Temporal changes in species composition of mixedwood stands in northwest New Brunswick: 1946–2008

Luke J. Amos-Binks, David A. MacLean, Jeremy S. Wilson, and Robert G. Wagner

Abstract: Patterns of softwood (SW) – hardwood (HW) change from 1946 to 2006 in 32 unharvested mixedwood (MW) stands in northern New Brunswick were analyzed using aerial photographs (1946, 1966, 1982, and 2006), sampled, and related to disturbance and stand conditions. Five stand development patterns were identified based on 1946 SW content (70%–80%, termed SW versus 30%–60%, termed MW) and change in SW content from 1946 to 2006 (SW-stable, SW-declining, MW-fluctuating, MW-stable, or MW-declining). Species composition was surprisingly changeable over this 60-year period, with change in SW content varying from +18% to –62%. High canopy cover reduction from 1946 to 1966 resulted from balsam fir (*Abies balsamea* (L.) Mill.) mortality due to old age and a 1950s spruce budworm (*Choristoneura fumiferana* Clem.) outbreak plus birch (*Betula* sp.) dieback. SW-stable stands that maintained SW composition from 1946 to 2006 (+7%) had more red spruce (*Picea rubens* Sarg.) than all other classes in which SW declined by 15%–47%. SW-declining stands were located on southerly aspects (189°) and had higher mean elevations (423 m) than other classes. Results suggest that balsam fir – tolerant HW MW stands may be naturally transitional due to disturbance, species, and stand conditions, which has significant implications for forest management designed to maintain static proportions of MW and SW stands.

Résumé : Les patrons de changement de la composition en essences résineuses et feuillues pendant la période 1946–2006 ont été étudiés dans 32 peuplements mixtes non coupés du nord du Nouveau-Brunswick à l'aide de photographies aériennes (1946, 1966, 1982 et 2006) pour ensuite être échantillonnés et reliés aux conditions de perturbation et de peuplement. Cinq patrons de développement de peuplement ont été identifiés en se basant sur le contenu en résineux observé en 1946 (peuplement résineux : de 70 % à 80 %; peuplement mixte : de 30 % à 60 %) et sur les changements du contenu en résineux de 1946 à 2006 (résineux stable, résineux déclinant, mixte fluctuant, mixte stable et mixte déclinant). De façon surprenante, la composition en espèces a beaucoup fluctué pendant cette période de 60 ans avec des changements du contenu en résineux de +18 % à –62 %. De fortes réductions du couvert de la canopée ont été produites de 1946 à 1966 par le dépérissement du bouleau (*Betula* sp.) et par la mortalité du sapin baumier (*Abies balsamea* (L.) Mill.) causée par son âge avancé et par l'épidémie de tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* Clem.) des années 1950. Les peuplements à résineux stable qui ont maintenu leur composition en résineux de 1946 à 2006 (+7 %) contenaient plus d'épinette rouge (*Picea rubens* Sarg.) que toutes les autres classes de peuplement dans lesquelles le contenu en résineux a diminué de 15 % à 47 %. Les peuplements à résineux déclinant étaient sur des versants sud (189°) et étaient situés à une altitude moyenne (423 m) plus élevée que celle des autres classes de peuplement. Les résultats indiquent que les peuplements mixtes à sapin baumier et à feuillus tolérants peuvent naturellement être en état de transition à cause de perturbations, des espèces en présence et des conditions du peuplement. Ces dernières ont donc des implications importantes pour l'aménagement forestier visant à maintenir des proportions statiques de peuplements mixtes et résineux.

[Traduit par la Rédaction]

Introduction

Managing stand types native to a region, often as a percentage of the landscape, is an important component of forest management planning. Concern about reduction in the number and area of mixed hardwood (HW) – softwood (SW) stands (hereafter termed mixedwood (MW)) has increased in recent years (e.g., Betts et al. 2003; Etheridge et al. 2005; Higdon et al. 2005) because stands are often managed for their primary SW or HW species. MW forests contain diverse tree species and conditions that provide a variety of values: habitat for birds (Girard et al. 2004), northern flying squirrels (*Glaucomys sabrinus*) (Ritchie et al. 2009), and white-tailed deer (*Odocoileus virginianus*) (Morrison et al. 2002), an important source of timber to forest industry, and reduced susceptibility to spruce budworm (*Choristoneura fumiferana* Clem.) defoliation compared with SW forest (Bergeron et al. 1995; Su et al. 1996; Camp-

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bell et al. 2008). MW stands are typical of the Atlantic Canada Acadian forest where boreal spruce (*Picea* sp.) and balsam fir (*Abies balsamea* (L.) Mill.) intersperse with northern HWs but differ from boreal MW forest by the presence of long-lived shade-tolerant species including sugar maple (*Acer saccharum* Marsh.) and red spruce (*Picea rubens* Sarg.).

Given relatively infrequent forest fires (estimated mean fire return intervals of 625 years; Wein and Moore 1977), the major natural disturbance affecting Acadian MW stand dynamics is spruce budworm outbreaks (Blais 1983). These outbreaks cause defoliation, growth reduction, and mortality of host balsam fir and spruce (e.g., MacLean et al. 1984; MacLean and Ostaff 1989) but only indirectly affect and may release the HW component.

Few long-term studies have documented stand dynamics of Acadian MW forest. Hughes (1960) observed that HW composition decreased by 4% and 23% from 1947 to 1956 in MW stands in northern New Brunswick due to birch (*Betula* sp.) dieback, and this altered the mature MW stand to an irregularly aged balsam fir-dominated stand. In Quebec, high budworm-caused mortality in SW-dominated late successional stands resulted in stand replacement, while lower mortality in MW or HW stands resulted in two-cohort or gap replacement dynamics (Bouchard et al. 2005). Budworm-caused mortality reduced SW canopy cover in MW forest and caused cyclic replacement of host species on lower slope position stands, but on upper slopes, host species were replaced with HWs (Bouchard et al. 2006). Reyes and Kneeshaw (2008) noted that conifer-dominated stands reestablished following disturbance but shrub and deciduous species dominated in mixed stands. Gap sizes influence recruitment, with small gaps favouring balsam fir and large gaps favouring yellow birch (*Betula alleghaniensis* Britt.), while species longevity, shade tolerance, and tree size were important in the maintenance of MW stands (Kneeshaw and Prévost 2007).

Etheridge et al. (2006) analyzed MW stand changes from 1945 to 2002 on a 190 000 ha forest in northwestern New Brunswick and found that only 16% and 18%, respectively, of harvested and unharvested MW forest present in 1945 remained as MW by 2002. Over the entire landbase, MW area declined by 19% from 1945 to 2002, and only 9% of MW stands present in 2002 were projected to remain as such under forest management (Etheridge et al. 2006). This significant reduction in MW stands raised questions about causes of such dramatic species shifts in MW forest and, indeed, whether MW stands are a transitional successional type. We conducted the present study on the same landbase as Etheridge et al. (2006) and determined the dynamics of 32 unharvested MW stands from 1946 to 2006. The objectives were to (*i*) determine patterns of change in tree species composition using aerial photographs from 1946, 1966, 1982, and 2006 and (*ii*) relate stand dynamics to stand and site characteristics and past disturbance. Specifically, we hypothesized that spruce budworm outbreaks render balsam fir – shade-tolerant HW MW a transitional stand type in which outbreaks periodically kill fir and convert MW to HW stands.

