, H2 and H3 had similar densities and basal area of live trees, but M1 had much higher density and basal area of dead trees (almost equal to that of live trees) and densities of live and dead saplings. Plot H2 had relatively high density of dead trees and live saplings, whereas H1 had low density of dead trees and saplings.

Table 2. Tree ($\geqslant$9.5 cm d.b.h.) and sapling (2.5–9.5 cm d.b.h.) abundance in old-growth stands of the Big Reed Forest Reserve. H1 to H3 – hardwood plots, M1 and M2 – mixed plots.

Plot	*Live trees*		*Dead trees*		*Sapling density*	
	Density	Basal Area	Density	Basal Area	Live	Dead
H1	475.5	27.4	181.6	12.7	763.3	181.6
H2	516.3	26.1	302.0	12.7	1055.1	275.5
H3	514.3	29.4	228.6	12.7	875.5	269.4
M1	512.2	29.6	451.0	27.0	1314.3	398.0
M2	649.0	33.7	189.8	9.5	783.7	263.3

Basal area in m^2/ha, density in stems/ha.

The hardwood plots were dominated by very shade-tolerant *Fagus grandifolia* and *Acer saccharum* (Table 3). *Fagus grandifolia* was the dominant species in terms of stem density (almost 50% of total), but *Acer saccharum* occupied roughly 75% of the total basal area in all three plots. *Picea rubens*, *Ostrya virginiana* (Mill.) K. Koch and *Abies balsamea* formed a minor component. In plot H1, which occurred at the highest elevation, *Abies balsamea* was absent and *Fraxinus americana* L. was present. Intermediate and tolerant species such as *Betula alleghaniensis* Britton and *Acer rubrum* L. were almost non-existent and there were no intolerant species. *Fagus grandifolia* also dominated the sapling layer (72–93%) in the hardwood stands, with 8 and 14% *Ostrya virginiana* in H3 and H1, and 10% *Acer saccharum* in H1 (Table 4).

Stem density and basal area in mixed plots were dominated by several species including *Picea rubens*, *Fagus grandifolia*, *Acer saccharum* and *Abies balsamea* (Table 3). *Ostrya virginiana*, *Acer rubrum*, and *Betula alleghaniensis* formed a small component in both plots. In addition, plot M1 had some *Tsuga canadensis* (L.) Carr, *Thuja occidentalis* L., and *Acer pensylvanicum* L., and thus the greatest tree-species richness. Neither of the plots had any intolerants. *Fagus grandifolia* dominated the sapling layer in mixed plots as well (82% in M1 and 45% in M2, Table 4). M2 also had 35% *Picea rubens*, 10% *Abies balsamea*

Table 3. Species composition (live tree density/ha (D) and basal area in m^2/ha (B)) of old-growth stands of the Big Reed Forest Reserve. H1 to H3 – hardwood plots, M1 and M2 – mixed plots.

Plot	H1		H2		H3		M1		M2	
	D	B	D	B	D	B	D	B	D	B
Species										
Acer saccharum$^{\bigcirc}$	186	21	206	18	173	22	55	5	82	15
Fagus grandifolia$^{\bigcirc}$	222	5	231	6	233	5	208	6	147	6
Picea rubens$^{\bigcirc}$	12	0	45	1	31	1	110	8	249	7
Abies balsamea$^{\bigcirc}$	0	0	16	0	45	1	45	1	157	4
Ostrya virginiana$^{\bigcirc}$	33	1	8	0	33	1	20	1	8	0
Tsuga canadensis$^{\bigcirc}$	0	0	0	0	0	0	20	5	0	0
Acer pensylvanicum$^{\bigcirc}$	0	0	0	0	0	0	12	0	0	0
Acer rubrum*	0	0	6	1	0	0	12	1	2	1
Thuja occidentalis*	0	0	0	0	0	0	8	1	0	0
Betula alleghaniensis**	0	0	4	0	0	0	18	2	4	0
Fraxinus americana**	22	1	0	0	0	0	0	0	0	0
Total	476	27	516	26	514	29	512	30	649	34

$^{\bigcirc}$very shade tolerant, *shade tolerant, **intermediate (Sources: Daniel et al. (1979); Burns and Honkala (1990)). Some discrepancies depending on site and region: *Picea rubens* very tolerant to tolerant, *Thuja occidentalis* very tolerant to intermediate.

Table 4. Density/ha of live/dead trees ($\geqslant$9.5 cm d.b.h.), and live/dead saplings (2.5–9.5 cm d.b.h.) of dominant species in old-growth stands of the Big Reed Forest Reserve. H1 to H3 – hardwood plots, M1 and M2 – mixed plots.

	Plot				
Species	H1	H2	H3	M1	M2
Trees					
Fagus grandifolia	223/88	231/174	233/112	208/120	147/94
Acer saccharum	186/39	206/25	173/33	55/ 0	82/12
Picea rubens	12/20	44/61	31/14	110/73	249/18
Abies balsamea	0/2	16/14	45/16	45/80	157/4
Saplings					
Fagus grandifolia	545/92	978/157	753/182	1088/94	355/18
Acer saccharum	80/22	12/8	8/2	4/0	4/0
Picea rubens	20/24	43/94	41/51	41/135	278/171
Abies balsamea	0/0	2/6	0/22	31/125	76/59

and 8% *Ostrya virginiana* whereas M1 had 10% *Acer pensylvanicum* in the sapling layer.

In plots H1, H2, and M1, there were equal or more dead *Picea rubens* and/or *Abies balsamea* than there were live stems (Table 4). In comparison, 28–43% of *Fagus grandifolia* stems were dead, and 11–17% of *Acer saccharum* stems in all plots (except in M1 where there was no dead *Acer saccharum*). Plot M2 had very low proportions of dead *Abies balsamea* and *Picea rubens* compared to other plots. In the sapling layer, there also were more dead than live *Picea rubens* and *Abies balsamea* in all plots but M2, where there was a high density of live saplings of both species. In hardwoods, 50–67% of the dead saplings were *Fagus grandifolia* with only 14–34% *Abies balsamea* and *Picea rubens*. However, 87% (M2) and 57% (M1) of the dead saplings in mixed forests, were *Abies balsamea* and *Picea rubens*.

Size and age structure

Of all trees, 15–21% were >35 cm d.b.h., and 3–9% were >50 cm d.b.h. (Figure 3). *Acer saccharum* and *Tsuga canadensis* attained the largest sizes and ages of all species on the plots, whereas *Abies balsamea*, *Fraxinus americana* and *Acer pensylvanicum* did not reach great sizes or ages (Table 6). *Fraxinus americana*, *Ostrya virginiana*, *Abies balsamea* and *Acer pensylvanicum* were mostly $\leqslant$25 cm d.b.h. in all plots, along with *Picea rubens* in hardwood plots (Figure 3). Most (89–97%) *Fagus grandifolia* were <35 cm d.b.h. *Picea rubens* in mixed plots and the few *Betula alleghaniensis*, *Thuja occidentalis*, and *Acer rubrum* were scattered through the range of size-classes.

