Using knowledge of natural disturbances to support sustainable forest management in the northern Clay Belt

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ABSTRACT

Several concepts are at the basis of forest ecosystem management, but a relative consensus exists around the idea of a forest management approach that is based on natural disturbances and forest dynamics. This type of approach aims to reproduce the main attributes of natural landscapes in order to maintain ecosystems within their natural range of variability and avoid creating an environment to which species are not adapted. By comparing attributes associated with natural fire regimes and current forest management, we were able to identify four major differences for the black spruce forest of the Clay Belt. The maintenance of older forests, the spatial extent of cutover areas, the maintenance of residuals within cutovers and disturbance severity on soils are major issues that should be addressed. Silvicultural strategies that mitigate differences between natural and managed forests are briefly discussed.

Key words: natural disturbance, landscape patterns, coarse filter, harvest pattern, volume retention, historic variability, even-aged management

RÉSUMÉ

Plusieurs approches conceptuelles sont à l'origine de l'aménagement écosystémique, mais un certain consensus semble exister actuellement sur le fait qu'il doit viser à reproduire des paysages naturels, i.e., des territoires aménagés qui conservent les principaux attributs des forêts naturelles. En créant des paysages avec des attributs forestiers semblables à ceux des paysages naturels, on vise à maintenir l'écosystème à l'intérieur des limites de variabilité naturelle. Ainsi, les espèces ne risquent pas de se retrouver dans un environnement auquel elles n'ont jamais été confrontées historiquement. En comparant le régime naturel des feux et son impact sur la dynamique forestière avec l'aménagement forestier actuel nous avons pu identifier certains écarts importants. Le maintien de forêts surannées, la dispersion spatiale des aires de coupes, la préservation de forêts résiduelles dans les aires de coupes et la sévérité des perturbations au sol constituent des enjeux importants à prendre en considération dans l'aménagement écosystémique des forêts de la ceinture d'argile. Des stratégies sylvicoles permettant de décroître l'écart entre l'aménagement et la dynamique naturelle sont brièvement discutées.

Mots-clés : perturbation naturelle, patron à l'échelle du paysage, filtre brut, patron de coupe, rétention variable, variabilité historique, aménagement équienne

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Introduction

Over the past decade, there has been an increasing interest in forest management approaches based on natural disturbance dynamics (Attiwill 1994, Bergeron and Harvey 1997, Angelstam 1998, DeLong 2002). The rationale is that management favouring the development of stand and landscape compositions and structures similar to those in natural ecosystems should maintain biodiversity and essential ecological functions (Franklin 1993, Hunter 1999). In other words, the conservation of native flora and fauna may be possible by emulating the size, frequency, pattern and severity of disturbances to which forest species have adapted over thousands of years (Hunter *et al.* 1988, Hunter 1990).

Fire is one of the most important ecological processes in North American boreal forests (Johnson 1992, Payette 1992). Forest fire regimes, defined by frequency, size, intensity, seasonality, type and severity (Flannigan 1993, Weber and Flannigan 1997), have a significant influence on many boreal forest attributes. Fire regimes affect the distribution of species (Desponts and Payette 1992, Flannigan and Bergeron 1998, Asselin *et al.* 2003, Le Goff and Sirois 2004), age-class distribution of stands (Bergeron *et al.* 2001), characteristics of wildlife habitats (Thompson *et al.* 1998, Drapeau *et al.* 2003, Nappi *et al.* 2004), vulnerability of forests to insect epidemics (Bergeron and Leduc 1998), and net primary production and carbon balance (Peng and Apps 2000). Fire regimes are important in boreal forests in that they have considerable spatial variations on several scales (Keane *et al.* 2004). This generates patterns of biological and ecosystem diversity on continental (Payette 1992), regional (Bergeron *et al.* 2001, 2004; Heyerdahl *et al.* 2001) or local scales. For instance, within the perimeter of a single fire event, there is a large variation in the type of legacies left after fire between areas affected by fires of low or variable severity (Schimmel and Granström 1996, Bergeron *et al.* 2002, Weisberg 2004), and even when fire severity is high (DeLong and Kessler 2000, Kafka *et al.* 2001).

One way to improve our forest management strategies to achieve ecological sustainability is to assess how current practices compare with natural disturbance regimes. Fig. 1A illustrates on three axes (time, size, severity) the possible variability that can characterize forest fire regimes. In the boreal forest, considerable amplitude may exist on each of these axes, and this can vary from region to region. The risk of a fire occurring is such that one site may burn two years in a row whereas another may be spared for several hundred years. Similarly, the area burned by a fire can vary from less than one hectare to hundreds or even thousands of square kilometres. Finally, while certain surface fires may only affect ground vegetation, an intense crown fire will kill virtually all trees in its path and may consume the forest humus layer down to the mineral soil. The combination of these characteristics—fire frequency, fire size and fire severity—and others make up the disturbance regime that is unique to an ecosystem or a forest region. Other than the variability imposed by permanent site features, which influence thermal, water and nutritional regimes, it is the disturbance regime that is responsible for the variety of forest habitats that occur in a region and thus determines the coarse filter on which maintenance of biodiversity should be based. In contrast to natural variability, we can represent the variability theoretically created by an intensive forest management regime involving, for example, the widespread use of plantations and stand-tending treatments. In this context, the interval between harvests, cutover size and their severity constitute a management regime whose variability would be considerably narrower than that of the natural disturbance regime and could even be outside the range of historic variability of this natural disturbance regime (Fig. 1B).