Methods

Study area

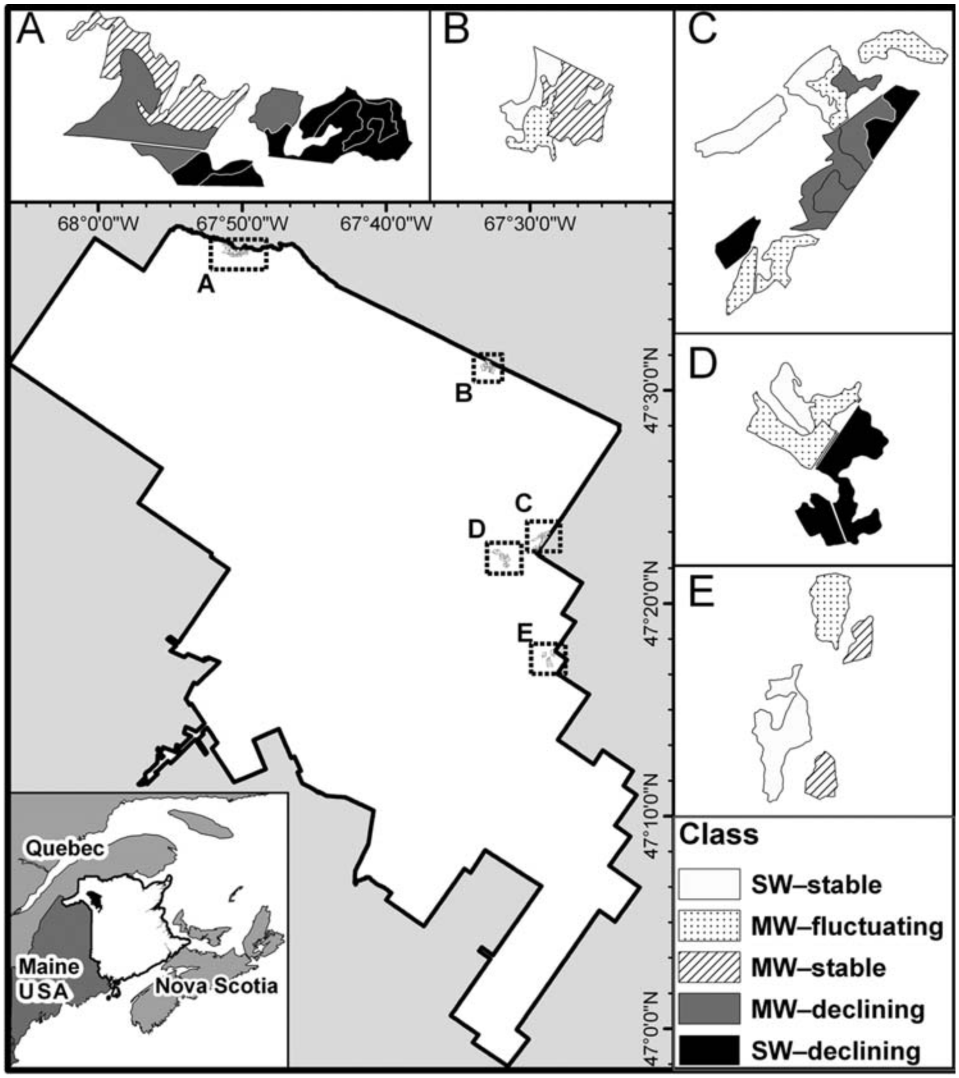
The study area is the J.D. Irving, Limited Black Brook District located in northwestern New Brunswick (Fig. 1). This 189 000 ha privately owned forest has been intensively managed since the 1950s. The landbase was originally purchased from the New Brunswick Railway Company in 1944. Most of the district is located in the Central Uplands Ecoregion (94%) where the effects of daily cold air drainage from higher elevation to valleys are evident in the distribution of SW and HW species (New Brunswick Department of Natural Resources (NBDNR) 2003). The lower valleys usually are made up of balsam fir and spruce. Mixed forests made up of balsam fir, spruce, and tolerant HWs (yellow birch, sugar maple, and American beech (*Fagus grandifolia* Ehrh.)) are generally present on slopes, while HW stands occupy upper slopes, hilltops, and ridges (NBDNR 2003). Southern slopes with a warmer topoclimate favour development of tolerant HW forests. Species like trembling aspen (*Populus tremuloides* Michx.) and pine (*Pinus* sp.) are relatively sparse due to the low frequency of fire in this ecoregion. The landbase includes four ecodistricts: Sisson (68%), Madawaska (26%), Restigouche-Upsalquitch (4%), and Saint John (1%) (NBDNR 2003). The dominant Sisson and Madawaska ecodistricts are at high elevations, experience abundant rainfall, and have generally similar species assemblages, although the Sisson ecodistrict has more low relief areas with reduced soil drainage, resulting in less tolerant HW and more coniferous and mixed forest. Successional dynamics are strongly influenced by spruce budworm and windthrow disturbances and by a long history of harvests and forest protection against insect outbreaks and fire.

In 1944, following acquisition of the landbase by J.D. Irving, Limited, a full timber inventory was performed. The southern, more accessible portion of the landbase had been harvested for approximately 40 years at the time of inventory, but no harvesting was reported in the northern portion before 1939 (Lussier and Grenier 1947). Lussier and Grenier (1947) reported good growth and quality for most species, with the exception of the birches, which were reported to have been declining for 5 years because of an unknown pathogen. The decline was so severe that Lussier and Grenier (1947) remarked that if the decline continued, birch would no longer appear as part of "overmature" stands. Defoliation records indicate that two separate spruce budworm outbreaks occurred in the area during 1947–1958 and 1971–1987. During the 1971–1987 outbreak, an aggressive protection plan was implemented using aerial insecticide application to reduce budworm-caused tree mortality.

Historical inventory and photo-interpretation data

Historical data available for the Black Brook District include aerial photographs from 1946, 1966, 1982, and 2006, a full timber inventory conducted between 1945 and 1947, and digitized annual aerial sketch maps of spruce budworm defoliation. The full set of aerial photographs from 1946 had been photo-interpreted and digitized for a previous project (Etheridge et al. 2006) to create a 1946-photograph-based GIS inventory. The scale of aerial photographs varied by measurement year: 1:15 000 in 1946, 1:17 500 in 1966 and

Fig. 1. Locations of 32 sampled stands on the J.D. Irving, Limited 190 000 ha Black Brook District in northwestern New Brunswick (black area in inset map) within five geographic areas (A-E). Sampled stands are grouped into five stand development classes based on SW content in 1946 and change in %SW content from 1946 to 2006.



