

Partial cutting as an analogue to stem exclusion and dieback in trembling aspen (*Populus tremuloides*) dominated boreal mixedwoods: implications for deadwood dynamics¹

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Abstract: In the winter of 1998–1999, two partial harvesting treatments that removed 33% (1/3) and 61% (2/3) of stand basal area were applied to even-aged trembling aspen (*Populus tremuloides* Michx.) stands and compared with unharvested control stands. Stands in the 1/3 treatment were low thinned, while stands in the 2/3 removal were crown thinned. Coarse woody debris dynamics were assessed during the following 6 years by means of permanent sampling plots and downed wood inventories. Between 1999 and 2004, tree mortality was, respectively, 18%, 17%, and 32% in control stands and 1/3 and 2/3 harvesting treatments. Although total snag density was similar between controls and partial cutting treatments, total snag basal area was significantly higher in controls in 2004. Between 1999 and 2004, net change in aspen snag density was positive for controls and negative for both partial cutting treatments. Partial cutting also exacerbated mortality of small-diameter white birch (*Betula papyrifera* Marsh.). Downed wood volume increased by 35 m³·ha⁻¹ in controls and by 25 m³·ha⁻¹ in the 2/3 harvesting treatment, while it decreased by 7 m³·ha⁻¹ in the 1/3 harvesting treatment. Coarse woody debris goals can be established in silviculture prescriptions; type, timing, and intensity of partial cutting are crucial to the outcome.

Résumé : À l'hiver 1998–1999, deux traitements de coupe partielle qui ont prélevé 33 % (1/3) et 61 % (2/3) de la surface terrière ont été appliqués à des peuplements équiennes de peuplier faux-tremble (*Populus tremuloides* Michx.) et comparés avec des peuplements témoins non traités. Les peuplements dans le traitement 1/3 ont été éclaircis par le bas tandis que les peuplements dans le traitement 2/3 ont été éclaircis par le haut. La dynamique du débris ligneux grossier a été étudiée au cours des 6 années suivant les traitements à l'aide de placettes d'échantillonnage permanentes et des inventaires du bois au sol. Entre 1999 et 2004, la mortalité arborescente a été 18 %, 17 % et 32 %, respectivement, dans les témoins et les traitements 1/3 et 2/3. Bien que les densités totales de chicots soient similaires entre les témoins et traitements de coupe partielle, la surface terrière de chicots (toutes espèces) était significativement plus élevée dans les témoins en 2004. Entre 1999 et 2004, le changement net de la densité de chicots de peuplier a été positif pour les témoins et négatif pour les deux traitements de coupe partielle. Les coupes partielles exacerbent aussi la mortalité des bouleaux à papier (*Betula papyrifera* Marsh.) de petits diamètres. Le volume du bois au sol a augmenté par 35 m³·ha⁻¹ dans les témoins et par 25 m³·ha⁻¹ dans le traitement 2/3 tandis qu'il a diminué par 7 m³·ha⁻¹ dans le traitement 1/3. Des objectifs spécifiques quant au maintien du débris ligneux grossier peuvent être établis dans des prescriptions sylvicoles; le type, le moment et l'intensité des coupes partielles sont critiques au résultat.

Introduction

Ecological forestry places an emphasis on understanding and working in harmony with natural patterns and processes (Seymour and Hunter 1999) and the diversification of silvicultural practices has been identified as an important measure for implementing ecological forestry or forest ecosystem management in the boreal forest (Bergeron et al. 2002; Greene et al. 2002). In this regard, silvicultural interventions may be considered as surrogates or analogues to natural processes involved in stand establishment, growth, and decline. In the absence of major disturbances such as fire, con-

siderable mortality occurs during normal stand development, initially due to competition for resources among individual stems and later primarily as a result of senescence and external factors (Smith et al. 1997). Depending on stand age, vertical structure, and species present, partial harvesting prescriptions in even-aged stands may emulate natural mortality processes in either the “stem exclusion phase” (up to maturity) in which intermediate and suppressed individuals are outcompeted for resource capture or a later “canopy transition phase” in which trees in the initial cohort, primarily dominants and codominants, lose vigor and die individually or in groups (Chen and Popadiouk 2002). In both cases,

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stem removal, injury to retained stems, and residual stand composition and structure influence immediate and future mortality and deadwood dynamics.

