SUSTAINABLE FOREST MANAGEMENT NETWORK

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A STATE OF KNOWLEDGE REPORT

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2010

Citation: Macdonald, S.E., Lecomte, N., Bergeron, Y., Brais, S., Chen, H., Comeau, P., Drapeau, P., Lieffers, V., Quideau, S., Spence, J., and Work, T. 2010. Ecological implications of changing the composition of boreal mixedwood forests. A State of Knowledge Report. Sustainable Forest Management Network, Edmonton, Alberta. 48 pp.

For an electronic version of this report, visit the Sustainable Forest Management Network website at http://sfmnetwork.ca
Print copies are available free of charge while supplies last.

Library and Archives Canada Cataloguing in Publication

Ecological implications of changing the composition of boreal mixedwood forests : a state of knowledge report / Ellen Macdonald ... [et al.].

Includes bibliographical references.

Type of computer file: Electronic monograph in PDF format.

Also available in print format.

ISBN 978-1-55261-225-5

1. Taiga ecology--Canada. 2. Taiga--Canada. 3. Forest biodiversity--Canada. 4. Sustainable forestry--Canada. 5. Forest management--Canada. 6. Forests and forestry--Canada.

I. Macdonald, Ellen, 1955-

QH541.5.T3E36 2010a 577.3’70971 C2010-902565-2

Photography
Front Cover (top to bottom):
- Dan MacIsaac
- Jane Stewart
- Dave Locky

Background:
- SFMN archives

Back Cover:
- Ducks Unlimited Canada

Design
www.c3design.ca

Printing

Priority Printing Ltd.

Printed in Canada

Cette publication est également disponible en français

Published May 2010

Foreword

The State of Knowledge program was launched by the Sustainable Forest Management Network (SFMN) to capture the knowledge and wisdom that had accumulated in publications and people over a decade of research. The goal was to create a foundation of current knowledge on which to build policy, practice and future research. The program supported groups of researchers, working with experts from SFMN partner organizations, to review literature and collect expert opinion about issues of importance to Canadian forest management. The priority topics for the program were suggested by the Network's partners in consultation with the research theme leaders. Each State of Knowledge team chose an approach appropriate to the topic. The projects involved a diversity of workshops, consultations, reviews of published and unpublished materials, synthesis and writing activities. The result is a suite of reports that we hope will inform new policy and practice and help direct future research.

The State of Knowledge program has been a clear demonstration of the challenges involved in producing a review that does justice to the published literature and captures the wisdom of experts to point to the future. We take this opportunity to acknowledge with gratitude the investment of time and talent by many researchers, authors, editors, reviewers and the publication production team in bringing the program to a successful conclusion.

Jim Fyles
Scientific Director

Fraser Dunn
Chair of the Board

Acknowledgements

Our research team would like to thank all the forestry professionals who took the time to meet us and answer our questions regarding the impacts of forest policy in the mixedwoods. We would also like to thank the researchers who provided unpublished data. Funding was provided by the Sustainable Forest Management Network.

Table of Contents

List of Figures

Executive Summary

In Canada, the highly productive southern boreal forest spans a total of six provinces and two territories. It is dominated by mixedwood forests composed of varying mixtures of broadleaf and coniferous trees. In recent decades, there has been increasing interest in environmental issues associated with forest management in this region, including maintenance of diverse forest values and ecosystem services. Mixedwood management has been promoted as a solution to issues of forest productivity, resistance, resilience, and biodiversity. Forest managers are presently confronted with the challenge of maintaining mixedwood landscapes (rather than managing stands for conifer or broadleaf trees alone), in the face of future changes in climate and disturbance regimes, to ensure the sustainability of this valuable resource.

As part of the "State of Knowledge" program of the Sustainable Forest Management Network (SFMN), a group of research scientists across Canada examined the current state of knowledge with respect to the potential ecological implications of altering forest composition in boreal mixedwood landscapes.

Our objective was to summarize the current state of knowledge regarding relationships of mixedwood composition to forest productivity, nutrient cycling, and biodiversity. Further, through interviews with forest practitioners and a literature review, we examined current management paradigms in mixedwood forests. These paradigms were considered in relation to natural dynamic processes in mixedwoods, and in the context of potential future climate change. From this, we identified important take-home lessons for forest managers.

Our interviews with forest practitioners clearly demonstrated that a wide variety of views exist about the impact of forest policy and management on stand diversity at the landscape scale. That being said, virtually all practitioners recognize that natural stand dynamics in the boreal mixedwoods are characterized by a gradual shift from broadleaf-dominated stands to either mixed or conifer-dominated stands.

From these interviews, it was also evident that, if given free reign, managers would select management approaches that are directly related to their opinion of current and past forest management and policy. For example, if a manager thinks policy has induced a loss of mixed stands on the landscape, (s)he is generally in favour of adopting practices that are inspired by natural stand dynamics (understory conifer planting, protection of advanced conifer growth during the harvesting of mixed and broadleaf-dominated stands, etc.). On the other hand, if a manager is of the opinion that management strategies have induced a loss of the conifer component on landscapes, (s)he is more likely to favour intensive practices that convert mixed and broadleaf-dominated stands into conifer-dominated stands.

Our review of the scientific literature on biodiversity responses to changes in boreal mixedwood composition demonstrated that different types of organisms display different relationships to forest composition. Overall, however, broadleaf-dominated, mixed, and conifer-dominated stands in the boreal mixedwood do not seem to host dramatically different biotic communities. In addition, only a few species appeared to be "mixedwood-specialists" (e.g., songbird species that had higher abundance in mixed forest stands). The richness and composition of living organisms in mixedwood forests are a reflection of the forest canopy composition and the associated structural and habitat features. In short, each mixedwood forest type across the broadleaf- to conifer- continuum is important for some species. Thus, in order to conserve biodiversity it will be important to maintain or recreate the structural and habitat features associated with the full range of forest types and ages.

With respect to stand productivity, our review suggests that mixedwood forest composition is closely related to forest floor conditions and the quality of the growing environment for trees. In mixed broadleaf-conifer stands, increasing the abundance of broadleaf trees, up to a point, may result in improved soil and environmental conditions for tree growth.

Furthermore, it appears that inclusion of low to moderate densities of broadleaf trees in conifer-dominated stands can result in better quality conifer stems, and sometimes more total wood volume at rotation age. Finally, by managing mixed stands as mixtures, by considering successional dynamics, and by carefully harvesting stems when the different component species are mature, it may be possible to obtain more wood from a given stand over several rotations.

Our current state of knowledge suggests that present forest management policy poses some risk by: 1) not allowing stands to age and change composition and structure according to natural stand dynamics; and 2) by failing to seriously consider past and future global climate change. A more precautionary approach to forest management in the boreal mixedwoods should be based upon:

1) The development of flexible standards that allow stands to change composition between and during rotations;
2) The development of a broader suite of alternative yield curves and targets within forest management plans, and adoption of a broad range of silvicultural practices (e.g., partial cutting, understory protection, underplanting of conifers in broadleaf-dominated stands) that "artificially age" stands in terms of both composition and structure. These may be effective for conservation of biodiversity and ecosystem function in managed mixedwoods.
3) In the face of climate change, there is a need to re-think concepts of local gene pool and seed tree zones to allow for innovative forest management and planning for future climate change by:

- Increasing regional genetic diversity by using tree seed sources from southern seed zones in some of our regeneration efforts;
- Increasing regional species diversity by establishing, on favourable sites within the eastern boreal mixedwoods (e.g., well-drained south-facing slopes), species and stand dynamics that resemble those of areas south of the current mixedwood zone;
- In the southern part of the western boreal mixedwoods, seriously examining the costs and benefits of silvicultural investments in the context of the likelihood of success, given climate change predictions;
- Increasing regional species diversity of areas north of the boreal mixedwood zone by establishing, on favourable sites, species and stand dynamics that currently occur in the mixedwood zone.

1.0 Introduction

1.1 Issues and objectives

The highly productive southern boreal forest in Canada is dominated by mixedwood forests in which the canopy contains varying mixtures of broadleaf (e.g., aspen, poplar, birch) and coniferous (e.g., spruce, fir, pine, cedar) trees. This forest region spans six Canadian provinces and two territories (BC, AB, SK, MN, ON, QC, YT, NwT). Within this region, canopy trees play a central role in forest ecosystem processes such as hydrology, nutrient cycling and net primary productivity. They also moderate the forest microclimate and form the trophic and structural template that supports a diversity of forest biotic communities.

We now know that "mixed" forest stands, in which two or more tree species are prominent in the canopy, can have higher productivity because of niche differentiation, optimization of resource use, enhanced nutrient cycling, and nurse crop effects (Kelty et al. 1992, Cannell et al. 1992, Man and Lieffers 1999). In the same way, mixed forests may have higher levels of biodiversity than "pure" stands, because they provide a greater variety of habitats.

Environmental issues associated with forest management have been increasing in recent decades, including maintenance of diverse forest values and ecosystem services (Berg et al. 1994, Haila 1994, Spence 2001, Foley et al. 2005). Thus, forest managers are presently confronted with the challenge of maintaining mixedwood landscapes (rather than managing stands primarily for either conifers or broadleaf trees), in order to ensure the sustainability of this valuable resource and future flow of a diversity of ecosystem goods and services, particularly in the face of future changes in climate and disturbance regimes.

Over the last few decades, forest managers and research scientists have come to appreciate the importance of the mixed nature of the boreal forest and to understand the need to focus on joint management, within some stands, for both broadleaf and conifer tree species. Mixedwood management has been promoted as a solution to maintain forest productivity, conifer resistance and resilience to stress and disturbance, and to maintain biodiversity (Cappuccino et al. 1998, Riihimaki et al. 2005, Fries et al. 1997, Wikstrom and Eriksson 2000, Mielikainen and Hynynen 2003).

Although many research initiatives and operational trials have occurred in the boreal mixedwoods, progress towards ecosystem management for mixedwoods has been limited by poor understanding of the ecological impacts of changing mixedwood forest composition.

In the absence of an integrated understanding of ecological relationships in mixed forests, we rely on economic drivers, operational guidelines, policies and regulation to promote management of mixedwood forests to meet particular strategic goals. Incorporating effective ecosystem management in mixedwood forests requires a broad underlying knowledge base because forest composition is inextricably tied to ecological function, productivity, and biodiversity.

We examined current paradigms of management in mixedwood forests in relation to natural dynamic processes in mixedwoods and in the context of potential future climate change.

As part of the "State of Knowledge" program of the Sustainable Forest Management Network, a group of research scientists across Canada examined the current state of knowledge with respect to the potential ecological implications of altering boreal mixedwood landscapes. Our objectives were as follows:

- to summarize the current state of knowledge regarding relationships of mixedwood composition to forest productivity, nutrient cycling, and biodiversity;
- to examine current paradigms of management in mixedwood forests in relation to natural dynamic processes, and in the context of potential climate change;
- to identify key take-home lessons for forest managers.

1.2 Changes and variability in mixedwood canopy composition

The composition of boreal mixedwood forests changes in both space and time. In general, following disturbance, forest canopies are initially dominated by shade-intolerant species (aspen, poplar, birch, pine). Over time, shade-tolerant species (typically conifers such as spruce and fir) slowly become more prominent in the canopy (Bergeron and Dubuc 1989, Bergeron 2000, Chen and Popadiouk 2002). This change in canopy composition over time is important for under standing ecological function and biodiversity relationships in mixedwood forests, because it confounds our ability to distinguish effects of forest composition from effects of forest age.

However, this successional gradient in canopy composition is also variable. It is influenced by site factors, the stand-initiating disturbance, regeneration processes of individual species and landscape forest composition (Bergeron and Dubuc 1989, Bergeron 2000, Chen and Popadiouk 2002, Peters et al. 2005). As a result, different mixedwood forest types (canopy compositions) may not necessarily be linked to stand age. For example, conifer-dominated and mixed forests (late-successional stage) can regenerate directly after fire (Bergeron 2000, Lieffers et al. 2008a). Alternatively, boreal aspen-dominated forests can exist for long time periods without substantial ingress of conifers into the canopy (Cumming et al. 2000, Peters et al. 2006). Thus, there are many different possibilities for mixedwood canopy succession (Figure 1).

