Describing condition-specific determinants of competition in boreal and sub-boreal mixedwood stands

by D. Scott Green[1]

There is a growing economic and ecological incentive in developing best-management practices for broadleaf-conifer mixedwood stands in boreal and sub-boreal regions of Western Canada. Current free-growing guidelines employed in these areas appear to be poor predictors of interactions between primary growth determinants and environmental conditions in these complex stands. Density-dependent relations between broadleaf and conifer components in mixedwood stands may vary across a range of conditions due to interactions discussed in this paper between primary growth determinants (i.e., light limitations, edaphic limitations and species-specific traits) and local environment. Clarifying these interactions will promote the development of adaptable tools that can be used to develop context-specific mixedwood management strategies.

Key words: mixedwood management, free-growing guidelines, boreal, sub-boreal, density-dependent competition

Il y a de plus en plus d'incitations économiques et écologiques reliées au développement des pratiques pour un meilleur aménagement des peuplements mélangés de feuillus et de conifères dans les zones boréales et sous-boréales de l'Ouest canadien. Les directives actuelles de régénération libre de croître utilisées dans ces zones semblent être de piètres indicateurs des interactions entre les facteurs primaires de croissance et les conditions environnementales au sein de ces peuplements complexes. Les relations basées sur la densité entre les composantes feuillues et résineuses des peuplements mélangés peuvent varier selon un ensemble de conditions découlant des interactions discutées dans cet article entre les facteurs primaires de croissance (par ex., limites associées à l'ensoleillement, limites découlant du sol et les caractéristiques spécifiques à l'espèce) et l'environnement local. Une meilleure connaissance de ces interactions permettra le développement d'outils versatiles qui pourront être utilisés pour élaborer des stratégies d'aménagement des forêts mixtes spécifiques au contexte.

Mots-clés : aménagement des forêts mixtes, directives de régénération libre de croître, zone boréale, zone sous-boréale, compétition dépendante de la densité

Introduction

In recent decades, the interest in managing broadleaf-conifer mixed tree species (hereafter, mixedwood) stands has grown with an improved understanding of their potential economic benefits (Kelty 1992, Sachs 1996, Comeau *et al.* 1999, Steele *et al.* 2001, Valkonen and Valsta 2001) and ecological benefits (Holbo *et al.* 1985, Mielikainen 1985, Morrison *et al.* 1988, Stathers 1989, Morrison *et al.* 1991, Watt 1992, Enns *et al.* 1993, McComb 1994, Taylor *et al.* 1994, Wang *et al.* 1995, Prescott *et al.* 2000). However, uncertainty about best-management practices in mixedwood stands has often been expressed in a default strategy of minimizing the incidence and growth of competing broadleaf tree species through intensive and expensive practices (even though management guidelines permit the presence of broadleaf competitors, see Simard 1996).

The development of effective management practices in boreal and sub-boreal mixedwood forests of Western Canada must incorporate the greater inherent complexity of broadleaf-conifer mixtures relative to single-species or mixed-species conifer forests (Simard 1996). Broadleaf and evergreen tree species have distinct growth patterns that manifest themselves following the initiation of mixedwood stands. Broadleaf species (such as *Populus tremuloides* Michx. [trembling aspen] and *Betula papyrifera* Marsh. [paper birch]) tend to grow faster than their conifer associates, commonly spruce and fir in boreal and sub-boreal regions (Simard 1990, 1996; Comeau 1996;

Peterson and Peterson 1996, Comeau *et al.* 1999, Yang *et al.* 2003), creating a high degree of structural complexity (i.e., stratified stands). Consequently, conifers are often relegated to understory conditions during early mixedwood stand development (Drew 1988, Valkonen and Valsta 2001).