1982, and 1:12 500 in 2006. Photographs from 1946 and 1966 were black and white, while those from 1982 and 2006 were colour. The 2006 GIS inventory was derived from near infrared images taken in 2005 and confirmed through ground sampling conducted by J.D. Irving, Limited.

The 1940s timber inventory was reported by northern (Grenier 1945) and southern (Lussier and Grenier 1947) portions of the land base. Cruise lines were established every 400 m in the north and every 800 m in the south and referenced to perpendicular baselines by compass. Transects 100 m by 10 m were established every 200 m to record species, diameter at breast height (DBH), and age class of all trees >10 cm DBH as well as stand origin (burn or cut). An additional 200 m^2 subplot was used to record trees <10 cm DBH. Historical data from the 1940s will be referred to as 1946 data for consistency. Annual spruce budworm defoliation data for the Black Brook district were obtained from digitized aerial sketch maps that have been maintained by NBDNR (Carter and Lavigne 1993).

Landscape changes in SW–HW content from 1946 to 2006

Change in SW–HW content of all unharvested stands was quantified by comparing GIS inventory data from 1946 and 2006. Unharvested stands were determined by excluding harvested and other areas that were treated silviculturally (thinning and planting). These areas were defined based on inventory records maintained by J.D. Irving, Limited and historical harvest maps that were scanned, georeferenced, delineated digitally, and incorporated into the GIS inventory. Potential sample stands were further refined by excluding areas that were identified as burned or in early stages of stand development in the GIS photograph inventory of 1946. Each stand in the 1946 and 2006 GIS data was categorized based on 10% SW categories from 0% to 100%. The 1946 and 2006 data were then overlaid into one layer that categorized the landscape by 10% SW classes in 1946 and 2006. Table 1 shows the distribution of the 10 665 ha

Table 1. Distribution of 10 665 ha of unharvested stands by %SW (0%–100% in 10% classes) in 1946 versus 2006 on a 190 000 ha landbase in northwestern New Brunswick.

		2006 %SW										
1946 %SW	Hectares	0	10	20	30	40	50	60	70	80	90	100
0	25	**100**	0	0	0	0	0	0	0	0	0	0
10	278	77	**15**	0	8	0	0	0	0	0	0	0
20	551	75	20	**0**	0	0	0	5	0	0	0	0
30	695	46	33	18	**0**	0	0	0	0	0	0	3
40	650	42	27	14	9	**8**	0	0	0	0	0	0
50	825	36	18	14	12	8	**7**	0	2	0	4	0
60	827	15	15	8	11	15	8	**6**	2	6	7	5
70	1081	10	0	8	12	9	10	6	**5**	6	15	18
80	1878	3	3	3	8	4	5	6	3	**8**	24	34
90	1383	0	0	0	4	5	0	0	7	9	**18**	57
100	2472	0	9	8	0	0	0	0	0	10	7	**66**

Note: Bold numbers show the percentage of the 1946 SW category that was in the same class in 2006.

of unharvested forest based on %SW categories in 1946 compared with 2006.

Determining patterns of change in SW–HW composition from 1946 to 2006

To quantify patterns of change in SW–HW composition, MW stands were classified based on (*i*) 1946 SW content, either 30%–60% or 70%–80% SW, and (*ii*) change in SW content from 1946 to 2006: greater than –40% SW (i.e., decline by >40%), –20% to –30% SW, –10% to +10% SW, or +20% to +30% SW. This approach resulted in a matrix of eight classes reflecting two initial (1946) SW contents and four SW changes from the 1946–2006 categories.

A subset of sample stands for the detailed photo-interpretation of within-stand 1946–2006 changes was selected from the above mentioned matrix in three steps. First, unharvested areas were identified that had a full series of aerial photographs of acceptable quality, with some areas excluded due to poor-quality photographs or excessive cloud shading. Regions were further refined with assistance from the management forester familiar with historical harvest on the landbase (Gaetan Pelletier, J.D. Irving, Limited, personal communication (2007)) to minimize the likelihood that harvest or other silvicultural activities had occurred. A total of five separate regions (Fig. 1) were selected, all in relatively remote areas near the eastern boundary of the landbase. Step two of the selection process involved randomly selecting stands that represented each of the eight classes of 1946 SW and 1946–2006 change patterns described above from each of the five regions. Due to low representation of area in the 1946 30%–60% SW with increasing SW class (+20% to +30% SW 1946–2006), stands were only selected from the remaining seven categories for a total of 35 sample stands. Step three involved confirming that no evidence of harvesting was present in the sample stands, initially determined during interpretation of aerial photographs based on signs of roads, skid trails, or stand disturbance and assessed again during site visits during the summer of 2008 (evidence of harvesting such as stumps, old roads, etc.). Three initially selected stands that showed evidence of harvesting during site visits were removed. Thus, a total of 32 stands were selected and photo-interpreted.

Photo-interpretation

A 50 m by 50 m grid was overlaid on the 1946, 1966, 1982, and 2006 aerial photographs of each sampled stand and georeferenced using permanent land features when possible (roads, dwellings, and rocky areas); in some instances, lakes and harvest boundaries had to be used for lack of more permanent features. Each 50 m grid cell was then photo-interpreted using 10 times magnification ocular lenses, recording %HW and %SW cover in 10% classes from 0% to 100%. Canopy cover was measured as the total cover of canopy trees tall enough to be distinguished from adjacent open ground or low vegetation. Total canopy cover was then calculated as the sum of HW and SW cover with a maximum value of 100% per cell. Identification of canopy cover by genus or species was not possible on the 1946 and 1966 black and white photographs, but SW and HW cover was easily discerned (SW darker than HW).

Classification of stand development classes

SW and HW contents of individual grid cells for each measurement year were calculated by dividing SW or HW cover by crown cover per cell. Average SW content per stand per year was then calculated from cell values per stand. When individual cells overlapped into adjacent stands, an area-weighted average was used so that only area within the sample stand was used. To examine trends in changes of species composition and stand development, sample stands were reclassified based on changes in SW content in three periods: 1946–1966, 1966–1982, and 1982–2006. Change in SW content ($\Delta\%\mathrm{SW}_t$) per period was calculated as

$$[1] \qquad \Delta\%\mathrm{SW}_t = \%\mathrm{SW}_t - \%\mathrm{SW}_{t-1}$$

Stands were grouped into stand development classes (hereafter termed classes) using a grouping algorithm based on similar (±15%) $\Delta\%\mathrm{SW}_t$ within and between periods. By adjusting the threshold value, the number of classes would either increase or decrease, but this either no longer differentiated classes by SW content in 1946 or created additional classes that varied only slightly in their SW content over time. A total of five unique classes resulted, which were named to reflect their 1946 species composition (SW or

MW) and 1946 to 2006 %SW trend (stable, fluctuating, or declining). Average changes in SW by class in the 1946–1966 and 1966–2002 periods, respectively, were (1) SW-stable +10% and less than –4%, (2) SW-declining –21% and –25% (3) MW-stable –5% and +4%, (4) MW-fluctuating +10% and –23%, and (5) MW-declining –15% and –12%. All classes were relatively stable from 1982 to 2006 with the exception of MW-fluctuating stands in which SW declined by 15%.