The composition of boreal mixedwood forests changes in both space and time.

Mixedwood forests are therefore dynamic, and it is possible to have stands that have a different composition but the same age, or a similar composition but different ages. In general, however, conifer-dominated stands are more prominent in forests that have not burned recently and hence more abundant in boreal forest landscapes where natural disturbance (e.g., fire) is less frequent (Figure 1, Lieffers et al. 2008a).

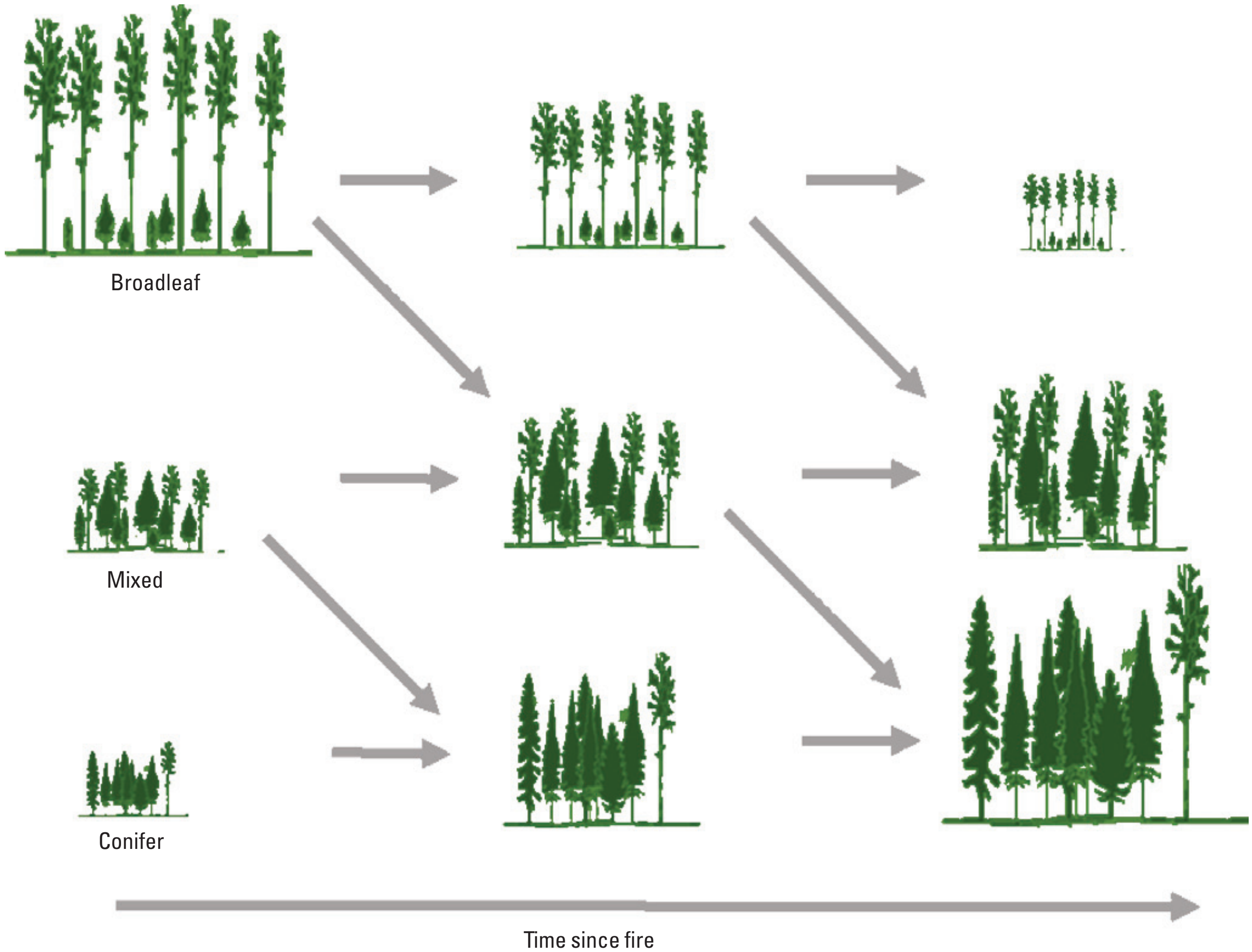


Figure 1. Spatial and temporal variation in stand canopy composition in the boreal mixedwoods. Note: size of the individual stands is proportional to their relative presence on the landscape at a given landscape age (time since fire).

2.0 Findings

2.1 Forest policy and boreal mixedwoods management: the point of view of practitioners

We interviewed over 40 forest practitioners in Alberta, Ontario, and Quebec to assess the state of knowledge regarding the ecological implications of altering the stand- and landscape-scale canopy composition of mixedwood forests. These interviews allowed us to obtain the opinion of forest practitioners on the ecological implications associated with current management policy in the boreal mixedwood. In particular, we sought to understand how, if given free choice, forest practitioners would do things differently.

Informal interviews were conducted and recorded in small groups at several different forestry companies and government agencies. We met with 42 individuals from 15 different organizations. To analyze the interviews, we listened to the recordings and extracted the main statements and opinions of forest practitioners.

> **We sought to understand how, if given free reign, forest practitioners would do things differently.**

We present here the predominant practitioner opinions with respect to natural stand dynamics, and policy impacts on forest cover, biodiversity and productivity. We also present what forest practitioners think should be done in order to find a balance between maximizing forest productivity and maintaining biodiversity.

KEY POINTS

- Most forest practitioners agreed that natural stand dynamics are characterized by a gradual replacement of broadleaf trees by conifer trees.
- Divergent views were expressed with respect to the impacts of policy on the maintenance of mixed stands on the landscape.
- Most forest practitioners agreed that, within the managed portion of boreal mixedwood landscapes, current forest policy engenders a replacement of old natural conifer stands by young managed conifer stands.
- The forest practitioners who believed that forest policy engenders a loss of mixed stands believed that current forest policy will lead to a loss of biodiversity. Those who felt that forest policy did not result in loss of mixed stands believed that forest policy does not have an impact on the maintenance of biodiversity.
- If allowed free choice in silvicultural approaches, those forest practitioners who believed that policy induced a loss of mixed stands and biodiversity were inclined to use management approaches that artificially aged stands (e.g., protection of understory conifer during harvesting of broadleaf trees).
- If allowed free choice in silvicultural approaches, forest practitioners who believed that policy in the past has induced a loss of conifer stands would be inclined to choose intensive tending techniques to establish conifer stands.

2.1.1 Views on natural stand dynamics in the boreal mixedwoods

When we showed interviewees a figure that depicts natural stand dynamics in the boreal mixedwoods, similar to the one in Figure 1, all practitioners agreed that this correctly describes stand development over time following natural disturbance in the boreal mixedwoods. Thus, all practitioners interviewed had a similar perception of stand development within mixedwood forests.

2.1.2 Views on policy impacts on forest composition

Mixing or unmixing?

Most practitioners agreed that in an attempt to meet "free to grow" standards, managers were adopting, as one practitioner described it, "creative approaches" that led to an "unmixing" of stands early in post-harvest stand development.

In other words, stands characterized by an intimate mixture of conifer and broadleaf trees were being converted into "segregated mixed" stands. That is, stands can be considered mixed (i.e. broadleaf and conifer trees are present) at one scale but at a finer scale the conifer and broadleaf stems are located in separate portions of the stand (see Figure 2).

Most practitioners agreed that in an attempt to meet "free to grow" standards, managers were adopting "creative approaches".

This being said, divergent opinions were expressed with respect to what happens to these young segregated mixed stands later in development (i.e. once these stands were classified as "free to grow"). Some practitioners were of the opinion that segregated mixed stands remained segregated through time ("Mixedwood segregation point of view", Figure 2A).

Others were of the opinion that as stands matured, conifer saplings established themselves in the broadleaf-dominated portion of the stand while broadleaf stems established or resprouted in the conifer-dominated portion of the stand ("Nature filling in the gaps point of view", Figure 2B). Hence, while these mixed stands may have been segregated when they were classified as "free to grow", as they mature they eventually become characterized by an intimate mixture of broadleaf and conifer stems.

Decreasing mean stand age

Most practitioners agreed that current policy resulted in a reduction of mean stand age of boreal mixedwood landscapes. They also agreed that a main difference between natural and managed boreal mixedwood landscapes was that current policy engendered a replacement of old natural conifer stands with younger managed conifer stands. These results suggest that current policy engenders, on the managed portion of the landscape, a gradual decrease in the amount of stands that are older than the rotation age.

Most practitioners agreed that current policy resulted in a reduction of mean stand age of boreal mixedwood landscapes.

Loss of conifer stands, and loss of tree diversity in conifer stands

Some practitioners were of the opinion that forest policies and associated management practices during the past few decades had engendered a loss of conifer stands in managed landscapes. This was attributed partly to selective harvesting of conifer during the initial periods of European settlement. However, some practitioners also felt that harvesting in recent decades has resulted in conversion of conifer-dominated stands into either mixed or broadleaf-dominated stands.

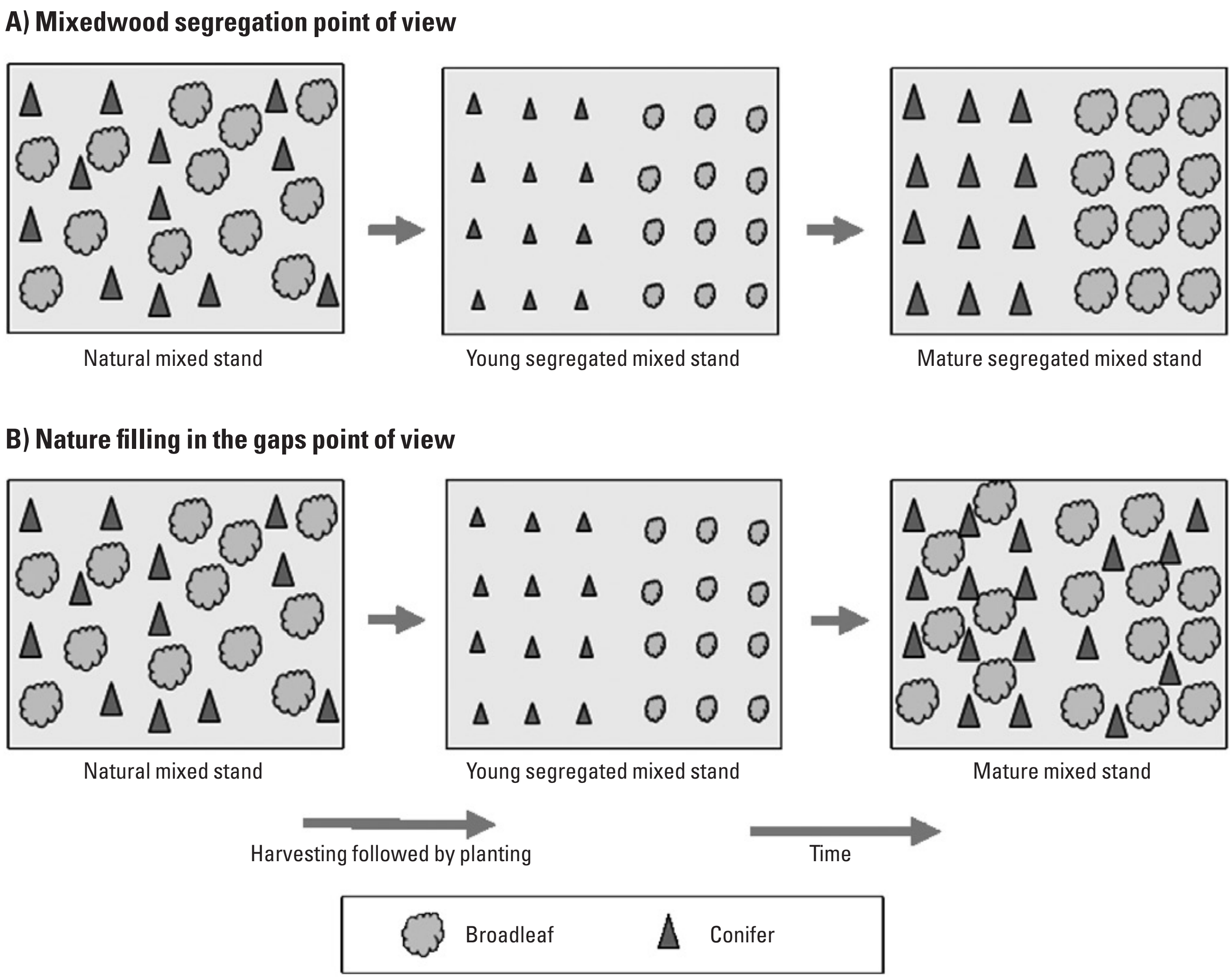


Figure 2. Practitioners' views on the impact of policy and practice on the maintenance of mixed stands in the boreal mixedwoods.