From an ecological viewpoint, mortality is as important a stand process as recruitment and growth, and dead and dying trees constitute biological legacies that are as important to ecosystem function and to the native community of organisms as live stems (Franklin et al. 2002). Moreover, a broader understanding of keystone processes associated with the utilization of deadwood is central to the development of forest conservation strategies. Production of deadwood has been associated with a myriad of ecological processes and functions (Bednarz et al. 2004) and deadwood or coarse woody debris (CWD), including snags (standing dead trees), logs (downed wood (DW)), and buried wood, is now recognized as a key feature of forest ecosystems (Harmon et al. 1986; Jonsson and Kruys 2001; Komonen 2003). In managed forests, the homogenization of forest structure and the increase in the proportion of younger forests in the landscape (Hagan et al. 1997; Bergeron et al. 2001) can potentially lead both to a scarcity of large-diameter, overmature live trees and snags and to a decrease in the quantity and quality of decaying logs (Grove 2002). Forest management interventions such as harvesting, site preparation, planting, and thinning also induce changes in the amount, size, distribution, and rate of decomposition of CWD (Wei et al. 1997; Fleming and Freedman 1998; Fraver et al. 2002).

The SAFE Project, a series of silvicultural experiments in the Lake Duparquet Research and Teaching Forest in the southeastern Canadian boreal forest, tests an ecosystem management model based on natural dynamics (Bergeron and Harvey 1997; Harvey et al. 2002). Briefly, the approach relies on varying silvicultural treatments to emulate natural dynamics. Clearcutting or other even-aged silvicultural systems are employed as surrogates for stand reinitiation by fire; partial cutting is used for modifying stand composition and structure similar to the process of natural succession from even-aged intolerant hardwoods to multicohort mixedwoods or conifer-dominated stands, and selection cutting is intended to mimic gap dynamics. Globally, the project tests the feasibility of using a variety of silvicultural treatments to maintain certain structural and compositional attributes of the natural forest mosaic, including those associated with old-age stands. This research provides an experimental framework for identifying the range and configuration of partial and selection cuts that will lead to desired stand development trajectories or conservation objectives and for understanding the productivity implications of these new systems.

The first phase of the SAFE Project was undertaken in approximately 75-year-old, even-aged trembling aspen (*Populus tremuloides* Michx.) stands. The initial response of these stands to harvesting has been reported in a number of papers (Bourgeois et al. 2004; Brais et al. 2004; Calogero-poulos et al. 2004; Belleau et al. 2006). The objective of the current study is to assess short-term (6 years) changes in CWD dynamics induced by two levels of partial harvesting (light low and heavy crown thinning) and to examine these treatments within the context of tree mortality in the natural stand development process. In this context, our primary hypotheses are that (i) partial cutting will result in a

short-term reduction in snag recruitment as a result of stem removal during treatments and (ii) recruitment of fresh DW will increase following partial cutting but well-decomposed DW will be higher in untreated controls.

Methods

Study area

The study is located in the Lake Duparquet Research and Teaching Forest in the Abitibi region of northern Quebec 45 km northwest of Rouyn-Noranda (48°86'–48° 32'N, 79°19'–79°30'W). The region is situated in the mixedwood zone of the boreal shield. The climate is continental with a mean annual temperature of 0.7 °C. Annual precipitation is 950 mm, 700 mm of which falls as rain from April to November (Environment Canada 2002). Soils are Grey Luvisols originating from glaciolacustrine clay deposits left by proglacial Lake Ojibway (Vincent and Hardy 1977). The study is conducted in aspen-dominated stands of fire origin dating from 1923 (Dansereau and Bergeron 1993).

