Post-Fire Development of Canopy Structure and Composition in Black Spruce Forests of Abitibi, Québec: A Landscape Scale Study

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Fire reconstruction and forest inventory maps provided an opportunity to study changes in stand-level characteristics following fire using a data set comprised of all forest stands of fire origin in an area of over 10 000 km^2. We assigned the date of the most recent fire occurrence to over 31 000 forest stands in an ecoforestry database. We categorized stands on different substrates into age classes to investigate differences in canopy composition, cover and height, and incidence of secondary disturbance. Stands with over 75% *Picea mariana* (Mill.) BSP dominated all age classes on organic sites. On other substrates, there was a change in canopy composition from deciduous stands and stands dominated by *Pinus banksiana* Lamb. to *Picea mariana* stands after about 100 yr. This transition was later for xeric sites. After a peak in canopy cover and height at about 100 yr, there was a decrease in the area occupied by stands with dense, tall canopies. Structural development was slower on less productive sites. There was little incidence of spruce budworm outbreaks. Partial disturbance by windthrow coincided with canopy break-up at 100 yr, but appeared to have little effect on overall canopy structure in later stages. Structural diversity was independent of compositional diversity; on organic sites, stands with similar composition had different canopy structure. Diversity of stands with different composition and structure was greatest in the first 150 yr following fire. Maintaining stands in different stages of structural development on the landscape would serve to maintain regional biodiversity.

Keywords boreal forest, canopy structural development, *Picea mariana*, spruce budworm outbreaks, stand-level structure, windthrow

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1 Introduction

Development of forest stands over time involves changes in both species composition and structure. Structural development is generally related to changes in composition, and is specifically associated with the density-independent mortality of the dominant tree species (Goebel and Hix 1997). For example, the mortality of a taller, early successional species can result in a shorter canopy height (Paré and Bergeron 1995). However, in some boreal forest ecosystems in which monospecific forest stands generally reestablish following fire (Carleton and Maycock 1978), this traditional view does not apply. Instead, structural development which is independent of changes in species composition may be the key process. The structural complexity which develops from this process acts indirectly on the abundance and distribution of species. Thus, one of the first steps towards developing strategies for forest management that conserve regional biodiversity is to determine structural development following fire.

Stand-level structural development, which we define as changes in canopy cover and height, can be related to the four-phase model of forest development by Oliver (1981). The stages of stand initiation, stem exclusion, understory reinitiation and old-growth have been linked to species replacement (e.g. Palik and Pregitzer 1993). However, we expect that stand-level structural development will follow these stages even in ecosystems dominated by one species. Changes in biomass, the basis of the biomass accumulation model (Bormann and Likens 1979), also reflect changes in canopy structure. For example, the end of the aggradation phase is characterized by the death of old dominant trees and replacement with younger trees (Bormann and Likens 1979), which could result in lower canopy height and cover.

Forest structure and composition are closely related to secondary disturbance, particularly spruce budworm outbreaks and windthrow, which are both common in eastern Canadian boreal forest. The incidence of spruce budworm outbreaks depends on species composition, in particular the abundance of *Abies balsamea* (L.) Mill. (MacLean 1980, Bergeron and Leduc 1998, Bergeron 2000), which varies with time since fire (Bergeron et al. 1995). Windthrow can vary with stand age, composition or structure (Mitchell 1995, Ruel 1995).

Changes in tree species composition, structural development and secondary disturbance can also depend on substrate (Gauthier et al. 1996). Successional rate has been positively correlated with soil nutrients, organic matter and moisture (Donnegan and Rebertus 1999). Biomass accumulation can be slower on sandy soils due to lower moisture-holding capacity (Johnson et al. 2000). Thus we expect faster structural development on more productive sites. In terms of secondary disturbance, windthrow hazard is greater for sites with poorer drainage, shallower rooting depth or organic soils (Mitchell 1995). However, the apparent relationship between site characteristics and mortality due to spruce budworm outbreaks in Quebec boreal forest (Dupont et al. 1991), has not always been validated (Bergeron et al. 1995).

We assessed post-fire development by determining changes in stand-level structure and dominant tree species composition with time since fire on different substrates. In this study, we focused on canopy composition, as well as canopy structure consisting solely of canopy height and canopy cover. Our specific objectives for each substrate were: 1) to determine the dominant canopy composition at different times since fire, 2) to assess changes in canopy structure with time since fire, 3) to relate the incidence of secondary disturbance to structural development, and 4) to identify age classes with the greatest diversity of stands with different canopy composition or structure. In the Canadian boreal forest, species dominance can shift from deciduous species or *Pinus* spp. to *Picea* spp. (Carleton and Maycock 1978, Bergeron and Dubuc 1989). However, the dominance of *Picea mariana* in stands of all ages on some substrates also allowed us to isolate structural development from changes in canopy composition. We hypothesized that changes in canopy structure would still be apparent on substrates with minimal differences in canopy composition, but to a reduced extent compared to other substrates.