A) view that policy engenders an "unmixing" of mixed stands.

B) view that policy may encourage an "unmixing" of mixed stands but that "nature fills in the gaps" as stands age. This changes young segregated mixed stands into mature stands with an intimate mixture of conifer and broadleaf trees (i.e. "true" mixed stands).

Some practitioners were of the opinion that forest policies and associated management practices during the past few decades had engendered a loss of conifer stands in managed landscapes.

Another interesting observation that was shared by some practitioners was the loss of tree diversity in pure conifer stands in the eastern portion of the boreal mixedwoods. These natural conifer-dominated stands are rarely pure stands as they often contain a mixture of pine, spruce, fir and cedar. This diversity of conifer tree species may be reduced by current policy which allows managers to replant stands with only one species. Some practitioners were concerned with the fact that this may result in the conversion of diverse conifer stands (stands that are composed of a variety of conifer trees) into monocultures of spruce, fir or pine.

2.1.3 Views on policy impacts on biodiversity

Practitioner views with respect to policy impacts on biodiversity were directly related to their views regarding policy impacts on the maintenance of mixed stands.

- Practitioners who believed that current policy would lead to a loss of mixed stands ("unmixing" the boreal mixedwoods) also believed that losing mixed stands at the landscape scale would lead to an eventual loss of biodiversity.
- Practitioners who were convinced that as stands matured "Nature was filling in the gaps", and hence that policy did not engender a loss of mixed stands at the landscape scale, believed that policy would not have an impact on biodiversity.

Some practitioners believed that relatively young conifer stands could provide the same type of habitat, and hence support an equivalent richness and abundance of biodiversity, as natural old conifer stands.

Interestingly, although all practitioners were of the opinion that current policy leads to a reduction in mean stand age at the landscape scale, only some of the practitioners believed that this would have an impact on biodiversity. This was because some practitioners believed that relatively young conifer stands could provide the same types of habitats as natural old conifer stands, and hence support an equivalent richness and abundance of biodiversity.

2.1.4 Views on policy impacts on stand productivity

We asked practitioners their opinion with respect to the impacts of policy on stand and landscape productivity. Regardless of their opinion on the impacts of policy on the maintenance of mixed stands, all practitioners were uncertain of the impacts of policy on stand or landscape productivity.

2.1.5 Views on how to maximize forest productivity and conserve biodiversity

Adopt strategies inspired by natural stand dynamics

Some practitioners felt that policy was resulting in a loss of mixed stands and that replacement of natural old conifer stands by younger managed conifer stands would result in a loss of biodiversity. They also believed that managers should adopt practices inspired by natural stand dynamics.

Management approaches favoured by these practitioners included underplanting conifer in broadleaf-dominated stands, and the protection of understory advanced conifer stems during the harvesting of broadleaf canopy trees. These practices were favoured because they allow broadleaf-dominated stands and mixed stands to develop into older mixed stands or conifer-dominated stands.

Establish more conifer stands

Another group of practitioners thought that current regeneration policies did not cause a loss of mixed stands. Rather, their opinion was that management and policy during the past few decades had caused a loss of conifer-dominated stands in managed landscapes. These individuals believed that a concerted effort should be made to establish conifer-dominated stands. This could involve intensive tending techniques designed to convert broadleaf-dominated or mixed stands into conifer-dominated stands.

2.1.6 Published studies on the impacts of forest policy on stand composition

There were differences of opinion among practitioners as to whether recent and current forest policy leads to an "unmixing" of mixedwood forests. Unfortunately, there is relatively little published information on this question.

Only a few landscape-level studies have looked at changes in the abundance of forest types through time. These studies indicate that management practices have led to a decrease in the abundance of conifer-dominated stands, and sometimes to a decrease in the abundance of mixed stands (e.g., Hearnden et al. 1992, Jackson et al. 2000, Franklin et al. 2005, Valeria et al. 2010).

Only a few landscape-level studies have looked at changes in the abundance of forest types through time.

Some would argue that this landscape change is simply an artefact of a landscape in which the conifer component had been artificially increased due to fire suppression. However, studies that used a benchmark that preceded the fire suppression era (i.e. mid 19th century) still demonstrated that management approaches in recent decades have led to a loss of the conifer component on the landscape (e.g., Jackson et al. 2000). Most of these studies also showed there are fewer mixed stands today than there were in the past. However, the main difference between past and present landscapes is the loss of conifer-dominated stands.

2.1.7 Conclusions

Our interviews clearly demonstrated that there exists a wide range of views with respect to the impact of forest management on stand diversity at the landscape scale, and its possible impact on biodiversity. That being said, virtually all practitioners recognize that natural stand dynamics in the boreal mixedwoods are characterized by a gradual increase in the conifer component of stands. This shift leads to the gradual replacement of broadleaf-dominated stands by either mixed or conifer-dominated stands.

These interviews also showed that, when given free choice, a forester's preferred management approach reflects their opinion about the impacts of recent management and policy on forest composition and biodiversity. If a manager thinks that policy has induced a loss of mixed stands on the landscape, s(he) is generally in favour of adopting practices that are inspired by natural stand dynamics (understory conifer planting, protection of advanced conifer regeneration during the harvesting of mixed and broadleaf-dominated stands etc.). On the other hand, if a manager is of the opinion that management strategies have induced a loss of the conifer component of boreal mixedwood landscapes, s(he) is more likely to favour intensive practices designed to convert mixed and broadleaf-dominated stands into conifer-dominated stands.

Given that our interviews revealed that forest practitioners have divergent opinions about the mixedwood forests, research should be undertaken to investigate the following questions:

1) How does stand composition evolve after trees have been classified as "free to grow"? (*Does Nature fill in the gaps?)*
2) Can young managed conifer stands provide the same type of habitats as old natural conifer stands? (*Does stand age matter for the maintenance of biodiversity?)*
3) Are there differences in conifer tree diversity in natural and managed conifer-dominated stands in the eastern portion of the boreal mixedwoods? (*Are we simplifying tree diversity in conifer-dominated stands in the eastern boreal?*).

When given free choice, a forester's preferred management approach reflects their opinion about the impacts of recent management and policy on forest composition and biodiversity.

2.2 Canopy composition and biodiversity: different roofs, different inhabitants?

As described above, the canopy composition of mixedwood forests varies in time and space (Figure 1). In turn this variation is expected to have an important influence on the presence and abundance of all other living organisms in the forest. For example, the relative abundance of broadleaf and conifer trees in the canopy controls light, forest floor conditions and below-ground resources. This in turn affects understory plant communities. Further, microclimatic conditions, food resources, and structural habitat features (e.g., deadwood) important for vertebrates and invertebrates vary with forest composition and age.

We examined available literature on vascular and non-vascular plants, soil microorganisms, arthropods, and songbirds for the Canadian boreal mixedwood forest to determine the relationships of species diversity and community composition to forest (canopy) composition.

KEY POINTS

- Mixed forests often have greater species richness because they include a combination of species found in broadleaf and conifer stands.
- Only in a few instances do mixed forests have *unique* species; however some species could be considered to be "*mixedwood specialists*" as they are more abundant in mixed as compared to broadleaf or conifer stands.
- Understanding the mechanisms that underlie species associations with different forest types can help us predict biodiversity and the influence of forest management practices upon it.
- To support all the different types of biota, it will be important to maintain some naturally-disturbed and unmanaged forests as well as some unmanaged older forests within the mixedwood landscape.

2.2.1 Canopy composition and biodiversity

There are a number of approaches to examining biodiversity relationships in mixedwood forests. For example, we can assess the abundance of particular types of species, the number of different species (richness), or species diversity (e.g., the Shannon index). We can also assess whether species are found in multiple forest types or are exclusive to stands of a particular canopy composition. In our synthesis, we examined species richness at the scale of forest stands (i.e., how many species of a given biotic group are found in broadleaf-dominated *vs.* mixed *vs.* conifer-dominated forest stands) as well as changes in species composition among these three forest types.

We saw several patterns for the relationship of species richness and community composition to forest canopy composition in boreal mixedwood forests. Different types of biota followed different patterns, as summarized below (see Figure 3).

Pattern 1. Same richness but different community: One possible pattern we anticipated was that broadleaf, mixed and conifer forests have similar species richness but each is characterized by a distinct biological community. Thus, only a few species are found in more than one forest type.

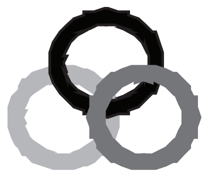
This pattern was not observed in any of the studies we examined.

Pattern 2. Similar richness and similar community: Broadleaf, mixed and conifer forests have similar species richness and most species are common to all stand-types, although their relative abundances may vary.

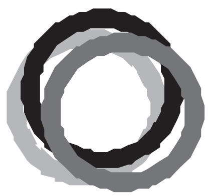
This pattern was observed for multiple studies on ground beetles in the boreal mixedwood forest of northwestern Quebec (O'Connor et. al. unpublished) and in northwestern Alberta (Work et al. 2004, Work et al. 2010). In both areas, all three mixedwood forest types had similar species richness and there was a high degree of overlap in the occurrence of dominant species among them. A larger synthesis of 10 ground beetle studies throughout Canada, most located in the boreal forest, corroborates these findings. It emphasizes that community differences between stand-types largely reflect differences in relative abundance of species rather than species found *per se* (Work et al. 2008). This was also the case for spiders (Work et al. 2004) and moths in mixedwood forests of northwestern Alberta (Morneau 2002).

Pattern 3. Mixed stands most diverse: Mixed forests have greater species richness than broadleaf or conifer stands because they host a combination of species found in both forest types.

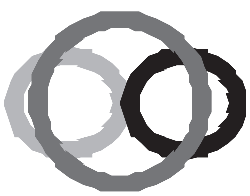
Size of circle = number of species
Overlap = number of species in common



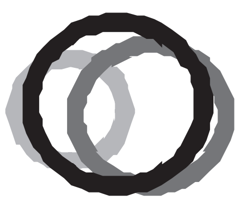
1. Same richness, different community: Broadleaf mixed and conifer stands have similar species richness but only a few species are found in more than one forest type. This patten was not observed for any type of organism in the studies we examined.