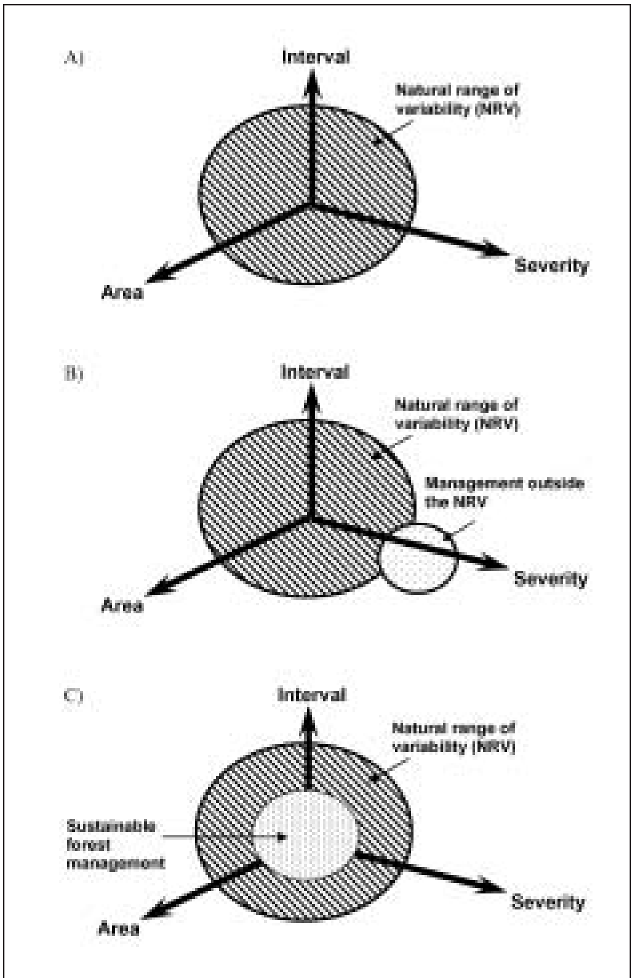

Fig. 1. Three dimensional conceptual model of fire regime variability in natural ecosystems (**A**) and managed ecosystems (**B** and **C**). In **B**, forest management produces a disturbance regime that incorporates little of the diversity of the natural regime. In **C**, management is illustrated as reproducing natural disturbances but with less variability.

Although the main objective of ecosystem management is to respect the inherent variability of natural disturbance regimes, in practical terms it often becomes a socially and economically acceptable compromise within the limits of historic variability. This management target is generally somewhere between the great variability generated by the natural regime and the homogeneity generated by a management regime aimed primarily at sustaining fibre yield (Fig. 1C).

In the following sections we consider each of the three variability axes that characterize fire regimes of the black spruce forest in the Clay Belt, i.e., fire frequency, size and severity, and discuss the major issues with regard to differences between fire and current forest management. We also provide suggestions for the development of new silvicultural and management planning practices that may reduce the gap between natural disturbances and current forest management.

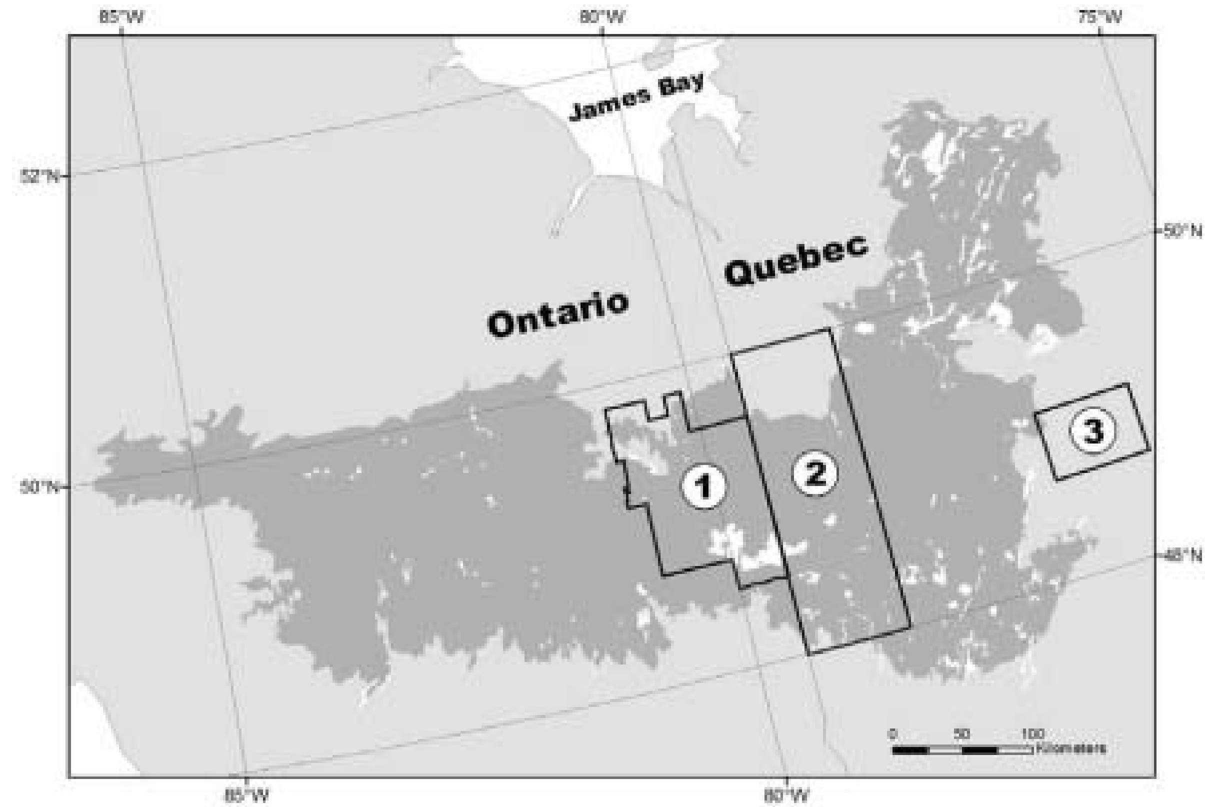

Fig. 2. Map of the northern Clay Belt with the location of the fire studies reported in Bergeron *et al.* 2001 within or near the Clay Belt.

Study area

The northern Clay Belt is located in the Boreal Shield ecozone of the Abitibi Plain ecoregion (Ecological Stratification Working Group 1996). This region borders the southern boundary of the James Bay Lowland ecoregion and extends from the western edge of the northern Clay Belt in Ontario to east of the Nottaway River and Lac au Goéland in western Quebec (Fig. 2). The ecoregion is marked by warm summers and cold snowy winters. Mean annual temperature is approximately 1°C. Mean summer temperature is 14°C and mean winter temperature is -12°C. Mean annual precipitation ranges from 725 mm in the west to 900 mm in the east. This ecoregion is classified as having a humid mid-boreal ecoclimate. Its mixed forest is characterized by stands of white spruce, balsam fir, paper birch and trembling aspen. Drier sites may have pure stands of jack pine or mixtures of jack pine, paper birch and trembling aspen. Wet sites are characterized by black spruce and balsam fir. Late successional stages on all site types tend to converge towards black spruce dominance (Harper *et al.* 2002). Understory in cold and wet sites is typically moss, as well as lichen. The ecoregion is underlain by Archean granitic intrusives and volcanic rocks. It is bounded on the north by Palaeozoic bedrock of the Hudson Basin, a source of carbonate-bearing glacial materials. The landscape is dominated by fine-textured, level to undulating lacustrine deposits. Intermixed within these deposits are bedrock outcrops and organic deposits. Occurrences of organic soils increase towards the north as elevation decreases, whereas rock outcrops are more numerous in the south and west of the ecoregion. Domed, flat and basin bogs are the characteristic wetlands found in over 50% of the ecoregion, with concentrations increasing towards the northern half. Gray Luvisols and Gleysols found on the clayey lacustrine and loamy tills are the dominant soils in the ecoregion. Poorly drained areas are characterized by Mesisols and Fibrisols, and Humo-Ferric Podzols occur on sandy deposits in the southern part of the ecoregion.