While the successional trajectories of such complex stands remain unclear, it is well established that the regeneration and growth potential of understory conifer crop trees in mixedwood stands is correlated to the density of competing broadleaf trees. These relations have been characterized in numerous mixedwood stands (e.g., Lieffers and Stadt 1994, Comeau *et al.* 1999, Messier *et al.* 1999, Jobidon 2000, Brandeis *et al.* 2001, Prévost and Pothier 2003, Valkonen and Ruuska 2003). Current management guidelines in Alberta and British Columbia, which are used to describe the "competition neighbourhood" around conifer crop trees in mixedwood stands (i.e., free-growing stocking standards), rely on distance-dependent relations confined to a small area around crop trees (MacIsaac and Navratil 1996, Lieffers *et al.* 2002). However, Lieffers *et al.* (2002) found that free-growing stocking standards failed to reasonably characterize light competition between broadleaf and conifer components in boreal mixedwood stands and that adequate sampling using current approaches would be operationally prohibitive.

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In fact, current free-growing standards employed in developing mixedwood stands may be too coarse-filtered to adequately describe competitive responses to a number of important growth determinants (in particular, light limitations, edaphic limitations and species-specific interactions.) and their interactions with environmental conditions (Green *In Review*).[2] This paper reviews current knowledge about such key density-dependent determinants of competitive relations among mixedwood components and the sensitivity of these factors to changes in environmental conditions in an effort to identify critical knowledge gaps that need to be addressed in the development of appropriate mixedwood management tools.

Light Limitations

Numerous researchers have suggested that competitive interactions between broadleaf and conifer components in mixedwood stands (at least in stratified stands) primarily reflect light limitations imposed by overstory broadleaf trees (e.g., Brand 1986, Simard 1996, Tanner *et al*. 1996, Comeau *et al*. 1999, Lieffers *et al*. 2002, Wang and Kimmins 2002). Further, light conditions mediated by both spatial and temporal factors may influence density-dependent relations between mixedwood components.

The spatial separation of broadleaf and conifer trees in stratified mixedwood stands results in inverse relations between broadleaf density and light interception (which is proportionally related to volume and biomass production, see Monteith 1972, Green 1998, Green *et al*. 2003) for mixedwood components. Light interception in the overstory increases with broadleaf stem density (or basal area), while light interception in the understory decreases (Comeau 2001, Comeau and Heineman 2003). Consequently, conifer survival, height growth and stem-volume increments in the understory have been shown to be negatively correlated with broadleaf stem density or basal area (Lieffers and Stadt 1994, Man and Lieffers 1997b, Jobidon 2000, Comeau 2001, Lieffers *et al*. 2002). Minimum understory light thresholds for conifer survival may be exceeded in dense broadleaf stands (Pinno *et al*. 2001) with light levels observed as low as 2% full light (Lieffers *et al*. 2002), which can result in high mortality among the most shade-tolerant conifers.

While the observed relations in mixedwood stands between overstory structure and understory light availability suggests a means to model light dynamics in mixedwood stands for management applications (Comeau 2001, Lieffers *et al*. 2002), there remains much uncertainty about how to operationally achieve and maintain target light levels for acceptable survival and growth of conifer crop trees. The spatial distribution of overstory broadleaf trees, for instance, creates considerable heterogeneity in understory light environments. Clumpiness in broadleaf tree patterns affects the amount, orientation and spatial distribution of leaf area, all of which have a strong bearing on the light environment and conifer growth in the understory (Pinno *et al*. 2001, Lieffers *et al*. 2002).

The temporal (phenological) separation of light utilization periods between deciduous broadleaf and evergreen conifer habits may be an important determinant of density-dependent relations in mixedwood stands (Man and Lieffers 1999).

Observations of photosynthetic productivity of understory conifer trees during the spring (and to a lesser degree autumn) broadleaf leafless periods suggest that these high-light windows may constitute an important ecological strategy to enhance the survival, growth and annual carbon balance of understory conifer trees (Baldocchi *et al*. 1984; Constabel and Lieffers 1996; Mielikainen 1996; Man and Lieffers 1997a, 1997b, 1999; Gill *et al*. 1998).