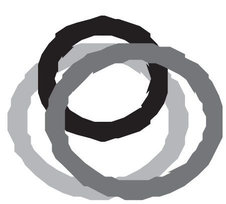
2. Similar richness, similar community: Broadleaf mixed and conifer stands have similar species richness. Most species are common to all stand types although their relative abundances may vary. Observed for: ground beetles,[1,2,3] spiders,[2] moths.[4]



3. Mixed stands most diverse: Mixed stands have greater richness than broadleaf or conifer stands because they host a combination of species found in both forest types. Observed for: vascular plants,[5,6] soil microbes,[7] saproxylic beetles,[8,9] songbirds.[10]



4. More conifers, more species: Species richness increases with conifer component because of the addition of species associated with the presence of conifers. Observed for: nonvascular plants,[11] forest beetles (litter-dwelling & saproxylic).[12]



5. More conifers, fewer species: Conifer forests have lower species richness than either mixed or broadleaf stands because certain species are 'missing' in conifer forest. Observed for: rove beetles,[13] vascular plants in black spruce/aspen mixtures.[14]

Figure 3. Patterns of species richness, and overlap in species composition between broadleaf-dominated, mixed, and conifer-dominated stands in the boreal mixedwood landscape, indicating patterns observed for different biotic groups. In the diagrams the sizes of the circles represent relative species richness while the overlap between circles indicates the proportion of species shared between stand types.

[1] O'Connor et al. (unpublished),[2] Work et al. (2010), [3] Work et al. (2004), [4] Morneau (2002), [5] Macdonald and Fenniak (2007), [6] Hart and Chen (2008), [7] Hannam et al. (2006), [8] Hammond et al. (2001), [9] Jacobs et al. (2007), [10] Hobson and Bayne (2000), [11] Caners et al. (unpublished), [12] Paquin and Dupérée (2001), [13] Work, et al. (unpublished), [14] Bergeron et al. (unpublished).

The occurrence of understory vascular plant species frequently corresponded to this pattern (but see # 5 for black spruce dominated forests). Most species occur in multiple forest types but mixed forest stands have higher species richness because they host a combination of species associated with a broadleaf canopy and those associated with a conifer canopy (Macdonald and Fenniak 2007, Hart and Chen 2008). However, this pattern may not apply if conifer-dominated forests are at an age where secondary disturbances, such as individual tree death, become important (Legaré et al. 2001, De Grandpré et al. 1993).

This pattern was also followed by soil microbial communities. These organisms, which are critically important for nutrient cycling and forest productivity, are a function of the forest floor (litter quality and quantity) and soil properties (pH, nutrients, carbon:nitrogen ratio)(Hannam et al. 2006). In mixedwood forests of northwestern Alberta, richness of the soil microbial communities (number of taxonomic groups or functional groups) was greater in mixed forests than in conifer or broadleaf stands (Swallow et al. 2009). This appears to also be true for ectomycorrhizae (Kernaghan et al. 2003) but may not always be the case for soil bacteria (Lamarche et al. 2004).

Saproxylic beetles are dependent upon standing or fallen deadwood and thus their richness and abundance are related to the amount and variety of deadwood substrates in a forest. Not surprisingly, then, species richness of saproxylic beetles was higher in mixed than in broadleaf- or conifer-dominated forests (Hammond et al. 2001, Jacobs et al. 2007). This likely is due to the greater abundance and diversity of deadwood substrates in mixed forest stands. These stands include dead snags and logs of both tree types and also have developed successionally to the point where there is a substantial supply of both deadwood types (conifer and broadleaf).

Occurrence of songbirds also appears to show this relationship. In a study of songbird communities in mixedwood forest stands of varying composition in Saskatchewan, the mixed forest stands had higher abundance and species richness of songbirds (Hobson and Bayne 2000). These stands, in turn, hosted a combination of species found in broadleaf- and conifer-dominated forests. Also, some species had particularly high abundance in mixed stands or mainly occurred in mixed forest stands. Five of these species (Swainson's Thrush, Blackburnian Warbler, Red-breasted Nuthatch, Black-throated Green Warbler, Bay-breasted Warbler) were identified as mixedwood specialists in a Quebec study because of their higher abundances in landscapes with a greater proportional area as mixed forest (Drapeau et al. 2000).

Each mixedwood forest type across the broadleaf-to-conifer continuum is important for some species.

Pattern 4. More conifer, more species: Species richness increases from broadleaf, to mixedwood to conifer stands because of the addition of species associated with the presence of conifers.

Broadleaf forests are generally recognized as having low abundance and richness of mosses and liverworts and this is likely due to heavy annual litterfall (which smothers forest floor mosses) and to low abundance and variety of establishment substrates (live and dead trees of different species, sizes, and decay stages) for these species. Richness and abundance of mosses and liverworts increases from mixed to conifer forests as the microclimate becomes moister, and a greater variety of substrates become available (Caners et al., unpublished). In particular, many liverwort species were found only in conifer-dominated forests.

Some groups of invertebrates showed a similar relationship to canopy composition. In a study that included both litter-dwelling and saproxylic beetles from mixedwood forest types in Quebec, Paquin and Dupérée (2001) found that conifer forests had the greatest species richness and more "unique" species than either mixed or broadleaf forest types.

Pattern 5. More conifer, fewer species: Conifer forests have lower species richness than either mixedwoods or broadleaf forests because certain species are "missing" in conifer forest.

Rove beetles are litter-dwelling insects that feed primarily on other insects. In many cases these animals hunt within mushrooms for flies and other animals that feed directly on fungi. Some species of rove beetles are known to feed directly on fungi. For this group of species, broadleaf-dominated and mixed forests had similar richness and many species were found in both forest types. Conifer forests, however, had lower species richness and lacked species that were found in the other two forest types (Work et al. unpublished).

This pattern was also followed by understory vascular plant communities in heavily conifer-dominated forests. In this case, particularly for black spruce dominated forests in the eastern Canadian boreal, understory communities may have lower richness and abundance of vascular plants than either mixed or broadleaf-dominated forests (Boucher et al., unpublished). This may be due to the negative influence of heavy shade and accumulation of forest floor mosses. Observations also indicate that dense white spruce stands may have very low understory vegetation diversity.

Summary

Clearly, different types of organisms display different relationships to forest composition. Overall, however, it does not seem that broadleaf-dominated, mixed, and conifer-dominated stands in the boreal mixedwood host dramatically different biotic communities, and only a few species appear to be "mixedwood-specialists" (e.g., songbird species that had higher abundance in mixed forest stands).

> **Different types of organisms display different relationships to forest composition.**

2.2.2 Forest composition, forest age, and species patterns

The occurrence and abundance of species in different forest types is often attributable to their particular habitat requirements. An understanding of these relationships is important for predicting patterns of biodiversity, and also for understanding the potential impacts of forest management on biodiversity. As we move across the gradient from broadleaf- to mixed to conifer-dominated forest, there are concomitant changes in microclimatic conditions, food sources, and structural habitats available. Further, as forests age along the successional trajectory, there are changes in forest structure that will drive patterns of variation in the associated biological communities.

For example, vascular understory plant species are closely associated with canopy composition at the stand scale (Macdonald and Fenniak 2007, Hart and Chen 2008) and also at the scale of small conifer-, mixed- or broadleaf-canopy patches within mixed forest stands (Chavez and Macdonald 2010). This has been attributed to the influence of canopy composition on microclimate, light, and forest floor and soil conditions.

Similarly, the occurrence and abundance of mosses and liverworts is determined by the availability of substrates and microsites (e.g., exposed mineral soil, presence of moist microsites, live trees of different species, and different types, species, sizes and decay stages of snags and downed logs) for which species have strong and specific affinities (Mills and Macdonald 2004, 2005). Thus, moss and liverwort abundance and richness in different forest types is a function of the availability and diversity of microsites.

Some arthropod groups that rely on large/old conifer trees are typically more common in mixed or conifer forests. Likewise arthropod species that depend upon dead wood (saproxylic beetles) also have greater richness in mixed forests because of the greater abundance and variety of dead wood. For rove beetles, however, reductions in species richness within conifer stands may be related to less broadleaf litter, which they depend upon for structural habitat, or it could be related to the abundance and diversity of fungi available as a food source. Thus, arthropod abundance and richness is dependent on a range of habitat conditions present throughout the gradient of stand types found in the boreal region.

These patterns also hold true for songbirds. For example, there are a number of habitat characteristics important for songbirds that may vary with mixedwood composition, such as singing perches, nesting sites, thermal or hiding cover, and plant or insect food sources. The Blackburnian Warbler was identified in a number of different studies as having a particular affinity for mixed forest (Drapeau et al. 2000, Hobson and Bayne 2000). A study conducted in New Brunswick also showed that this species was associated with mixed forest composition at the scale of a small patch. Its greater abundance in mixed stands was explained by the availability of small patches that contained large broadleaf and conifer trees, which are used for both foraging and singing (Young et al. 2005).

The richness and composition of living organisms in mixedwood forests are a reflection of the forest canopy composition and the associated structural and habitat features important for some species.

In summary, the richness and composition of living organisms in mixedwood forests are a reflection of the forest canopy composition and the associated structural and habitat features. These vary spatially and temporally (Brassard et al. 2008a, 2008b). Each mixedwood forest type across the broadleaf-to-conifer continuum is important for some species.

2.2.3 Can we maintain the forest type – biodiversity relationships in managed forests?

It is difficult to say how biodiversity will develop in relation to forest composition in managed mixedwood forests. North America has a very short history of managing mixedwood forests. Thus, there has not yet been enough time to observe the effects of management practices on the structural development and biodiversity of these forests. However, in Fennoscandia boreal forests have been managed for well over a century. In that region, the major causes of species extirpation or decline have been attributed to declines in broadleaf trees, deadwood and wildfire (Kuuluvainen 2002).

Some experimental studies in Canada are also beginning to yield information on the short-term effects of forest management on biodiversity. There is evidence that forest harvesting practices are driving the forest landscape outside its natural range of variability and that this has consequences for the associated biological communities (e.g., Imbeau et al. 2001, Haeussler and Bergeron 2004, Cyr et al. 2009). Also, several studies have shown that early post-fire forests host unique biotic communities and that salvage harvesting dramatically changes these (Bradbury 2006, Koivula and Spence 2006, Koivula and Schmiegelow 2007, Kurulok and Macdonald 2007, Macdonald 2007). Thus, maintaining some unmanaged post-fire forests is important for biodiversity conservation across the range of mixedwood stand types and ages.

Other studies are beginning to provide important information on how innovative harvesting approaches can be used to create forest structural and habitat characteristics. These characteristics have been shown to help retain or facilitate rapid redevelopment of biotic communities of arthropods, birds, amphibians and mammals following harvest (Norton and Hannon 1997, Buddle et al. 2000, Schieck et al. 2000, Harrison et al. 2005, Haeussler et al. 2007, Hart et al. 2009, Work et al. 2008, Swallow et al. 2009, Work et al. 2010). For example, understory vascular plant communities respond relatively quickly to the influence of canopy redevelopment (Craig and Macdonald 2009). This suggests that the maintenance of these communities can be achieved by using management practices that affect canopy composition.

Maintaining some unmanaged post-fire forests is important for biodiversity conservation across the range of mixedwood stand types and ages.

It is also important to understand that some of the important habitat features of mixed forests are not available until sufficient time has passed since disturbance (e.g., large live trees or advanced decay stages of deadwood). Furthermore, some species require long time periods to re-establish after disturbance, either because of dispersal limitations or habitat requirements (e.g., mosses or liverworts). On the other hand, early post-disturbance forests are characterized by some unique structural and environmental characteristics, upon which certain “disturbance-” or “fire-” dependent species rely. Thus to conserve biodiversity it will be important to maintain or recreate the structural and habitat features associated with the full range of boreal mixedwood forest types and ages.

2.3 Canopy composition, growing conditions and tree productivity

The influence of individual tree species on ecosystem processes and attributes is dependant on multiple traits (Eviner and Chapin 2003). For example, canopy trees directly influence environmental and edaphic conditions in the understory, including microclimate, litter quantity and quality, nutrient cycling and pH. Canopy trees are also the prime determinants of forest biomass accumulation and productivity.