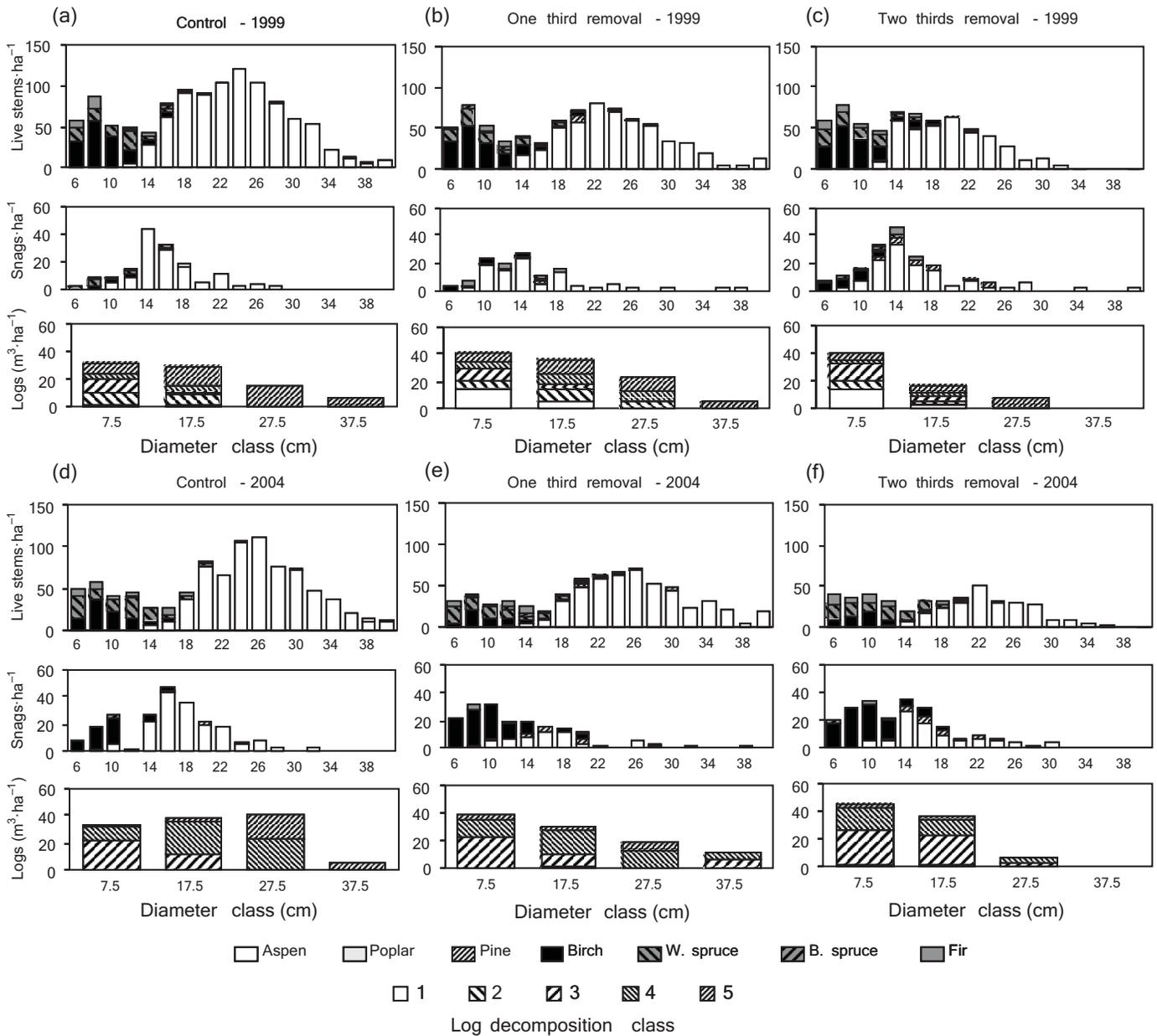
Field methods

In the winter of 1998–1999, four levels of forest harvesting, including a no-harvest control, two intensities of partial harvesting, and a clearcut treatment, were applied according to a complete block design with three replications of each treatment. The two partial cut treatments were aimed at removing approximately one third (1/3) and two thirds (2/3) of merchantable basal area. Treatments were assigned randomly, but some minor adjustments were made so that partial cutting treatments were assigned to areas where softwood understory regeneration density was relatively high. Experimental units ranged from 1 to 2.5 ha. In partial cuts, trees to be removed were marked prior to harvesting. Stands in the 1/3 removal treatment were low thinned with nonvigorous aspen stems removed, while stands in the 2/3 removal treatment were essentially crown thinned with vigorous co-dominant and dominant aspen stems preferentially selected. Harvesting was done manually in all treatments and stems were delimiting on site. (For a more complete description of the harvesting treatments, see Brais et al. 2004.)

Before harvesting, and in all experimental units, five 400 m² permanent circular sample plots (radius = 11.28 m) were established. All stems (trees and high shrubs) greater than 5.0 cm diameter at breast height (DBH) (1.3 m) were identified, tagged, and DBH measured. In a 100 m² quarter of each plot, all stems between 2.0 and 4.99 cm DBH were also tagged and DBH measured. Following harvesting, in the spring of 1999, a tally of remaining stems was conducted in all sample plots of the partial cuts to estimate residual basal area and change in stem density and diameter distribution. The inventory was conducted again in the fall of 2004.

The volume of DW was estimated by triangular-transect method in 1999 following harvesting and again in 2004. One 30 m sided triangle (Van Wagner 1982) was sampled in each experimental plot. Along each transect line, the frequency of DW was recorded by species, diameter class (5 cm: 2.5–7.5 cm, 10 cm: 7.6–12.5 cm, 15 cm: 12.6–17.5 cm, and 17+ cm: 17.6 cm and greater), and five decomposition classes (Daniels et al. 1997).