The size-class distributions of live trees on all plots were reverse-J shaped with a slight peak at mid (31–45 cm d.b.h) size-classes in most plots (Figure 3). Chi-square contingency table analysis indicated significant differences among plots ($\chi^2_{36,\,<0.001}=130.31$). Standardized deviates indicated that M1 had more than expected in the sapling category, with less than expected in the 10–15 cm class. H1 had more than expected in 10–15 and >50 cm classes, and

Table 5. Spatial patterns and interactions derived from univariate and bivariate K distributions of species in old-growth stands of the Big Reed Forest Reserve. Scale of clustering was small (≤ 15 m), mid (15–28 m), and large (>28 m). Bivariate association was − (negative), + (positive) or 0 (neutral) between indicated species at indicated scales.

	Univariate K distribution results				
Plot	*F. grandifolia*	*A. saccharum*	*P. rubens*	*A. balsamea*	Other species
H1	small-large	small	—	—	random
H2	small	small	—	—	small
H3	small	random	—	—	small, large
M1	small	small-mid	small	—	large
M2	random	random	small-mid	small-mid	—

	Bivariate K distribution results		
Plot	*F. grandifolia*	*A. saccharum*	*P. rubens*
H1	− AS small-mid	+ other mid	—
H2	− all small	+ other small	—
H3	− all small-mid	0 other	—
M1	0 all	− PR small	—
M2	− all small-large	0 PR and AB	+ AB large

AS - *Acer saccharum*, PR - *Picea rubens*, AB - *Abies balsamea*, other species - included *Picea rubens* and *Abies balsamea* in hardwood plots, H1 to H3. M1 and M2 - mixed plots.

M2 less in the sapling class and more in the 15–25 cm classes.

Abies balsamea and *Picea rubens* had reverse-J shaped diameter distributions for live trees in H1, H3, and M2, and for total trees (live plus dead) in H2 and M1 (Figure 3). *Fagus grandifolia* also displayed a tendency towards a reverse-J shape diameter distribution with small peaks in mid-larger size-classes in all plots but M2 (Figure 3). *Fagus grandifolia* in plot M2 was bimodal with two strong peaks at <15 cm and 21–25 cm size-classes. The pattern did not change even when dead trees were added in.

Acer saccharum did not approach a reverse-J shape distribution of size-classes on any plot (Figure 3). In plots M2 and H3, *Acer saccharum* was present in larger numbers in the larger size-classes, unimodal in M2, and bi-tri modal in H3 with peaks in larger size-classes. In plots M1 and H2, *Acer saccharum* diameter distribution was bimodal (mid-large size-classes) and in plot H1, it was tri-modal (lots of very small, medium and large trees). Adding in dead trees did not alter the overall pattern for *Acer saccharum*.

All plots were uneven or irregular-aged with three apparent recruitment peaks – early 1800s, 1860s–70s and 1920s–40s, each 60 years apart (Figure 4). Recruitment in recent decades was not included because only a small proportion of trees <9.5 cm d.b.h. were cored. *Fagus grandifolia* and *Ostrya virginiana* recruitment followed the three peaks closely. *Acer saccharum* recruitment occurred on all plots in the early 1800s and 1860s–70s, but only in H1 in the 1920s–40s. *Picea rubens* also followed the three recruitment peaks, but the first peak was a little delayed and variable from plot to plot. In addition the mixed plots also had some *Picea rubens* regeneration in the early 1900s. *Fraxinus americana* (in H1), *Acer pensylvanicum* (in M1), and *Abies balsamea* were primarily recruited in the 1920s–40s period, and *Betula alleghaniensis* in the 1870s.

Diameters of all species were significantly correlated with age except for *Abies balsamea* in plot H1 (Table 7), but the correlation coefficients were not very high except for *Acer saccharum* in H1 (0.85). There was a wide range of sizes for a given age class, and of ages for a given size class (Figure 5). The strength of the relationship varied considerably among plots and species (Table 7).

Canopy structure

For all species, a lower percentage of trees were suppressed in mixed plots compared to hardwood plots (Table 8). Few trees were in dominant positions and hence the dominant and codominant classes were combined. Approximately equal numbers of trees

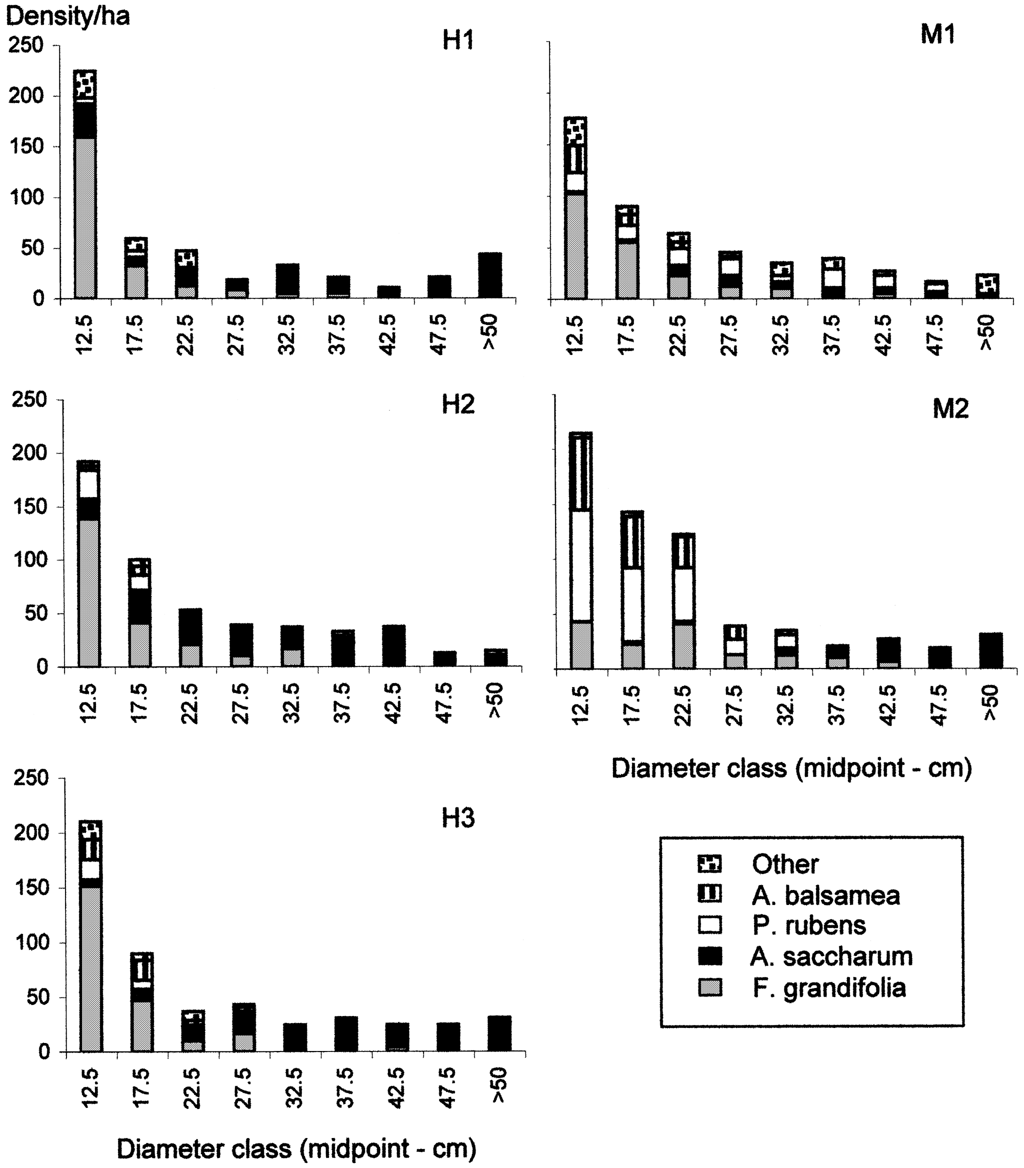

Figure 3. Diameter distributions by species for live trees on five sample plots. Sapling (2.5–9.5 cm d.b.h.) numbers were very high and are not depicted.

were in suppressed, intermediate, and codominant plus dominant positions in hardwood plots, whereas 46% and 53% of the trees were in codominant plus dominant positions in M2 and M1, respectively, with 2% in gaps (Figure 6). Chi-square contingency table analysis indicated that there were significant differences in crown class distributions among plots ($\chi^2_{8,\,<\,0.000}=58.99$). There were more trees in M1 in the codominant plus dominant class, less in M2 in the intermediate class, and less in H1 in the codominant plus dominant class. M1 had a low proportion (13%) of suppressed trees.

