SECTION 4: Plant Community Management

TABLE OF CONTENTS

4 Plant Community Management 1
Requirements of Plant Species and Interactions 1
4.1 Paradigms, Principles, and Integration 1
4.1.1 Paradigms of Plant Community Management 1
4.1.2 Key Principles in Plant Community Management 3
4.1.3 The Role of Integration in Plant Community Management 3
4.2 Plant Species Interactions 3
4.2.1 Autecology of Boreal Species 5
White Spruce 5
Aspen 6
Balsam Poplar 8
Tall Shrubs - Willow and Alder 8
Medium Shrubs – Cranberry and Honeysuckles 9
Raspberry (Rubus ideaus) 9
Fireweed (Chamerion angustifolium) 10
Reedgrass (Calamagrostis canadensis) 10
4.3 Silvicultural Implications 14
4.3.1 White spruce and aspen 14
4.3.2 Aspen – White Spruce and Reedgrass 23
4.3.3 Aspen – Aspen Intra-specific Competition 25
4.4 Literature Cited 26

4 PLANT COMMUNITY MANAGEMENT

REQUIREMENTS OF PLANT SPECIES AND INTERACTIONS

APPROACH AND STRUCTURE

This section of the Silviculture Guide addresses the interactions of plant species in mixedwood forest stand development. Interactions are discussed from an ecological perspective before management implications are drawn. This approach will help silviculturists more fully understand the biology underlying the interactions and therefore be better able to assess and manage interactions between species toward specific management objectives.

This section begins with a discussion regarding the evolution of vegetation management for silviculture through three paradigms (Reactive, Agro-military, Integrated) to place the approach of this Guide in context. Next, fundamentals of plant species interactions, focusing on crop tree species and critical competing species that limit crop tree establishment and growth, are discussed. The objective is to provide silviculturists with guidance in assessing, interpreting, and managing interactions between plant species over the critical first 10 to 15 years of plant community development.

4.1 PARADIGMS, PRINCIPLES, AND INTEGRATION

Forest stand development is a subset of the larger process of plant community development. Community composition and structure change with time and with changes in the environment. This is an interdependent process where meso-scale environmental change is frequently both a function of, and an enabler to, changes in the plant community.

Mixedwood management of boreal systems offers a wide array of management outcomes. To minimize constraints on the management system, this discussion attempts to embed forest stand development in the broader context of plant community development.

4.1.1 PARADIGMS OF PLANT COMMUNITY MANAGEMENT

Wagner (2005) has described the evolution of forest vegetation management through three historical phases, as follows:

Reactive: The earliest attempts at vegetation management waited until the desired forest stand condition was in jeopardy. At this time, the silviculturist would move to control community development (i.e. reduce competition) to the point where the management objective was no longer threatened. This approach to vegetation management is still frequently encountered in settings where silviculturists manage to regulatory requirements. In these environments, the silviculturist often develops an institutional reactive approach. That is, plant community structure is viewed entirely through a “competition-focused filter” with community assessments and prescriptions timed to meet regulatory requirements in a cost-effective manner.

Agro-military: This is still a common approach wherein silviculturists recognize the potential for plant community conditions that will jeopardize the desired “crop” species and proactively move to prevent that condition from arising. Again, the silviculturist views the plant community from a competition viewpoint focusing on a single desired crop species or, at best, a narrow array of acceptable species. Generally, this approach is effective in achieving outcomes for the crop but does so at considerable cost. These costs can be financial or biological. Biological costs may be a reduction in diversity (particularly when measured using indices that include both species and numbers of individuals), changes in habitat values, and a general simplification of the forest into a stand of trees. The agro-military approach is most commonly encountered on private lands with high potential forest productivity (e.g. exotic antipodean pine plantations, eucalyptus plantations in South America and South Africa, and southeastern short rotation pine production in the United States of America – often referred to as short-rotation intensive culture (SRIC) silviculture).

Integrated: This approach stresses working with the general flow in plant community development and attempting to nudge it in a desired direction. It anticipates changes that will occur in the community and proactively deploys treatments to direct plant community development. This approach has merit in a mixedwood context for several reasons:

- It focuses on plant communities, not stands, and allows the silviculturist to consider and value complexity in stand structure. It provides a platform for both choosing a desired mixedwood composition and working toward achieving it.
- It recognizes changes in the plant community over time and provides the opportunity to emulate “natural” community development, and manage towards a specific community structure and composition.
- It recognizes the role of happenstance (or stochasticity) in plant community development, fostering flexibility in forest management and placing substantial value on operational monitoring.
- It allows for better integration of multiple species with diverse niche requirements into stand management objectives and, hence, into prescriptions.