Fig. 1. Diameter distribution of live stems, snags, and downed logs in control stands, in light low thinning treatment (1/3), and in heavy crown thinning treatment (2/3) (a–c) immediately after harvesting (1999) and (d–f) six growing seasons after harvest in 2004.



Data analyses

Data analyses were done using FREQ, GLM, and MEANS procedures of the SAS statistical package. Stand diameter distributions were tabled at the sampling plot level and averaged by experimental units (five plots per unit, total = 45) and again within experimental units (three replications per treatment). Parametric analysis of variance was conducted according to a complete randomized design with three treatments (the clearcut treatment is not included in this study) and three replications per treatment. We used a least significant difference test ($\alpha = 0.05$) to assess differences between partial harvesting and control treatments.

Results

Natural stands

The even-aged aspen stands at SAFE originated from a fire in 1923 (76 years prior to harvest). Aspen stem diameter distribution followed a normal curve with stems smaller than 14 cm DBH virtually absent (Fig. 1a). Shade-tolerant species, balsam fir (*Abies balsamea* (L.) Mill.) and white spruce (*Picea glauca* (Moench) Voss), as well as white birch (*Betula papyrifera* Marsh.) dominated the smaller diameter classes. Stand density at the time of treatment (>5 cm DBH, all species) was 1125 stems·ha⁻¹ (Table 1) or 983 stems·ha⁻¹ (≥ 10 cm DBH) and mean aspen diameter was 24.2 cm. Snag

Table 1. Characteristics of boreal trembling aspen stands submitted to different prescriptions of partial harvesting immediately and 6 years after harvesting.

Variable	1999				2004			
	Harvesting treatment				Harvesting treatment			
	Control	1/3	2/3	SD	Control	1/3	2/3	SD
Live stem density (stems·ha ⁻¹)	1125	805	647	141	928	665	442	147
Live stem basal area (m ² ·ha ⁻¹)	42.9	29.3	14.9	1.5	40.9	29.8	13.1	1.9
Mean trembling aspen diameter (cm)	24.2	25.3	20.8	3.2	26.5	27.4	24.7	3.7
Trembling aspen mortality (stems·ha ⁻¹ ·6 years ⁻¹)					173	52	123	25
Trembling aspen mortality (%·6 years ⁻¹)					20	11	32	3.1
White birch mortality (stems·ha ⁻¹ ·6 years ⁻¹)					57	108	102	55
White birch mortality (%·6 years ⁻¹)					40	60	67	13
Snag density (snags·ha ⁻¹)	148	123	183	107	225	178	212	61
Trembling aspen snag density (snags·ha ⁻¹)	123	93	118	67	167	60	88	35
Snag basal area (m ² ·ha ⁻¹)	3.1	2.4	3.8	1.6	5.1	2.8	3.5	0.4
Fresh downed wood (m ³ ·ha ⁻¹)	30.1	53.5	40.3	8.0	34.3	38.6	50.9	4.8
Well-decomposed downed wood (m ³ ·ha ⁻¹)	50.9	51.4	22.2	39.3	81.8	59.2	36.4	36.8

Note: Significant differences (least significant difference test, $\alpha = 0.05$) between harvested and control stands are in bold type.

diameter distribution lagged behind that of living trees (Fig. 1a) and snag density was 148 stems·ha⁻¹ of which 129 were aspen or balsam poplar (*Populus balsamifera* L.). Snags accounted for 12% of total standing stems (7% of basal area) in 1999. DW volumes were 30.1 m³·ha⁻¹ for fresh (classes 1–3) and 50.9 m³·ha⁻¹ for well-decomposed (classes 4 and 5) wood. The largest proportion of DW was in the small diameter classes (<22.5 cm) and large DW pieces were only found in the advanced decomposition classes (Fig. 1a).