Spruce budworm defoliation data

Annual aerial sketch-mapped defoliation data have proven to be an accurate means for predicting forest response from spruce budworm attack (MacLean and MacKinnon 1996; Taylor and MacLean 2008). Methods of data collection as parts of operational surveys were described by MacLean and MacKinnon (1996) and Carter and Lavigne (1993). The maps classified areas independently of stand boundaries based on four defoliation classes: nil (0%–10%), light (11%–30%), moderate (31%–70%), and severe (71%–100%). Midpoint values of defoliation classes were used for all calculations. Individual stand defoliation values were determined by overlaying digitized aerial sketch maps, by year, on boundaries of the 32 sample stands. If a stand contained more than one defoliation class in a given year, an area-weighted average was calculated.

In addition to annual defoliation by year, cumulative defoliation was calculated as a measure of the overall impact of multiple years of defoliation. Cumulative defoliation time series (CD_t) were calculated using relative foliage mass for a given age of foliage (from Kleinschmidt et al. 1980) to weight current defoliation (C) in year t (MacLean et al. 2001):

$$[2] \qquad CD_t = 0.28C_t + 0.26C_{t-1} + 0.22C_{t-2} + 0.13C_{t-3} + 0.08C_{t-4} + 0.03C_{t-5}$$

Annual and cumulative defoliation time series from 1945 until 2008 were created for each sampled stand. These were then used to calculate several spruce budworm outbreak severity measures per sample stand and outbreak period: sums of annual and cumulative defoliation, number of years of moderate to severe defoliation, duration of outbreak, first and last year of moderate-severe defoliation, and years of aerial protection. Differences in severity of spruce budworm outbreak measures across stand development classes were analyzed using ANOVA.

Field sampling

Three prism plots were established in each of the 32 sample stands in the summer of 2008 using a 2.0 m^2/ha basal area factor angle gauge. Prism plots were established in specific grid cells (50 m by 50 m) in each sample stand, selected based on the grid cell's %SW cover in each photo-interpretation measurement year, to match the mean SW content of the stand over time. Sample prism points were established at the center of grid cells with the aid of a GPS. At each sample point, all trees >6 cm were measured to determine DBH (centimetres), height (metres), canopy class (suppressed, intermediate, codominant, or dominant), and identified to species. These variables were used to calculate stand density, basal area, and volume per stand and to create 2008 diameter distributions by species for comparison with similar data from the 1946 inventory.

Results

Changes in SW–HW content from 1946 to 2006

The landscape analysis identified 10 665 ha as unharvested from 1946 to 2006, and changes in SW–HW content over this period varied widely across the 1946 SW–HW gradient (Table 1). HW-dominated (<20% SW) and SW-dominated (>80% SW) stands of 1946 were stable, with ≥90% of the area in these classes within 10% of the 1946 value by 2006. However, three-quarters of the area of HW-dominated (20%–30% SW) MW stands in 1946 experienced ≥20% reductions in SW cover from 1946 to 2006. The area of MW (40%–60% SW) and SW-dominated (70%–80% SW) MW stands in 1946 were particularly unstable, with 34%–46% of the area experiencing ≥40% reductions in SW cover from 1946 to 2006, while only 12%–16% of the area stayed within 10% of the 1946 value by 2006. In SW-dominated MW stands, 32%–39% of the area had ≥20% reductions from 1946 to 2006 and 33%–34% showed increases of ≥20%, while only 17%–35% remained within 10% of their 1946 value.

Characteristics of stands by development class

The five stand development classes were found to have substantially different tree species composition over time (Fig. 2). SW-stable and SW-declining stands were both dominated by SW (~80%) initially (1946), but whereas SW-stable was fairly stable over time, SW-declining experienced significant reductions (28%–60%) in SW cover by 1982. The three MW classes all had 37%–70% SW in 1946 but their trajectories varied. MW-fluctuating stands fluctuated with increased SW (0%–26%) from 1946 to 1966 followed by a sharp decline from 1966 to 1982, MW-stable stands were relatively stable over time, and MW-declining stands underwent significant declines (20%–33%) from 1946 to 1982. The patterns of SW change over time were likely related to variation in disturbance events across the region and differing stand characteristics among the different classes.

Table 2 summarizes site and stand characteristics and stand-level change of the sample stands by stand development classes. Aspect differed (p = 0.001) between classes, with MW-stable and MW-declining having a southeasterly aspect (mean of 145°), SW-declining having a predominantly southern aspect (189°), and SW-stable and MW-fluctuating having westerly aspects (238 and 285°). Elevation also differed (p = 0.026), with SW-stable and MW-stable having lower elevation (318–358 m) than MW-declining and SW-declining (423–441 m), while MW-fluctuating was intermediate (404 m). There were no differences (p = 0.209) among classes for stand density (400–730 stems/ha), basal area (21.1–26.0 m^2/ha), volume (151–218 m^3/ha), DBH (18.3–25.7 cm), or slope (8–17°).

Sample stands represented two ecosites (5 and 7) present on the landbase. Ecosites represent enduring features at the scale of a landform that reflect the moisture, nutrient, and topoclimate regimes of the particular site. Ecosites 5 and 7 both represent well-drained sites, but ecosite 7 has higher

Fig. 2. Temporal change in SW content based on photo-interpretation of images from 1946, 1966, 1982, and 2006 for 32 sampled stands grouped into five stand development classes based on SW content in 1946 and change in %SW content from 1946 to 2006. The black line represents the average SW change trajectory for stands in each class and the grey lines represent trajectories for each stand.