More specifically, there are important differences between broadleaf and conifer species in terms of their ecological characteristics and functions. Canopy composition is, therefore, expected to have an important influence on ecosystem processes such as nutrient cycling, decomposition, and productivity. Further, as forest composition changes through succession in mixedwood forests, ecosystem attributes, such as light transmission, soil temperature, and deadwood characteristics are influenced by the changes in species composition over time. In this section, we synthesize our knowledge with respect to the influence of canopy composition in boreal mixedwoods on:

1) Nutrient cycling and decomposition,
2) Soil conditions for tree growth, and
3) Wood quality and volume.

KEY POINTS

- Growing conditions for trees are usually more favourable in mixed stands than in pure conifer stands.
- Decomposition rates are faster in mixed stands than in pure conifer stands.
- "Adding" low densities of aspen to spruce stands can result in increased total volume at rotation age.
- Spruce "added" to aspen stands do not negatively affect aspen productivity.
- Protecting understory spruce while harvesting mature aspen stems could result in harvesting more wood in the long term.

2.3.1 The influence of canopy composition on soil nutrient dynamics and growing conditions

Litter quality and decomposition rates

Parent material, climate, atmospheric deposition and topography are important determinants of soil nutrient content, particularly for cations such as calcium. In closed canopy forests, however, availability of nutrients (particularly nitrogen) relates largely to decomposition of litter. The rate of decomposition is controlled by temperature and moisture as well as by the chemical and physical nature of the litter (Paré and Bergeron 1996, Prescott 2002). Further, time since disturbance, mineral soil properties (e.g., pH), microclimate (soil temperature and moisture) and coarse woody debris can also influence nutrient dynamics in forests. Below we explore the role of canopy composition and coarse-woody debris in more detail.

Time since disturbance, mineral soil properties (e.g., pH), microclimate (soil temperature and moisture) and coarse woody debris are important controlling influences on nutrient dynamics of forests.

Canopy composition

In what ways does canopy composition influence nutrient availability in forests? Canopy composition influences litter quantity (e.g., deciduous versus evergreen species), quality (e.g., chemical and physical differences between broadleaf and needle litter), rooting patterns and nutrient requirements (Prescott 2002) as well as the forest floor and soil microenvironment. Together these drive decomposition and hence the release of nutrients in forest soils.

For example, conifer-dominated forests are expected to have slower rates of nutrient cycling (compared to broadleaf) because conifers produce less litter each year, needle litter decomposes more slowly than broadleaf litter, and also because the low light at forest floor

(Constabel and Lieffers 1996) and the thick feather-moss cover (Macdonald and Fenniak 2007) reduce soil temperature, slowing the rate of decomposition.

Broadleaf forests, on the other hand, are expected to have higher nutrient availability because they produce higher volumes of litter that is more readily decomposable and they also have warmer soil conditions, leading to more rapid decomposition. Broadleaf trees such as aspen also improve soil conditions by transporting nutrients from deep in the soil and then contributing these back to nutrient cycling through litter fall.

Decomposition has also been shown to be more rapid in forest floors of broadleaf than conifer stands (Prescott et al. 2000), and Jerabokova et al. (2006) showed that nitrogen availability was directly related to the relative abundance of broadleaf trees in boreal mixedwoods. Broadleaf litter is of higher quality and can also result in less acidic forest floor conditions, promoting higher forest floor microbial biomass and activity and decomposition (Bauhus et al. 1998, Prescott et al. 2000, Jerabokova et al. 2006, Hannam et al. 2006, Swallow et al. 2009). However, Prescott et al. (2000) showed that these differences in quality between broadleaf and conifer litter disappear within the first three years of decomposition.

Within mixedwood forests, there is conflicting information as to a potential nutrient cycling benefits of these forests. Looking just at litter decomposition, Prescott et al. (2000) found that mixed litters did not decompose more quickly than either "pure" broadleaf or conifer, but Jerabokova et al. (2006) found that mixed stands had the highest rates of nitrogen mineralization. Rothe and Binkley (2001) reviewed the topic of nutrient dynamics in mixed forests and concluded that, in terms of nutrient inputs and soil nutrient supply, mixed stands are most often intermediate between the two monocultures.

The relative importance of litter quantity, quality and decomposition rate in terms of the effect of canopy composition on nutrient availability is also unclear. In a review of nutritional dynamics in mixed forests Rothe and Binkley (2001) found that there were only minor differences in decomposition rate across a mixed compositional gradient from broadleaf to mixed to conifer-dominated. Prescott (2002) concluded that the primary effect of canopy composition on nutrient availability was due to differences in litter quantity and nutrient content rather than decomposition rate; i.e., there are more nutrients to cycle but they do not necessarily cycle more quickly.

Coarse woody debris

Nutrient fluxes from coarse woody debris (CWD) are a small component of the total ecosystem nutrient cycle (Laiho and Prescott 2004). Initially CWD may be a net sink of nutrients, but over the long term is a minor nutrient source. Thus, if the CWD component is removed by harvesting, the capacity of ecosystems to accumulate nutrients from external sources may be critical to the maintenance of forest productivity.

Decomposition rates of wood differ among tree species; aspen wood decomposes much more quickly than either spruce or pine (Brais et al. 2006). The timing of nutrient release during wood decomposition also varies by tree species. For example, aspen releases a large pulse of nutrients very early in the downed woody debris decay cycle whereas the major pulse of nutrient release from birch doesn't occur until about 40 years. For spruce the initial nutrient release is low, and then nutrients are released at a slow and steady rate from about 20 to 80 years (Brais et al. 2006). Having a diversity of tree species, therefore, results in greater variation in the timing of nutrient release from deadwood over time.

> **Mixedwood forests of different canopy composition almost certainly differ in terms of nutrient dynamics and availability.**

Summary

In summary, mixedwood forests of different canopy composition almost certainly differ in terms of nutrient dynamics and availability. It is not clear, however, that "mixed" forest stands necessarily have higher rates of litter or downed wood decomposition or that they exhibit higher soil nutrient availability. The natural mixedwood dynamic, in which broadleaf and coniferous trees change in dominance over time, is likely important for the long-term nutrient dynamics of these forests.

Forest composition effects on soil conditions

Studying the effect of forest composition on tree growing conditions is challenging because it requires comparison among environmentally similar sites that host different forest types (relative abundances of broadleaf and conifer trees). Here we aim to summarize studies that examined how canopy composition affects soil growing conditions for trees.

Increasing dominance by conifers over time is accompanied by deteriorating soil conditions for tree growth.

Brais et al. (1995) studied a mixedwood successional gradient in northwestern Québec and showed that as stands age and become increasingly dominated by conifers, soil nutrient status changes dramatically. For example, soil pH and cation exchange capacity decreased, and this was associated with a decline in availability of several soil nutrients, including phosphate, calcium, potassium and magnesium. At the same time, soil organic carbon increased with time since disturbance. Nitrogen availability remained relatively unchanged across this compositional / temporal gradient – likely because microbial immobilization of nitrogen takes place. Although we cannot uncouple the effects of composition and forest age in this study, it does demonstrate that increasing dominance by conifers over time is accompanied by deteriorating soil conditions for tree growth.

A study in the black spruce feathermoss area of northwestern Québec supported the idea that addition of trembling aspen to conifer-dominated forests improves growing conditions for trees. In their study, Légaré et al. (2005a) controlled for stand age by comparing stands of the same age but different canopy composition. Stands along a compositional gradient from pure black spruce to a mixture of black spruce and trembling aspen were studied. They found that soil pH, cation exchange capacity and wood decomposition rates increased with increasing aspen. These conditions could lead to increased soil nutrient availability. This study, in the black spruce feathermoss region, clearly suggests that as the broadleaf component of the conifer dominated stands increases, soil conditions for growth and decomposition improve.

In the western boreal forest, broadleaf forests (as compared to conifer or mixedwood stands) had greater litter depth, warmer soil temperatures, and greater total nitrogen in the mineral soil and organic layer. These stands, however, did not differ in soil moisture or available nitrate, ammonium or phosphate (Macdonald and Fenniak 2007). In addition, small deciduous-dominated patches within mixed stands (as compared to coniferous patches in the same mixed stands) had a shallower organic layer depth and lower soil available nitrate, but higher available calcium and magnesium. They also had warmer, wetter soils (Chavez and Macdonald 2010). This study in the western boreal forest shows that even at small spatial scales the amount of broadleaf trees in the canopy has a positive influence on tree growing conditions.

Increasing abundance of broadleaf trees, up to a point, in conifer-dominated mixedwood stands may result in improved soil and environmental conditions for tree growth.

Soil microbial communities, which are important determinants of decomposition and nutrient immobilization, also differ among mixedwood forest types (but see Lamarche et al. 2004). Hannam et al. (2006) showed that conifer and mixed forests were similar to one another in terms of soil microbial community composition, but different from broadleaf-dominated forests. This was attributed to the influence of conifers on forest floor pH and nitrogen concentration, as well as to the higher contribution of moss to organic matter in conifer-dominated forests. Bauhus et al. (1998) found a decline in forest floor organic matter quality, microbial biomass, and nutrient use efficiency as stands aged and aspen abundance decreased in a mixedwood successional gradient in northwestern Québec. These studies demonstrate that the dominance of broadleaf trees in the canopy has positive effects on microbial communities and processes.

Summary

All these studies suggest that mixedwood forest composition may influence forest floor conditions and the quality of the growing environment for trees. Increasing abundance of broadleaf trees, up to a point, in conifer-dominated mixedwood stands may result in improved soil and environmental conditions for tree growth.

2.3.2 Influence of forest composition on wood quality and volume

"Mixed" forests, in which two or more tree species are prominent in the canopy, are often considered to have high productivity. However to date there has been no synthesis to confirm that this is true for the boreal mixedwood.

Experts found that total stand volume at rotation age increased with increasing aspen abundance up to about 40% of total stand basal area.

Légaré et al. (2004, 2005b) examined stand-level tree productivity across a compositional gradient from pure black spruce to mixed aspen-black spruce. They found that total stand volume at rotation age increased with increasing aspen abundance up to about 40% of total stand basal area. In all cases this increase in stand volume was due to the addition of trembling aspen volume and in most, but not all, cases this increase in trembling aspen did not negatively affect black spruce volume (Figure 4). Further, the quality of the black spruce increased, as the volume was distributed among fewer but larger stems. A recent study by Cavard et al. (2010) showed that this additive effect is no longer present once the proportion of aspen reaches 50%.

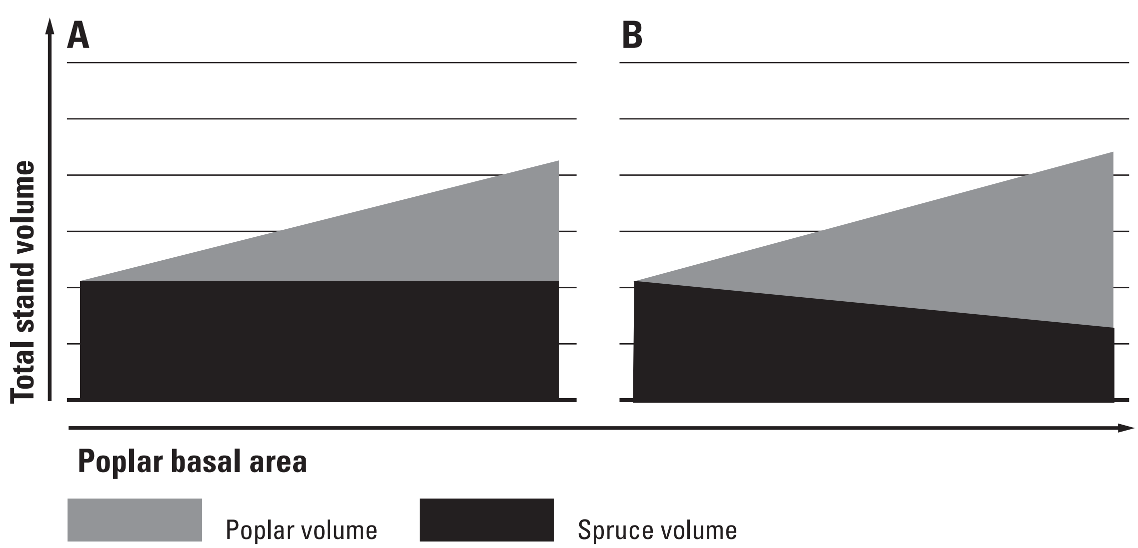


Figure 4. Variation in total trembling aspen and black spruce volume at rotation age with different relative amounts of trembling aspen in black spruce dominated forests in northwestern Quebec. In (A) the poplar volume is additional to the spruce volume; in (B) there is some loss of spruce volume, which is more than compensated for by addition of poplar volume (adapted from Légaré et al. 2005b).