However, the relative importance of temporal separation in light utilization for understory conifer trees in mixedwood stands may vary with broadleaf density. High-light windows may be particularly important for conifer survival and growth at moderate to high broadleaf densities. In a pilot study looking at the growth of shade-tolerant subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) saplings under variable densities of paper birch cover in central British Columbia (Fig. 1, unpublished data – D.S. Green 2002 [see Comeau *et al*. 1998 for a description of the study site and mixedwood stand structure]), the spring high-light window provided little apparent benefit at the endpoints of overstory broadleaf stem densities (i.e., high and low). Bi-weekly measurements of radial stem growth (using high-resolution band dendrometers) and relative photosynthetic photon flux density (PPFD) (i.e., the ratio of understory PPFD and ambient PPFD taken under cloudy conditions just above each target fir sapling) for understory fir saplings permitted an assessment of temporal growth trends during the deciduous leafless period. No measurable stem growth occurred during the spring high-light (leafless) window below a light threshold of about 60% full light, which corresponded to a light level of about 7% full light during mid-summer (see Fig. 1D). At such high cover densities, shading by broadleaf branches may sufficiently restrict light levels in the understory during the deciduous leafless period to create secondary limitations (e.g., delayed snowmelt and near-frozen soils, which can hinder biophysical processes such as root conductance of water; see Teskey *et al*. 1984, Jurik *et al*. 1988, Man and Lieffers 1997a). As broadleaf densities decreased below the highest levels observed in the pilot study (i.e., increasing understory light availability), conifer saplings utilized increasing portions of the spring leafless period for measurable stem growth (see Fig. 1C). At low broadleaf densities in this pilot study, stem growth trends during the leafless period were similar to trees growing under full light (see Fig. 1B). At these low levels of cover, understory light-availability differences between the leafless and leafed period may not be significant in terms of photosynthetic production or secondary limitations.

Edaphic Limitations

While generally considered to be less limiting than light in mixedwood stands, competition for edaphic resources may play an important role in relations between broadleaf and conifer components (Comeau *et al*. 1999, Man and Lieffers 1999). As with light limitations, density-dependent relations in mixedwood stands may be influenced by edaphic conditions mediated by both spatial and temporal factors. Some studies suggest that broadleaf and conifer species may exploit different edaphic niches in mixedwood stands due to a spatial separation in rooting zones (Laitakari 1934, Strong and La Roi 1983, Kabzems and Lousier 1992, Mielikainen 1996, Man and Lieffers 1999). While the adaptive importance of such a spatial separation is