Between 1999 and 2004, live stem density decreased from 1125 to 928 stems·ha⁻¹ in control stands (Table 1) (from 983 to 822 for stems ≥ 10 cm DBH). Aspen and balsam poplar mortality was 20% (or 173 stems·ha⁻¹) and the snag proportion of standing stems increased from 12% to 20% over the 6-year period. Snag basal area increased from 7% to 11% of total basal area over this period. Mean aspen diameter increased to 26.5 cm (Table 1). This increase resulted mostly from the higher survivorship of larger stems (>26 cm). Stated inversely, aspen mortality during this period occurred mostly in the smaller diameter classes (16–22 cm DBH) (Figs. 1d and 2a). Forty-four percent (SD = 11%) of stems in diameter classes 18–28 cm moved to a larger class in the course of the 6-year period. A high rate of mortality was observed for white birch (40%, 57 stems·ha⁻¹). Net recruitment of birch snags between 1999 and 2004 was largely limited to the smallest classes (6–10 cm DBH) (Figs. 1d and 2d). Total snag density increased to 225 stems·ha⁻¹, of which 167 were aspen, and snag diameter distribution still lagged 10 cm behind that of live stems (Fig. 1d). There were very few snags >26 cm DBH in untreated stands. Total DW volume increase from 81.0 to 116.1 m³·ha⁻¹. Fresh DW volume remained constant, while that of well-decomposed DW increased (Table 1).

Immediate effects of harvesting

Differences in prescription between partial harvesting treatments were apparent in residual diameter distributions (Figs. 1b and 1c). Live stem density decreased to 805 and to 647 stems·ha⁻¹ immediately following the 1/3 and 2/3

removal treatments, respectively (677 and 512 stems·ha⁻¹ ≥ 10 cm DBH). The 1/3 treatment removed more stems in the 14–16 cm classes but a similar amount in the 18–20 cm classes as the 2/3 treatment, while removal in the 2/3 treatment was concentrated in the 22–32 cm classes. As a result, mean aspen diameter increased to 25.3 cm in the 1/3 removal treatment, while it decreased to 20.8 cm in the 2/3 treatment (Table 1). Snag densities were 123 and 183 snags·ha⁻¹ in the 1/3 and 2/3 treatments, respectively, and not significantly different from that of control stands. In the 1/3 treatment, snags accounted for 13% of standing stems, a value similar to that of the control (12%) immediately following treatment, but were markedly higher (22%) after the 2/3 treatment. Harvesting induced an immediate and significant increase in fresh DW in only the 1/3 removal treatment (Table 1). Well-decomposed wood was not significantly affected by partial harvesting immediately following treatments, although volume in the 2/3 treatment was half that of control stands (Table 1).

Short-term changes in stand dynamics induced by harvesting

Live stem density decreased from 805 to 665 stems·ha⁻¹ in the 1/3 removal treatment (from 677 to 523 stems·ha⁻¹ ≥ 10 cm DBH), while basal area remained more or less constant (29.8 m²·ha⁻¹) and significantly lower than that of control stands over the 6-year period. Snag proportion increased to 21% of standing stems in the 1/3 treatment in 2004, which was similar to that of controls (20%). Mean aspen diameter increased to 27.4 cm as a result of mortality in the smaller diameter classes and survivorship of larger stems. A general increase (61%) of stems in diameter classes 18–28 cm moved to a larger 2 cm class in the course of the 6-year period, a proportion not significantly larger than that of control stands. Mean aspen diameter was not significantly larger than that of control stands. Combined aspen and balsam poplar mortality was 11% (52 stems·ha⁻¹) over the 6-year period and was significantly lower in terms of absolute numbers and proportion compared with control stands. Birch mortality was very high (60%, 108 stems·ha⁻¹). Snag density increased to 178

stems·ha⁻¹ of which 60 were aspen, a number significantly lower than in control stands. Fresh DW volume decreased (Table 1) and was comparable with control stand volume, while well-decomposed wood remained stable.

In the 2/3 removal treatment, live stem density decreased from 647 to 442 stems·ha⁻¹ (DBH > 5 cm) or from 512 to 365 stems·ha⁻¹ (DBH ≥ 10 cm) during the 6-year posttreatment period, while basal area decreased from 14.9 to 13.1 m²·ha⁻¹. Mean aspen diameter increased to 24.7 cm mostly as the result of the same factors as in the 1/3 removal: mortality of smaller stems, particularly birch, and an increase in stem diameter of larger surviving stems. Seventy-five percent of stems in the 18–28 cm diameter classes moved to a larger class in the course of the 6-year period, a proportion significantly higher than that of control stands. Aspen mortality over the 6-year period was 32% (123 stems·ha⁻¹), significantly higher, proportionally, than in control stands. Birch mortality in the 2/3 treatment was similar to that in controls in terms of absolute numbers but significantly higher (67%) in terms of proportion. Snag density increased only slightly to 212 snags·ha⁻¹ of which 88 were aspen. Snags accounted for a third (32%) of standing stems in the 2/3 treatment 6 years following harvesting. Fresh DW increased to 50.9 m³·ha⁻¹, a value significantly higher than that of control stands.