Researchers have used several approaches to investigate changes in forest structure and composition with time. Although repeat measurements on permanent plots is the most ideal method (e.g. Hofgaard 1993), it is not feasible for long time periods or at large spatial scales. Diameter or height distributions used to infer past and future developmental stages may represent differential growth rates rather than successional trends (Bergeron and Dubuc 1989, Bergeron 2000). Both size structure and dendroecology (e.g. Bergeron 2000) would be very labour intensive for large areas. The chronosequence approach, in which stands of different ages are compared to provide insight into changes over time, is subject to criticism that differences could be due to site characteristics rather than stand age (Johnson 1992, Linder 1998, Bergeron 2000), particularly when the sample size is small. Our approach of combining an ecological forest inventory database with fire reconstruction maps, partially overcomes these shortcomings by analyzing trends for different site types and by using a very large data set. In one of the first applications of this approach, we provide an overall assessment of stand-level structure along a post-fire chronosequence at the landscape scale.

2 Materials and Methods

2.1 Study Area and Database

Our 10 000 km^2 study area in the Abitibi region, Québec, was situated between 78°30´W and 79°31´W, was bounded by 49°N to the south, and extended up to 50°10´N in the north with an additional extension to 50°22´N in the Maskutchi region. This area is part of the Clay Belt of Ontario and Québec, a physiographic unit composed of clay deposits left by pro-glacial Lake Ojibway (Vincent and Hardy 1977); organic soils, tills and glaciolacustral deposits are also common. The topography is generally flat. Mean annual temperature is –2.5 to 0 °C; the length of the growing season is 150 to 160 days and total precipitation is 700 to 800 mm (Robitaille et al. 1998).

Our study area is part of the Lake Matagami Lowland ecological region, within the *Picea mariana*–moss bioclimatic domain (Saucier et al. 1998). Most of the area is dominated by *P. mariana* which tends to form monospecific, even-aged stands with a continuous moss layer dominated by *Sphagnum* spp. In this ecosystem, large and frequent fires kill most trees and aboveground vegetation (Viereck 1983). Fire cycle length has increased from 53 yr before 1850, to 141 yr between 1850 and 1920, to 326 yr since 1920; mean stand age is 139 yr (Bergeron et al. 2001).

The Ministry of Natural Resources ecoforestry database (Ministère des Ressources Naturelles du Québec 1994) includes information for each stand: area, surficial deposit and moisture regime. In addition, the following data on forest stands were available for analysis: canopy composition, canopy height, canopy cover, and incidence of windthrow and spruce budworm outbreaks. Data were not available on within-stand structural variables such as tree size distribution or deadwood material. The methodology used by the Ministry of Natural Resources was based on aerial photo interpretation. The dominant tree species composition was based on the proportion of coniferous or deciduous trees, and the dominant species (Table 1). Nomenclature follows Farrar (1995). Canopy height was determined using the average height of the dominant and co-dominant trees, and was divided into six classes (>22 m, 17–22 m, 12–17 m, 7–12 m, 4–7 m, 1.5–4 m). Canopy cover, the proportion of the area occupied by the projected cover of tree crowns, was deter-

Table 1. Classification of canopy composition (Ministère des Ressources Naturelles du Québec 1997). (For cover type codes associated with the classification, see Appendix.)

Name	Description	
Picea mariana	>50% conifer	>75% *Picea mariana*
Pinus banksiana	>50% conifer	>50% *Pinus banksiana*
Other conifer	>50% conifer	<75% *Picea mariana* and <50% *Pinus banksiana*
Deciduous	>50% deciduous	

mined using four classes (80–100%, 60–80%, 40–60%, 25–40%). Partial and complete disturbance (including partial and total windthrow, and light and severe spruce budworm outbreak) were defined as the destruction of trees over 25–75% and >75% of the area, respectively. Photo interpretation was done shortly after the last spruce budworm outbreak in 1970–1987 (Bergeron et al. 1995).

2.2 Data Analysis

By overlaying fire reconstruction maps (Bergeron et al. 2001) onto the forest inventory maps that accompanied the ecoforestry database, we assigned a date since last fire to every forest stand in our study area. The fire reconstruction maps were developed by dating postfire tree cohorts and using other dendrochronological techniques for fires before 1880, and using archives and aerial photographs for fires after 1880. We checked the fire dates on the maps, and assigned residual stands (assessed using age class, structure and composition) to the previous fire. Since the resolutions of the two sets of maps were not equivalent, we minimized error by discarding stands of uncertain attribution (1.4% of stands). We also excluded any stands that were harvested (15.7%) or classified as non-forest (26.3%). Our final database (the remaining 56.5%) consisted of 31 033 forest stands and covered an area of 429 577 ha (Table 2).

In order to investigate changes over time in canopy cover, height, tree composition and incidence of secondary disturbance, we categorized stands into time-since-fire classes using 25 yr intervals for the past century and 50 yr intervals thereafter (Table 2). These age classes included stands originating from many different fires throughout the study area (e.g. more than 25 yr since 1900). Younger stands covered less area due to a decrease in fire frequency, possibly because of climatic factors and fire suppression (Bergeron et al. 2001). The area and number of stands generally represent the sample size for analysis. However, some young stands or those that had experienced secondary disturbance had missing data since the regenerating forest was too young to assess the structural characteristics. We do not present results from the youngest 0–25 yr old class because data were available for less than 2% of the area. Although we include the 25–50 yr old class, data were available for only slightly more than 50% of the stands.