4.1.2 KEY PRINCIPLES IN PLANT COMMUNITY MANAGEMENT

Wagner (2005) offers 10 principles for successful forest vegetation management. Described from a conifer production standpoint, these principles illustrate five concepts critical to mixedwood reforestation success:

1. Prompt (or timely) implementation of silvicultural treatments is critical to success, regardless of treatment type (site preparation, planting, vegetation management).
2. The "commensal nurse" benefits of mixedwood silviculture may reduce risk of catastrophic climatic or weather effects on white spruce, but they come with a cost in growth reduction.
3. Site preparation is the time when silviculturists have the broadest array of treatment options, and thus it should not be undervalued as an opportunity to explore or use some of these options.
4. Regardless of tree species or origin, herbaceous competition with crop trees may be significant in the early phases of plant community development.
5. Site-dominating species pose a substantial and potentially enduring challenge to less dominant woody species (Wagner considers deciduous tree species and reedgrass to be site dominating species).

4.1.3 THE ROLE OF INTEGRATION IN PLANT COMMUNITY MANAGEMENT

Wagner (2005) does not address the importance of an integrated approach to forest stand establishment. Understanding the unique benefits or strengths of an array of treatments allows the silviculturist to integrate treatments to most effectively "nudge" the plant community at a critical time, thus better assuring success and likely optimizing silviculture costs. Optimization implies that while costs of treatment may not be minimized, risk of failure is reduced, thereby reducing the likelihood of needing to deploy high cost remedial treatments.

4.2 PLANT SPECIES INTERACTIONS

Plants in a community interact (as species and as individuals) in several characteristic manners. Understanding these interactions is critical to identifying the need, opportunity and means to influence plant community development. Although foresters frequently use the following terms to describe interactions between plants (at either the individual or species levels), formal definitions have been drawn from the glossary in "Essentials of Ecology" by Townsend, Begon and Harper (2002):

Competition is "an interaction between two (or more) organisms (or species), in which, for each, the birth and/or growth rates are depressed and/or the death rate increased by the other organisms (or species)."

Commensalism is “an interaction in which one organism (or species) beneficially affects a second organism (or species), but the second has no effect (good or bad) on the first.”

Facilitation is “the influence of one species that enables a second species by changing the conditions encountered.”

Symbiosis is “the intimate living together of two dissimilar organisms in a relationship beneficial to one or both species.”

Amensalism is “an interaction between species in which one species is inhibited and the other is unaffected.”

Tolerance describes the relative capacity of an organism to grow or thrive when subjected to an unfavorable environmental factor. It is defined as “where an unfavorable environmental condition has little or no effect on a species”. Martin and Gower (1999) define and offer specific examples of the tolerance of tree species:

- Tolerant species are able to grow or thrive under competitive conditions; an example of a highly tolerant tree species is hemlock or beech.
- Intolerant species are not able to grow or thrive (or possibly even survive) under competitive conditions – an example of a highly intolerant tree species is aspen or lodgepole pine.
- Intermediate species survive under competitive conditions but thrive under less competitive conditions – an example of an intermediate tolerant tree species is white spruce.

The following terms describe categories of ecological description used to characterize species or communities (Townsend et al. 2002):

- Autecology is “ecology dealing with individual organisms or individual species of organisms.”
- Synecology is “ecology that deals with the structure, development, and distribution of ecological communities.”

Understanding the autecology and synecology of dominant species is critical to successful mixedwood management. With this understanding the silviculturist is well equipped to anticipate and proactively address stages in plant community development that pose silvicultural challenges.

4.2.1 AUTECOLOGY OF BOREAL SPECIES

The following brief descriptions of the autecology of key boreal species provide a foundation for plant community management and foster the integrative approach taken in this manual. The following references underpin the summaries presented here:

For tree species: Burns and Honkala (Technical Coordinators). Silvics of North America. USDA Forest Service Handbook 654. Available from: http//www.na.fs.fed.us/Spfo/pubs/silvics_manual

For most boreal species: Arnup, R.W., Dowsley, B.J., Buse, L.J., and Bell, F.W. 1995. Field Guide to the Autecology of Selected Crop Trees and Competitor Species in Northeastern Ontario. Northeast Science and Technology, Ontario Ministry of Natural Resources, FG-005.