Major Forest Management Issues Needing To Be Addressed On the Clay Belt

Fire frequency and its implications for forest age structure

At first glance, an even-aged management approach appears to resemble the natural disturbance regime if the timber harvest rotation age approaches that of the natural fire cycle. However, a full even-aged regulation does not produce an age-class distribution similar to that of natural distribution, even for forest rotations that are as long as the fire cycle. Indeed, in an even-aged management context, a forest is considered to be fully regulated when stand age classes are uniformly distributed throughout a territory. Thus, in theory, after one complete rotation in a region submitted to a 100-year rotation, no stands over the rotation age will exist. The same region submitted to forest fires intense enough to generate even-aged stands will, at equilibrium, present a completely different age class distribution of stands composing the forest. Assuming that the probability of burning is inde-

Table 1. Average age of the natural forest and proportion of old-growth forests in or near the Clay Belt forest of Quebec and northeastern Ontario (numbers refer to location on Fig.2). Data from Bergeron *et al.* (2001).

Territory	Average age	% of forests 100 years	% of forests 200 years
1. Eastern Ontario	172	78	32
2. Western Abitibi (Quebec)	139	57	23
3. Eastern Abitibi (Quebec)	111	54	15

pendent of stand age (as is generally reported for studies in the boreal forest; Johnson 1992, Johnson *et al.* 1998), the forest age structure will, again theoretically, resemble a negative exponential curve, with about 37% of the forest being older than the fire cycle (Johnson and Van Wagner 1985). This means that for a fire cycle and a forest rotation of similar duration, forest management will not spare any forest that exceeds rotation age whereas fire will maintain over 37% of the forest in older age classes. This difference is fundamental because it implies that full regulation in an even-aged management regime will result in the loss of over-mature and old-growth forests, often judged to be essential to the maintenance of biodiversity. Previous work (Bergeron *et al.* 2001) in or near the Clay Belt (Table 1, Fig. 2) shows that the natural mosaic contains more than 50% of forests older than 100 years, and more than 15% of forests older than 200 years, meaning that over-mature and old-growth forests historically are a major part of the forested landscape in these regions. Moreover, Cyr *et al.* (2005) report that large tracts of black spruce forests have not burnt for thousands of years in the Clay Belt region. Although trembling aspen or jack pine can establish themselves following fire (see Gauthier *et al.* 2004 for detailed succession pathways), stand establishment following fire is often dominated by an initial cohort of spruce, which can give rise to a dense even-aged forest originating principally from seed (Fig. 3). At maturity, this stand structure is gradually replaced by a more open forest containing stems originating from the fire and regeneration partly of layer origin. In the prolonged absence of fire, these stands develop into uneven-aged stands maintained by layering and characterized by an even more open and heterogeneous structure. Fig. 3 also illustrates the proportion of the different stand types according to the estimated fire cycle for the Quebec Clay Belt and a normal forest rotation of 100 years. Thus, **the amount of forest habitat that is over timber rotation age (in over-mature and old-growth stands) represents the first major difference between managed and natural disturbance-dominated landscapes in the Clay Belt.**

Fire size, extent of regeneration areas and their implications for the spatial configuration of the forest mosaic

What becomes evident when illustrating the frequency of fire occurrence by different size classes is that whereas the majority of fires are smaller than 1000 ha, these fires are generally responsible for less than 10% of the total area burned in western Quebec (Fig. 4A). Consequently, it is primarily large fires