Abies balsamea and *Picea rubens* had the highest proportion of stems in the suppressed class followed by *Fagus grandifolia* (Table 8). Most *Fagus grandifolia* in hardwood plots were in intermediate to suppressed positions, whereas in mixed plots, they were codominant to intermediate (Figure 6). *Acer saccharum* were mostly codominant everywhere. *Picea rubens* and *Abies balsamea* were mostly suppressed in hardwood plots, but occurred in all crown classes

Table 6. Maximum tree sizes and ages by species on the sample plots in old-growth stands of the Big Reed Forest Reserve.

Species	Max. d.b.h. (cm) at 1.4 m height	Max. age (years)
Tsuga canadensis	79.6	436
Acer saccharum	76.4	313
Acer rubrum	66.5	193
Thuja occidentalis	53.0	154 +
Betula alleghaniensis	51.8	188 +
Picea rubens	49.3	246
Fagus grandifolia	48.0	213
Ostrya virginiana	33.6	192
Abies balsamea	31.7	93 +
Fraxinus americana	23.8	156
Acer pensylvanicum	16.3	56

+ cores incomplete due to heart-rot.

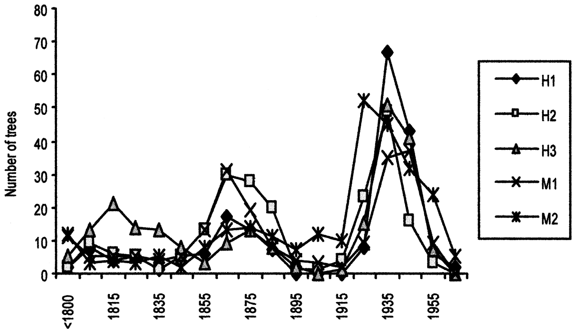

Figure 4. Age distributions of trees ⩾ 9.5 cm d.b.h. on five sample plots.

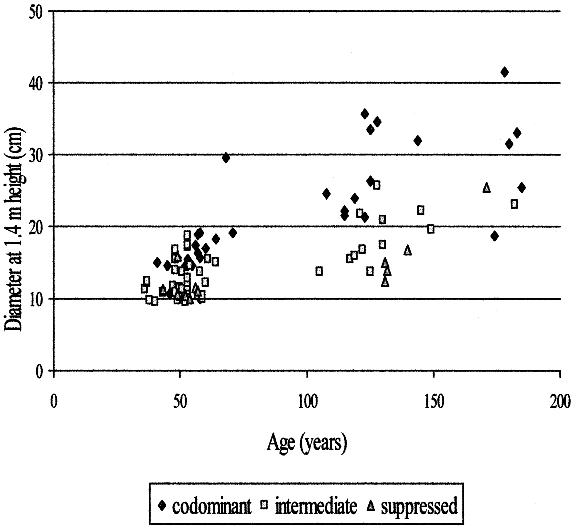

Figure 5. Age versus diameter at 1.4 m height for *Fagus grandifolia* on plot M1.

Table 7. Spearman's rank correlation coefficient between d.b.h. and age for the four most common species on plots where n > 20; in old-growth stands of the Big Reed Forest Reserve. H1 to H3 – hardwood plots, M1 and M2 – mixed plots.

Species	Plot H1	H2	H3	M1	M2
Fagus grandifolia	0.43^{b}	0.61^{b}	0.47^{b}	0.69^{b}	0.74^{b}
Acer saccharum	0.85^{b}	0.53^{b}	0.26^{a}	0.53^{a}	—
Picea rubens	—	0.70^{b}	—	0.58^{b}	0.31^{b}
Abies balsamea	—	—	0.28	—	0.39^{b}

^{a}significant at ∝ = 0.05, ^{b}significant at ∝ = 0.01.

in mixed plots. The few *Tsuga canadensis* in M1, which were also old and large, were in codominant positions. Other less common species were of codominant or intermediate crown class in all plots.

Spatial patterns and interactions of live trees

Live trees overall were randomly distributed on all plots except for a minimum distance (2–7 m) between trees (e.g., Figure 2). In plots H2 and H3, live *Fagus grandifolia* were clustered at small spatial scales around 10 m, and strongly negatively associated with all other species at small-mid scales up to 18 m (Table 5). In plot H3, *Acer saccharum* trees were randomly dispersed, and independently distributed relative to "other species" (i.e., species besides *Fagus grandifolia* and *Acer saccharum* in hardwood plots), which in turn were strongly clustered at 7–15 m and >34 m. On plot H2, *Acer saccharum* and "other species" were clustered at small scales <12 m and positively associated with each other at scales of 11–12 m. On H1, *Fagus grandifolia* was clustered at 10–31 m, and independently distributed of "other species", which in turn were randomly to regularly distributed. *Acer saccharum* trees were clustered at small scales <12 m on H1, and negatively associated with *Fagus grandifolia* up to about 19 m, but clustered with "other species" at 22–24 m.

In mixed plot M1, live *Fagus grandifolia* and *Picea rubens* were clustered at small scales around 10 m, and *Acer saccharum* at 7–25 m (Table 5). All other species combined in M1 were concentrated only at large scales (29–34 m). *Fagus grandifolia* was independently distributed with respect to *Picea rubens* and *Acer saccharum*, whereas *Picea rubens* and *Acer saccharum* were negatively associated with each other at 14–15 m. In plot M2, live *Fagus grandifolia* and *Acer saccharum* were randomly-regularly distributed, and *Picea rubens* and *Abies balsamea* (strong