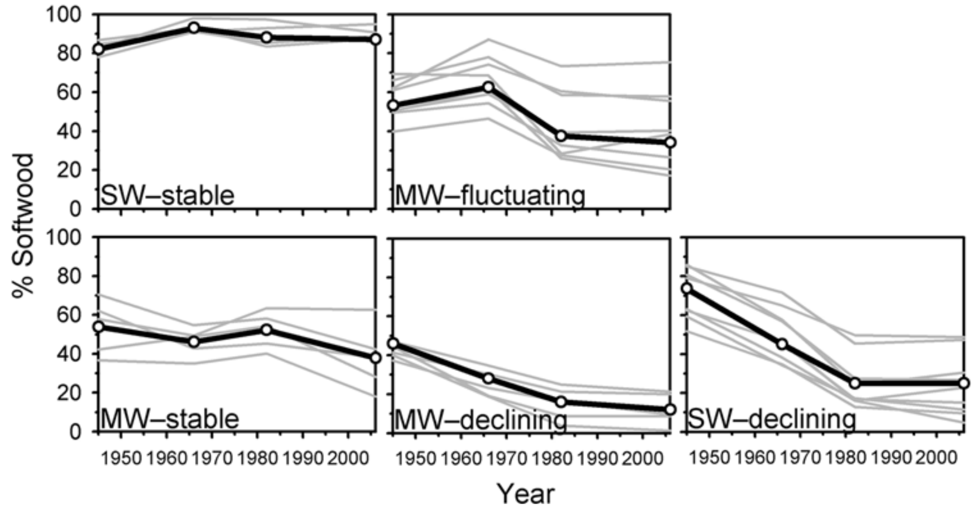
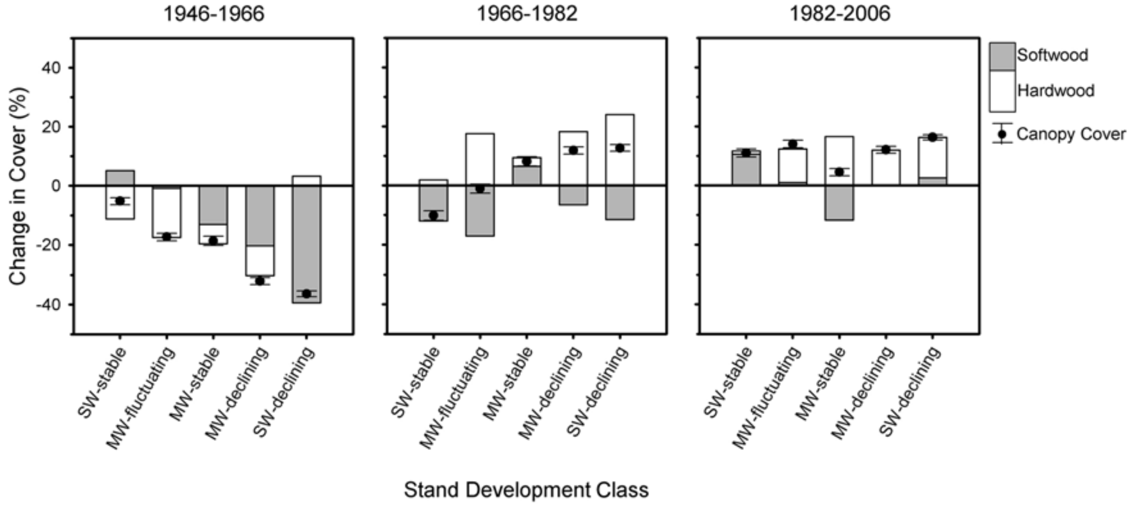


Table 2. Mean ± 1 SE stand characteristics data for 32 sampled stands grouped into five stand development classes defined based on SW content in 1946 and the pattern of change in %SW content from 1946 to 2006.

	Stand development class					ANOVA	
	SW-stable	MW-fluctuating	MW-stable	MW-declining	SW-declining	*F* (df = 4)	*p*
Stand characteristics							
No. of stands	4	8	6	5	9		
Density (trees/ha)	696±86	730±64	673±36	400±49	696±47	0.639	0.640
Basal area (m^2/ha)	26.0±2.3	25.7±0.4	22.9±0.8	21.1±1.3	23.3±0.9	0.525	0.718
Volume (m^3/ha)	218±21	181±3	164±5	151±9	157±7	1.252	0.313
DBH (cm)	20.3±1.5	20.7±0.7	18.3±1.1	25.7±1.4	19.1±0.5	1.372	0.270
Aspect (°)	285±2a	238±5a	145±15b	145±14b	189±5c	4.920	0.001*
Slope (°)	17±1	10±0	8±1	10±0	13±0	1.576	0.209
Elevation (m)	358±26a	404±10ab	319±7a	441±5b	423±6b	3.267	0.026*
No. of stands							
Ecosite 5	2	2	5	0	0		
Ecosite 7	2	6	1	5	9		
Species composition (%)							
Balsam fir	19.0±8.9	27.9±2.4	30.0±5.2	8.8±1.9	30.6±2.1	0.639	0.639
Red spruce	57.7±9.5a	12.9±1.8b	1.7±0.5b	6.2±1.7b	15.2±2.2b	10.377	0.001*
White spruce	4.5±2.2	2.4±0.9	2.9±0.8	0.0±0.0	0.0±0.0	1.128	0.364
Other softwood	0.4±0.2	3.1±1.1	0.4±0.1	0.0±0.0	0.0±0.0	0.744	0.571
Red maple	6.6±3.0	4.6±0.8	5.6±1.2	1.1±0.3	11.2±1.7	0.886	0.486
Sugar maple	0.0±0.0a	14.0±2.2a	16.9±3.7a	46.8±7.2b	13.8±1.6a	2.828	0.044*
Yellow birch	5.2±1.9a	24.9±1.8b	27.7±4.2b	31.6±4.6b	18.9±1.4b	2.991	0.036*
Other bardwood	6.7±2.3	10.2±1.5	14.6±3.3	5.4±1.5	10.1±2.6	0.817	0.525
Softwood composition (%)							
1946	83±0	56±1	52±2	42±0	71±1		
1966	93±0	66±1	47±1	27±2	50±1		
1982	89±1	43±2	51±1	15±1	25±1		
2006	90±0	41±2	37±2	12±1	24±1		
Change 1946–2006	+7	–15	–15	–30	–47		

Note: Stand characteristics and species composition were determined using plot data in 2008, while SW composition was based on interpretation of four sets of aerial photographs from 1946 to 2006. Ecosites: 5, moderate nutrient regime, well drained; 7, rich nutrient regime, well drained. Letters (a and b) indicate significant differences among stand development classes. An asterisk indicates significance at $p < 0.05$.

Fig. 3. Average positive or negative change (increase or decrease) in %SW and %HW cover by time period for five stand development classes based on SW content in 1946 and change in %SW content from 1946 to 2006. Overall change in canopy closure (sum of change in SW and HW cover) is shown by the black circle ± 1 SE of the mean.



productivity. Most stands in MW-fluctuating (75%), MW-declining (100%), and SW-declining (100%) were classified as ecosite 7, whereas most MW-stable (80%) stands were classified as ecosite 5 and 50% of SW-stable stands were classified as ecosite 7.

Species composition based on ground sampling in 2008 differed among classes (Table 2). Red spruce content was higher ($p < 0.001$) for SW-stable at 57%, with all other classes substantially lower (2%–15%). Sugar maple content was higher ($p = 0.044$) in MW-declining stands at 47%, while others ranged from 0% to 17%. Yellow birch content was lowest in SW-stable (5%), lower ($p = 0.036$) than in other classes (19%–32%). No differences in balsam fir, white spruce, other SW, red maple, or other HW content were found ($p > 0.05$).