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[2] Consideration of these factors in this paper will be limited to stratified mixedwood stands to minimize the potential complexity of the issues.
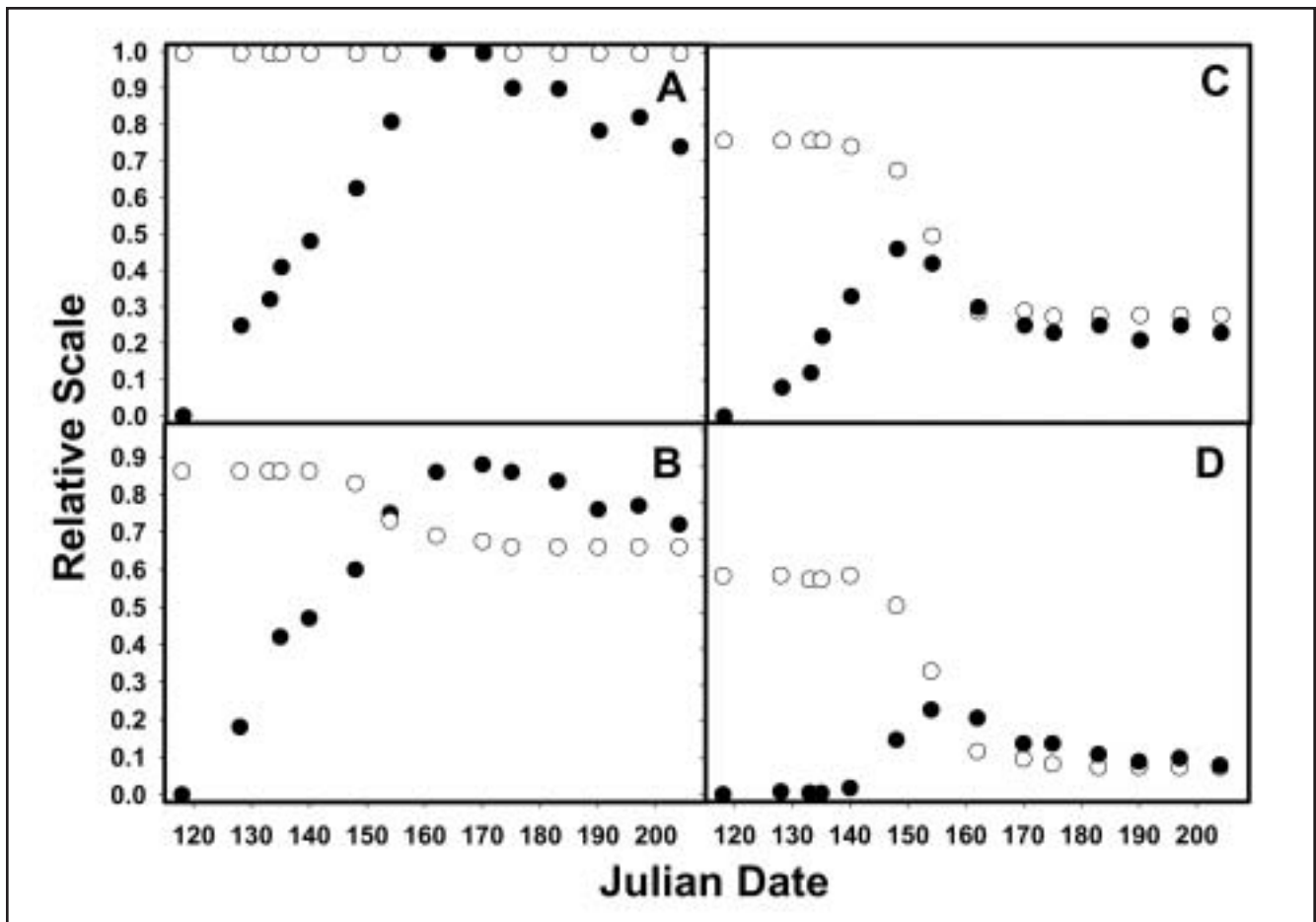
Fig 1: Transmittance of photosynthetically active radiation as a fraction of full light (0.0-1.0 on Relative Scale; open circles) and relative stem-wood production (0.0–1.0 on Relative Scale; filled circles) by Julian date for subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) saplings growing under variable densities of paper birch (*Betula papyrifera* Marsh.) cover at the Spey Creek research site (central B.C. – N 53º 54' 882, W 122º 21' 167) during the growing season of 2002. Relative Stemwood Production was scaled to the peak growth of the fastest growing tree (**1A**). Figures show trends typical under no paper birch cover (**A**), under low-density paper birch cover (**B**), under medium-density paper birch cover (**C**) and under high-density paper birch cover (**D**).

not clearly understood, the potential benefits will likely increase with stand density as competition for edaphic resources intensifies and as biophysical processes influence important factors such as soil temperature and nutrient mineralization.

The temporal separation of light utilization periods between deciduous and evergreen habits should also influence competition for edaphic resources in mixedwood stands. The reduced demand on edaphic resources by broadleaf trees during their leafless periods should help to sustain the potentially high photosynthetic rates of understory conifers given the enhanced light availability at these times (particularly in the spring, due to the longer days and higher solar angles relative to fall leafless periods) (see Man and Lieffers 1997b). The importance of temporal separation in leafing habits on the availability of edaphic resource for understory conifers may vary with broadleaf density in a manner similar to that described for light.