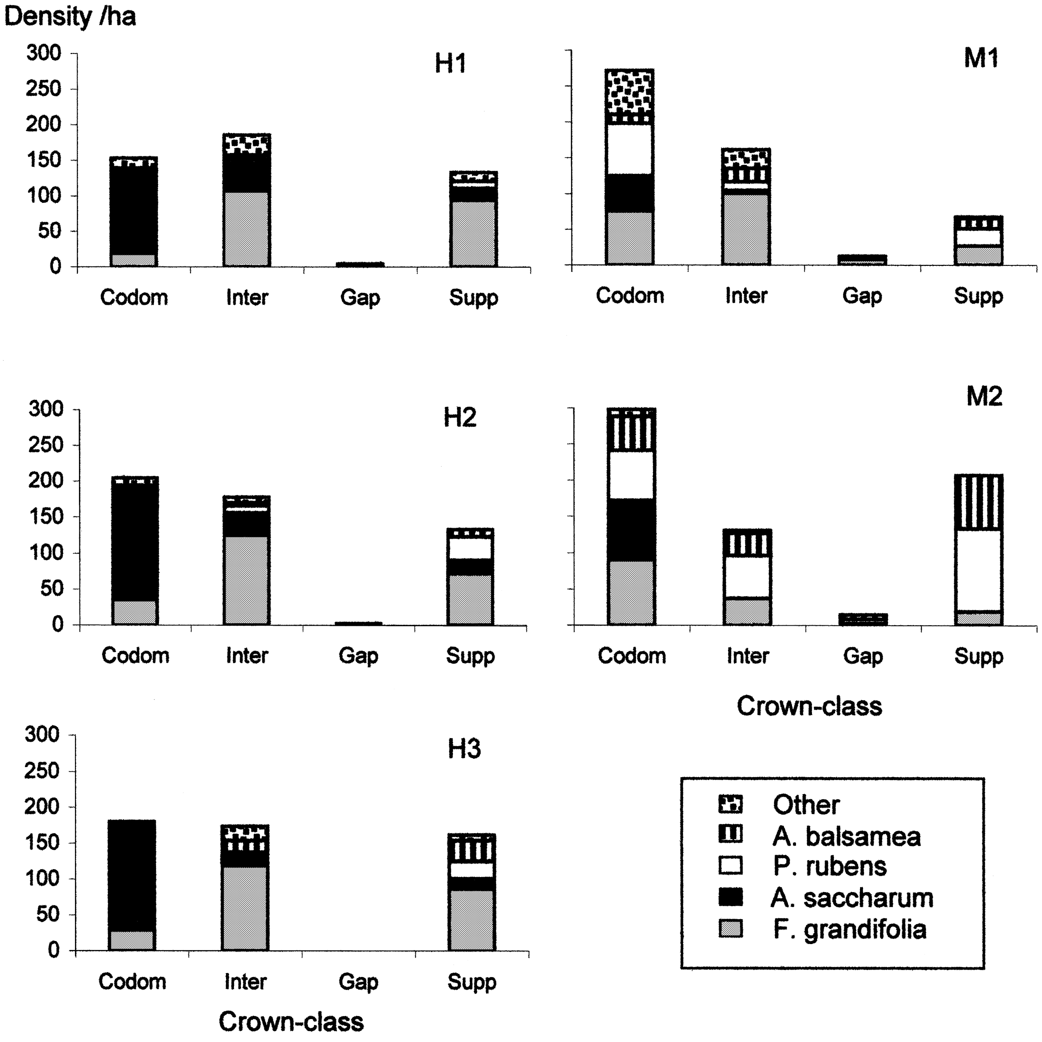

Figure 6. Crown-class (codominant + dominant, intermediate, gap and suppressed) distribution by species on sample plots.

Table 8. Percentage of trees of each species under suppressed conditions in hardwood and mixed plots; in old-growth stands of the Big Reed Forest Reserve.

	Hardwood			*Mixed*	
Species	H1	H2	H3	M1	M2
Acer saccharum	9	9	8	0	0
Ostrya virginiana	29	0	25	0	0
Fagus grandifolia	42	31	37	12	13
Abies balsamea	—	63	64	32	47
Picea rubens	83	73	80	22	46
Other species	10	0	—	2	0
All species combined	29	26	31	13	32

peak at 16 m) were clustered at 2–27 m. *Fagus grandifolia* was negatively associated with all the other species, including *Picea rubens* at 11–16 m, *Abies balsamea* at ⩾26 m, and *Acer saccharum* at 7–11 and 15–18 m. *Acer saccharum* had a neutral relationship with the two conifer species, which in turn were clustered together at large spatial scales ⩾25 m.

Dead wood: type abundance and spatial patterns

In plots H2, H3 and M2, dead trees were also randomly to regularly dispersed, whereas in H1 and M1, they were clustered at small spatial scales <10 m. Snags made up 32–66% and uprooted trees 20–35% of the total density of dead trees. Snag density was 80–151 stems/ha (8–20 snags/ha >35 cm d.b.h.) and uprooted tree density was 31–90 stems/ha (6–20 uproots/ha >35 cm d.b.h.). There was a relatively

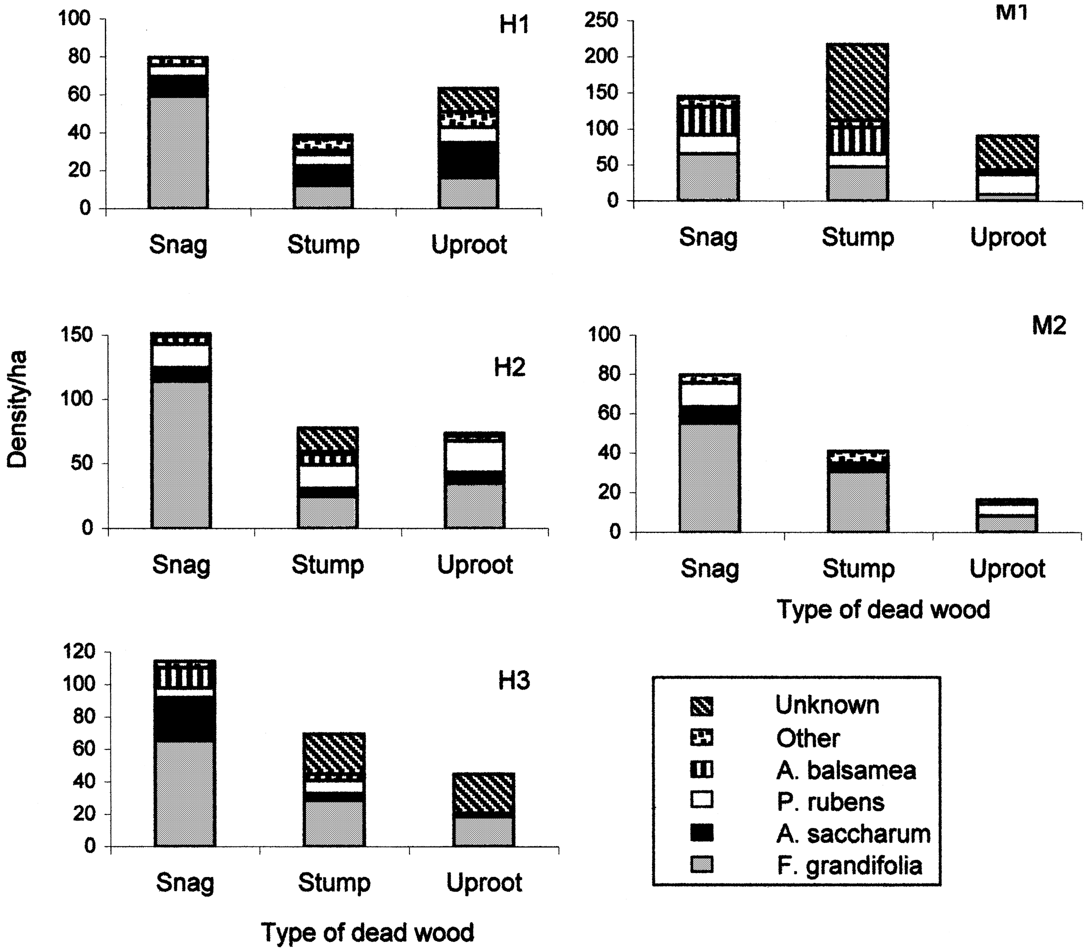

Figure 7. Density of dead wood type by species on sample plots.

even distribution of dead trees among stumps, snags and uprooted across size classes lines with no particular sizes of trees tending to uproot or be snags.