Discussion

Stand structure and development phase

The diameter distribution of control stands reflects what is known of natural dynamics following fire on these sites, that is, the dominance of a first cohort of fast-growing, shade-intolerant species with a gradual increase of slower growing, more shade-tolerant species into the shrub and canopy layers (Bergeron 2000; Brassard and Chen 2006). (The presence and mortality of white birch in the subcanopy are discussed later.) The observed diameter distribution of live and dead stems is also characteristic of aspen stands prior to breakup. In even-aged aspen stands, this relationship of dead to live stem diameter distribution is a reliable indicator of stand development phase and of general stand vigor (Pothier et al. 2004; Senecal et al. 2004). The fact that mean snag diameter lags about 10 cm behind that of live trees and that there are very few snags in dominant size classes indicates that these 80-year-old aspen stands with merchantable stem density of 983 stems·ha⁻¹ are not yet in decline. This is somewhat surprising given that Pothier et al. (2004) estimated that decline in aspen stands generally begins around 60 years when stem density has decreased to about 720 stems·ha⁻¹. Although the age and live stem density of our control stands are considerably greater than these values, the fact that the snag proportion of standing stems increased from 12% to 20% between 1999 and 2004 does indicate that the transition toward decline is indeed underway.

The self-thinning analogue

The notion of linking silviculture to natural stand processes is fundamental to this study. Low thinning, such as in the 1/3 partial cut treatment, is the silvicultural equivalent to the mortality process in the stem exclusion stage in that it

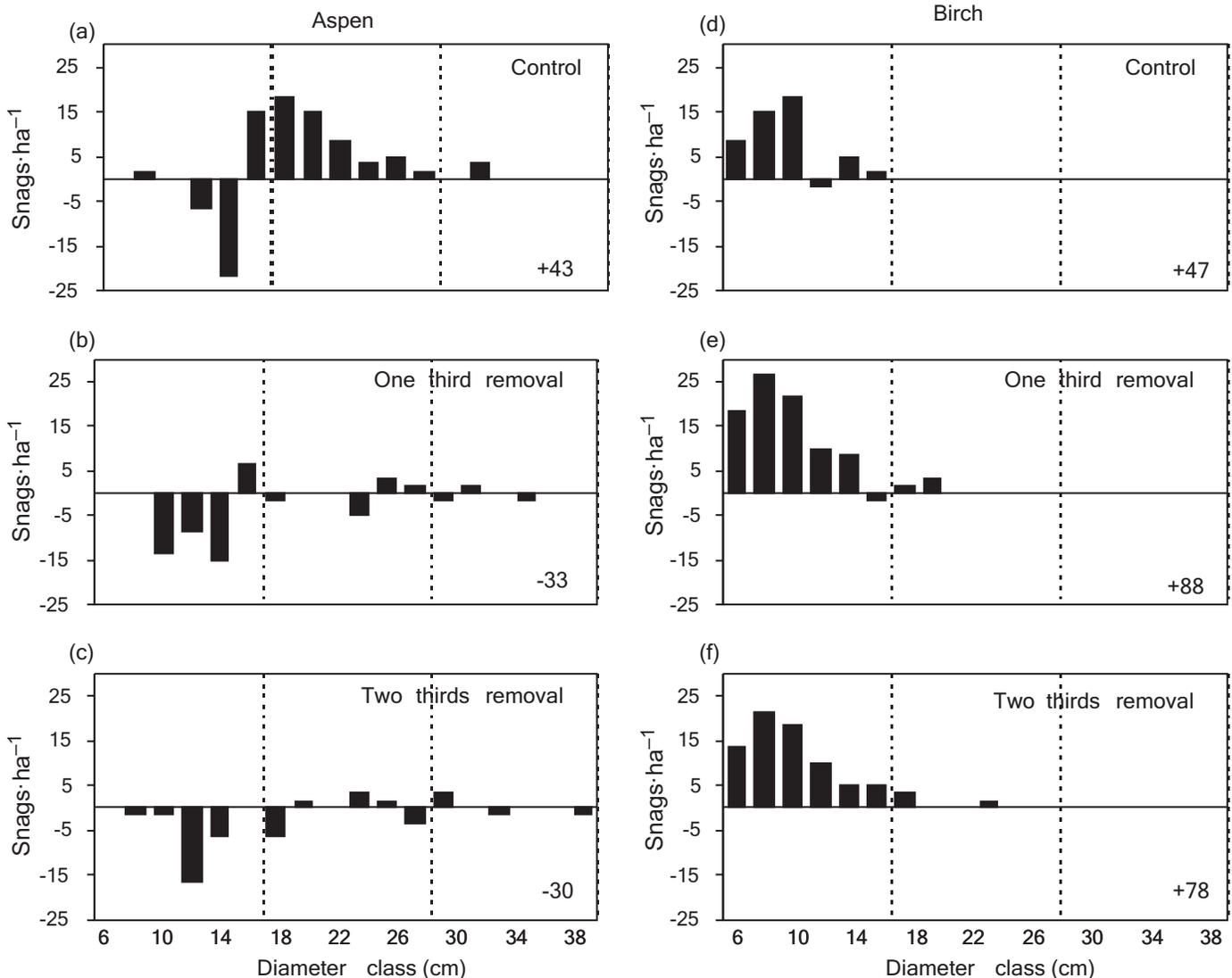
removes smaller, suppressed, and less vigorous stems destined to fall out of the live canopy in the relative short term (imminent mortality). The major difference between the natural process and its silvicultural analogue is that in removing live trees, thinning reduces the density of both live and dead stems and recruitment of DW. Given the positive aspen snag recruitment in untreated stands between 1999 and 2004 (Fig. 2a) and net decreases in aspen snags during the same period in the two thinning treatments (Figs. 2b and 2c), it is clear that DW recruitment of aspen will be higher over the next decade in untreated stands. The 1/3 thinning operation itself did generate significantly higher fresh DW than controls immediately following the treatment, particularly in the smaller diameter classes (Fig. 1b), but DW values were similar to those of controls in 2004 (Table 1). Much of this fresh DW consisted of branches and tops left from on-site delimiting as well as collateral felling of small or dead stems. Interestingly, most freshly fallen wood from silvicultural operations differs from that in untreated stands in that, in the latter, aspen trees usually die standing, or at least wood decomposition as a result of fungal infection begins before trees actually fall (Hill et al. 2005). These authors found wood-decaying fungi to be the predominant factor responsible for tree mortality and standing and snapped snags to be the most frequent gap makers in young aspen stands.