To investigate differences in structural changes on different substrates, we divided the dataset into four site types based on surficial deposit and moisture regime (similar to those being established by the Québec provincial forest inventory program, Thuy Nguyen pers. comm.; Table 3). The site types represent a gradient of productivity, from the least productive organic hydric sites to the most productive fine subhydric sites. Coarse and thin soil, the two xeric site types, both have intermediate productivity. Stands were not distributed evenly among the four site types (Table 2). Fine and organic site types were well

Table 2. Number of forest stands and surface area for each age class; also the midpoint age of each age class, and the proportion of the area occupied by different site types.

Time since fire class	Approx. age (yr)	Midpoint age (yr)	Number of stands	Total area (ha)	Proportion (%) by site type			
					Fine	Coarse	Organic	Thin soil
1975–1997	0–25	12	1210	34983	59.6	0.5	32.7	7.2
1950–1974	25–50	38	889	12645	83.7	4.4	9.4	2.4
1925–1949	50–75	62	307	3986	77.2	0.8	10.4	11.6
1900–1924	75–100	88	11867	153128	68.8	15.0	10.4	5.7
1850–1899	100–150	125	3378	41533	62.6	16.4	19.2	1.8
1800–1849	150–200	175	6643	90160	64.7	3.3	30.1	1.9
1750–1799	200–250	225	4852	66264	59.8	3.2	35.9	1.1
1700–1749	250–300	275	1816	25425	63.6	3.9	32.3	0.2
Before 1700	300–350	325	71	1453	86.0	0.0	14.0	0.0

Table 3. Site type classification: name, description, moisture regime and surficial deposit codes (Ministère des Ressources Naturelles du Québec 1997).

Name	Description	Moisture regime	Surficial deposit codes
Fine	Glacial till and glaciolacustrine deposits	Mesic-hydric	1, 1A, 1AA, 1AAR, 1AR, 4GA, 4GAR
Coarse	Moraine, and fluvio-glacial, fluvial, shallow water glaciolacustral and eolian deposits	Xeric-mesic	1BI, 2A, 2AE, 2BD, 2BE, 3, 4GS, 9
Organic	Organic layer >40 cm	Hydric	7, 7R
Thin soil	Rock substrate, soils <50 cm	Xeric-mesic	R

represented in most of the age classes; however there were not as many stands on coarse and thin soil sites, particularly in the oldest age classes and the 50–75 yr old class on coarse soils.

For each age class within each site type, we calculated the relative area (divided by total area within each category) covered by stands for different classes of canopy composition (using groups defined in Table 1), cover and height. The average canopy cover and height was determined using the midpoints of the classes (25 m for the >22 m height class). Stand diversity was calculated using Shannon's index separately on the proportion of stands with different classes of canopy composition or structure: composition, height, cover, and the combination of cover and height. For secondary disturbance, we determined the percentage of the area affected by spruce budworm outbreaks and windthrow. We also calculated the proportion of stands with *Abies balsamea* as the dominant or co-dominant species (for cover type codes, see Appendix).

3 Results

3.1 Canopy Composition

The abundance of stands with >75% *Picea mariana* increased with time since fire on all site types, approaching 90% of stands in the oldest age classes (Fig. 1). Stands with >75% *P. mariana* dominated all age classes on organic sites. On fine sites, the proportion of area occupied by stands with >75% *P. mariana* was particularly low in the younger age classes and then increased rapidly with time since fire. Stands dominated by *Pinus banksiana* were most abundant in the intermediate 75–100 yr old stands on coarse and thin soil substrates; but these stands were also present in later stages, even up to 200 yr following fire. Other conifer-dominated stands with other species such as *Abies balsamea, Larix laricina* (DuRoil) K.Kock, *Betula papyrifera* Marsh. or *Populus tremuloides* Michx. (see Appendix), were common in intermediate 75–200 yr old classes on all substrates except organic. Deciduous stands dominated the youngest age class on fine substrates, and were also common on coarse and thin soils sites in intermediate age classes.

Diversity of stands with different canopy composition was generally greatest for the younger or intermediate-aged stands, and then decreased substantially with time since fire (Fig. 2a). Diversity was lowest on organic sites. Values were similar among the other three site types, but the trends with time since fire were different. On fine substrates, diversity was highest in the youngest age classes, whereas the peak in diversity occurred in the intermediate stages (75–200 yr) for the coarse and thin soil sites.

3.2 Structural Development

Forest structure varied considerably along the chronosequence. Most stands were relatively open with 20 to 60% canopy cover, except in the 50–75 and 75–100 yr age classes which had higher proportions of dense stands (over 60% cover, Fig. 3a). Except for the youngest 25–50 yr age class with