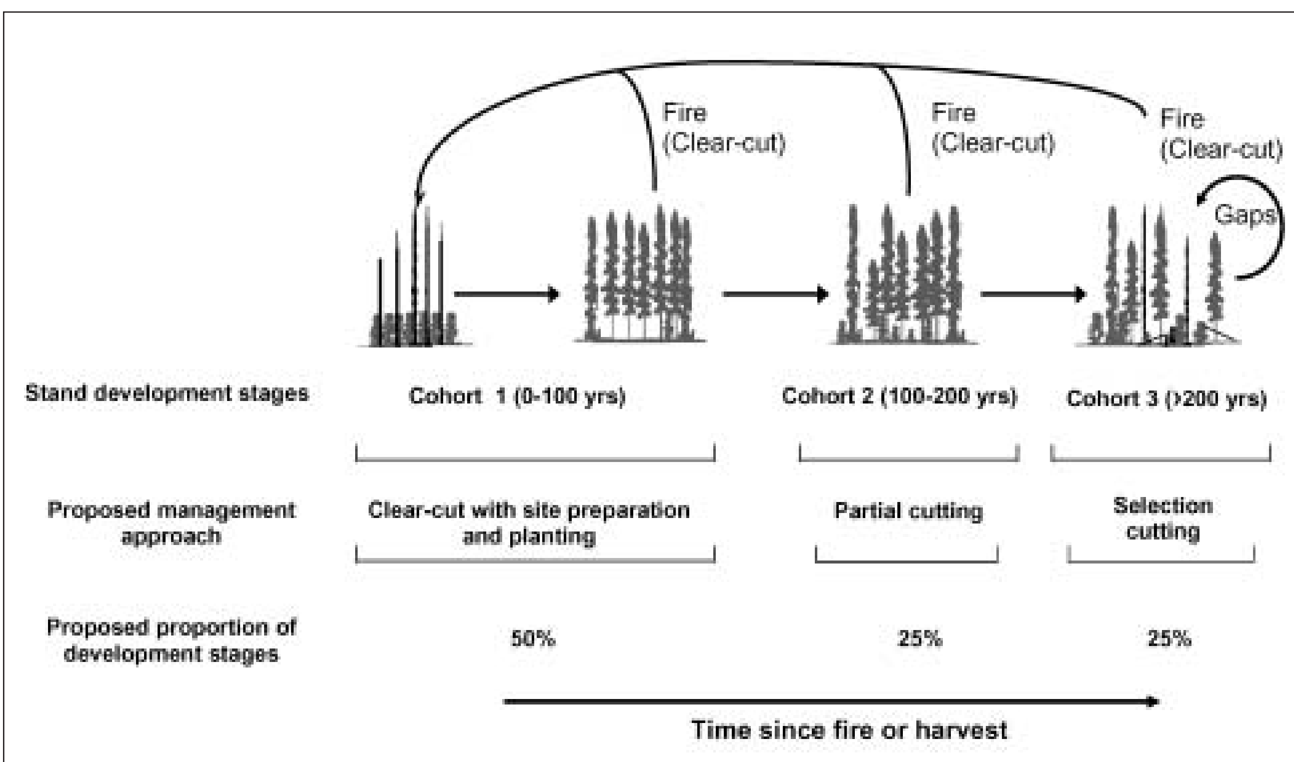

Fig. 3. Natural stand dynamics and silviculture proposed for the Clay Belt black spruce forest. The arrows going from left to right represent time since the last fire or clearcut. Also note the proportion of different stand structural development stages according to a 140-year fire cycle and a 100-year forest rotation. Adapted from Bergeron *et al.* (1999).

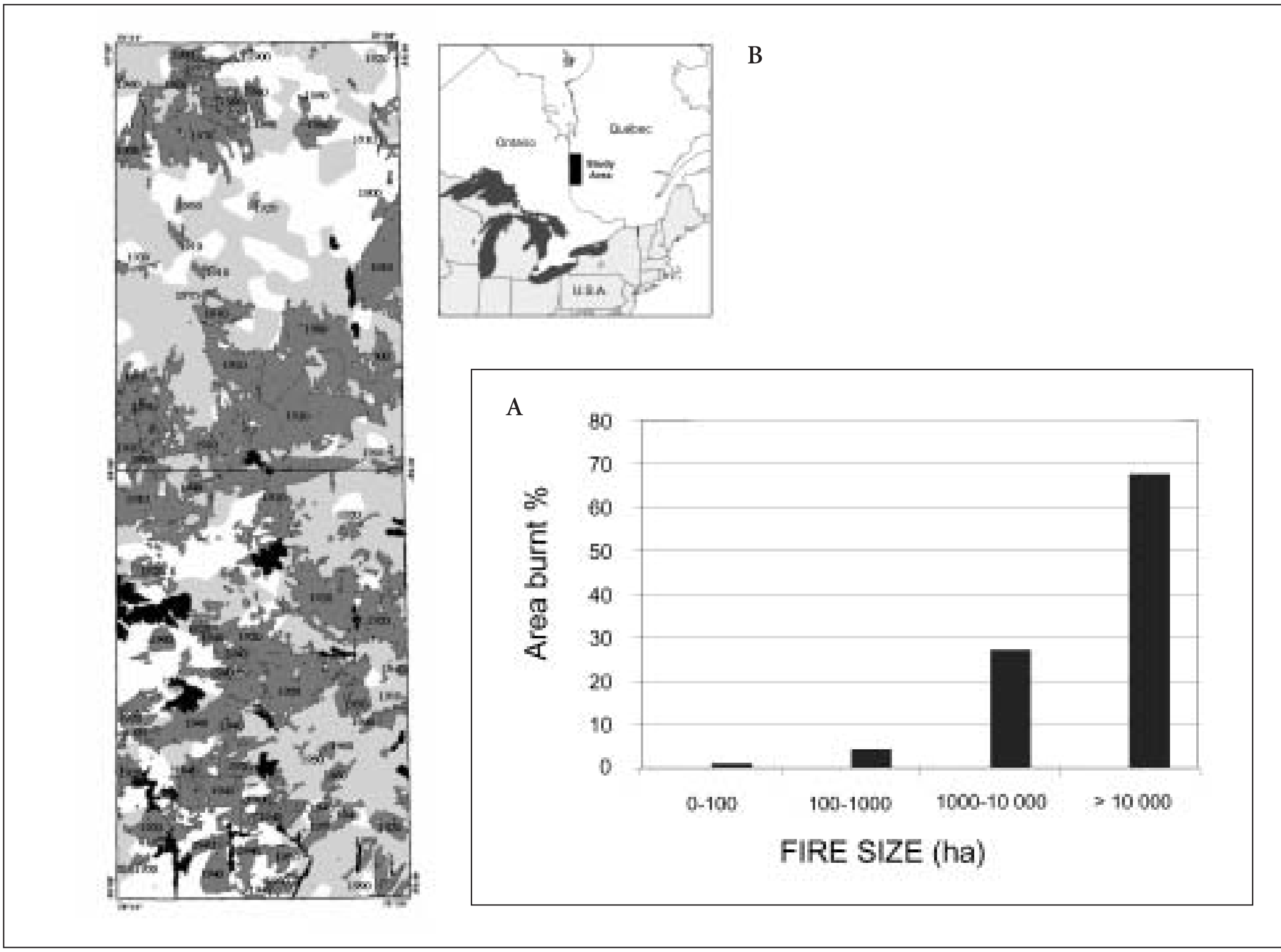

Fig. 4. A) Size distribution of fires in the boreal forest of western Quebec for the period 1940–1998. **B**) Time since fire map showing patterns of stands originating from fire of different ages for the Quebec Clay Belt (from Bergeron *et al.* 2004). All fires that occurred in the 1900s are identified by the decade during which they occurred, fires that occurred between 1801 and 1900 are represented by grey areas, and fires that occurred before 1800 are represented by white areas.

(those over 1000 ha) that are responsible for the natural regeneration of the forest and that generate a given age structure and spatial configuration of forest cover types (Johnson *et al.* 1998). At the high end of fire size distribution are fires that cover very large areas. In fact, among those fires over 1000 ha, the 10% that are over 20 000 ha are alone responsible for 40% of the total area burned. Over the last 60 years, almost 55% of the area burned in the black spruce zone of western Quebec ranged from 950 to 20 000 ha (Bergeron *et al.* 2002). With respect to the spatial distribution of these regeneration areas, or a minimal distance to be maintained between these areas, there is very little existing evidence that fires tend to be clustered in the landscape within a region (Perron 2003). Our studies on fire reconstruction (Bergeron *et al.* 2004) showed that recent fires were well dispersed over all the study area and that regeneration patches originating from old fires were large and well dispersed over the landscape (Fig. 4B).