Changes in canopy cover

Over time, changes in SW–HW canopy cover differed among stand development classes. From 1946 to 2006, there was a gradient of declining average canopy cover across classes experiencing average changes in canopy cover of –5%, –6%, –10%, –11%, and –12%, respectively (Fig. 3). The largest reductions in canopy cover occurred from 1946 to 1966 in all classes except SW-stable, with values ranging from –18% to –38%. From 1966 to 1982, canopy cover of SW-stable stands declined by 10%, but that of MW-stable, MW-declining, and SW-declining increased by 8%–12% (Fig. 3). From 1982 to 2006, all classes showed recovery of canopy cover by 2%–14%.

HW canopy cover declined by 8%–18% only from 1946 to 1966 in all classes except SW-declining (Fig. 3). From 1966 to 1982 and from 1982 to 2006, HW canopy cover increased in all classes: MW-fluctuating, MW-declining, and SW-declining by >19% from 1966 to 1982, and all classes except for SW-stable had increases of 11%–17% from 1982 to 2006 (Fig. 3). In contrast, HW cover in SW-stable stands varied little (<2%) from 1966 to 1982 and from 1982 to 2006.

The most significant periods of change in SW cover differed depending on development class. MW-stable, MW-declining, and SW-declining experienced their greatest reduction in SW cover of 12%, 21%, and 39%, respectively, from 1946 to 1966 (Fig. 3). SW-stable and MW-fluctuating differed in that their greatest period of reduction in SW cover occurred from 1966 to 1982 at 12% and 17%, respectively. MW-stable was the only class to show a reduction in SW content from 1982 to 2006. Periods of increase in SW cover were rare, occurring only in SW-stable, MW-stable, and SW-declining, and all <10%.

Changes in species composition and stand characteristics

Species composition and diameter distributions by class from the 1945 timber cruise and data collected in 2008 are shown in Fig. 4. In 1945, balsam fir was the dominant component of stands by density, comprising 52%–65% of total stems per hectare, and ranged from 200 to 384 stems/ha. However, by 2008, balsam fir content had declined in all classes (8%–30%) and only made up 123–174 stems/ha. SW-stable stands had the most spruce (21%) in 1945, with other classes having 13%–17%. By 2008, SW-stable stands still had the most spruce (59%) and had increased substantially, while other classes remained low (2%–15%). Species of spruce were not identified in the 1945 cruise, but most sampled in 2008 were red spruce. Tolerant HW density increased from 45–125 stems/ha in 1945 to 123–466 stems/ha by 2008. Tolerant HW content in 1945 was lowest in SW-stable at 8% versus 15%–32% in the other classes; tolerant HW in other classes increased to 38%–77% by 2008.

Overall stand density in 1945 was highest in SW-stable (591 stems/ha) and MW-fluctuating (512 stems/ha) with all other classes being lower at 384–415 stems/ha (Fig. 4). By 2008, density had increased across all classes to 696–730 stems/ha, except MW-declining (400 stems/ha). Average DBH in 1945 was lower at 19.0–19.4 cm for SW-stable and MW-fluctuating versus 20.1–22.5 cm in other classes. By 2008, average DBH had increased substantially in MW-declining (25.7 cm), increased slightly in SW-stable and MW-fluctuating (20.3–20.7 cm), and decreased slightly in MW-stable and SW-declining (18.3–19.1 cm) (Table 2). Although differences in sampling method exist between the

Fig. 4. Diameter distributions in 1945 and 2008 for sampled stands grouped into five stand development classes based on SW content in 1946 and change in %SW content from 1946 to 2006. The 1945 data are from plots in a timber cruise and the 2008 data are from three sampled plots in each of 32 stands.

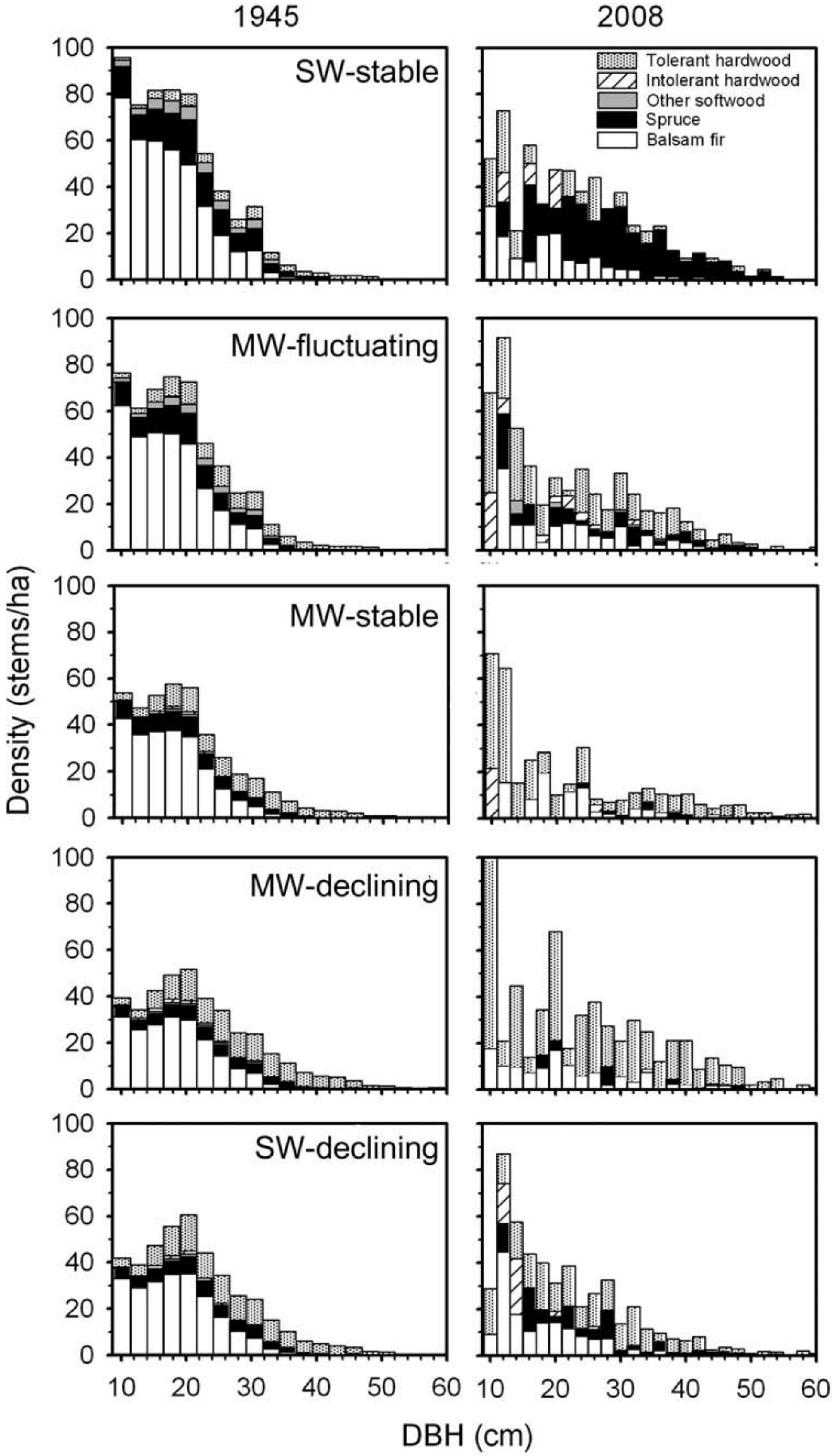
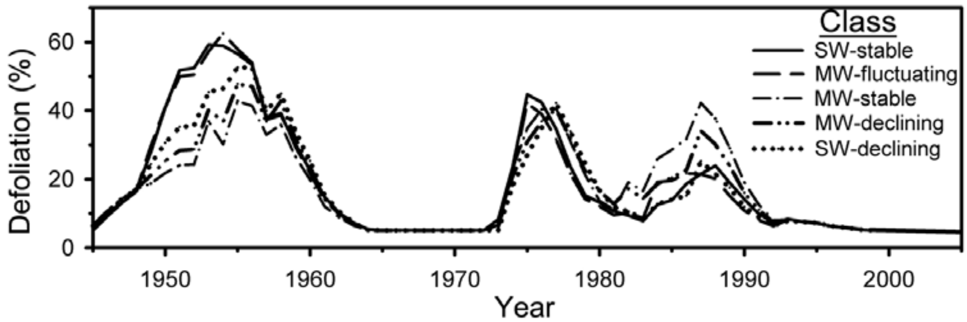