Overall, chi-square contingency table analysis indicated significant differences between plots in the type of dead material present ($\chi^2_{8,0.00}=38.33$) (Figure 7). Plots H2, H3 and M2 had more snags, then stumps followed by uproots, and the snags were randomly to regularly distributed. Plot H1 had fewer stumps and more uprooted trees than expected, and the dominant dead wood type, snags, were clustered at 2–9 m. Plot M1 had more stumps and fewer snags than expected, and there was a strong clustering of uprooted trees at 5–14 m and stumps at 9–12 and 15–16 m.

Most dead *Fagus grandifolia* (54–67%) were snags and only a small proportion were uprooted (Figure 7). Most dead *Acer saccharum* were snags but a considerable proportion were uprooted as well in H1 and H2. Dead *Abies balsamea* were mostly snags or stumps, whereas dead *Picea rubens* were mostly snags or uproots.

Volume of downed wood >15 cm d.b.h. ranged from 31–39 m^3/ha in plots M2, H1 and H3, whereas there were 57 and 74 m^3/ha in M1 and H2, respectively. Log density ranged from 116–190 stems/ha. In most plots, 29–39 stems/ha, or 18–23% of the logs were $\geqslant 35$ cm d.b.h (Figure 8). In H1, 30% of the logs were $\geqslant 35$ cm d.b.h. Log diameter distributions were not significantly different between plots as per chi-square analysis. Downed wood volume was largely (68%) comprised of *Acer saccharum* in H1, *Acer saccharum* and *Fagus grandifolia* in M2 and H3, *Picea rubens* in M1, and all three species in H2.

Downed log orientation was significantly different between plots ($\chi^2_{7,<0.001}=85.72$) and not uniformly distributed ($\chi^2_{7,<0.005}=21.5$ to 54.9) (except in H2) (Figure 9). In two plots (H1 and H3) with steeper

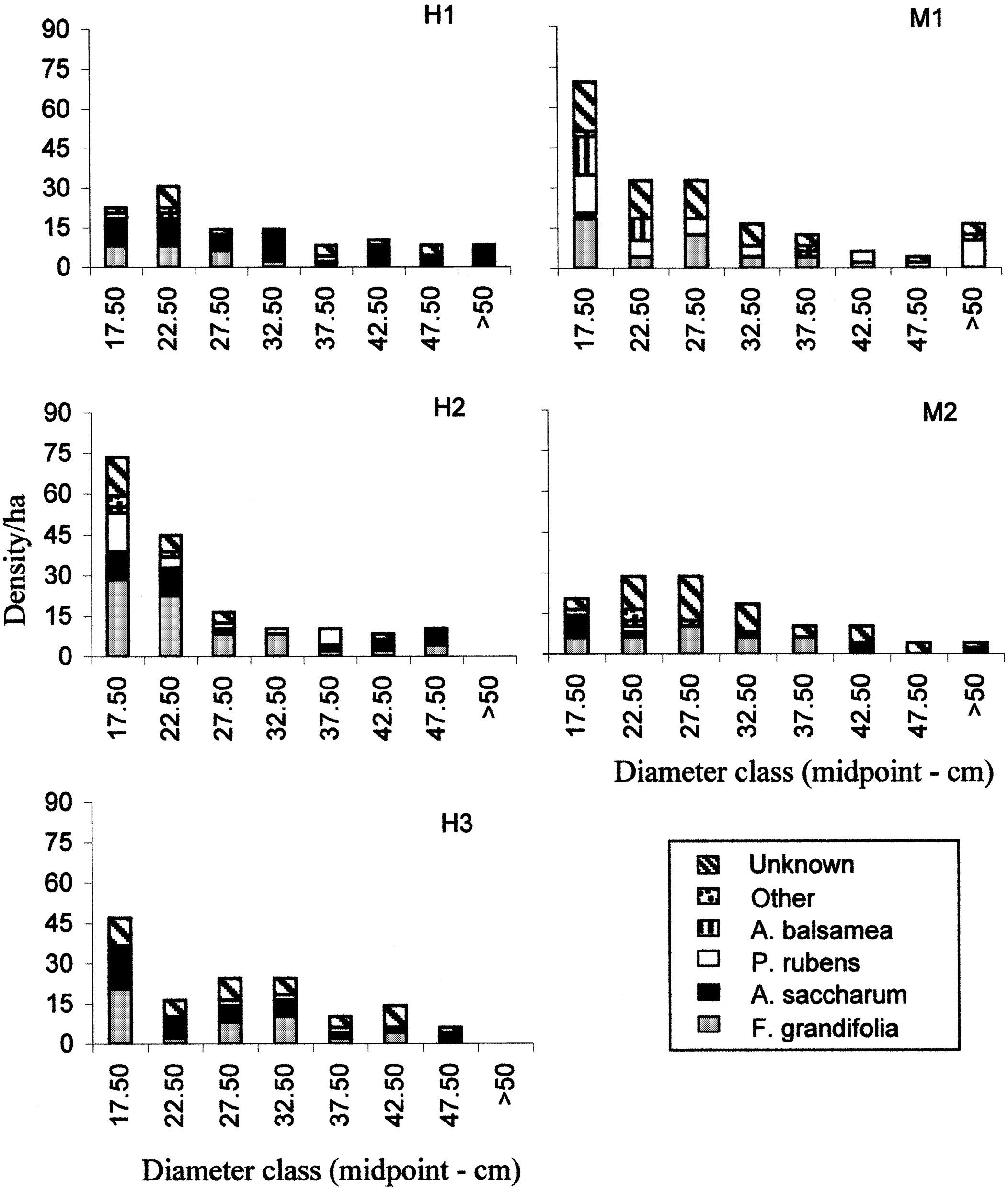

Figure 8. Log diameter distributions by species on five sample plots.

slopes, most downed logs followed the aspect of the plot, i.e., southeast-south. In H2, a plot with gentler slopes, orientation of downed logs was not different from a uniform distribution. In the two gentle slope, low elevation mixed plots, there was some directionality in orientation beyond that of falling downhill. In M1 (aspect north-northwest), downed logs were mostly oriented north-northeast-east, and in M2 (aspect northeast-north), downed logs were oriented in any direction between north-east-south. There were only a few logs with southwest-west-northwest orientations on both plots.