Current regulations in Quebec and, to a lesser extent, in Ontario limit the size of individual cutblocks to relatively small areas (dozens or hundreds of hectares at most). However, they do not address the issue of the spatial extent of cutover areas and their adjacency in space over time. Whereas lightening-caused wildfires can easily spread over thousands of hectares (Bergeron *et al.* 2002), they are rarely adjacent to one another in the landbase over the 25 to 30 years time period where regeneration areas are still in early seral stages (Belleau *et al.* 2007). For a similar time frame, industrial timber harvesting has usually resulted in a much larger spatial extent of regeneration areas than the one resulting from cumulative wildfires (Perron 2003), whether cutblocks within regeneration areas are dispersed (Delong and Tanner 1996) or clustered (Perron 2003). **Important differences in the size and spatial extent of regeneration areas thus make up the second important difference between currently managed forests and naturally disturbed forests.**

Fire severity and its implications for the remaining stand structure

One of the most persistent beliefs shared by many foresters in North America is that fires in the boreal forest are generally severe; that is, that they induce the mortality of most trees within their perimeter. Moreover, several studies have shown that only about 5% of burnovers generally subsist as interior forest islands, untouched by fire (Eberhart and Woodard 1987, Kafka *et al.* 2001, Bergeron *et al.* 2002), a figure that may approach the proportion of remnant forest left by the forest industry within cutover areas. A corollary, even-aged harvesting is often presented as being more or less as severe as a fire and, as such, it is thought to contribute in a similar manner to natural regeneration processes of the forest.

However, wildfires, especially those that extend over very large areas and burn for longer than a day, will present variations in severity along their path, leaving green trees following their passage (van Wagner 1983, Turner and Romme 1994, Kafka *et al.* 2001). Fire severity mapping in Quebec (Kafka *et al.* 2001) recognizes *de facto* the existence of this phenomenon by including the class "mixture of green crowns and reddened crowns with green-crown dominance" in order to designate zones where fire has had a low impact. Far from being a marginal phenomenon, these "low severity zones" may occupy up to 50% of a burnt area, depending on the type of forest burnt and, especially, the prevailing weather conditions (Fire Weather Index) prior to and during the fire (Bergeron *et al.* 2002). Not only do those trees that survive the passage of a fire appear to play a determining role in regenerating burns (Greene and Johnson 2000), they also constitute wildlife refuges or shelters (Schieck and Hobson 2000, Morissette *et al.* 2002) in the regenerating forest, and contribute to increasing the spatial heterogeneity of the forest mosaic resulting from the fire. Current practices in Quebec and, to a lesser extent, in Ontario do not include permanent or temporary retention that emulates fire patterns. Within these harvested regeneration areas in Quebec, the only fragments of mature forest are linear cut-block separators, linear riparian buffer strips, and unproductive or inaccessible forest patches. Furthermore, the 20-m riparian strips along streams and lakes provide linear remnant habitats that can be partly harvested, and upland forest strips (60 to 100 m wide) between cut-blocks are fully integrated into the annual allowable cut (AAC) and are harvested when adjacent cut-blocks regeneration reach 3 m in height. **Lack of sufficient green retention in cutover areas is the third important difference between natural disturbances and forest management.**

Fire severity effects on soils and its implications for stand structural development and productivity

Because of its flat topography, forests in the Clay Belt are very susceptible to paludification. Paludification is the gradual conversion of a dry forest to a forested peatland via the accumulation of organic material and water table rise (Taylor *et al.* 1987, Viereck *et al.* 1993, Fenton *et al.* 2006). It occurs topographically in dips and successionally in areas with low to moderate slopes and fine-textured soils, two conditions that are found in the Clay Belt. Reconstruction of fire history in the Clay Belt (Lefort *et al.* 2003, Bergeron *et al.* 2004) has revealed that a large part of the landscape is covered by old-growth forests and that the importance of successional paludification has been underestimated in the past. Subsequent work demonstrated that, following high-severity fires, black spruce stands on slight slopes will undergo a gradual change through natural succession from a dense, dry (unpaludified) productive stand to an open, wet (paludified) unproductive stand over a period of 200 years (Lecomte *et al.* 2005; 2006 in press (Fig. 5A)). The accumulation of organic matter within black spruce stands on the Clay Belt was determined to be caused primarily by the climate and the presence of black spruce. However, this accumulation is accelerated by an increase in *Sphagnum* moss cover and ericaceous plants (Fenton *et al.* 2005), but is slowed by the presence of aspen (Légaré *et al.* 2005a). As a consequence of these changes associated with the process of paludification, the quality of substrates available for tree growth decreases because, whereas *Sphagnum* moss is a good substrate for germination, it is a poor quality substrate for tree nutrition as compared with humus derived from *Pleurozium schreberi*, a feather moss (Lavoie *et al.* 2007). Paludification therefore causes a significant decrease in tree productivity (Simard *et al.*, in press) through nutrient limitation and high water table rise.

Whereas paludification can be reversed by fire, our previous work has demonstrated that some fires do not consume entirely the organic layer of the forest floor, which has a strong influence on future stand structural development. After such low-severity fires, the advanced state of paludification of the stands influences forest floor composition, tree regeneration and stand productivity, which in turn will inhibit future stand closure throughout succession, and therefore accelerate paludification rate (Lecomte *et al.* 2005; 2006a,b; Fig. 5A). This is particularly worrying when we see that the predominant harvesting practices currently applied (CPRS in Quebec and CLAAG in Ontario) remove the tree layer while leaving the organic layer (forest floor) intact. Interestingly, although these practices were designed to increase yields and reduce regeneration costs by protecting advance regeneration, their effect is similar to low-severity fires. Hence, these practices may be leading to increased paludification on low-topography Clay Belt sites and significant losses in stand productivity (Fig. 5B). Thus, **low disturbance severity on soils in cutover areas is the fourth major difference between current forest management practices and fire.**

Towards Solutions

Maintaining over-mature and old-growth forests

The creation of permanent or floating reserves protecting the remaining old-growth forests is part of the solution (Cumming *et al.* 1996), but it is probably insufficient compared with the abundance of old-growth forests in the pre-industrial landscape. Development of silvicultural techniques that maintain or restore old-growth forests' compositional, structural and functional characteristics at different scales in the landscape is an important option to explore.