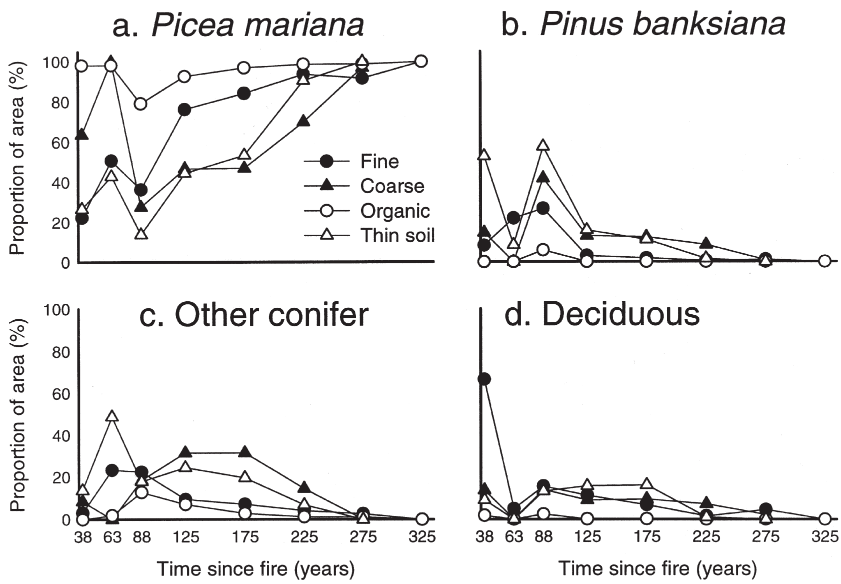

Fig. 1. Canopy species composition of stands in different age classes on four site types; proportion of area occupied by the following composition classes: *Picea mariana* (a); *Pinus banksiana* (b); other conifer (c); deciduous (d). See Table 1 for a description of canopy composition classes, and Table 3 for a description of site types.

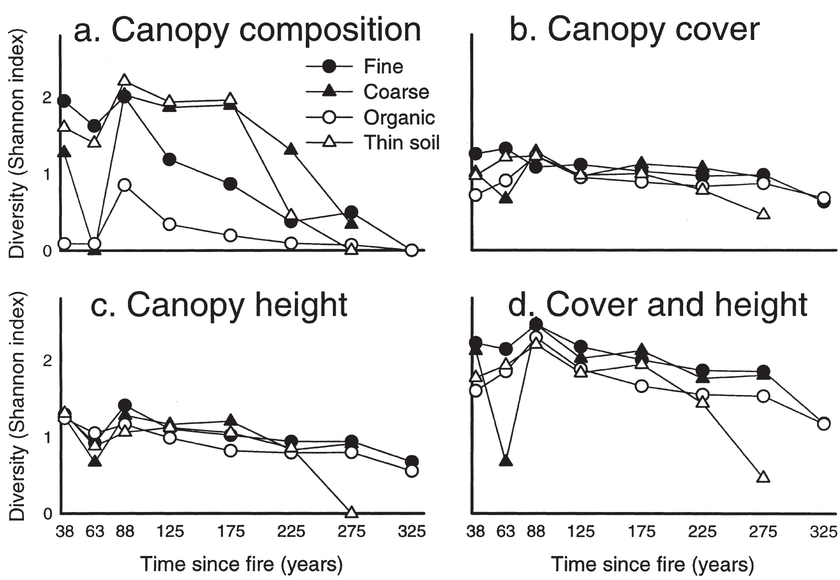

Fig. 2. Diversity, using Shannon index, of stands with different characteristics in different age classes on four site types, based on: canopy species composition (a); canopy cover (b); canopy height (c); both cover and height (d). See Table 3 for a description of site types.