WHITE SPRUCE[1]

White spruce is a long-lived conifer species of intermediate tolerance that is able to enter the plant community at a wide range of times in the plant community assembly cycle. Depending on seed availability, site conditions, and competition, white spruce can behave as anything from a pioneer species through to a late successional species. For example, on mesic sites where a hot summer wildfire destroys the aspen root mat, white spruce and aspen can both act as pioneer species, growing together as seed-origin cohorts, especially if disturbance occurs in a white spruce seed year (see below). Conversely, on sites where a less intense wildfire initiates community development without significant disruption of the aspen root mat, white spruce may be excluded from the overstory of the developing community by aspen competition. Over time, as the overstory of aspen breaks down, white spruce saplings in the understory are released from competition, grow vigorously, and enter the canopy decades after the community-initiating disturbance.

White spruce reproduces from seed, producing small quantities of seed for several years, followed by abundant seed crops for typically one or two years. Seeds are about mid-size (for the boreal forest) and winged. Seeds can be dispersed over great distances by wind, especially skimming along the surface of crusted snow (seed drop occurs in late autumn and continues throughout the winter) but the vast majority of seeds fall within a few hundred meters of the parent tree. White spruce is not an obligate outcrossing species (it can self-pollinate) but it

[1] Material on white spruce is based on Nienstaedt, H., and Zasada, J.C. 1990.

generally cross-pollinates. There is some evidence that white spruce can also reproduce vegetatively by layering.

Site characteristics favoring white spruce are mesic to moist moisture regime. medium to rich nutrient regime, and moderately fine (silt) soil textures. White spruce will tolerate only moderate drought and therefore is seldom found on sites susceptible to periodic, sustained drought (coarse soils or exposed outcrops). Pure white spruce stands are frequently found on rich, alluvial sites like the floodplains of large rivers.

White spruce's intermediate tolerance means it tends to survive under competition and can prosper in mixed species stands. This may be due to white spruce cycling nutrients more slowly than pioneer species and hence benefiting from increased nutrient availability when in association with pioneer species. Hangs et al. (2002) were unable to demonstrate that the release of nutrients from decomposing aspen foliage resulted in increased nutrient availability to white spruce. Conversely, Carmosini et al. (2003) found an increase in nitrogen mineralization from fallen aspen foliage following harvest. Furthermore, other tree or tall shrub species provide white spruce seedlings shelter from late season frost (new growth of white spruce flushes very early in the spring), shelter from warm winter winds, and from being struck by an endemic insect pest (white pine weevil, *Pissodes strobi*). According to Taylor et al. (1996) the mechanism of this effect is overstory shading masking host tree silhouettes at the time of beetle flight.

ASPEN[2]

Understanding aspen autecology is critical to successful mixedwood management. Aspen is a crop species and one of the two most successful inundatory invaders (abundant and aggressive post-disturbance regeneration) species in the boreal forest. Aspen's success as an aggressive invader means it functions as a strong competitor with most other woody species during the early dynamic stages of plant community development. The need to understand aspen autecology is reinforced by current aspen silvicultural regimes relying on clonal propagation and minimal intervention for success. To oversimplify, silvicultural interventions are far more efficient in reducing aspen abundance than they are in enhancing aspen abundance or distribution.

[2] Material on aspen is based on Perala 1990.

As an intolerant, inundatory, invading pioneer tree species, aspen tends to aggressively colonize a wide array of disturbed sites, unless the disturbance removed or destroyed the aspen root mat.

Aspen reproduces clonally (from root suckers or basal sprouts) and from seed. If a site is drastically disturbed (intense wildfire or deep soil disruption), aspen invasion is likely to be from seed; if less drastically disturbed, the site will likely be invaded vegetatively by root suckers arising from aspen on the site prior to disturbance. Aspen are dioecious (individual trees are either male or female) therefore only female clones produce seed. Aspen produce an abundant seed crop each spring except in extremely dry years. Maini and Horton (1966) determined that a single female aspen tree produced 7 million seeds. Aspen seed is highly viable; however, germinants require a minimum of two weeks to a month of warm, moist conditions before they are able to survive drought. This is due to slow growth of the main root of aspen seedlings, forcing germinants to depend on a ring of fine downy hair-like roots for water uptake for several days to two weeks. The narrow environmental window for successful aspen establishment from seed has often led to the importance of seed dispersal in aspen's role as an invader being overlooked. Aspen seed is much smaller than conifer seed and is carried in white, downy "fuzz" resulting in movement by wind and/or water over great distances.