The use of rotations of variable length in proportions similar to those observed in the natural fire regime is a possible alternative to fixed rotations (Burton *et al.* 1999, Seymour and Hunter 1999, Fig. 3a) in order to maintain over-mature and old-growth forests. However, this approach may be applicable only in ecosystems where species are long-lived and can thus support longer rotations. In boreal forests composed of relatively short-lived species, this approach would probably lead to fibre loss and a decrease in allowable cut. Alternatively, Bergeron *et al.* (1999) have suggested that silvicultural practices aimed at maintaining the structural and compositional characteristics of over-mature stands in treated stands could, in boreal regions, guarantee the maintenance of habitat diversity while only slightly affecting allowable cut (Gauthier *et al.* 2004). It would be possible to treat some stands by clearcutting followed by seeding or planting (or another even-aged

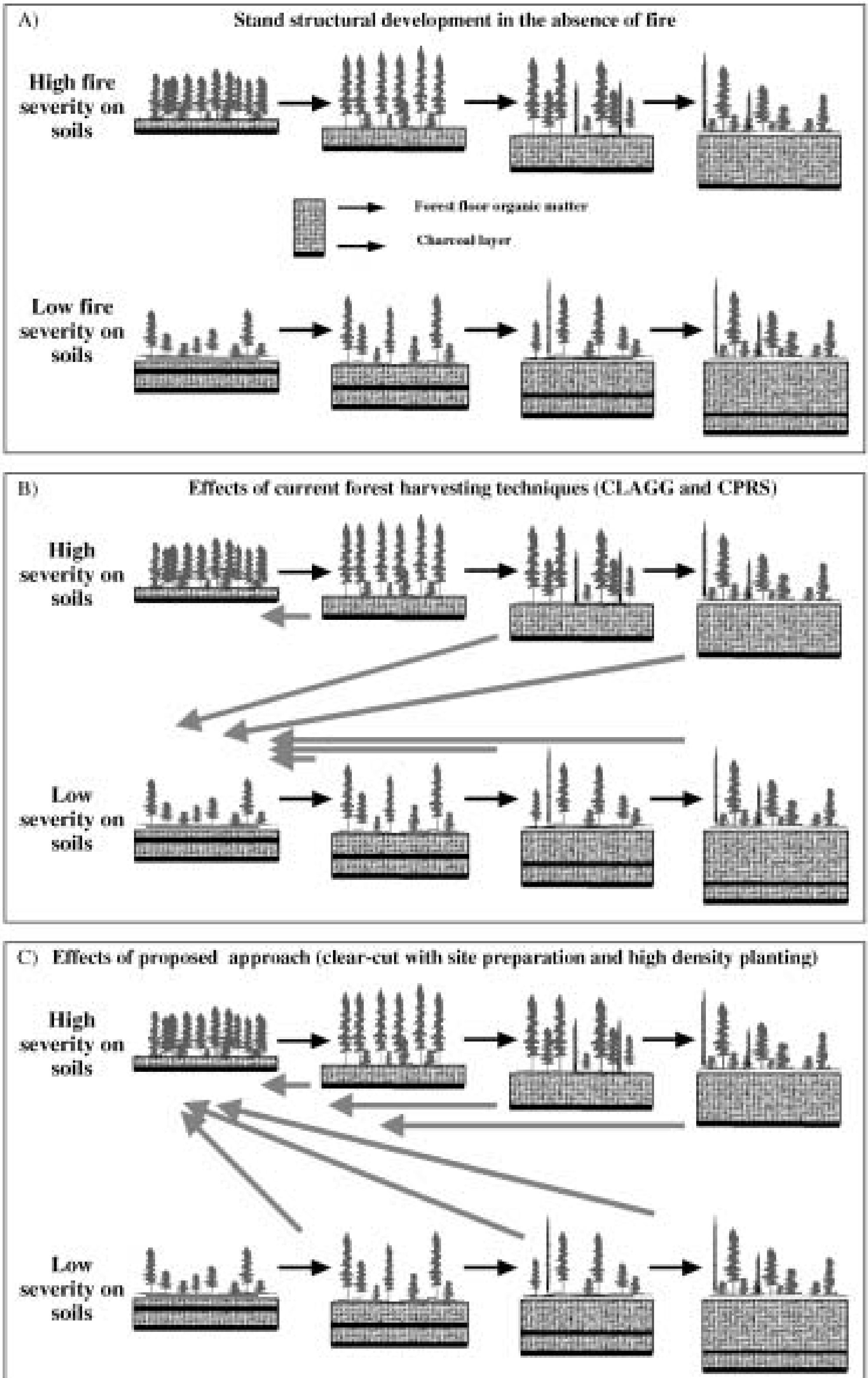

Fig. 5. A) Effects of soil-borne fire severity on stand structural development and the accumulation of forest floor organic matter. Adapted from Lecomte *et al*. (2006b). **B**) Effects of current forest management approaches in Quebec (CPRS) and Ontario (CLAAG). **C**) Proposed management approach that favours the establishment of dense productive stands with the use of clearcutting, site preparation (scarification, control burning), and high-density planting.

silvicultural system whose outcome resembles the effect of fire). Other stands could be managed using partial cuts that approach the natural development of over-aged stands. Still other stands could be managed with selection harvesting in order to reflect the dynamics of old-growth stands (e.g., see Harvey *et al.* 2002 or Gauthier *et al.* 2004).

A simple example illustrating relationships between natural dynamics and management of the black spruce forest is presented in Fig. 3. Varying silvicultural practices is intended to develop a forest composition and structure comparable to natural stands. Thus, the even-aged structure of the first cohort originating from fire could be generated by clearcutting followed by natural or artificial regeneration. The irregular structure of the second cohort would be maintained or stimulated by partial cutting practised in stands with even or uneven-aged structure (Groot 2002). In the case of the uneven structure of the third cohort, it could be generated by selection harvesting to mimic gap characteristics in old-growth stands. The proportion of stands submitted to each of these treatments will vary depending on the natural disturbance cycle and maximum harvest age (Bergeron *et al.* 1999, Gauthier *et al.* 2004). Partial cutting prescriptions should be done while taking into account the fact that sites may be very susceptible to paludification and hence likely to express low tree productivity following the treatment (see section on fire severity).