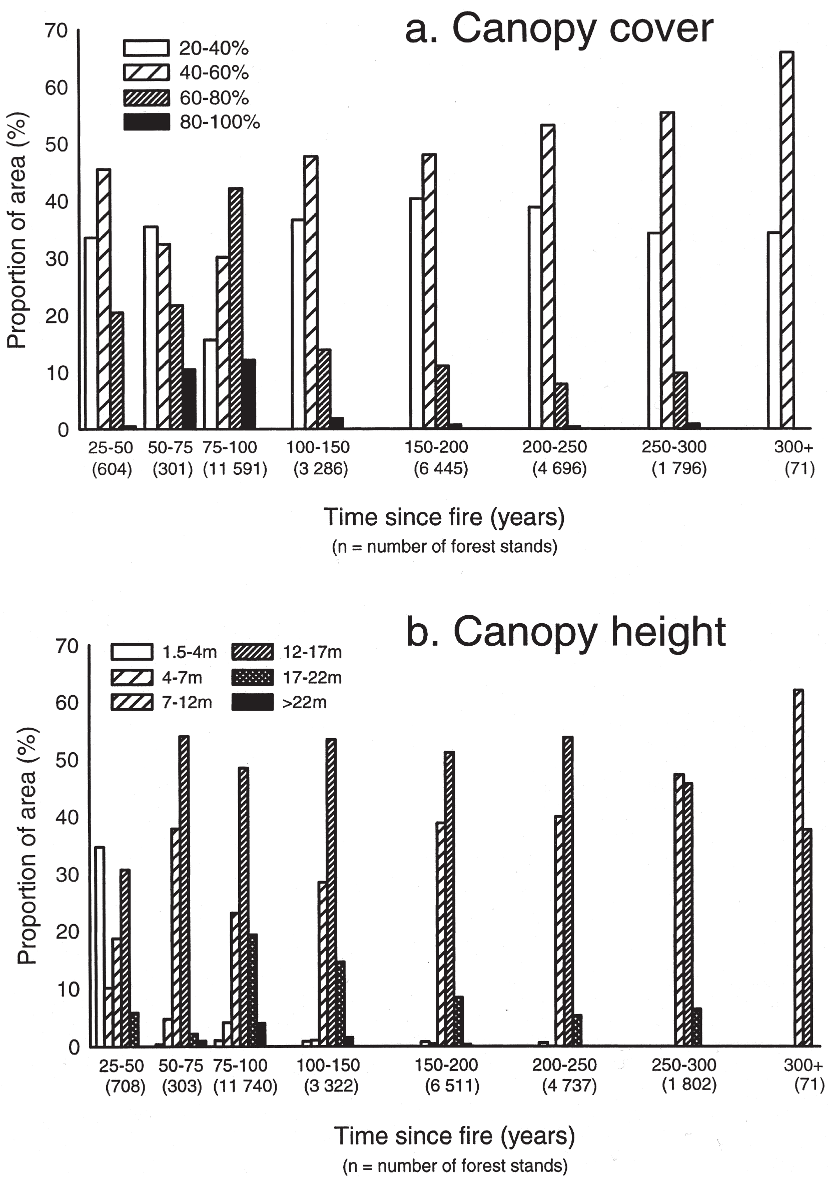

Fig. 3. Structural characteristics of stands in different age classes; proportion of area occupied by different classes of canopy cover (a) and height (b).

high proportions of stands with shorter trees, the vast majority of stands were 7–17 m tall (Fig. 3b). The proportion of stands taller than 17 m was greatest in the 75–100 yr age class.

Trends in average canopy cover and height differed slightly among the four site types (Fig. 4). Average cover was greatest at 75–100 yr for all site types except for coarse substrates which had the highest cover at 50–75 yr (Fig. 4a). Peaks in canopy height were slightly earlier for fine and thin soil substrates (75–100 yr) than for coarse and organic substrates (100–150 yr, Fig. 4b). The

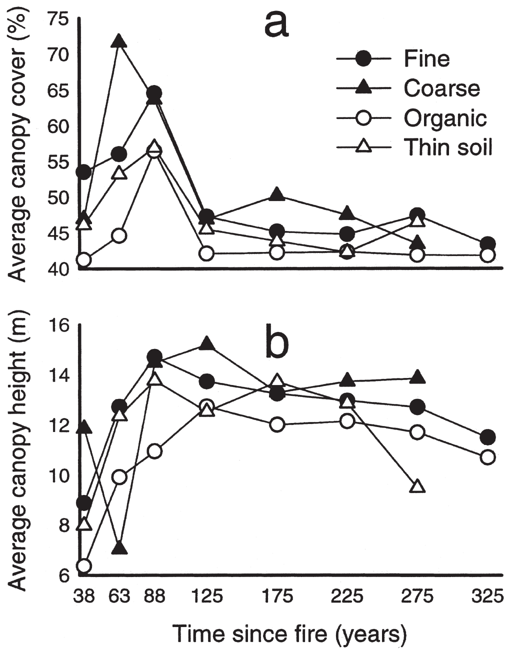

Fig. 4. Stand level characteristics at different times since fire on four site types: average canopy cover (a); average canopy height (b). See Table 3 for a description of site types.

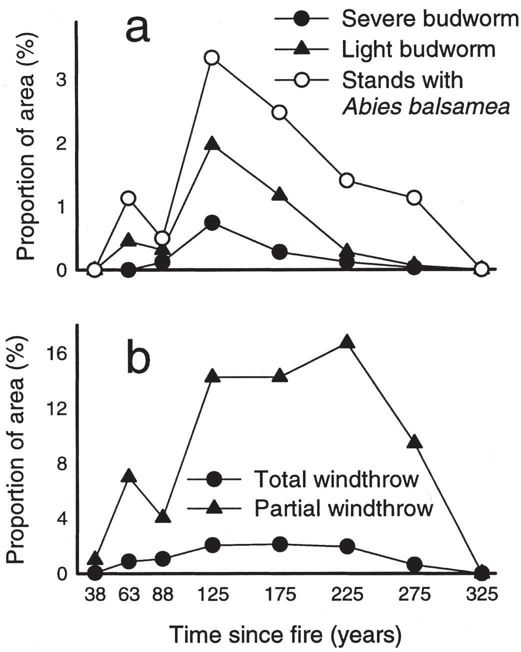

Fig. 5. Incidence of secondary disturbances in different age classes; proportion of area occupied by stands affected by: severe and light spruce budworm outbreaks (a); total and partial windthrow (b). The percentage of area covered by stands with *Abies balsamea* in the canopy is included in (a).

peaks in canopy height and cover coincided for fine and thin soils; however, they were offset for coarse and organic substrates where 100–150 yr old sites had lower canopy cover, but greater height than 75–100 yr old sites (Fig. 4b).

Intermediate age classes had the greatest diversity of stands with different structural characteristics (Fig. 2b–d). There were few differences in diversity among site types except for lower diversity in the 50–75 yr old age class on coarse substrates, and an earlier peak in diversity based on canopy cover for fine substrates.

3.3 Secondary Disturbance

Secondary disturbance was most common in stands of intermediate age (Fig. 5). The overall incidence of spruce budworm outbreak was very low in all age classes with less than 1 and 2% of stands affected by severe and light budworm outbreaks, respectively (Fig. 5a). The 100–150 yr old stands were the most affected by spruce budworm, and also had the highest proportion of *Abies balsamea*. Windthrow was more common than spruce budworm outbreaks, affecting more than 16% of the area occupied by the 100–250 yr old stands (Fig. 5b). Most windthrow only partially disturbed the forest stands.