The potential exploitation of different edaphic and light niches (spatial and temporal) may partly explain the observation that

mixedwood stands may be more productive than single-species stands (Kelty 1992, Simard 1996, Man and Lieffers 1999).

Species-Specific Interactions
Density-dependent relations in mixedwood stands may vary due to species-specific interactions between and within functional groups (i.e., deciduous broadleaf vs. evergreen coniferous). Broadleaf species may differ in their light interception potential on a given site and/or in relations between light interception and stand traits such as basal area or stand density. For instance, light measurements taken in the understories of boreal mixedwood stands of trembling aspen or paper birch of variable densities indicated dramatically different relations between light availability and stand basal area (unpublished data – P.G. Comeau), with birch attenuating considerably more light at a given basal area (about 88% vs. 50% full light at 10 m^2 ha^{-1} basal area for birch and aspen, respectively) (also see Comeau 2001, Comeau and Heineman 2003). Additionally, broadleaf

species may vary in the phenology of leaf out and senescence, resulting in differences in the effective period of temporal separation between deciduous and evergreen mixedwood species. The author is not aware of any studies that have examined phenological differences among deciduous mixedwood species. However, during the spring of 2002 and 2003, such differences were observed at the Spey Creek research site (central B.C.) with trembling aspen leafing out about a week before paper birch, which could effectively reduce the spring high-light window for conifer photosynthetic production in aspen-dominated mixedwood stands. Interactions between light absorption potential at a given basal area and phenology (i.e., timing of leaf out/leaf drop) in different broadleaf species could either increase species distinctions through additive effects (e.g., lower light attenuation at a given basal area associated with later leaf out) or mute species distinctions through compensating tradeoffs (e.g., lower light attenuation at a given basal area associated with earlier leaf out).

Understory conifer species appear to differ in the minimum light thresholds at which survival and growth are severely curtailed (Kobe 1996, MacIssac and Navratil 1996, Simard 1996, Kobe and Coates 1997, Wright *et al.* 1998, Lieffers *et al.* 2002). Stewart *et al.* (2001) found that white spruce (*Picea glauca* [Moench] Voss) survival in boreal mixedwood stands decreased rapidly below about 10% of full light, while Lieffers and Stadt (1994) identified 8% full light as a minimum light level. Reported observations suggest that minimum light levels vary among other western boreal conifers, including 4% full light for lodgepole pine (*Pinus contorta* Dougl. *ex* Loud var. *latifolia* Engelm.) (Messier 1996), 1% full light for subalpine fir (Klinka *et al.* 1992) and 2.5% full light for balsam fir (*Abies balsamea* [L.] Mill.) (Parent and Messier 1995).

Further, intra-species variability in reported minimum light thresholds suggests different responses among geographically distinct populations and/or under different environmental conditions. For example, Eis (1970) found that the critical light threshold for white spruce survival in central B.C. (about 15% full light) was nearly twice that observed in boreal forests by Lieffers and Stadt (1994). Additionally, Awada and Redmann (2000) reported considerable variation in mortality at low light levels among different populations of white spruce from western and central Canada.

Light requirements for potential growth of conifer seedlings and saplings may also vary among species and conditions. Peak height growth for some boreal conifers (e.g., white spruce and balsam fir) has been shown by some studies to occur between 40–60% full light (Shirley 1945, Logan 1969, Lieffers and Stadt 1994, Comeau 2001), while Jobidon (2000) found that height increments for white spruce increased all the way to full sun. Peak stem radial and/or volume growth among many boreal and western conifers appears to occur near full light (Eis 1967, Logan 1969, Lieffers and Stadt 1994, Wright *et al.* 1998, Jobidon 2000, Comeau 2001). However, stem radial-growth trajectories in response to light availability differ among ecologically distinct conifer species (Wright *et al.* 1998). Conversely, some tree species may achieve peak radial growth under shading cover. Logan (1969) found that stem volume production for shade-tolerant balsam fir was greater at 45% than at 100% sunlight. Further, the growth responses of distinct tree species to light availability may vary among environments (Wright *et al.* 1998), as was noted previously for seedling/sapling responses to minimum light

thresholds. Consequently, conifer species appear to differ in their capacity to tolerate broadleaf cover, and some environmental factors appear to influence the relationship.