Maintaining landscape structure

In ecosystems that experience large-scale natural disturbances such as the boreal forest, it is assumed that biodiversity is likely to be tolerant to these landscape-scale changes. Thus, a key issue that must be addressed when planning for biodiversity maintenance in harvested forests is not to determine whether habitat fragmentation *per se* has an impact on organisms but rather whether the level of fragmentation planned for harvesting purposes is within or outside the range of natural fragmentation tolerated by the organisms. Hence, spatial patterning of cutover areas and intervening forest tracts (mature and over-mature) in the landbase are critical for maintaining adequate forest conditions for biodiversity, particularly since persistence in fragmented landscapes depends on multiple populations and their capacity to interact (Opdam 1991, Hanski *et al.* 1996, Bennett 2003). Knowledge of the size, spatial and temporal distribution of regeneration areas created by wildfires can provide guidelines for the design of harvested units for both their size and adjacency in space and time. This should mitigate the negative impacts on biodiversity (Kouki and Väänänen 2000, Smith *et al.* 2000) that often result from current forest management, where the spatial extent of regeneration areas resulting from harvesting is not planned within the range of natural forest fragmentation. From a strategic planning perspective, empirical information on fire size and spatial and temporal extent should be incorporated into spatially explicit models with simulation routines that could allow the derivation of management guidelines. These guidelines could specify the level at which harvested regenerating areas (regenerating forests less than 4 m in height) should be aggregated in time (spatial constraint) and the agglomeration size distribution over an entire rotation period (Belleau *et al.* 2007). Given that large fires will continue to burn in managed landscapes, spatially explicit models should incorporate large fire events in their modeling routines and thus derive guidelines on the size and spatial extent of harvesting areas that account for the persistence of large wildfires in the landbase. This could mitigate the potential cumulative effects of natural and anthropogenic disturbances that current managed forests experience. Indeed, as there are no considerations for the spatial patterning of cutover areas over time and space, the cumulative effects of adjacency of regeneration areas that originate from harvesting and wildfires are likely to be worst under current management practices.

Maintaining remnant habitats

The fact that fire severity is variable within burns and does not kill all trees implies major improvements in the amount and configuration of forest habitat retention (mature and over-mature cover types) within timber harvested regenerating areas. Indeed, current retention in managed forests is not planned with the perspective of maintaining comparable forest conditions as in naturally disturbed regenerating areas, nor is it planned to maintain sufficient amounts of suitable habitat for forest-dwelling species. To do so, a first step could be to determine the range of variation in the amount, size, shape and spatial arrangement of green forest patches left within wildfires (see Perron 2003, for instance). The same approach could be used for single trees or clumps of unburned trees in burned forests. The relative importance of unburned patches and unburned trees within low severity zones should also be assessed to determine the range of variation in the spatial patterning of the overall green retention within wildfires. Such information could provide general guidelines with regard to the total amount of green retention to be left in cutover areas. Bergeron *et al.* (2002) provide some insights on the overall proportion of fire skips within a set of 35 wildfires that burned in northwestern Quebec in the summers of 1995 and 1996. Kafka *et al.* (2001) provide more detailed information on the spatial configuration of retention areas in a wildfire in Lake Crochet, Quebec. First, they found that lightly burned zones were distributed throughout the entire burn. Second, fire skips (unburned patches) averaged 52 ha in size and were frequently surrounded by lightly burned zones, suggesting a high degree of connectivity between the burned matrix and unburned vegetation. Third, contrary to current harvested landscapes, the shape of most of these remnants in wildfires is not linear, thereby providing more suitable interior habitat conditions than remnants in current managed landscapes. Overall, studies on landscape patterns in wildfires show that green retention is not a marginal phenomenon within wildfires and thus prompt the implementation of better retention strategies in cutover areas (Cissel *et al.* 1999). One way to improve green retention strategies, particularly with regard to the spatial arrangement of remnants, is to assess and measure their capacity to achieve sustainable landscape functions (refuges, dispersal channels, or both) for biodiversity. Such information could be provided by studying organisms' responses to the spatial arrangement of remnant habitats within wildfires. For instance, in managed landscapes, several studies have investigated organisms' responses to remnant habitats' shape, size and spatial arrangement. In regenerating areas of the boreal black spruce forest in northwestern Quebec, Mascarúa López *et al.* (2006) found that the entire forest structure in linear riparian buffers and cut-block separators is affected by edge effects. They conclude that wider corridors would be required to offer interior forest conditions. Darveau *et al.* (1995) showed that 20-m riparian buffers could not retain forest-dependent bird species over time. Rheault *et al.* (2003) also found that epiphytic lichens biomass was lower in the first 50 m of clearcut forest edges than within the forest interior. The response of these lichens to edge conditions suggests that linear riparian buffers (20 m wide) and upland strips (60–100 m) are unlikely to offer suitable refuge conditions for epiphytic lichens. Implementing green retention within the range of natural variation in spatial patterning of habitat remnants within harvested regeneration areas will require an ongoing assessment of the efficiency of such an approach on organisms' responses through comparisons with naturally disturbed landscapes.

Finally, the size of regenerating areas, their dispersal in time and space, and the amount and arrangement of green retention within these cutover areas point towards two key issues of landscape-level requirements for effective conservation of biodiversity in fragmented managed landscapes, i.e., how much habitat is needed (percent cover both between and within regenerating areas) and how should it be dispersed in the landbase (habitat configuration). Whereas knowledge from vegetation patterns induced by wildfires is likely to provide coarse-filter management targets on the amount and spatial arrangement of green retention, the effectiveness of such a strategy requires to be assessed through direct response of organisms to these landscape patterns, preferably through a multi-species approach (Block *et al.* 1995, Roberge and Angelstam 2004, Huggett 2005) that targets forest species that are the most sensitive to habitat fragmentation and alteration (Lambeck 1997, Imbeau *et al.* 2001, Drapeau *et al.* 2003, Guénette and Villard 2005). Quantitative measures of the effectiveness of the planning process should be based on comparisons of the response functions of these species in naturally fragmented landscapes with those resulting from management operation. Permanent retention of habitats within managed landscapes will necessarily imply adjustments in yield expectations given the philosophical shift from a silvicultural system that traditionally focused on tree growth and yield to a system where a proportion of the trees are retained to meet ecological management objectives other than growth and yield.