The most common invasion strategy of aspen is by root suckering. Aspen roots bear large numbers of buds capable of forming individual stems. If there is loss of apical dominance (the stem attached to the root mass is cut or broken off) and soil temperatures increase, these buds are triggered and a massive emergence of new stems (called suckers) occurs. Reduced levels of suckering occur if aspen roots are exposed to increased temperatures in the soil without apical dominance being disturbed, as might occur if an area were logged for conifers and the mature aspen was left standing. In effect, aspen trees are super-organisms capable of generating large numbers of stems from existing root systems to rapidly occupy the aboveground portion of disturbed sites. The genetic make-up of these stems is identical; such large aspen clumps are clones. Furthermore, even if root buds are not stimulated (and suckering has not occurred), aspen root occupancy of a site with even moderate densities of mature aspen will be very high.

Thus, aspen invasion of a previously uncolonized site may be a two-generation process – the first generation invading from seed, thereby gaining a foothold on the site, and the second generation effecting site dominance following less drastic disturbance.

These complementary reproductive strategies make aspen an adaptable and successful invader after a wide range of disturbances. Suckers grow and develop much more quickly than seedlings (aspen or conifer), due to their use of an existing, well-developed root system.

In order to thrive, aspen requires a mesic moisture regime and it does best on medium to rich sites. Sustained or frequent drought conditions will exclude aspen from a site. Aspen site regime requirements are similar to those of white spruce, although white spruce will tolerate wetter sites than aspen.

BALSAM POPLAR[3]

Balsam poplar is a pioneer species on the sites to which it is best adapted, and slightly behind the earliest pioneer species such as aspen and lodgepole pine. An intolerant species, balsam poplar is somewhat more shade tolerant than aspen (or lodgepole pine), and is best suited to moist sites (sub-hygric to sub-hydric). Balsam poplar is often an invader of secondary successional sites.

Balsam poplar has a wide array of reproductive strategies. It produces an abundant, highly viable seed rain very similar to that of aspen. It can reproduce from basal sprouts if cut or broken off. As well, buried stems and branches can produce roots and act as cuttings. Once established, balsam poplar can reproduce from root suckers that, while less vigorous than those of aspen, can quickly achieve site dominance.

Balsam poplar is most commonly found on moist to hygric sites, showing its best growth on rich, alluvial, sub-hygric sites. While balsam poplar is able to tolerate medium to slightly poor nutrient regimes, it does best on medium-rich to rich sites.

TALL SHRUBS - WILLOW AND ALDER[4]

Alder and willow (35 species of which occur in Alberta) are found on a wide array of sites. Both reproduce from seed and basal sprouts (if stem is broken or cut off). Dense, almost pure stands of alder (*Alnus tenufolia*) or willow are often found in riparian or hygric to sub-hydric habitats.

Conversely, other willow species and alder (*Alnus viridis*) frequently occur on xeric sites where poor nutrient regimes exclude most other shrub species; on these sites, they occur in association with lodgepole pine. Both alder and willow can invade recently burned areas very aggressively from seed. Minor disturbance or light browsing can stimulate basal sprouting of these species, as can mechanical damage or cutting.

[3] Material on balsam poplar taken from Zasada and Phipps (1990)
[4] Material taken from Arnup *et al.* (1995)

MEDIUM SHRUBS – CRANBERRY AND HONEYSUCKLES[5]

Cranberry and honeysuckle shrub species are seed bankers producing numerous to abundant hard seeds annually, which can persist in soil for several years to several decades. Seed production is regulated by climatic conditions. These species produce their seed in or as an edible structure.