The incidence of secondary disturbance varied among site types. Spruce budworm outbreaks were more prevalent on fine and thin soil sites than on organic and coarse sites (Fig. 6a). The peak in spruce budworm outbreaks with time since fire was slightly later for fine sites than for sites with thin soil. The trends with time since fire for spruce budworm and the proportion of stands with *Abies balsamea* coincided for thin soil and organic sites, but were offset by one age class for fine and coarse sites (Fig. 6a, b). The

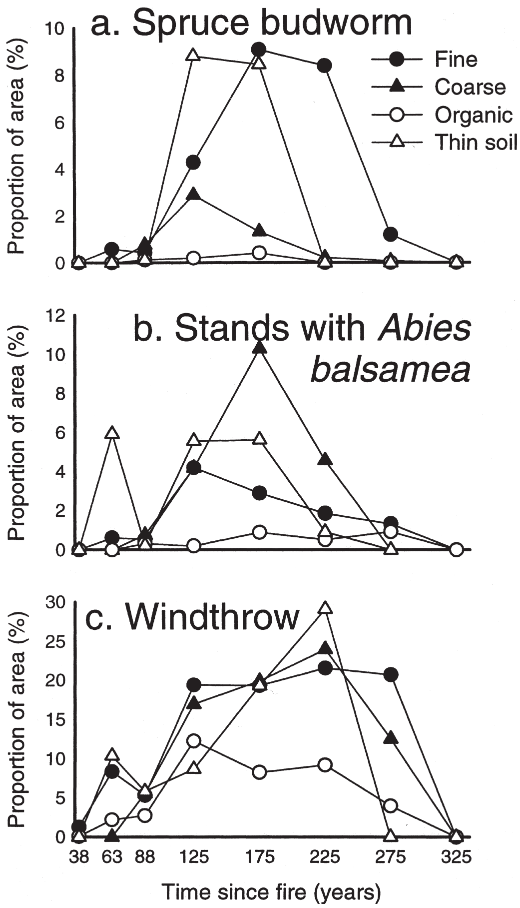

Fig. 6. Incidence of secondary disturbances in different age classes on four site types; proportion of area occupied by: stands affected by spruce budworm outbreak (a); stands with *Abies balsamea* in the canopy (b); stands affected by windthrow (c). See Table 3 for a description of site types.

incidence of windthrow was similar among site types except for organic sites which were much less affected by windthrow (Fig. 6c).

4 Discussion

4.1 Canopy Composition

The ecoforestry inventory measures and the fire occurrence dates on a very large number of stands provided a thorough, general overview of the main trends in post-fire stand development in our study region. Changes in canopy composition were evident in the first century following fire on most substrates. Stand-level canopy species dominance shifted from deciduous stands or stands dominated by *Pinus banksiana* to stands with over 75% *P. mariana*; however, some monospecific *Picea mariana* stands established immediately after fire. The presence of *Picea mariana* in the subcanopy of intermediate-aged deciduous and *Pinus banksiana* dominated stands (Harper et al. unpubl.), and the presence of a few late-intermediate aged deciduous and *P. banksiana* stands, suggests that canopy succession explains, in large part, the transition towards dominance by *P. mariana*.

Similar transitions from deciduous or *Pinus* sp. to *Picea* sp. have been observed in other studies in the Canadian boreal forest (Carleton and Maycock 1978, Bergeron and Dansereau 1993). However, further south near Lac Duparquet, mixedwood stands are maintained through recruitment of deciduous trees in gaps (Bergeron 2000). Gap disturbance creates favourable microsites for other species in many ecosystems (e.g. Kuuluvainen 1994, Frelich and Reich 1995). In our study area, there was no evidence of other tree species regenerating in *P. mariana* stands. The development of an extensive thick *Sphagnum* moss layer prevents seedling establishment (Boudreault et al. 2002). This allows the dominance of *Picea mariana* which reproduces mainly by layering in old-growth forests and is tolerant of cold, wet, nutrient poor conditions (Viereck 1983).

The timing of the change in canopy composition on different site types reflects a productivity gradient. Differences in canopy composition among site types were evident even in the early stages. *Picea mariana* stands developed immediately after fire on organic sites where there appeared to be virtually no change in species composition. This could be due to the lack of seed source for other species if the pre-fire composition on these organic sites was exclusively *P. mariana*. On the most productive fine sites, deciduous species such as *Populus tremuloides* prefer clay substrates, and therefore colonize and dominate the youngest stands.

On all site types except organic, there was an apparent shift in dominance from stands with *Pinus banksiana* in the canopy to stands with over 75% *P. mariana* at about 100 yr following fire. This transition occurred sooner on more productive fine sites than on xeric coarse and thin soil sites, due to faster growth and subsequent mortality of *P. banksiana*. Rates of succession have been found to be greater on sites with higher soil nitrogen and moisture (Donnegan and Rebertus 1999). Alternatively, on coarse and thin soil sites, stands with *P. banksiana* may burn rather than become dominated by *P. mariana.* Gauthier et al. (2000) found a slightly longer fire interval on organic sites, but no detectable difference among other site types. Thus it is unlikely that fire interval length alone could explain the different transitions in canopy composition. Most likely, rapid growth of *P. mariana* on the more productive fine sites leads to an earlier change in dominance, although *P. banksiana* may still persist within stands with over 75% *P. mariana*.