Discussion

Density, dominance and species composition

Basal area values (26–34 m^2/ha) and live tree densities (475–649 stems/ha) for the northern hardwood

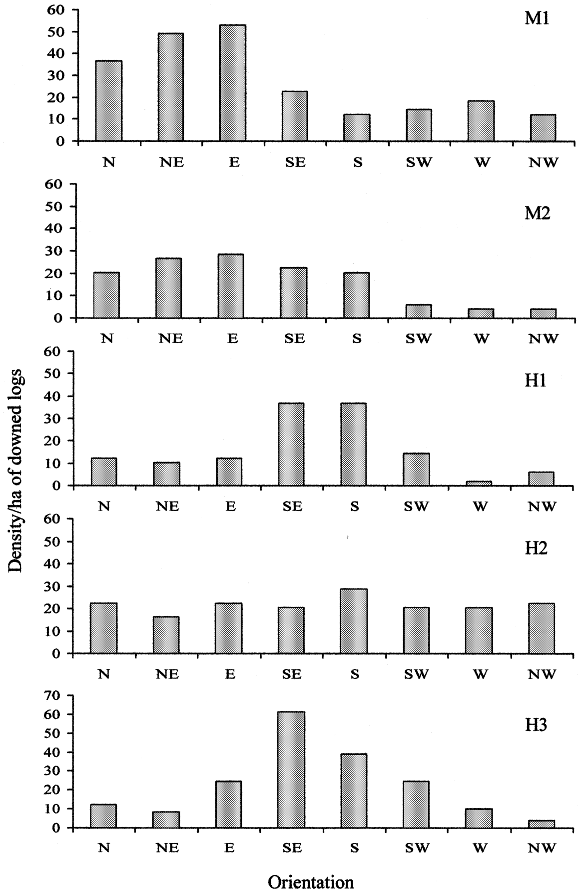

Figure 9. Downed log orientation on sample plots.

and mixed forest types at Big Reed Forest Reserve were comparable to that of the spruce-northern hardwood forests of New Hampshire (22–30 m^2/ha, 566 stems/ha) (Leak 1973; Martin 1977; Gore and Patterson 1985; Leak 1987), and the Adirondacks, New York (29–35 m^2/ha, 535 stems/ha) (Leopold et al. 1988; Whitney 1994). Other northern hardwood forests and mixed hemlock-white pine-northern hardwood forests in northwestern Pennsylvania, the Lake States, and Vermont generally had higher basal areas (∼>40 m^2/ha) and lower densities (283–450 stems/ha) (Morey 1936; Stearns 1951; Bormann and Buell 1964; Whitney 1984; Mroz et al. 1985), but in Massachusetts, basal areas (34–37 m^2/ha) were similar though densities (347–415 stems/ha) were lower again (Dunwiddie and Leverett 1996). Mixed mesophytic forests in the central hardwood region had lower densities (160–456 stems/ha) and a wide range of basal areas (23–60 m^2/ha) (Whittaker 1966; Parker 1989; Martin 1992; Boerner and Kooser 1991; Muller and Liu 1991). Spruce-fir forests of Maine and New Hampshire generally had higher basal areas (>40 m^2/ha) and densities (>700 stems/ha) (Oosting and Billings 1951; Foster and Reiners 1983). The low basal areas in spruce-northern hardwood associations in northern Maine when compared to north-central and more southern forests of similar type could perhaps be related to climatic factors, i.e., shorter growing season which restricts tree growth (Whitney 1994).

Overstories and understories of both mixed and hardwood plots were dominated by very shade-tolerant tree species with relatively low importance of tolerant to intermediate species, and no intolerant species at all. The dominance of shade-tolerant species corresponds with expectations based on pre- or early-settlement surveys of forests in Maine (Cary 1894; Hosmer 1902; Lorimer 1977). One of the mixed plots (M1), with higher disturbance in recent times (as suggested by high abundance of dead trees and saplings), did have greater diversity though still no intolerant species such as *Betula papyrifera* and *Populus* spp. Hardwood plots were dominated by *Acer saccharum* (in basal area) and *Fagus grandifolia* (in density), with the addition of *Picea rubens* and some *Abies balsamea* in mixed plots. Saplings were mainly *Fagus grandifolia* in all plots with the addition of *Picea rubens* in mixed plots. All of this is suggestive of low disturbance levels that kept out intolerant species and allowed release of very shade-tolerant saplings in the understory and dominance of the forest by them. Overstory composition was similar to that of spruce-northern hardwood associations of northern New Hampshire (Martin 1977; Foster and Reiners 1983; Leak 1987; Gemborys 1996; Crow et al. 1994; Royte et al. 1996) with perhaps a lower proportion of *Betula alleghaniensis*. Composition also was comparable to northern hardwood forests in the Northeast, except for the addition of *Picea rubens* and *Abies balsamea*, and a lower proportion of *Tsuga canadensis* and *Betula alleghaniensis* (Nichols 1913; Hough and Forbes 1943; Bormann and Buell 1964; Siccama 1971; Foster 1988; Woods and Cogbill 1994; Dunwiddie and Leverett 1996). Lack of *Acer saccharum* saplings in most plots in this study suggested potential change in forest composition towards *Fagus grandifolia* dominance in hardwood plots except in the more open exposed plot H1. However, considerable *Acer saccharum* was observed in the seedling layer in all plots, and *Acer saccharum* being more gap opportunistic than *Fagus grandifolia* (Canham 1985, 1990), could be successfully recruited into the canopy given larger frequent gap occurrences (Poulson and Platt 1996). Similar transition tendencies towards *Fagus grandifolia* dominance at the expense of *Acer saccharum* was observed by Brisson et al. (1994) in an old-growth forest in southern Quebec in the absence of perturbation. In the Bowl, New Hampshire, and in central Vermont, sapling composition was similar to the overstory composition of *Fagus grandifolia* and *Acer saccharum* (Bormann and Buell 1964; Leak 1973; Martin 1977).

Each shade-tolerant species was found in many different canopy positions. In mixed plots, smaller proportions of all species were found in suppressed conditions though density of stems overall was higher or comparable with that of the hardwood plots, perhaps due to more conical, compact crowns and greater area in gaps at the current time (personal observation), and thus greater light penetration.

Size and age structure

Ages of different species in the hardwood and mixed forests of Big Reed Forest Reserve approached the maxima found in other similar eastern old-growth forests, 200–350 years for the hardwoods, and 200–400 years for the conifers (Nichols 1913; Oosting and Billings 1951; Bormann and Buell 1964; McIntosh and Hurley 1964; Leopold et al. 1988; Brisson et al. 1992; Blozan 1994; Dunwiddie et al. 1996; Dunwiddie and Leverett 1996). Maximum age of 246 years for *Picea rubens* was on the lower end (Cogbill (1996) found >300-year old *Picea rubens* in Maine, New York and New Hampshire). Maximum sizes (Table 6) of different species were much smaller than those found in similar eastern old-growth forests, 85–130 cm for *Tsuga canadensis*, >90 cm for *Acer saccharum*, 60–98 cm for *Fagus grandifolia*, 67–78 cm for *Picea rubens*, 120–135 cm for *Betula alleghaniensis* and *Fraxinus americana* (Nichols 1913; Cline and Spurr 1942; Bormann and Buell 1964; Leak 1973; Cogbill 1996; Dunwiddie and Leverett 1996), but were comparable for *Tsuga canadensis* and *Acer saccharum* in the Lake States (Stearns 1951). Maximum ages and sizes for *Acer saccharum* and *Fagus grandifolia* were more comparable to those in Quebec (Brisson et al. 1992).