Longpré et al. (1994) also found that jack pine trees were larger when grown in mixture with paper birch, although this wasn't the case for mixtures with aspen. Another study in Alberta indicated that stand-level productivity (mean annual increment) may be 15 to 20% higher for mixed stands as compared to either pure aspen or pure white spruce stands, although it is unclear how this would translate into merchantable volume at rotation age (Man and Lieffers 1999, MacPherson et al. 2001). Similarly, a study in Minnesota showed that mixed forests had greater mean annual increment than did either "pure" aspen or spruce stands (Edgar and Burk 2001).

Protecting and maintaining understory conifers (10-20 cm DBH) when the mature broadleaf trees are harvested can shorten the next rotation and hence allows more harvests within a given time period.

These results from studies of natural stands are supported by recent research on 15-year-old managed mixtures of white spruce and trembling aspen in Alberta. These studies showed that low densities (up to 1000 stems/ha) of trembling aspen had no effect on growth of planted white spruce (Griffiths 2008). Both white and black spruce may grow less vigorously under closed broadleaf canopies, but they can maintain themselves in the understory and the canopy may, in fact, protect them from frost damage (Groot and Carlson 1996, Filipescu and Comeau 2007).

In addition, mixed species stands at rotation age often contain understory conifers that can be protected during harvesting operations. Studies have shown that these trees show improved growth following removal of the broadleaf canopy (MacIsaac and Krygier 2004). Further, simulations over numerous rotations have demonstrated that by protecting and maintaining these understory conifers (10-20 cm DBH) when the mature broadleaf trees are harvested, it is possible to shorten the next rotation. This, in turn, allows more harvests within a given time period (Figure 5) (Comeau et al. 2005).

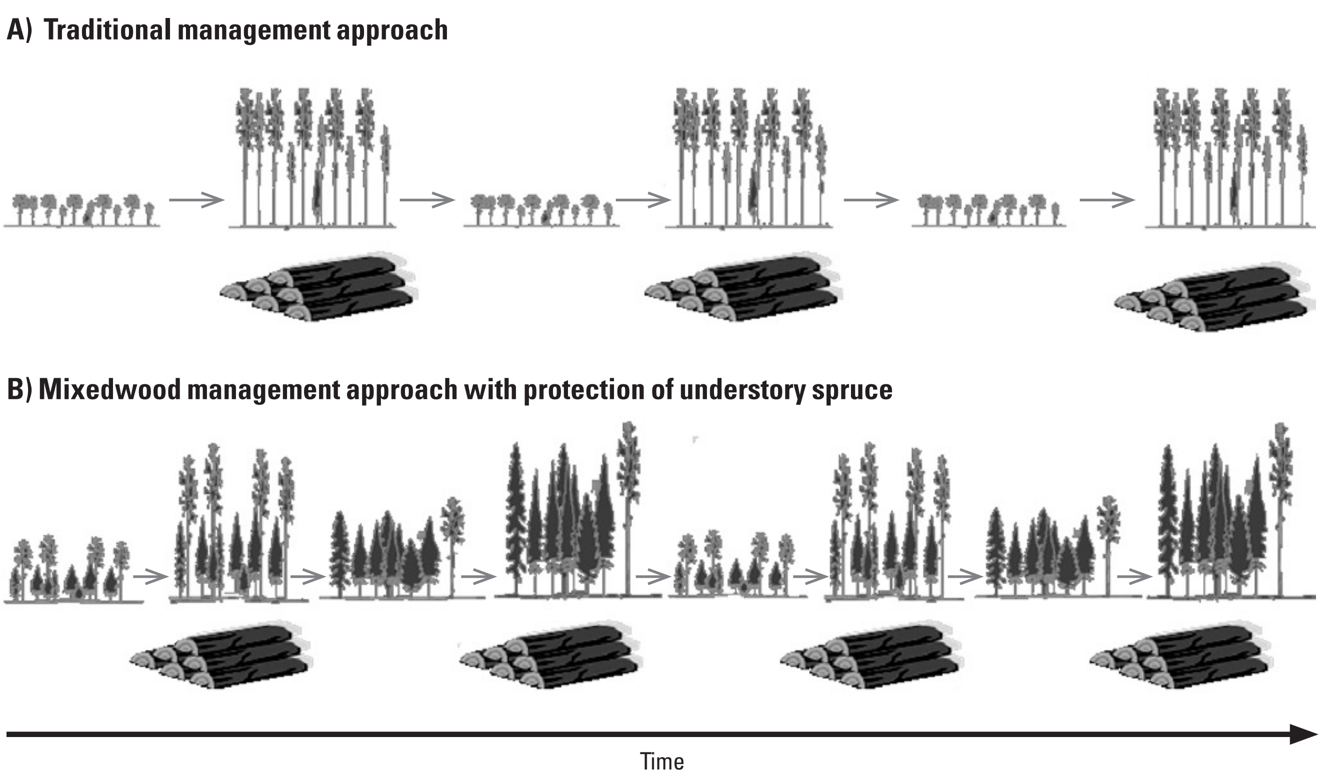


Figure 5. Comparison of hypothesized number of harvests for a given time period under (A) traditional management and (B) mixedwood management using understory protection (partially based on Comeau et al. 2005).

Despite this information, there is still a need to understand trade-offs between frost protection, light availability and competitive effects as related to densities and spatial arrangements of species in mixed plantations. This will enable managers to precisely define conditions for productivity advantages in mixed stands (Voicu and Comeau 2006, Man et al. 2008).

In conclusion, the literature (Edgar and Burk 2001, Chen et al. 2003, Kelty 2006, Szwagrzyk and Gazda 2007) suggests that mixed stands are most likely to exhibit increased productivity (compared to either of their "pure" counterparts) when they are:

- comprised of a mixture of shade-tolerant and shade-intolerant species,
- when they are vertically structured,
- when there is inclusion of a nitrogen-fixing species, or
- when fast-growing species are added to the mix.

It appears that inclusion of low to moderate densities of broadleaf trees in conifer-dominated stands can result in better quality stems, and sometimes more total wood volume at rotation age.

From the available studies of natural and managed stands it appears that inclusion of low to moderate densities of broadleaf trees in conifer-dominated stands can result in better quality conifer stems, and sometimes more total wood volume at rotation age. By managing mixed stands as mixtures, by considering successional dynamics, and by carefully harvesting stems when the different component species are mature, it may be possible to obtain more wood from a given stand over several rotations.

2.4 Boreal mixedwood management: minimizing risk in a changing climate

In the previous sections we demonstrated the potential importance of forest composition for biodiversity and productivity across the broadleaf to conifer compositional gradient in the boreal mixedwood forest. On this basis, we can conclude that it is important to consider the influence of management effects on forest composition. In this section we consider how mixedwood management could be less risky if managers and policy makers kept in mind: (1) natural stand and disturbance dynamics and (2) past and projected global climate change.

KEY POINTS

- Post-fire stand dynamics in mixedwoods are generally characterized by a gradual shift in canopy composition from broadleaf to coniferous-dominated stands over time.
- Current policy focuses on replacing what we cut. This may maintain the current proportion of stand types found in boreal mixedwood landscapes, but it does not respect the natural successional dynamics of these forests. This may be risky.
- A precautionary approach to managing boreal mixedwoods should allow the tree composition of some stands to change through time while maintaining a variety of stand types across the landscape.
- Boreal mixedwood management strategies designed to ensure adaptation to climate change should assist species to colonise favourable sites north of their current extent.

2.4.1 Replacing what we cut: risky?

Once a certain stand type, always the same stand type?

After fire, the natural stand dynamics of boreal mixedwoods are characterized by a gradual shift from broadleaf-dominated to conifer-dominated stands (Figure 1, Figure 6). Unmanaged stands 0-80 years old are dominated by broadleaf species while the presence of conifer-dominated stands increases with age (time since fire) of the landscape (Lieffers et al. 2008a, Figure 6).

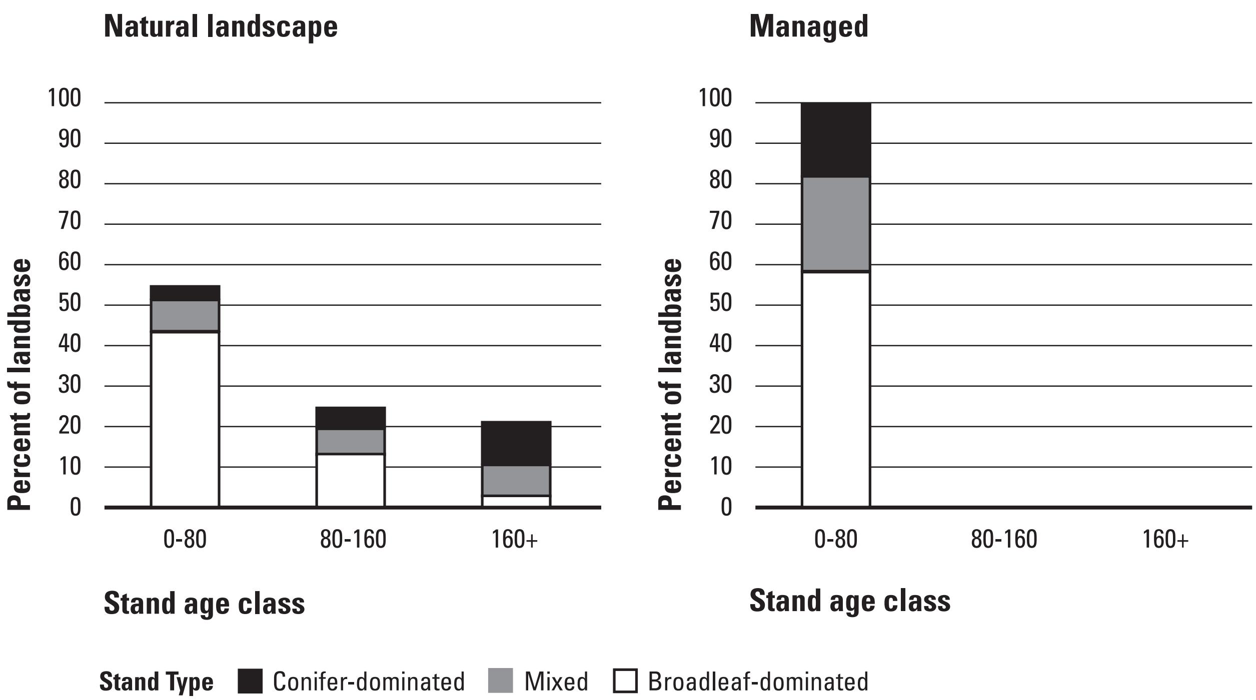


Figure 6. Proportion of forest stand types in an unmanaged (natural) unharvested boreal mixedwood landscape under a 100-year fire cycle (from Lieffers et al. 2008a), and in a theoretical managed boreal mixedwood landscape under current forest policy. The overall proportions of each stand type were set to be the same in both natural and managed landscape types. Clearly age-class distribution of managed landscapes can be very different from "natural" landscapes even if both have the same overall proportions of conifer-dominated, mixed and broadleaf-dominated stands.