This results in wide dispersal of the seed by animal vectors. Following a hot fire (that strips away the insulating organic mat on the soil surface) the banked seeds germinate and quickly capture the site. Reduced soil disruption associated with logging results in less dramatic seed bank response. However, if mechanical site preparation is used, seed bank induction (i.e. germination induced by favorable conditions arising from site preparation) will result. Thus, the presence of these species in the understory prior to harvest indicates a likelihood of them being present after harvest. Abundance of these species after harvest will depend on the level of soil disruption associated with harvest and with site preparation for planting.

Bracted honeysuckle (*Lonicera involucrata*) and beaked hazel (*Corylus cornuta*) tend to be found on sub-hygric sites, while cranberry (*Viburnum* sp.) is found on mesic sites. Tolerance varies between these species but all are able to survive (or thrive) in the open environment that follows clearcutting.

RASPBERRY (*RUBUS IDEAUS*)

Raspberry is a deciduous shrub that produces biennial woody stems. A seed banking species, raspberry can produce up to 26,000 seeds/m2 over four years under ideal growing conditions, and under a forest canopy it will produce >75 seeds/m2 per year with 60 percent constancy. These seeds can persist in soil for more than 50 years (Oleskevich et al. 1996). Soil disturbance and increases in soil surface temperature associated with harvesting stimulate germination of the raspberry seed bank which, though unlikely to pose competition to deciduous crop species, can pose substantial competition to white spruce seedlings or germinants. Raspberry can also reproduce by vegetative means allowing it to quickly expand its coverage in openings and disturbed sites.

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[5] Material taken from Arnup *et al.* (1995)

FIREWEED (*CHAMERION ANGUSTIFOLIUM*)

Fireweed is a perennial forb that spreads by seed and expands site occupancy through root reproduction from pseudo-rhizomes. Some taxonomists identify two subspecies of fireweed depending on habitat and size. Only the shorter sub-species occur in Alberta. As a pioneer species fireweed tolerates a wide range of climatic, soil, and altitudinal conditions. It is most commonly found on sandy loam to loamy soil textures. Fireweed does not compete well with aspen or reedgrass but frequently invades reforested areas following herbicide use to control one or both of these species. Fireweed can offer white spruce seedlings substantial competition.

REEDGRASS (*CALAMAGROSTIS CANADENSIS*)

Reedgrass is a long-lived perennial grass found in late successional plant communities. It will tolerate moisture regimes from mesic to moist but prefers sub-hygric. Rich sites are most favorable to reedgrass; however, it will tolerate medium nutrient regimes. Reproduction is by seed and rhizomes (underground stems carrying vegetative reproductive buds). Reedgrass produces an annual crop of abundant, very small seed. Invasion of late successional communities is via seed into small openings (serules) of mineral soil created by blowdown on older or dead trees. Reedgrass requires moist mineral soil for germination. However, once established, reedgrass' shade tolerance allows it to survive and develop a rhizome mat at the duff-mineral soil interface. Unlike raspberry and bracted honeysuckle, bolting of rhizome buds causes reedgrass invasion following logging. Reedgrass has been called a disclimax species (Collins 2001), "a relatively stable ecological community often including kinds of organisms foreign to the region and displacing the climax because of disturbance, especially by man" (Merriam-Webster 2006). This post-harvest disclimax behavior of reedgrass can make it a particularly pernicious invader of recently harvested moist, rich sites. Mechanical site preparation treatments that break-up, mix or stir the organic-mineral soil interface exacerbate reedgrass problems by breaking up rhizomes thereby stimulating sprouting.

As part of their review of reedgrass autecology and synecology, Lieffers et al. (1993) offer an interesting conceptual model that addresses four successional stages that are important to understanding the ecology of reedgrass. Figure 4.1 is adapted from their work, and presents the seral stages in a more linear framework, while Figure 4.2 shows the same process amended to accommodate the disclimax hypothesis.