Influence of Environmental Factors in Density-Dependent Mixedwood Relations

Density-dependent growth relations between broadleaf and conifer components in mixedwood stands may vary moving across primary environmental gradients toward harsher conditions (e.g., higher elevation and/or latitude; steeper, more northerly slope aspect; increased continentality) due to interactions between local environment and light limitations, edaphic limitations and/or species-specific traits (Green *In Review*).

Cold soil and air temperatures, which tend to be more prevalent with increasing elevation/latitude and on northerly slope aspects in northern ecosystems, are known to be key limiting factors in tree growth and reproduction (Tryon and Chapin 1983, Van Cleve *et al.* 1983, Bonan 1992, Navratil 1996, Loehle 1998, Landhäusser *et al.* 2001). The growth responses of trees to thermal conditions may differ markedly between broadleaf and conifer species, altering their relative dominance in mixedwood stands across environmental gradients (Van Cleve *et al.* 1983, Landhäusser *et al.* 2001, Landhäusser *et al.* 2003). Landhäusser *et al.* (2001) found strong positive relations between soil temperature (5–25°C) and numerous growth characteristics (including whole-plant growth, leaf production, root production, net photosynthesis and stomatal conductance) for trembling aspen seedlings. These general trends have been confirmed for trembling aspen and *Populus balsamifera* L. [balsam poplar] by other studies (Tryon and Chapin 1983, Landhäusser *et al.* 1996, Landhäusser and Lieffers 1998, Landhäusser *et al.* 2003). Conversely, Landhäusser *et al.* (2001, 2003) observed slight or no changes in key growth characteristics with increasing soil temperature for white spruce seedlings. Other studies have shown a similar insensitivity to soil temperature for other spruce species, including *P. engelmannii* Parry ex. Engelm. [Engelmann spruce] (Day *et al.* 1990), *P. sitchensis* (Bong.) Carr. [sitka spruce] (Turner and Jarvis 1975) and *P. mariana* (Mill.) B.S.P. [black spruce] (Tryon and Chapin 1983). Further, a low sensitivity to cold soil temperatures may be common among a range of western and boreal conifers. Huxman *et al.* (2003) observed relatively high carbon uptake rates in subalpine conifer forests (i.e., lodgepole pine, Engelmann spruce and subalpine fir) during periods of depressed soil temperatures in the early growing season.

Additionally, several studies suggest that key mixedwood conifer species are relatively tolerant of near-freezing air temperatures. Studies have shown a relatively flat photosynthetic response to air temperatures between 5 and 15°C for lodgepole pine, subalpine fir and Engelmann spruce (Huxman *et al.* 2003) and between 10 and 25°C for Engelmann spruce (DeLucia and Smith 1987). Man and Lieffers (1997b) found a similar photosynthetic insensitivity for white spruce between 5 and 25°C in the spring and fall, when light is most abundant in understory. During the summer, photosynthesis at saturating irradiance increased with temperature, but there was little difference at lower light levels (e.g., below 150 μmol PAR, which would be common in mixedwood understories at moderate broadleaf densities — see Constabel and Lieffers 1996). Sub-freezing air temperatures during the growing season are known to impede photosynthesis in trees (Öquist 1983, Man and

Lieffers 1997b, Lamontagne *et al.* 1998, Krasowski and Simpson 2001), but again, some evidence suggests that conifers may be less sensitive than deciduous species. At sub-freezing air temperatures, Lamontagne *et al.* (1998) found that black spruce and jack pine (*Pinus banksiana* Lamb.) were less sensitive to photosynthetic inhibition and less prone to irreversible damage than trembling aspen. Combined, these studies suggest a convergence in growth indicators and determinants between a variety of broadleaf and conifer species as soil and air temperatures decrease in mixedwood stands due to increasing environmental harshness.