4.2 Structural Development

Overall, structural development coincided with changes in dominant species composition. However, changes in forest structure were still apparent where there was little change in canopy composition, both on organic sites in our study area and in a *Picea abies* forest (Svensson and Jeglum 2001). These results provide evidence for our hypothesis that changes in canopy structure would occur, but to a lesser degree, on substrates with minimal changes in canopy composition. Therefore, structural development is partly independent of species replacement. Most likely, the same processes that initiate species turnover (mortality and subsequent recruitment of new trees in the canopy), also affect structural development whether the structural cohorts are of the same or different species.

Overall, stages of structural development in our study area mirror those of the biomass accumulation model (Bormann and Likens 1979) and the stand development stages (Oliver 1981). However, since we were unable to determine the development of individual stands, we could not rule out alternative pathways, such as continuous recruitment in open spruce forests (Sirois and Payette 1989). The first stage of structural development, reorganization (stand initiation), was not directly assessed with our sampling design. The second, aggradation (stem exclusion), phase lasted up to 100 yr following fire, as evidenced by the increase in the proportion of stands with greater canopy cover and height. This duration is longer than in faster-growing *Populus*-dominated forests (25–35 yr, Palik and Pregitzer 1993; up to 75 yr after fire, Paré and Bergeron 1995). However, increases in height and volume from 68 to 140 yr, and from 124 to 196 yr after fire in old-growth *Pinus sylvestris* and *Picea abies* stands in Sweden (Linder 1998) indicate similar timing of structural development. The longer duration in these coniferous forests is probably due to the slow growth of *Picea mariana* seedlings and saplings (Johnson 1992), since most *P. mariana* establishment occurs in the first few years after fire (Sirois and Payette 1989, St.-Pierre et al. 1992).

The transition (understory reinitiation) phase starts to occur at about 100 yr on most site types when the canopy becomes more open. The level of resolution of our data is too coarse to determine the length of this phase. The decrease in cover could be related to the transition from *Pinus banksiana* stands to the more open *Picea mariana* stands. This is similar to the change from a taller to a shorter canopy following the mortality of *Populus tremuloides* in forests south of our study area (Paré and Bergeron 1995). On organic sites, however, this change in structure is independent of change in species composition, and is most likely related to the mortality of the first cohort of taller trees.

Changes in different structural components do not necessarily occur simultaneously during the transition phase. Structural development is the outcome of different processes which can act independently. For example, canopy height is the result of growth, whereas the decline in canopy cover at stand break-up is most likely due to mortality from age-related factors such as disease and windthrow. On coarse and organic sites, trees may grow slower and mature after canopy break-up because of excess moisture in organic soils, or low moisture and nutrient availability in sandy soils (Johnson et al. 2000). Earlier peaks in canopy height on fine and thin soil sites may be explained by higher productivity on fine sites, and may be an artifact of low sample size on the nutrient poor thin soil sites.

In the final stage of structural development, at about 150 yr following fire, there was minimal change in canopy cover and height on all site types, and a gradual transition to *Picea mariana* stands on organic and fine sites. Open forests with discontinuous canopies are maintained on all site types due to paludification, a process in which soil temperature, nutrient availability and productivity decrease with time since fire with the build-up of thick moss and organic layers (Van Cleave et al. 1983, Paré and Bergeron 1995).

4.3 Secondary Disturbance

Secondary disturbance from windthrow and, to a lesser extent, spruce budworm outbreaks, was prominent in the intermediate age classes (100–300 yr), together affecting almost one fifth of forest stands. These results probably underestimate the total amount of partial disturbance since levels of disturbance with <25% of trees affected were not included. The increase in levels of spruce budworm outbreak and windthrow at about 100 yr coincided with canopy break-up during the transition phase of structural development.

The incidence of spruce budworm outbreak was closely related to the proportion of stands with *Abies balsamea*, the preferred species of spruce budworm. *Abies balsamea*, a late successional species, decreased in abundance with time since fire since the increase in *Sphagnum* spp. cover favours *Picea mariana* which can reproduce vegetatively by layering. Another study also found a relationship between mortality due to budworm and the amount of *A. balsamea* rather than stand structure (MacLean 1980). Although Bergeron et al. (1995) and Bergeron and Leduc (1998) found that mortality due to spruce budworm outbreaks was not related to site characteristics, we found a low incidence of outbreaks for coarse sites which had a relatively high proportion of stands with *A. balsamea* in the canopy, and the reverse trend for fine sites. This could be due to the dominance of *Pinus banksiana*, a non-host species, on many coarse and thin soil sites, whereas most stands on intermediate-aged fine sites were dominated by *P. mariana*, another host species.

Windthrow is dependent on canopy structure (Mitchell 1995). Greater canopy height made intermediate aged stands more susceptible to windthrow (Smith et al. 1987, Mitchell 1995, Ruel 1995). Some forest stands may have been opened up by windthrow during the transition phase. Alternatively, a decrease in canopy cover from other causes may have reduced stability in these *P. mariana* stands with poor rooting substrate (Smith et al 1987, Ruel 1995). Intermediate-old stands may have experienced windthrow because of higher proportions of stands dominated by *Picea mariana*, which is shallow rooted and thus more vulnerable to windthrow (Viereck 1983, Smith et al 1987, Ruel 1995). In the oldest stands, trees had grown in more open conditions where diameter growth is favoured over height growth (Ruel 1995), and would therefore have been less prone to windthrow.