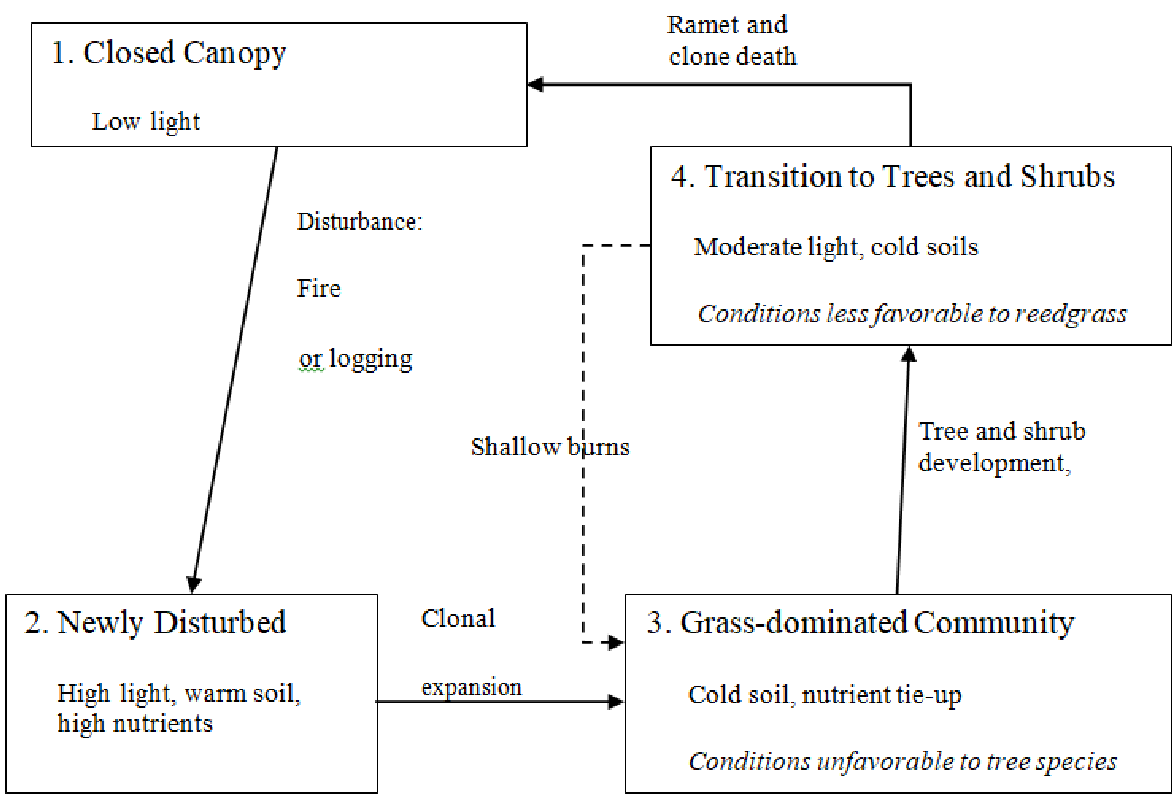

Figure 4.1. Successional stages for reedgrass in boreal mixedwood forests (after Lieffers et al. 1993).