Tree species at the Reserve were found in numerous size and age classes as expected based on pre- or early-settlement surveys of forests in Maine (Cary 1894; Hosmer 1902; Lorimer 1977). For all species combined, and for *Picea rubens*, *Abies balsamea* and *Fagus grandifolia* individually, size-class distributions were reverse-J shaped with slight peaks at mid size classes, presumed to be indicative of continuous recruitment and thinning. Lorimer (1980) suggested that relatively light disturbances could cause the small diameter peaks due to gap responses of understory stems. *Acer saccharum* was skewed towards larger sizes in plots M2 and H3, with very few small stems. In plots M1 and H2, it was bimodal, leaning to the mid-large size classes, and in H1, it was trimodal, the only plot with small *Acer saccharum* stems. Similar to the results from this study, *Fagus grandifolia*, *Picea rubens*, and *Abies balsamea* in the Bowl, New Hampshire had reverse-J shaped diameter distributions, and *Acer saccharum* had a bimodal distribution, though at small-mid size classes (Leak 1973). Brisson et al. (1992) found a flat diameter distribution for *Acer saccharum* but a reverse-J shaped distribution for *Fagus grandifolia* in Quebec.

Age distributions were uneven but not all-aged. There were definite episodic recruitment peaks for all species (as in Hett and Loucks (1976); Lorimer (1980); Payette et al. (1990); Moesswilde's (1995); Cogbill (1996)), and not the negative exponential or power function distributions as expected for long-lived shade-tolerant species (Hett 1971; Leak 1975; Hett and Loucks 1976). Long-lived shade-tolerant species were represented in all age class peaks, except for *Acer saccharum*, which in the 1920s–40s period was recruited mainly in H1, the only plot with young and small *Acer saccharum*. In contrast, in the Bowl in New Hampshire, Leak (1974) and Leak (1975) found that *Fagus grandifolia* and *Acer saccharum* had negative exponential or power function distributions characteristic of stationary populations, whereas *Picea rubens* had a bell-shaped age structure characteristic of a declining population. Parshall (1995) found that *Acer saccharum* with a negative exponential diameter distribution was replacing *Tsuga canadensis* with its bell-shaped distribution, because of frequent drought events in Upper Michigan. Almost all species had synchronous episodic recruitment patterns in the Big Reed Forest Reserve. Such age class peaks could be due to disturbance and/or drought (Lorimer 1980).

Correlations between age and diameter were significant for the dominant species but rather weak except for *Acer saccharum* in H1, the relatively open plot with *Acer saccharum* present in even the small size and age classes. Each age class had a wide range of diameters and each diameter class had a spread of ages as found by Moesswilde's (1995) in the spruce/fir forests in the same Reserve, Tyrrell and Crow (1994a) in north-central hemlock-hardwood forests, and Oosting and Billings (1951) in northern hardwoods in the White Mountains, New Hampshire. Risks associated with inferring age structure from size structure are evident in this study. Age structure was more episodic than would be inferred from the diameter distribution alone. This is to be expected particularly in stands dominated by shade-tolerant species where vertical stratification may occur (Smith et al. 1997). Differential growth and mortality rates, and suppression in the understory with periodic gap release of any aged-stems in the area disturbed could result in poor correlations between diameter and age (Oosting and Billings 1951).

Spatial patterns of live trees

The random distribution of live trees could be related to maximum occupancy of space. Spatial patterns of individual tree species appeared to be related to life history characteristics, recent disturbance patterns, and structural characteristics such as tree sizes, and provided insight into the processes underlying stand composition and structure.

Fagus grandifolia, a heavy-seeded, very shade-tolerant species found in numerous strata formed small-scale clusters, perhaps the effect of clustering around parent trees (Tubbs and Houston 1990), root sprouting (Russell 1953; Ward 1961), and also release in small gaps. Root sprouting is abundant in forests following outbreaks of beech bark disease, including Maine and the Adirondacks of New York (Houston 1975), and small gaps are the predominant disturbance type in the mixed and hardwood forests of the Big Reed Forest Reserve (Chokkalingam 1998). Clustering at small to large scales in H1 suggested release in small to large gaps on this more open exposed site. A random distribution in M2 was perhaps due to lower recent disturbance that restricted clustered release in gaps and promoted stem thinning. *Fagus grandifolia* was negatively associated with all other species in most plots, perhaps due to the clustering of shade-tolerant saplings around parent trees, and deep shade cast by the numerous crown layers (Canham et al. 1994).

Acer saccharum, a lighter-seeded (compared to *Fagus grandifolia*), shade-tolerant species (Godman et al. 1990), was randomly distributed in plots less disturbed in recent times (H3 and M2) with some clustering in more disturbed plots, perhaps relating to gap response. H3 and M2 were also the plots where *Acer saccharum* were mostly large codominant trees which could be expected to be randomly distributed. *Acer saccharum* was independent of or clustered with other species (other than *Fagus grandifolia*), perhaps due to the lighter shade cast by its crowns (Canham et al. 1994), and its ability to respond more strongly to gaps than *Fagus grandifolia* (Canham 1985, 1990; Poulson and Platt 1996). *Abies balsamea* and *Acer saccharum* were found to have relatively similar regenerative traits in terms of strong response to small canopy gaps (Houle and Payette 1991). *Abies balsamea* and *Picea rubens* were clustered at small-mid scales in mixed plots indicating gap response. Other species (including *Abies balsamea* and *Picea rubens*) formed small-scale clusters in H2 and H3 responding to gaps in a beech-dominated matrix, and forming large-scale concentrations in H3 due to within-site topographic variation. In H1, the more open plot, they were randomly distributed.

Contrary to the results in this study, northern hardwoods including *Acer saccharum* and *Fagus grandifolia* in Ontario and Indiana were found to be nearly randomly distributed in studies using quadrat and nearest neighbor measures (Payandeh 1974; Williamson 1975; Ward and Parker 1989), a result of either regional differences or methodology used. However, more shade-intolerant species and conifers were clustered at scales corresponding to gap sizes as in this study. *Fagus grandifolia* sprouts are relatively more important in the northeastern part of its range (Ward 1961), which could explain the increased tendency for clustering in this study.

Dead wood

In the present study, the sizeable proportion of dead *Picea rubens* and/or *Abies balsamea* (equal or more than live stems of the same species) in both the understory and overstory in all plots but M2 testified to the effects of the recent spruce budworm outbreak (~ 1976–85, (Seymour 1992)). Evidence of the budworm outbreak was also visible as radial growth declines (Chokkalingam 1998) on surviving spruce trees in all plots. The effects of the budworm outbreak on these plots were surprising considering that the higher species diversity and low conifer component of mixed and hardwood stands were expected to make them less vulnerable to budworm outbreaks compared to spruce-fir forests (Osawa et al. 1986; Irland et al.

1988). Also, *Picea rubens* was expected to be less susceptible than *Abies balsamea* to the budworm (Irland et al. 1988), but proportions of dead *Picea rubens* trees and saplings to live stems in our study were often equal to or higher than those for *Abies balsamea* (from Table 4). This appears to be in agreement with land managers' perceptions (Irland et al. 1988) that given high levels of infestation for a long enough time, both spruce and fir became equally vulnerable, and also the vulnerability of host species in mixed stands approached that of conifer stands.