The dieback analogue

Although the physiological processes involved in dieback are considerably different from harvesting, heavy partial cutting, crown thinning, or coppice methods in aspen stands may be considered silvicultural analogues to stand breakup or dieback. Where there is sufficient understory of tolerant softwoods, Lieffers et al. (2003) suggested that a “natural shelterwood”, limited to the removal cut, can be used to simulate dieback in aspen stands. The dieback analogue in our study, the 2/3 partial cut treatment, aimed at maintaining a dispersed canopy cover through removal of most but not all dominants and codominants. Because clones tend to be small in our study region and ramets of different aspen clones spatially interspersed (Namroud et al. 2005), thinning of dominants may resemble the pattern of natural dieback mortality in these stands. However, this treatment would probably have limited application in areas where clone sizes are typically much larger. Moreover, thinning of dominants is a questionable practice in aspen stands where crowns of intermediate and overtopped stems are generally small and trees lack vigor, thus reducing the probability of good growth response of residuals. Indeed, whereas harvesting imminent mortality of smaller, suppressed stems in the 1/3 treatment reduced aspen snag recruitment (tree mortality), leaving smaller, less vigorous stems in the 2/3 removal treatment had the opposite effect of higher residual mortality (snag density) in the smaller diameter classes.

The natural process of dieback in aspen stands may act rapidly or mortality may shift gradually from self-thinning of smaller stems to senescence and general decline of dominants and codominants. Wellington et al. (1950), cited in Ghent (1958), stated that breakup of aspen stands may be as short as 5–7 years following 2 or 3 years of defoliation by the forest tent caterpillar (*Malacosoma disstria* Hbn.) or

Fig. 2. Difference in number of snags of (a–c) trembling aspen and (d–f) white birch between 1999 and 2004 for control, 1/3 thinning, and 2/3 thinning treatments. Bars above 0 represent a net increase between 1999 and 2004 in number of snags for a diameter class. Bars below 0 represent a net decrease in the number of snags and recruitment of downed wood from snags during the same period. The number in the bottom right corner of each panel is net change in snag density.



take as long as 20 years in the absence of infestation. According to Frey et al. (2004), the factors involved in aspen dieback are numerous and can have a compounding effect on the rapidity of tree decline and mortality. Complete defoliation by tent caterpillar occurred in our stands only in 2001 but that year and 2002 also experienced unusually dry summers and it is likely that these factors together influenced mortality.