Notes: For the natural landscape, data for relative abundance of forest types within each age class were adapted from real data for northeastern Alberta from Lieffers et al. (2008a). The proportion of each stand age class on the natural landscape was estimated using the method described in Bergeron et al. (1999) assuming a 100-year fire cycle and 80 years for transitions from broadleaf to mixed or mixed to conifer. Data for the managed landscape are theoretical. They assume an 80-year rotation, and assume that the proportion of the managed landscape occupied by each stand type is the same as the overall average (all age-classes) for the natural landscape.

The effect of time on forest composition has not been considered in previous forest management policy, but is predicted to be a critical consideration in successful long-term management of boreal mixedwood landscapes.

The effect of time on forest composition has not been considered in previous forest management policy. However, time is predicted to be a critical consideration in successful long-term management of boreal mixedwood landscapes (Bergeron and Harvey 1997, Harvey et al. 2002).

Stand dynamics imposed by current policies: Does a change in age structure matter?

Current forest management regulations across Canada are focused on re-establishing the stand type that was harvested. However, there is some concern that mixed stands are being converted to either broadleaf- or conifer-dominated stands.

Guidelines are also designed to maintain the same proportion of each stand type on the landscape over time. This approach fails to embrace the natural stand dynamics described previously, and can lead to management approaches that are expensive and difficult because they are at odds with this natural succession.

> **Even if current forest management policy does maintain the same proportion of stand types on the landscape, the proportions of stand age classes will almost certainly be altered.**

In addition, given current rotation lengths, eventually most stands within the managed portion of the landscape will be younger than 80 years. Thus, even if current forest management policy does maintain the proportion of stand types on the landscape, the proportions of stand age classes will almost certainly be altered as compared to an unmanaged landscape (Figure 6).

As described above in section 2.2, structural features of forests that change with composition and age have an important influence on biodiversity. As a result of the policy-induced change in age structure, forests may lack these features that provide critical habitat for a diversity of species. Is this risky? While many forest ecologists may answer yes, there is little scientific data to support this notion. Few studies have compared boreal mixedwood forests of similar composition but different age. Further, given the relatively short history of management in the boreal mixedwoods of Canada, comparisons between older managed and older unmanaged conifer forests are not possible. It is difficult to say whether this should be of concern.

We do know that biotic communities vary with mixedwood canopy composition because of species-specific habitat requirements, as was described above in section 2.2. Further, mixedwood forests of varying composition and age differ in terms of the habitat features they provide. On this basis, we can predict that, to the extent that current forest management policies affect the composition and age structure of boreal mixedwood forests, they may be risky from a biodiversity point of view. For example the structural and species diversity associated with old stands may be lost, if these stands no longer exist. Further research is needed in this area.

2.4.2 The pre-industrial forest obsession

Once a boreal mixedwood landscape, always a mixedwood landscape?

Forest managers need guidance in determining what proportions of each stand type and stand age class should be maintained in boreal mixedwood landscapes now and in the long term. Forest ecologists (e.g., Barrette and Bélanger 2007) and forest certification standards (e.g., Forest Stewardship Council) suggest using the pre-industrial forest condition as a benchmark.

In boreal mixedwood landscapes the pre-industrial forest condition usually represents what existed prior to intensive forest operations, i.e., about 50 years ago in much of Canada. Adoption of the pre-industrial forest condition as a guide, however, represents a fairly static view of forest landscapes. Indeed, it implies that the composition of boreal mixedwood landscapes in the recent past is the single objective we should strive to maintain into the future.

This approach to landscape management, which can be characterized as the "pre-industrial forest obsession", fails to embrace the following:

1) the arrangement of boreal mixedwood stands on the landscape was not always as it appears today, and
2) projected global climate change may favour an encroachment of boreal mixedwood forest further north, in turn altering stand types and stand dynamics in a given area.

For example, during the early parts of the Holocene (6000 years ago) when the Earth's temperature was warmer than it is today, areas in the eastern boreal region of Canada that are currently dominated by boreal mixedwoods were occupied by species that are currently found further south in the Great-Lakes Saint-Lawrence biome (Carcaillet et al. 2001, Figure 7). In western Canada during this period, some areas in the southern portion of the current boreal mixedwood forest were occupied by aspen parklands and grasslands while boreal mixedwoods were found further north than they are today (Strong and Hills 2005, Figure 8).

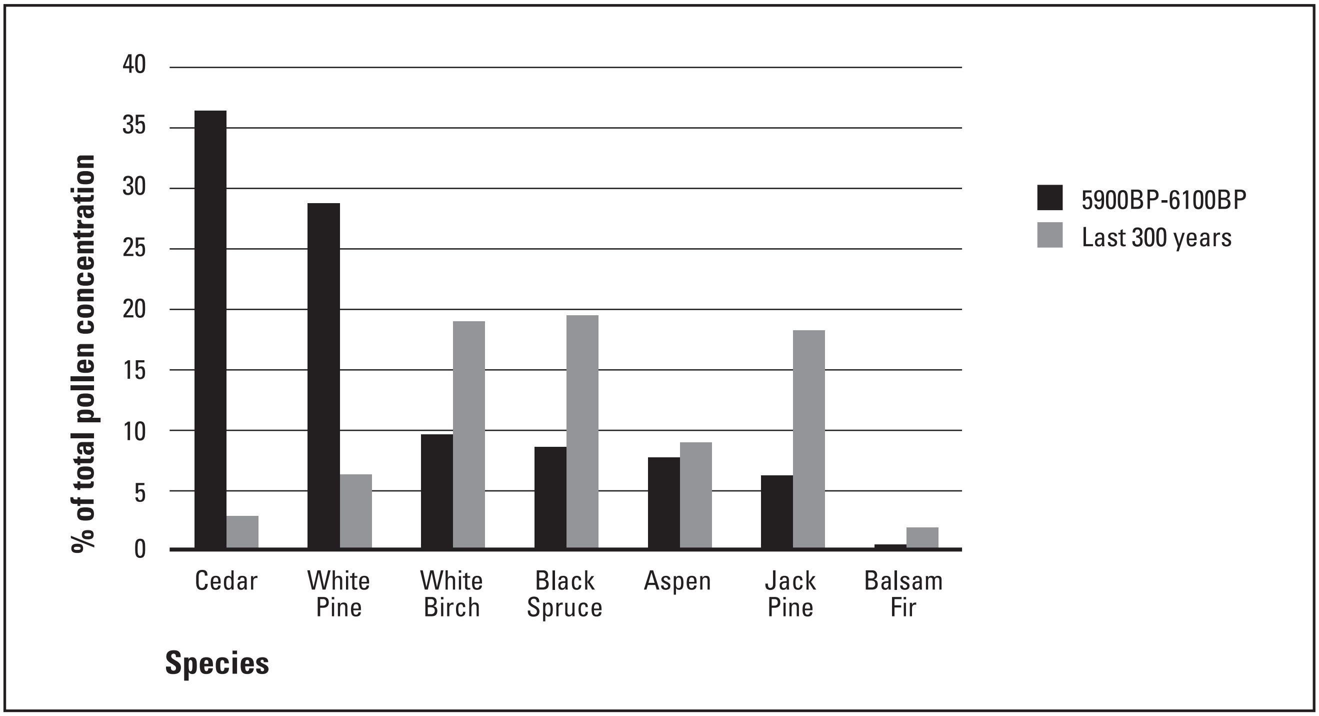


Figure 7. Relative abundances of tree species' pollen 6000 years ago (6100 to 5900 years before present, BP) and in the past 300 years, based on analysis of a lake core from the boreal mixedwoods in northwestern Quebec (based on Carcaillet et al. 2001).

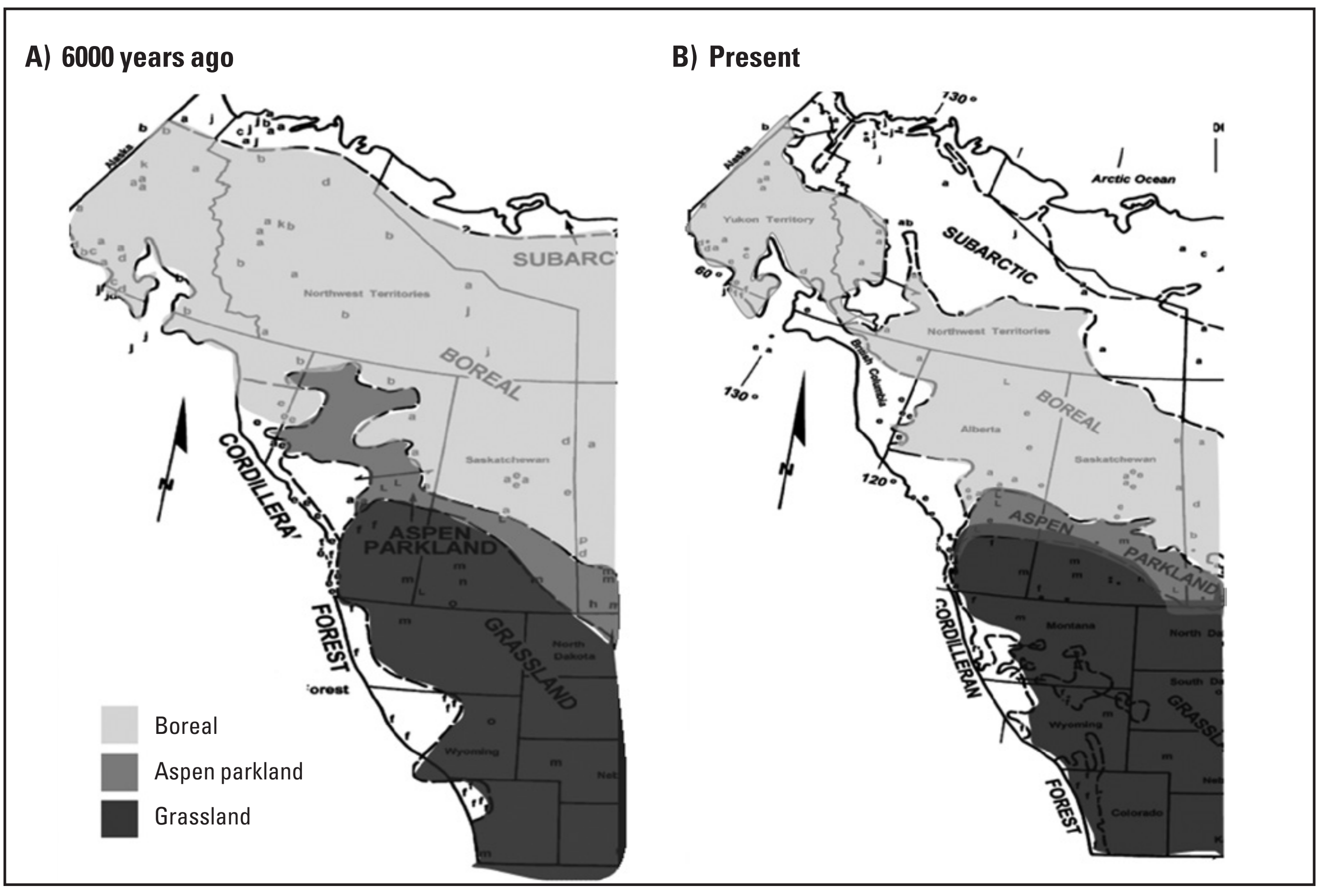


Figure 8. The extent of boreal, aspen parkland and grassland landscapes in western Canada (A) 6000 years ago and (B) at present (adapted from Strong and Hills 2005).

Planning in the face of uncertainty

It is increasingly likely that, regardless of mitigation measures, the next century will be characterized by shifts in global weather patterns and climate regimes. Meanwhile, considerable uncertainty remains about the direction and extent of climatic change at a regional scale. This poses significant challenges for forest ecosystem managers.