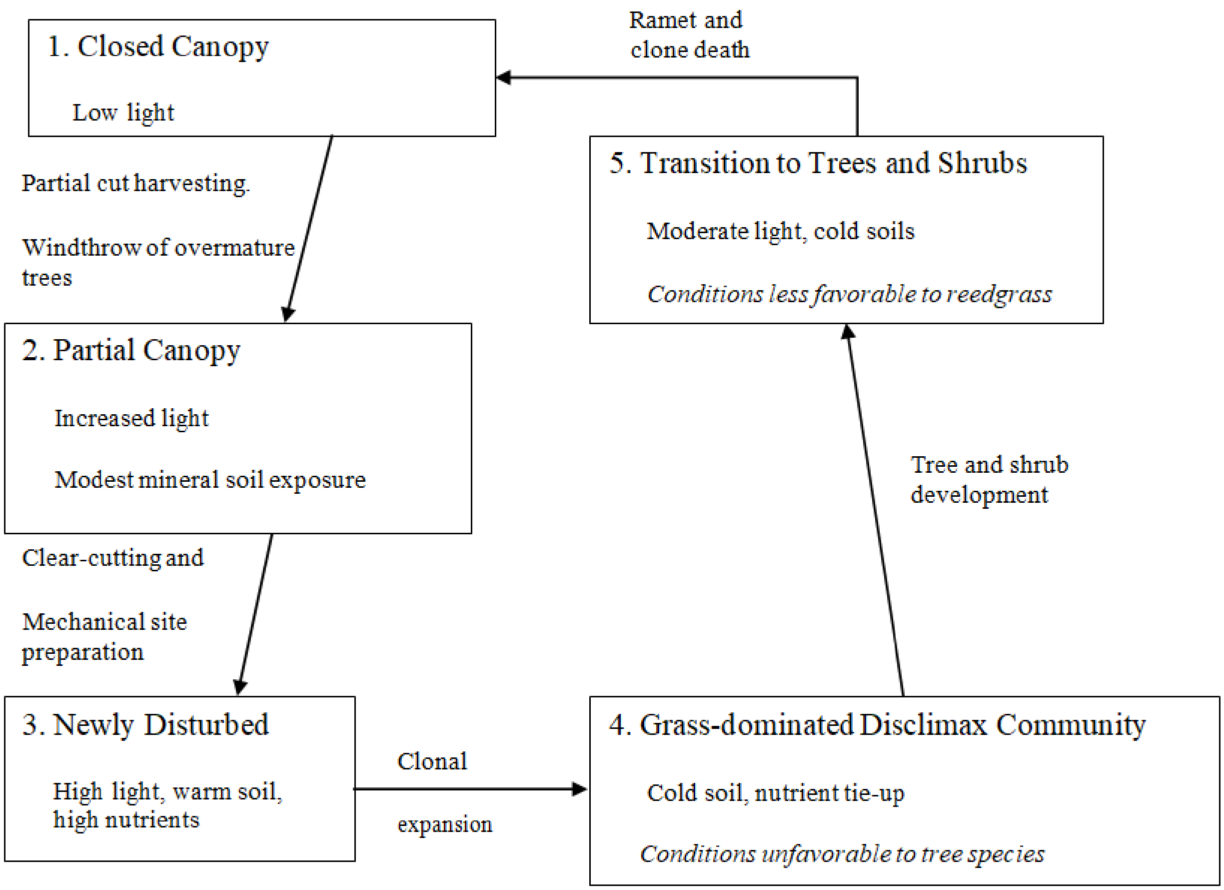

Figure 4.2. Successional stages for reedgrass in the boreal mixedwood forest under the disclimax hypothesis. (Figure 1 from Lieffers et al. (1993), adapted to reflect the "disclimax" hypothesis).

Table 4.1. Autoecology of key boreal mixedwood species

Autecological Factor	White spruce	Black spruce	Aspen	Balsam poplar	Alder	Willow	Raspberry	Reedgrass
Sere	Mid	Plastic	Pioneer	Pioneer	Pioneer	Pioneer to late	Plastic	Late
Tolerance	Mid.	Int.	Int.	Int.	Int.	Varies with species	Plastic	Mid.
Reproduction	Seed	Seed Layer	Suckers Sprouts Seed	Sprouts Seeds Suckers Cuttings	Seed Sprouts	Seed Seed bank Sprouts	Seed Seed bank Suckers	Rhizomes Seed
Optimal moisture regime	Mesic to sub-hygric	Mesic to sub-hydric	Mesic	Moist to sub-hygric	Submesic to hygric	Variable	Moist to hygric	Mesic to sub-hygric
Drought tolerance	Medium	Low	Low	Low	High	Variable	High	Low to medium
Site richness	Medium to rich	Low to medium	Medium to rich	Rich to medium	Medium to rich	Medium to rich	Low to medium	Medium to rich
Response to:								
Wildfire	Loss of site	Invasion	Inundatory invasion	Invasion by seed	Inundatory invasion	Loss of site	Loss of site	Loss of site
Ground fire	Invasion	Site dominance	Loss of site or invasion	Loss of site	Re-invasion	Loss of site	Loss of site	Invasion

4.3 SILVICULTURAL IMPLICATIONS

The interactions discussed below are generalized to major interactions and the impacts of harvesting, reforestation, and exclusion of fire.

4.3.1 WHITE SPRUCE AND ASPEN

Aspen can limit white spruce growth and survival (Comeau et al. 2006). Though white spruce is an intermediate tolerant species capable of surviving substantial competition, growth is reduced in the presence of competition.

White spruce and aspen perform best on similar site types (mesic, medium to rich) leading to direct competition. This interaction is exacerbated by rapid aspen domination of cutovers through reproduction by suckering. Newton (2002 pers. Comm.) suggests mixed species tree communities perform best when species do not share similar root space and have similar rates of height growth. This does not describe the relationship between white spruce and aspen, which does not meet either criterion. The temporal shift in dominance associated with most boreal mixedwood stands suggests that aspen and white spruce often function as temporal mixtures where site dominance is traded between species over time.