Reversing the effects of paludification

Aggressive site preparation or prescribed burning followed by high density planting or seeding (4000 stems/ha) are potential silvicultural techniques that might reverse paludification (Fig. 5C). One of the key issues is our ability to correctly identify sites that are already paludified or susceptible to becoming rapidly paludified. Compositional changes in the understory during succession in the absence of fire involve a replacement of feathermosses by hummock and ultimately hollow *Sphagnum* spp. (Fenton and Bergeron 2006). The relative abundance of these different bryophyte species in the understory should guide foresters as to whether they should decide prescribe aggressive site preparation techniques. Productive sites with a predominant feathermoss understory could be managed using partial or selection cutting whereas sites with a significant proportion of hummock or hollow *Sphagnum* species should be clearcut with site preparation or prescribed burning. Interestingly, a large portion of the landbase that is currently classified as unproductive may have been productive before undergoing successional paludification. These stands represent a currently unexploited forestry potential in the region on which we could capitalize with aggressive site preparation techniques.

Mixedwood management is also a very efficient way to prevent paludification. Aspen litter inhibits bryophyte invasion of the understory, and favours soil fertility (Légaré *et al.* 2005a,b). While we do not propose increasing aspen proportions to levels not observed in the pre-industrial landscape, we do propose modifying current precommercial thinning techniques that favour coniferous species over deciduous species. Maintaining an optimal mixture of aspen and spruce after precommercial thinning should decelerate the process of paludification and not only maintain the eventual volume in spruce, but also add an additional volume in aspen (Legaré *et al.* 2005a,b).

Conclusion

An important outcome of current management methods is a reduction in the amount of old-forest habitats that were present in historic landscapes. One management option to avoid this outcome, which has a negligible impact on timber supply, is to rely more on uneven-aged silviculture to maintain a high proportion of forests with structural characteristics resembling those encountered in over-mature and old-growth forests.

Significant disruption of the old-forest continuity by natural disturbances is another common feature of boreal landscapes, but the spatial arrangement in time and space differs from that created by current forest management. Thus, it will become critical to plan more rigorously in space and in time, not only for harvested areas but also for unharvested forests between and within regenerating cutovers. This calls for a major shift in the forest management philosophy that was traditionally aimed at harvesting merchantable volumes. Variable retention of forest habitats and structural elements that make up the biological legacies (*sensu* Franklin *et al.* 2000) must be integrated in strategic and tactical planning processes, not as a constraint but rather as a requirement to reach ecological sustainability in managed forests. Perhaps Harris's (1984) proposal of a management approach that generates a shifting mosaic of stands of varying ages can be projected in space and time for the boreal forest, leading to a landscape mosaic of regenerating areas of different ages interspersed with large tracts of mature, over-mature and old-growth forests.

In naturally disturbed landscapes, organisms, particularly forest-dependent species, have evolved in a context where populations could benefit from suitable forest conditions over a large proportion of the landbase, but this proportion becomes more limited in remnant habitats of recently burned landscapes. Hence, even though organisms may be adapted to varying habitat fragmentations in time and space, the systematic shift in the proportion of mature and older forests versus young ones that industrial even-aged management has generated in the eastern boreal forest (Bergeron *et al.* 2002, Harper *et al.* 2002) raises concerns about the capacity of such conventional even-aged management to maintain biodiversity in managed landscapes. The resulting fragmentation of older forests may exert a pressure on biodiversity that is above its tolerance. It is thus important to implement retention strategies that reduce the gap between current managed landscapes and naturally disturbed landscapes, both within and between cutover areas. This should become a high priority for resource managers and conservation planners given the rate at which natural forests are converted to cutover landscapes in the boreal forest throughout Canada.

The implementation of such a retention strategy should also be set forth with a monitoring scheme to assess its effectiveness. In an adaptive management context, multi-species approaches as described above could help in refining the management guidelines derived from natural disturbance regimes by providing complementary targets based on the tolerance of organisms to forest removal with regard to both the extent of regeneration areas and, within cutover areas, the spatial arrangement of remnant habitats. Refinements could come from the detection of critical thresholds in species responses (Guénette and Villard 2005) with regard to distance from unharvested large tracts between cutover areas (Kouki and Väänänen 2000, Leboeuf 2004), to isolation among remnants within regenerating areas or to the availability of key structural attributes—for instance, standing deadwood—within remnants.

Finally, and probably what is the most important for the achievement of sustainable forest management on the Clay Belt, the aggressive reversal of forest paludification during or after harvesting must be addressed. The widespread use of harvesting techniques that "protect" the forest floor humus during forest operations is particularly worrisome as this may be greatly enhancing the degree and extent of paludification on the Clay Belt. By mimicking the effects of fires that only partially consume the forest floor, these "careful" logging techniques may actually be accelerating the process of paludification and inhibiting post-disturbance stand closure. This may not only have detrimental effects on eventual timber yields but also on biodiversity as large expanses of productive closed stands, which are known to harbour distinct species assemblages, become rare. In order to diminish differences in disturbance severity on soils between burnt and harvested forests, we propose that managers prescribe aggressive site preparation techniques in post-harvest stands that are already paludified or susceptible to becoming rapidly paludified.

We recognize that by suggesting the use of partial and selection cuts with little soil disturbance we are encouraging paludification on the one hand while on the other hand countering paludification by suggesting the application of aggressive site preparation treatments in cutover areas. While these suggestions may appear to be contradictory, in the end it is a question of balance and compromise between maximizing tree productivity and maintaining biodiversity. Given the decrease in stand productivity associated with an increase in the degree of paludification, partial and selection cuts, contrary to aggressive site preparation techniques after clearcuts, may not allow stands to fully express their tree productivity potential. However, given that many boreal species are adapted to over-mature and old-growth stands, these post-partial or post-selection cut stands should increase the potential of managed landscapes to conserve biodiversity as compared with even-aged managed landscapes. With that being said, given the lengthening of the fire cycle during the past century and the widespread use of silvicultural treatments that promote paludification during the past decades, most Clay Belt landscapes are characterized by 1) a predominance of open forest that resemble old-growth forests, and 2) a scarcity of young productive and over-mature stands. Hence, today, Clay Belt forest managers should 1) concentrate on the establishment of dense productive stands with the use of aggressive site preparation techniques, 2) use a variety of partial cutting techniques to maintain and recreate over-mature stands, and 3) carefully prescribe the appropriate treatment by taking into account silvicultural feasibility, paludification levels and potential future productivity. These approaches should enable forest managers to significantly increase forest yields while having little or no effect on overall landscape biodiversity. In the long term, when forest managers will have succeeded in establishing significant tracts of dense productive stands, they should envision prescribing appreciable amounts of selection cuts.

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