In mixed plot M1, adding back the dead tree component suggested an increase in the proportion of hardwoods in the overstory and understory with a reduction in the conifer component as a result of the budworm outbreak (from Table 4). The hardwood plots were affected by both the recent bud worm outbreak and the continued effects of beech bark disease since the 1940s–50s (Houston 1975), and adding back the dead tree component suggests a reduction in the relative proportions of *Picea rubens*, *Abies balsamea*, and *Fagus grandifolia*, and an increase in the *Acer saccharum* component in the overstory (from Table 4). Similarly in the sapling layer, relative conifer density has decreased again, but *Fagus grandifolia* increased in two plots, and *Acer saccharum* in H1. Recent disturbance events appear to have slightly enhanced the hardwood component of the mixed plot M1, and the overstory *Acer saccharum* component and understory *Fagus grandifolia* component of the hardwood plots. Increase in understory *Fagus grandifolia* with mortality of canopy stems may be due to its root-sprouting ability (Houston 1975). Mixed plot M2 had surprisingly low numbers of dead *Picea rubens* and *Abies balsamea* and did not appear to have been affected much by the recent budworm outbreak despite relatively high spruce/fir composition. Plot M1 with lower spruce/fir proportions (even when adding back the dead tree component) and greater species diversity was affected more by the recent outbreak. Both plots had relatively similar age ranges and distributions.

Similar to Moesswilde's (1995) results for spruce/fir forests at Big Reed Forest Reserve, 22–33% of the total basal area was dead in most plots in this study as well. Also in the Adirondacks, New York, 20–35% of the basal area was dead in hemlock-northern hardwood, spruce-northern hardwood, and spruce-fir forests (Leopold et al. 1988). In M1, a mixed plot in this study more affected by the recent spruce budworm outbreak, 47% of the basal area was dead. Cogbill (1996) reported that dead basal area nearly equaled or exceeded live basal area in most old-growth spruce-fir stands across Maine, New Hampshire, New York and Vermont. Total dead basal area in the mixed and northern hardwood forests in the Reserve (i.e., 10–16 m^2/ha) corresponded with that in northern hardwood and hemlock-northern hardwood types in the Northeast, whereas values were much higher in spruce-fir forests (21–61 m^2/ha) (Leopold et al. 1988; Moesswilde's 1995; Cogbill 1996). Also standing dead basal area (4.2–7.0 m^2/ha, 11–19% of total standing basal area) in hardwood and mixed forests of Big Reed Forest Reserve were similar to the 0.9–7.1 m^2/ha and 3–15% in northern hardwood and hemlock northern hardwood types of the Northeast USA, and much lower than the 23–43% in spruce fir forests (Tritton and Siccama 1990; Dunwiddie and Leverett 1996). Spruce-fir types tend to occupy cooler, moister, more stressful, north-facing or higher-elevation environments, where there may be higher mortality and slow decay rates (Tritton and Siccama 1990).

Density of snags and logs >20 cm d.b.h. (39–65, and 94–120 stems/ha, respectively) at Big Reed Forest Reserve were much higher than the 5–12 snags and 51 logs/ha found in old-growth mixed mesophytic forests of Kentucky (McComb and Muller 1983; Muller and Liu 1991). However volumes of downed wood $\geqslant 20$ cm d.b.h. (29–64 m^3/ha - this study) were similar to the 47.8 m^3/ha in Kentucky (Muller and Liu 1991), suggestive of the smaller sizes of trees in northern Maine. Results from most other studies were not comparable due to differences in minimum sampling diameters and definitions for inclusion in dead class. Most dead *Fagus grandifolia* were snags, indicating the effect of the much-evident beech bark disease with gradual crown thinning, growth reduction and mortality of standing stems (Krasny and Whitmore (1992); Gavin and Peart (1993), and personal observation) in the aftermath forests. *Picea rubens* and *Acer saccharum* were found as either snags or uprooted trees, whereas *Abies balsamea* uproots were not common. *Picea rubens* and *Abies balsamea* in Vermont and New Hampshire also tended to die while standing due to widespread dieback and decline, in which insects and diseases, wind stress, and air pollution have all been implicated (Worrall and Harrington 1988; Perkins et al. 1992). Weakened trees were found more susceptible to windthrow. Whether a tree tended to get uprooted or form a snag did not appear to depend on its size in this study, whereas Brewer and Merritt (1978) found that larger trees were more likely to get uprooted in a northern hardwood forest in Michigan. Perhaps larger trees in the more sloping terrain of Big Reed Forest Reserve tended to bring down/uproot neighboring smaller trees in their path as they fell.

Plot H1, perhaps due to its exposed topographic position, had more uprooted trees, and also snags and dead trees overall formed small-scale clusters. In M1, the other more disturbed plot, dead trees were clustered at small scales because of uproot and stump clusters. In the three less-disturbed plots (H2, H3 and M2), snags were the dominant type of dead wood and were regularly to randomly distributed. Snags were also the predominant mode of mortality in hemlock-northern hardwood forests of the Lake States (Tyrrell and Crow 1994b), and in subalpine spruce-fir forests of the Northeast (Battles and Fahey 1996). The preponderance of snags over stumps and uprooted trees tend to favor the regeneration/slow release of shade-tolerant tree species (Jonsson and Dynesius 1993).

Downed-log orientation may be related to plot composition. In hardwood plots, if slopes were steep, downed logs were oriented downhill, else with no particular tendency. But in mixed plots, with gentler slopes, downed logs favored particular orientations not totally explained by plot aspect, there being a lack of southwest-west-northwest orientations. Treefalls were perhaps related to the passage of cold fronts (summer thunderstorms and winter gales) with a northwesterly peak wind direction, and also prevailing westerly winds through the year (Bormann and Likens 1979; Foster 1995). Hurricanes would have caused the opposite treefall direction (Foster and Boose 1992). Brewer and Merritt (1978) found that downed log orientations in a northern hardwood forest in Michigan were also related to wind direction, perhaps indicative of the greater importance of wind disturbances in that region that affect even the more strongly rooted hardwood-dominated forests. In a mixed mesophytic forest in Kentucky, Muller and Liu (1991) found that downed logs tended to be oriented downhill.

Conclusions

Structural characteristics of northern hardwood and mixed forests at the Big Reed Forest Reserve in northern Maine were most comparable to spruce-northern hardwood forests of northern New England and the Adirondacks, New York, especially The Bowl in New Hampshire, and most characteristics matched expected patterns for old-growth forests of the region. Hardwood and mixed forests at Big Reed Forest Reserve had distinctly different species composition, but they did not segregate out in terms of most structural characteristics. The plots occupied a range of values for each structural characteristic more related to topographic position and recent disturbance history than species composition. H1, a hardwood plot on upper exposed slopes, had distinctly different characteristics such as lower live and dead tree and sapling densities than the other plots, and was thus more open. Recent disturbance history in terms of the continued effects of beech bark disease had a greater effect on hardwood plots, whereas a spruce budworm outbreak affected the plots with greater conifer density more than it did other plots.

Detailed investigation of large (0.49 ha) sample plots helped characterize both quantitatively and in fine resolution, the structure, pattern, and elemental interactions in hardwood and mixed plots at Big Reed Forest Reserve, and also provided some insights into the underlying processes possibly responsible for such characteristics. The inclusion of saplings, dead wood, age distributions, spatial pattern, and interactions extended this study beyond that of a stand description at a single point in time, and provided some idea of forest dynamics and temporal change. The comparability of the results to other eastern old-growth studies enhanced the extrapolative quality of the results, and provided methodological guidelines for future studies. Recent disturbance and topographic position appear to be important in explaining current structure and dynamics of hardwood and mixed forests at Big Reed Forest Reserve in northern Maine.

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