Fig. 5. Average percent cumulative spruce budworm defoliation from 1945 to 2008 for sampled stands grouped into five classes based on SW content in 1946 and change in %SW content from 1946 to 2006.



1945 cruise data (fixed area) and the sample plots (prism points) established in 2008, it is unlikely that sampling method was responsible for the observed changes in density and species composition, since it is straightforward to determine number of trees by species and DBH class.

Spruce budworm outbreaks

Two distinct spruce budworm outbreaks occurred in the region from 1947 to 1958 and from 1972 to 1987. Cumulative and current defoliation values indicated that the 1972–1987 outbreak had two clear peaks, likely attributed to aggressive insecticide protection programs to minimize the impact of the outbreak (Fig. 5). The 1950s outbreak began on average 1.8–3.4 years earlier in SW-stable and MWfluctuating stands compared with other classes (p = 0.002) but the outbreak duration was only longer than MW-stable (7.3–9.0 versus 5.5 years, p = 0.008) (Table 3). This difference in outbreak length was associated with lower current (p = 0.034) and cumulative defoliation (p = 0.007) (305% and 436%) in MW-stable compared with other classes (385%–420% and 553%–616%) (Table 3). No differences (p > 0.05) were found between classes for the 1972–1987 outbreak, but Fig. 5 indicates that MW-stable peak cumulative defoliation during the second part of the outbreak was higher (42%) when compared with other classes (20%–30%). MW-stable stands also experienced a longer outbreak (9.5 years) when compared with the other four classes (3.1–6.8 years). In contrast with the 1950s outbreak, MW-stable stands did demonstrate greater reductions in SW canopy cover than other classes following the 1970s–1980s outbreak (Figs. 3 and 5).

Discussion

Natural changes in species composition within unharvested stands result from tree mortality caused by disturbance or senescence and subsequent replacement by trees that re-inhabit newly available growing space (Lorimer 1985; Oliver and Larson 1996). If intensity of disturbance varies across a landscape or if the disturbance affects species differently, then postdisturbance conditions will vary (MacLean 1980; MacLean and Ostaff 1989). The resulting stand condition can promote the development of some species and reduce the competitive advantages of others and also predispose stands to certain kinds of future disturbances (Morin 1994; Erdle and MacLean 1999; Bouchard et al. 2006).

The relatively stable pattern of SW content in SW-stable stands reflected only minor changes in canopy cover (<10%) in all periods (Fig. 3) and likely resulted from the occurrence of a large amount of red spruce relative to dominance by balsam fir in the other four classes (Table 2). The mean year of establishment for red spruce in SW-stable stands was 1881 (±7.5 SE) compared with 1942 (±5.7 SE) for balsam fir. Given that stand origin likely dated back to the 1870s spruce budworm outbreak and the long-lived nature of red spruce (Gordon 1985) compared with balsam fir, less red spruce mortality would be expected during the period 1946–1966. Red spruce experiences only 41% as much defoliation (Hennigar et al. 2008) and less budworm-caused mortality (MacLean 1980; Bergeron et al. 1995) than balsam fir. The slight increases in SW content from 1946 to 1966 resulted from reduced HW (Fig. 3) caused by birch dieback, which resulted in SW composing a larger percentage of overall canopy cover.

MW-fluctuating stands experienced a loss of 18% of HW canopy from 1946 to 1966 (Fig. 3), likely due to birch dieback in the 1940s (Gibson 1953; Bourque et al. 2005) and that resulted in a slight increase in SW content during this period. SW-stable and MW-fluctuating stands experienced the greatest defoliation during the 1947–1956 outbreak (Fig. 5) but in fact experienced the least reduction in SW canopy cover. This outcome may reflect a lack of accuracy of the 50- to 60-year-old defoliation assessment and lower resolution than more recent defoliation survey data, which have been used to predict forest responses in SW-dominated stands during the most recent outbreak (MacLean and MacKinnon 1996; Taylor and MacLean 2008). MW-fluctuating stands experienced a significant reduction in SW canopy cover from 1966 to 1982 (Fig. 4), which could have resulted from mortality induced by the second spruce budworm outbreak, which began in 1972 (Fig. 5), decline that began in 1946–1966, or more likely a combination of both. This, combined with increased HW (Fig. 3) from 1966 to 1982 and from 1982 to 2006, led to decline in SW from 1966 to 2006.

The stable pattern of SW content in MW-stable stands (Fig. 2) reflected relatively low reductions in both SW and HW cover from 1946 to 1966 and only minor changes in canopy cover from 1966 to 2006 (Fig. 3). MW-stable were the only stands that showed SW decline (12%) from 1982 to 2006. Although no differences (p > 0.05) were detected for 1972–1987 spruce budworm outbreak metrics, MW-stable stands did show a clear secondary pulse of defolia-

Table 3. Statistical comparison of metrics for two spruce budworm outbreaks (1947–1958 and 1972–1987) for sampled stands grouped into five stand development classes based on change in %SW content from 1946 to 2006.