Subcanopy white birch

Because white birch is generally considered shade intolerant, its presence in the subcanopy (Fig. 1) may seem surprising. However, the same subcanopy status and mortality of birch, as well as its clumpy distribution as a result of stump sprout origin, have been observed in nearby stands on similar sites dominated by aspen (Bergeron and Charron 1994) and by jack pine (*Pinus banksiana* Lamb.) (Béland et al. 2003). Clearly, birch grows slower and attains lower maxi-

mum heights than aspen and jack pine and manages to survive in the subcanopy for several decades in this region. In this respect, its dynamic reflects a higher tolerance to shade than aspen and jack pine. Bergeron and Charron (1994) attributed birch mortality in a mature natural stand to an outbreak of forest tent caterpillar, possibly exacerbated by successive dry summers, similar to what the region experienced in 2001 and 2002. While we would have thought that birch would respond positively to small canopy openings, partial cutting under these conditions appears to exercise an additional stress on residual stems (Figs. 2d–2f).

Large, persistent legacies

More than 80 years after the fire from which these stands originated, remnants of predisturbance stands were still apparent as large, well-decomposed logs. Snags of jack pine trees established following the previous fire in 1760 must have been present in small numbers in the forest matrix that

burned in 1923 (Dansereau and Bergeron 1993). Jack pine snags can remain standing for over 100 years (Dansereau and Bergeron 1993). This and the slow decomposition rate of jack pine logs (Brais et al. 2006) would account for their presence on the forest floor of 80-year-old aspen stands. However, the high standard deviation associated with average load of well-decomposed large logs (Table 1) reflects the sporadic nature of the phenomenon. Neither partial cutting strategy specifically aimed at maintaining these particular attributes into the future, although the possibility to do so still exists.

Management implications

The notion of silvicultural treatments as analogues to or facilitating natural stand-level processes affecting tree establishment, growth, and mortality is basic to the concept of forest ecosystem management. From a silvicultural viewpoint, the timing and intensity of partial cutting treatments are designed to preempt a good part of natural mortality and anticipate potential recruitment or site occupation by advance regeneration. Low thinning, as an analogue to natural self-thinning, may have the effect of retarding stand breakup or at least of maintaining a first cohort stand structure. Although the aspen diameter distribution curve is flattened as a result of removal focussed on smaller stems (Fig. 1e), stand diameter distribution retains some of its normality. In the short term, a lower mortality rate may be expected than in higher density control stands. In contrast, crown thinning in the 2/3 treatment, as an analogue to stand dieback, has the potential effect of accelerating stand development. Heavy removal of dominants and codominants should create an environment that is more favorable for growth response of understory spruce and fir as well as aspen suckers, thus producing a multicohort stand structure sooner than either the 1/3 or untreated control stands. In this case specifically, the moderate density of softwoods in the understory does not necessarily bode well for a fully stocked transition into a mixedwood composition in the short term (Fig. 1f). However, because the treatment resulted in fairly open residual stands, it initially produced dense suckering ($>63\,000$ stems·ha⁻¹, Brais et al. 2004).

While our stands were essentially entering a transition phase from self-thinning to dieback, low thinning better captured the current natural mortality process than crown thinning. This said, the low thinning was remarkably evenly applied in these stands, resulting in very little opening of the stand canopy (Brais et al. 2004). Use of crown thinning at a lower intensity than 61% or possibly of a variant of group selection (normally applied to uneven-aged stands) or 20% to 35% gap cuts may have more closely reflected natural gap formation reported to occur in aspen stands of comparable or older age (Haeussler 2004; Hill et al. 2005). Certainly, in terms of refining this natural disturbance based silvicultural approach, the use of “free thinning”, a mix of low and crown thinning aimed at removing less vigorous trees from all broad diameter classes (Smith et al. 1997), would be worth experimenting. Variations of these scenarios are currently being simulated using SORTIE-ND (Coates et al. 2003). Along with the density and distribution of residual cover, the size of residual stems to be left for biodiversity values, particularly for cavity nesting bird and mammal spe-

cies, is important (Drapeau et al. 2002; Ferguson and Archibald 2002). This suggests that specific retention guidelines for large-diameter trees should be included in both self-thinning- and dieback-emulation treatments.

Conclusions

Partial harvesting induced short-term changes in CWD dynamics through direct physical impacts on existing standing and DW or through changes in residual stem diameter distribution and mortality rates. Treated stands conserved many features of control stands, as large-diameter live stems and snags and considerable DW were still observed. However, it is evident that untreated stands with their higher density and basal area will eventually generate more snags and DW than thinned stands. In the context in which long-term maintenance of CWD constitutes an issue for maintenance of biodiversity, ecosystem integrity, and productivity, harvesting prescriptions should include CWD management objectives such as input rates and diameter distribution.

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