Overall, there was not much difference in windthrow among site types despite differences in windthrow hazard for different soils and rooting depths (Mitchell 1995, Ruel 1995). However, windthrow was unexpectedly lower for organic sites despite poor drainage, organic soils and the dominance of the more vulnerable *Picea mariana*. Trees grown in conditions of lower canopy height and cover in these organic sites could have been more resistant to windthrow (Smith et al. 1987, Mitchell 1995, Ruel 1995).

In boreal forest ecosystems, changes in structure from secondary disturbances such as windthrow, insects or disease may allow the re-establishment of early successional species and the maintenance of mixedwood stands. For example, there was a shift towards mixed deciduous stands in Quebec following spruce budworm outbreaks (Bergeron and Dansereau 1993). However, in our study area in northwestern Quebec, the incidence of secondary disturbance in the intermediate age classes appeared to have little effect on canopy composition. In relation to structural development, secondary disturbance most likely contributed to decreases in canopy cover and height during canopy break-up in the transition phase. However, further decreases in canopy cover were not apparent at later stages when partial windthrow was still common. Thus, the effects of secondary disturbance on overall canopy structure were minimal in the old-growth stages of structural development.

4.4 Structural Diversity

Structural diversity was independent of tree species diversity; canopy structure varied among stands whether they had similar or different composition. Structural diversity was similar among all site types despite substantially lower diversity of stands with different canopy composition on organic sites. Structural diversity also generally remained high throughout stand development while diversity based on composition decreased in the later stages. Stand-level diversity for both composition and structure was greatest during the early intermediate stages around canopy break-up. At this transition stage, different timing for changes in forest structure within different stands resulted in a variety of different types of canopy structure on the landscape.

Although 75–100 yr old stands had the highest among-stand composition and structural diversity, stands of all ages contribute to structural diversity on the landscape. Younger stands have unique structural characteristics such as tall, dense canopies; and slightly older age classes had the highest incidence of secondary disturbance. Due to longevity and more open canopies, the oldest stands could provide other structural attributes including high amounts of coarse woody material (Ohlson et al. 1997) and gaps (Kuuluvainen 1994) that contribute to local, within-stand diversity. Forest stands of different ages can be produced through a natural disturbance regime or by extending harvesting rotation length (Bergeron et al. 2002). Different stages of structural development can be simulated through diversified silvicultural treatments (Bergeron et al. 2002). From an ecosystem standpoint, our results of stand-level canopy development suggest that maintaining different stages of structural development should provide the variety of stand-level structural characteristics on the landscape that are necessary to preserve regional biodiversity.

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Appendix. Cover type codes and their descriptions (Ministère des Ressources Naturelles du Québec 1997). Descriptions include the conifer proportion of the basal area, and the composition of the conifer and deciduous components. Canopy classes refer to our classification of canopy composition (Table 1).

Canopy class	Code	Description [a)]			
		% conifer	Conifer [b)]	Deciduous	Other
Picea mariana	EE	>75%	>75% Pm		
	EEC	>75%	>75% Pm		<40% canopy cover
Pinus banksiana	EPG	>75%	50–74% Pm, Pb co-dominant		
	PGBB	50–74%	>50% Pb	>50% Bp	
	PGE	>75%	50–74% Pb, Pm co-dominant		
	PGFI	50–74%	>50% Pb	>50% Pt or Bp	
	PGPE	50–74%	>50% Pb	>50% Pt	
	PGPG	>75%	>75% Pb		
Other conifer	EBB	50–74%	>50% Pm	>50% Bp	
	EFI	50–74%	>50% Pm	>50% Pt or Bp	
	EME	>75%	50–74% Pm, Ll co-dominant		
	EPE	50–74%	>50% Pm	>50% Pt	
	ES [c)]	>75%	50–74% Pm, Ab co-dominant		
	MEE	>75%	50–74% Ll, Pm co-dominant		
	MEME	>75%	>75% Ll		
	RBB	50–74%	No species dominant	>50% Bp	
	RE	>75%	Pm important but <50%		
	RFI	50–74%	No species dominant	>50% Pt or Bp	
	RPE	50–74%	No species dominant	>50% Pt	
	RPG	>75%	Pb important but <50%		
	SBB [c)]	50–74%	>50% Ab	>50% Bp	
	SE [c)]	>75%	50–74% Ab, Pm co-dominant		
	SFI [c)]	50–74%	>50% Ab	>50% Pt or Bp	
	SPE [c)]	50–74%	>50% Ab	>50% Pt	
	SS [c)]	>75%	>75% Ab		
Deciduous	ALF	<25%		>25% Al	
	ALM	26–50%		>25% Al	
	BB	<25%		>50% Bp	
	BBE	26–50%	>50% Pm	>50% Bp	
	BBPG	26–50%	>50% Pb	>50% Bp	
	BBR	26–50%		>50% Bp	
	FIS [c)]	26–50%	>50% Ab	>50% Pt or Bp	
	BBS [c)]	26–50%	>50% Ab	>50% Bp	
	PES [c)]	26–50%	>50% Ab	>50% Pt	

[a)] Based on basal area
[b)] Species codes: Ab = *Abies balsamea*, Al = *Alnus* spp., Bp = *Betula papyrifera*, Ll = *Larix laricina*, Pb = *Pinus banksiana*, Pm = *Picea mariana*, Pt = *Populus tremuloides*
[c)] Stands with *Abies balsamea*