	Stand development class					ANOVA	
	SW-stable	MW-fluctuating	MW-stable	MW-declining	SW-declining	*F* (df = 4)	*p*
1947–1958 budworm outbreak severity measures							
Sum of current defoliation (%)	420.1±30.1a	411.4±27.7a	305.4±22.7b	404.0±33.1a	385.0±16.8a	3.044	0.034*
Sum of cumulative defoliation (%)	616.8±31.2a	612.4±30.1a	436.1±22.4b	565.49±50.3a	553.5±29.6a	4.477	0.007*
First year of defoliation	1949.3±0.3a	1949.1±0.1a	1952.5±0.5b	1951.4±0.9b	1951.2±0.7b	5.557	0.002*
Last year of defoliation	1958.3±0.8	1958.1±0.4	1958.0±0.4	1959.0±0.1	1958.6±0.3	0.826	0.520
Outbreak duration (years)	9.0±0.7a	9.0±0.4a	5.5±0.8b	7.6±1.0a	7.3±0.6a	4.333	0.008*
Years moderately to severely defoliated	10.0±0.7a	9.8±0.5a	5.5±0.8b	8.0±1.2a	7.7±0.7a	5.062	0.004*
Years protected	2.9±0.1	2.9±0.1	2.5±0.2	2.5±0.2	2.6±0.1	1.345	0.279
1972–1987 budworm outbreak severity measures							
Sum of current defoliation (%)	359.3±103.8	341.2±48.7	460.6±51.2	340.0±32.7	369.0±22.2	1.025	0.412
Sum of cumulative defoliation (%)	382.8±107.7	368.2±49.0	501.9±52.4	370.4±38.2	374.3±24.5	1.282	0.301
First year of defoliation	1974.8±0.3	1974.9±0.1	1976.8±1.7	1975.8±0.4	1975.7±0.2	1.218	0.326
Last year of defoliation	1979.0±3.4	1978.0±1.7	1986.3±2.1	1982.6±2.7	1982.3±1.8	2.121	0.106
Outbreak duration (years)	5.0±3.7	3.1±1.8	9.5±2.5	6.8±2.3	6.7±1.6	1.203	0.332
Years moderately to severely defoliated	4.8±2.4	3.5±1.2	6.8±1.5	3.4±0.9	3.7±0.5	1.380	0.267
Years protected	4.6±0.5	4.6±0.3	3.8±0.9	3.3±0.8	2.6±0.5	2.187	0.097

Note: Stand development classes are defined by SW content in 1946 and the pattern of change thereafter. Data are from annual aerial spruce budworm defoliation surveys. Letters (a and b) indicate significant differences among stand development classes. An asterisk indicates significance at $p < 0.05$.

tion from 1982 to 1987, greater than any other stands (Fig. 5), which may account for the reduction of SW cover.

The decreases in SW composition (Fig. 2) and SW canopy cover (Fig. 3) in MW-declining and SW-declining stands coincided with the 1947–1956 spruce budworm outbreak. Defoliation values were, however, lowest in MW-declining and SW-declining stands, even though they did experience the greatest reduction in SW cover from 1946 to 1966. Perhaps the most significant causal factor in the reductions of SW canopy cover observed during this period resulted from stand age and origin. Etheridge et al. (2005) previously identified that in 1945, 85% of the forest was 70–120 years old and many of these stands likely originated from the 1870s spruce budworm outbreak in Maine and New Brunswick (Blackman 1919; Tothill 1923; Swaine and Craighead 1924). This outbreak likely gave rise to a young forest that would have been lightly damaged by the 1910s budworm outbreak. By 1946, much of the balsam fir originating following the 1870s outbreak would have been approaching ages susceptible to mortality from wind, pathogens, and spruce budworm (Sprugel 1976; Ruel 2000; Taylor and MacLean 2005). This difference in the effect of the outbreak is consistent with the supposition that more severe mortality is evident during every second spruce budworm outbreak (Blais 1981), but stands may have already been in a declining state prior to the outbreak. Further reductions in SW canopy cover evident in MW-declining and SW-declining stands from 1966 to 1982 could be due to the 1970s budworm outbreak (Fig. 5), continued decline that began in 1946–1966, or more likely a combination of both. Increases in HW in 1966–1982 and 1982–2006 could be attributed to in-growth of HW species into canopy gaps created in the previous period; HW replacement of the SW reduction in 1946–1966 (Fig. 3) indicates conditions that favoured HW species. MW-declining and SW-declining stands were also the most open from 1946 to 1966 following reduction of 31%–38% canopy cover (Fig. 3), which allowed HW species to take advantage of the new growing space. Shade-tolerant SW species (balsam fir and spruce) are more effective competitors in small canopy gaps (Osawa 1994; Kneeshaw and Prévost 2007), as is yellow birch in large canopy gaps (Kneeshaw and Prévost 2007). MW-declining and SW-declining stands were also all on the higher productivity ecosite 7 (Table 2), further enhancing HW recruitment.

Our results corroborated the overall shifts in MW stand types from 1945 to 2002 previously identified by Etheridge et al. (2006) but also found that the variety of patterns of stand development was surprisingly complex. Similar development patterns to those in MW-fluctuating, MW-declining, and SW-declining stands were observed in Quebec by Bouchard et al. (2006), with decreases in SW canopy cover following the 1980s spruce budworm outbreak and subsequent increases in HW canopy cover. In contrast with our study, stands studied by Bouchard et al. (2006) did not sustain a major spruce budworm outbreak in the 1950s. The legacy effect of budworm-caused mortality on stands leaves them more vulnerable to wind disturbance events and can cause rapid stand decline (Taylor and MacLean 2009). The combined effects of three mortality factors (spruce budworm, birch dieback, and stand age) significantly thinned stands and predisposed remaining trees to additional mortality from wind events. The combined effect of these mortality factors likely accounted for the period of significant reduction in canopy cover from 1946 to 1966 and the observed changes in SW content.

Management implications

Our results revealed that proportions of SW and HW tree species in MW stands are highly variable over time and space. Five distinct classes of development occurred within sampled stands in this forest, but others undoubtedly exist. Variation in development of stands resulted from effects of various and often interacting disturbances: spruce budworm, birch dieback, wind throw, and natural senescence, the resulting stand conditions, and species-specific response to the new stand conditions. Mature balsam fir was particularly vulnerable to mortality from natural senescence and from budworm-caused mortality from 1946 to 1966. When combined with the birch dieback episode during this same period, heavy mortality occurred in MW stands. The long-lived nature of red spruce, combined with its low susceptibility to budworm defoliation (Hennigar et al. 2008), resulted in stands with a considerable red spruce component being stable. In contrast, stands with substantial balsam fir, a short-lived species with high susceptibility to spruce budworm, had large declines (15%–47%) in SW content over time. In this sense, balsam fir – tolerant HW stands in northern New Brunswick appear to be a temporally transitional MW stand type, whereas red spruce – tolerant HW stands common in Maine, southern New Brunswick, and Nova Scotia are more stable.

Our results suggest that caution is needed when monitoring the abundance and health of MW forests, as not all MW stands have similar successional patterns. The observed stand development patterns can inform the design of silvicultural practices aimed at creating or maintaining MW stands.

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