> **It is increasingly likely that, regardless of mitigation measures, the next century will be characterized by shifts in global weather patterns and climate regimes.**

Nonetheless, we need to incorporate expected future environments into ecosystem management planning. Within a century, or much sooner in some regions, projections indicate that using the recent historical landscape as a template for forest ecosystem management may lead to failure.

Is our focus on maintaining the landscape-scale pattern of mixedwood forest composition risky? In theory, likely yes, given that trees regenerated today will determine the stand composition for at least the next 60 to 80 years, and many of these species and populations may no longer be adapted for the future climate.

> **Managers and policy makers could, on a limited portion of the landscape, adopt practices that are inspired by stand dynamics that occur south of the boreal mixedwood.**

Rather than being inspired only by the stand dynamics that currently occur in the boreal mixedwoods and the landscape patterns of the recent past, managers and policy makers could, on a limited portion of the landscape, adopt practices that are inspired by stand dynamics that occur in forests south of boreal mixedwood landscapes. Similarly, to maintain the proportion of Canadian landscapes that will be characterized by boreal mixedwood dynamics, some portion of the landscapes that are currently north of boreal mixedwoods could be allocated to practices inspired by boreal mixedwood stand dynamics. In the end this should increase the region's resilience to global climate change by increasing the stand and species diversity.

2.4.3 What can managers and policy makers do?

Our current state of knowledge indicates that present forest management policy poses some risk by:

1) not allowing stands to age and change composition and structure according to natural stand dynamics, and
2) by failing to seriously consider past and future global climate change.

> **Our current state of knowledge indicates that present forest management policy poses some risk.**

A more precautionary approach to forest management in the boreal mixedwoods should be based on:

- The development of flexible standards that allow stands to change composition between and during rotations;
- The development of a broader suite of alternative yield curves and targets within forest management plans, and adoption of a broader range of silvicultural practices (e.g., partial cutting, understory protection, underplanting of conifers in broadleaf-dominated stands) that "artificially age" stands in terms of both composition and structure. These may be effective for conservation of biodiversity and ecosystem function in managed mixedwoods.

- In the face of climate change, there is a need to re-think concepts of local gene pool and seed tree zones to allow for innovative forest management and planning for future climate change by:
  - Increasing regional genetic diversity by using tree seed sources from southern seed zones in some of our regeneration efforts;
  - Increasing regional species diversity by establishing, on favourable sites within the eastern boreal mixedwoods (e.g., well-drained south-facing slopes), species and stand dynamics that resemble those of areas south of the current mixedwood zone;
  - In the southern part of the western boreal mixedwoods, seriously examining the costs and benefits of silvicultural investments in the context of whether they are likely to survive to the end of rotation given climate change predictions;
  - Increasing regional species diversity of areas north of the boreal mixedwood zone by establishing, on favourable sites, species and stand dynamics that currently occur in the mixedwood zone.

3.0 Implications and recommendations

Our state of knowledge on the implications of changing the composition of boreal mixedwood forests has clearly increased in recent years, through a variety of research programs and on the ground applications. However, many more experimental trials and studies need to be completed before alternative silvicultural approaches will be firmly entrenched in forest policy.

Many more experimental trials and studies need to be done before these alternative practices will be firmly entrenched in forest policy.

Here we list the implications of our findings on management and forest policy. We then proceed to list the research needs with respect to the management of boreal mixedwoods.

3.1 Implications for management and policy

Applying innovative silvicultural approaches to facilitate mixedwood management presents certain challenges for implementation. However, we do currently have a strong knowledge base with respect to several of the silvicultural approaches that could be used to meet objectives for mixedwood management (see Appendix). Here we also summarize some key points for managers and policy makers to consider when implementing these techniques.

- **Maintain the full range of mixedwood canopy types as a mosaic of patches at a variety of scales. Embrace the diversity of successional pathways to maintain biodiversity and possibly increase stand productivity.** This can be achieved by:
  - Carefully managing conifer and broadleaf trees as intimate mixtures to maximize stand productivity;
  - Retaining conifer seed trees to facilitate natural regeneration;
  - Protecting conifer understory to enhance recovery and increase productivity.

- **Maintain the habitat elements associated with different mixedwood stand types and ages.** This can be achieved by:
  - Using understory retention and other partial-harvest systems;
  - Actively managing for deadwood.

- **Recognize the biodiversity value of both young and old forests and their associated habitat features.** This can be achieved by:
  - Maintaining naturally disturbed forests (i.e. not salvage log all disturbed forests) to conserve populations of disturbance-dependent species;
  - Maintaining unmanaged old-growth forests to conserve populations of "old-growth"-dependent species.

- **Re-think concepts of local gene pool and seed tree zones to allow for innovative forest management and planning for future climate change.** This can be achieved by:
  - Using tree seed sources from southern seed zones in at least some of our regeneration efforts (i.e., assisted migration);
  - Establishing, on favourable sites within the eastern boreal mixedwoods, species and stand dynamics that resemble those of areas south of the current mixedwood zone;
  - Establishing, on favourable sites in areas north of the western boreal mixedwood zone, species and stand dynamics that currently occur in the mixedwood zone.

3.2 Implications for research

Compilation of this synthesis provided insight into our current understanding and also identified knowledge gaps. On this basis, we have identified the following research needs:

- **Given current uncertainty about the effects of forest management (current and recent past) on forest composition and dynamics in the boreal mixedwood regions there is a need to further explore these questions by:**
  - Investigating how stand tree composition evolves after stands have been classified as "free to grow";
  - Comparing conifer tree diversity in natural and managed conifer-dominated stands in the eastern portion of the boreal mixedwoods;
  - Comparing landscape-level diversity relative to presettlement and current characteristics of mixedwood landscapes.

- **While evidence suggests that biodiversity is strongly linked to forest composition, age, and habitat features, there is a need to expand our knowledge regarding the biodiversity implications of changing mixedwood forest composition.** This can be approached by:
  - Comparing the biodiversity found in natural stands of different composition types and ages;
  - Comparing biodiversity in managed stands and natural stands for a diversity of mixedwood compositions and ages (including evaluating implications of different silviculture and management practices).

- **To optimize productivity of mixedwood forests while incorporating consideration of biodiversity implications, there is a need to better understand the influence of forest composition on productivity and how different management options can be most effectively applied to mixedwoods.** This can be approached by:
  - Comparing the productivity of stands for a diversity of mixedwood compositions and ages;
  - Continuing to study the positive and negative impacts of protecting the conifer understory;
  - Continuing to examine alternative approaches for regenerating and managing mixedwood stands;
  - Undertaking and studying assisted migration of mixedwood tree species and stand dynamics as a strategy for adaptation to climate change.

4.0 Conclusions

- Natural stand dynamics in mixedwoods are generally characterized by a gradual shift in canopy composition from broadleaf-dominated to coniferous-dominated stands over time.
- Variation in canopy composition (broadleaf – mixed – conifer) in the boreal mixedwood has an important influence on nutrient cycling and growing conditions for trees.
- There is some evidence that mixed forests have greater productivity than "pure" conifer or broadleaf forests.
- The biotic communities of the boreal mixedwood are related to forest composition and age because these determine the habitats provided therein.
- Mixed forests often have distinct biotic communities including a combination of species found in broadleaf and conifer-dominated forests with higher overall abundance and species richness .
- We lack knowledge on the longer-term implications of forest management on biodiversity in mixedwoods. However, there is reason for concern, particularly over potential loss of naturally-disturbed forests and old forests.
- A precautionary approach to managing boreal mixedwoods should allow the tree composition of some stands to change through time. It should also incorporate a variety of silvicultural approaches in order to maintain the natural variation in species mixtures.
- Boreal mixedwood management strategies designed to ensure adaptation to climate change could include assisted migration of species and incorporation of stand dynamics that are likely to be appropriate for future climates.

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Appendix

Silvicultural options for boreal mixedwoods: recent research

A number of publications over the past 15 years have proposed approaches to ecosystem management and explored a diversity of silvicultural options for boreal forests (Lieffers et al. 1996, Harvey et al. 2002, Haeussler et al. 2004, Gauthier et al. 2009).

Bergeron and Harvey (1997) proposed increasing integration of natural stand dynamics in silviculture as a means of maintaining stand-level processes such as regeneration and succession. This would also help attain forest-level goals of ecosystem or forest type diversity in the eastern boreal mixedwood. This approach was expanded upon by Harvey et al. (2002) to propose specific treatments including seed tree systems, careful logging to protect advanced regeneration, single- and group-selection and shelterwood cuttings.

Using this system, treatments with the greatest retention are designed to maintain compositional and structural heterogeneity in stands, and encourage acceleration of succession to develop the structural characteristics of older coniferous stands. In this context, characteristic mixed stands of broadleaf and coniferous species are considered an intermediate, transitional phase of stand development on mesic sites. Similarly, the diversity of silvicultural treatments is intended to reflect the gradient of natural disturbances that drive this ecosystem, from high-intensity crown fires to insect outbreaks and gap dynamics.

Some of the treatments and the general approach proposed for ecosystem management of eastern mixedwoods are being tested in the SAFE (*sylviculture et aménagement forestier écosystémique*) project (Brais et al . 2004). Among reported results, Bourgeois et al (2004) found that heavy thinning (60% of basal area) in mature, aspen-dominated stands resulted in a positive growth response in understory balsam fir. They concluded that this treatment would favour transition to a more complex structured mixedwood than would a lighter (30%) thinning. Haeussler et al. (2004) concluded that diffuse, low-impact partial harvesting in these same stands did not generate the structural or plant diversity characteristics of over-mature mixedwoods. Thus, they suggested that diversifying the size of stand openings and the degree of soil disturbance would increase stand-level biodiversity.

Harvey and Brais (2007) examined partial cutting treatments in aspen-dominated mixedwoods as analogues to natural mortality processes of self-thinning and stand break-up and their influence on dead wood production. Finally, building on artificial seeding work done by Calogeropoulos et al. (2004) in eastern boreal mixedwoods, Greene, Harvey and Brais are currently evaluating operational approaches to enhancing white spruce regeneration. They are doing this by synchronizing understory scarification in mixed and aspen-dominated mixed stands, and seed tree and site scarification treatments in open post-spruce budworm stands with mast years.

Lieffers et al. (1996) proposed a variety of "natural and semi-natural" silvicultural options based upon the diversity of natural stand types found in the western boreal mixedwood. They suggested that an ecosystem management approach for mixedwoods could include: underplanting of conifers in broadleaf-dominated stands, understory protection of conifers when harvesting the broadleaf canopy, shelterwood and seed tree systems to promote natural regeneration of conifers, and single tree and group selection systems to maintain natural heterogeneity within stands.

More recently, Comeau et al. (2005) further elaborated harvesting and regeneration options for mixedwoods with respect to creating different forest compositional and structural types. They describe options for creating stands with single- and two-storied mixtures of broadleaf and conifer trees or in which both types of species are maintained as a mosaic of small patches.

They explore the costs and yields associated with options such as seeding, post-harvest planting, underplanting, understory protection, strip clearcutting and row thinning. Their analysis suggests a yield advantage for understory protection (Comeau et al. 2005). Further, the "Continuous Cover" management approaches they discuss could prove attractive for maintaining habitat attributes of mixedwood forests and addressing public concerns about clearcutting.

Recent improvements in our understanding of the interactions of conifer and broadleaf species growing in intimate mixtures suggests that the influence of "competing" broadleaf saplings on white spruce growth is complex and is not well-expressed by free-to-grow assessments using small plots (Lieffers et al. 2008b).

Experimental studies are beginning to provide the necessary information to optimize yields while managing these species as intimate mixtures (Groot and Carlson 1996, Voicu and Comeau 2006, Filipescu and Comeau 2007, Lieffers et al. 2008b, Man et al. 2008). Another recent study suggested that natural regeneration of spruce is a viable option for achieving partial stocking in stands that were aspen-dominated before harvest (Martin-Demoor et al. 2010).

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