Such distinct responses to temperature between broadleaf and conifer species could alter the role of edaphic limitations, light limitations and species-specific interactions across the range of conditions in which mixedwood stands occur. Consequently, density-dependent relations in mixedwood stands may be quite condition- or site-specific (Green *In Review*). Edaphic limitations on colder sites would likely change the competitive dynamics between components in mixedwood stands compared to warmer sites, as growth characteristics (and presumably, demand for edaphic resources) among broadleaf and conifer species appear to be more similar on cold sites. In boreal regions, for instance, thick organic layers can limit soil warming (Viereck 1970, Navratil 1996, Landhäusser *et al.* 2003), which may favour conifers once soils thaw in spring. At high stand densities, where competition for edaphic resources is likely greatest, the shift in stand dynamics among broadleaf and conifer species between warm and cold sites should be most evident.

Light limitations on colder sites may also create different competitive dynamics between broadleaf and conifer species in mixedwood stands compared to warmer sites. As average conditions become colder (or otherwise harsher), the leaf-area potential on a site tends to diminish (Waring and Schlesinger 1985, Skre 1993, Constabel and Lieffers 1996, Kabzems and Garcia 2004). A reduction in broadleaf light interception on cold sites should create more favourable light conditions in the understory for less cold-sensitive conifer species. The actual capacity of conifers to exploit better light environments on cold sites may depend upon species-specific factors, as various conifers demonstrate unique adaptation to different environmental stresses that may be associated with increased radiation loads (e.g., water stress; see Man and Lieffers 1997a).

Additionally, the importance of temporal separation in light utilization between deciduous and evergreen habits in mixedwood stands may vary between warm and cold sites. Delays in leaf flush or advances in leaf drop among broadleaf species on cold sites (e.g., at high elevations/latitudes and on north-facing slopes) due to extended periods of depressed air/soil temperatures in the early or late growing season spring (Myking and Heide 1995) may further increase the high-light growth opportunity for conifer species suited to cold conditions.

However, temperature likely interacts with other climate factors (e.g., moisture availability) to determine density-dependent relations (Chen *et al.* 2002). In wetter regions, climate conditions at higher elevations and latitudes may considerably extend the period of snowcover in spring, decreasing the effective high-light period for understory conifers. In drier, regions (e.g., more continental), early snow-free conditions may occur even at higher broadleaf densities, effectively increasing the high-light period for understory conifers once the soils have thawed. Similarly, slope aspect may interact with latitude, elevation, and continentality, diminishing the importance of temporal separation in high latitude/elevation and high snowfall areas where snowcover would tend to persist on northern slope aspects.

Finally, environmental harshness may alter relations between broadleaf and conifer species during the initiation of mixedwood stands. For example, Navratil (1996) found that aspen suckering decreased in cold soils, potentially diminishing the early dominance of broadleaf species in mixed stands in harsher environments.

Conclusions

Given the considerable uncertainty regarding the condition-specific determinants of density-dependent relations and succession in mixedwood stands, the development of spatially explicit management tools is paramount (Chertov *et al.* 2003, Harper and Kabzems 2003). Current free-growing guidelines for mixedwoods in Alberta and British Columbia appear to be too coarse-filtered to predict the relative importance of key growth determinants and environmental factors across the wide range of conditions in which mixedwood stands are found. Future research must clarify the level of spatial detail required to predict optimal broadleaf densities across a diverse landscape, which remains a significant knowledge gap. It is entirely possible that mixedwood stands in close proximity may vary considerably in the competitive relations among broadleaf and conifer components due to large differences in conditions mediated by factors like elevation and slope aspect (Green *In Review*). And, the next generation of stand models and management standards must give attention to such important factors.

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