More recently, Pitt et al. (2015) examined the interaction of reedgrass, aspen and white spruce at the time of forest establishment, clearly demonstrating the equivocal relationship between white spruce and aspen as one of facilitation at the cost of growth loss due to competition.

Several facilitative commensal interactions characterize the relationship between young seedling (or seed origin) white spruce and aspen, including:

- Aspen foliage cycles primary nutrients very efficiently while white spruce foliage cycles nutrients (nitrogen, phosphorus, potassium, and micronutrients) slowly. Aspen takes up nutrients and drops them annually with leaf fall, thus making the nutrients released from the decomposing foliage readily available to white spruce. In this way, aspen may render nutrients more available to white spruce (Arnup et al. 1995). Hangs et al. (2002) could not find quantitative evidence of this effect. Conversely, Carmosini et al. (2003) found an increase in nitrogen mineralization from fallen aspen foliage following harvest. This may be of more benefit to white spruce on nutrient–poor sites.

- White spruce flushes early in the growing season, making it vulnerable to late spring or early summer frost. If it is part of an intimate mixture with aspen (with emerging leaves), the seedling is less likely to be damaged by frost due to the emerging aspen canopy moving the boundary layer of freezing air above the white spruce seedling (Comeau et al. 2006).
- Aspen cover also traps snow and moves the temperature boundary layer above the height of white spruce seedlings when warm subsiding winds (chinooks) result in winter temperatures substantially above freezing (ibid.). If relatively young white spruce seedlings (less than three growing seasons after planting) are subject to above freezing temperatures while their roots remain frozen, they will quickly deplete all water in their foliage through transpiration and become desiccated (McDonald 1996 pers. Comm.) See the Winter Injury Tool for a more thorough discussion of this phenomenon. Depending on the temperature and duration of exposure, desiccation may result in injury (ranging from slight to severe) or mortality.
- Aspen cover reduces the likelihood of white spruce being struck by the white pine weevil (*Pissoides strobi*) (Comeau et al. 2006). This insect pest endemic to Alberta's boreal forest flies above the canopy seeking spruce (white, black, Engelmann) seedlings or saplings. Upon finding young trees of these species, the female weevil descends and lays an egg at the base of the current terminal leader. When the egg hatches, the weevil larva mines the cambium of the current leader causing loss of both growth and apical dominance. Spruce seedlings and saplings in an aspen dominated canopy are less easily identified by weevils and therefore less subject to weevil strike. According to Taylor et al. (1996), the mechanism of this effect is overstory shading masking host tree silhouettes at the time of beetle flight.

The Aspen White Spruce Facilitation and Competition Tool summarizes these interactions against a temporal scale. This is a "thought" tool intended to help the practitioner identify and consider facilitative and competitive interactions between aspen and white spruce over time. The temporal time scale in the tool is nominal and will vary with risk factors inherent to the site, aspen density, and condition/performance of both aspen and white spruce over time.

The relationship between aspen and white spruce also involves direct competition for light, moisture, nutrients, and possibly root space. Of these, competition for light has been examined the most thoroughly. Lieffers et al. (1998) found that at 40 percent of full sunlight, white spruce height growth was not reduced compared to full sunlight. Comeau et al. (1993) suggest a light level of 66 percent of full sunlight as a "reasonably attainable" level of light for white spruce growth. They suggest that white spruce volume is reduced by any competition for light; however, the management effort required to manage aspen densities to a level where full sunlight was available to white spruce would be too high. The volume gain associated with full sunlight over 66 percent of available light is also substantially less than the gain associated with making 66 percent light available versus less than 50 percent.

In effect, the relationship between these species is complex. The facilitative benefits white spruce derives from association with aspen come with a cost in reduced growth due to the competitive aspects of this same relationship. In some cases, growth losses and mortality due to winter injury or grass competition may exceed those which would occur under an intact young aspen canopy. The complexity of the interaction between white spruce and aspen is exacerbated by the site requirements of these species. White spruce will survive and reach commercial size on sites wetter than aspen will tolerate, while aspen will survive on sites drier than white spruce. However, both species attain maximum growth and productivity on modal sites as described by the edatopic grid (See Edatope(s) 4, 5, 16; Figure(s) 4.3, 4.4, 4.5).

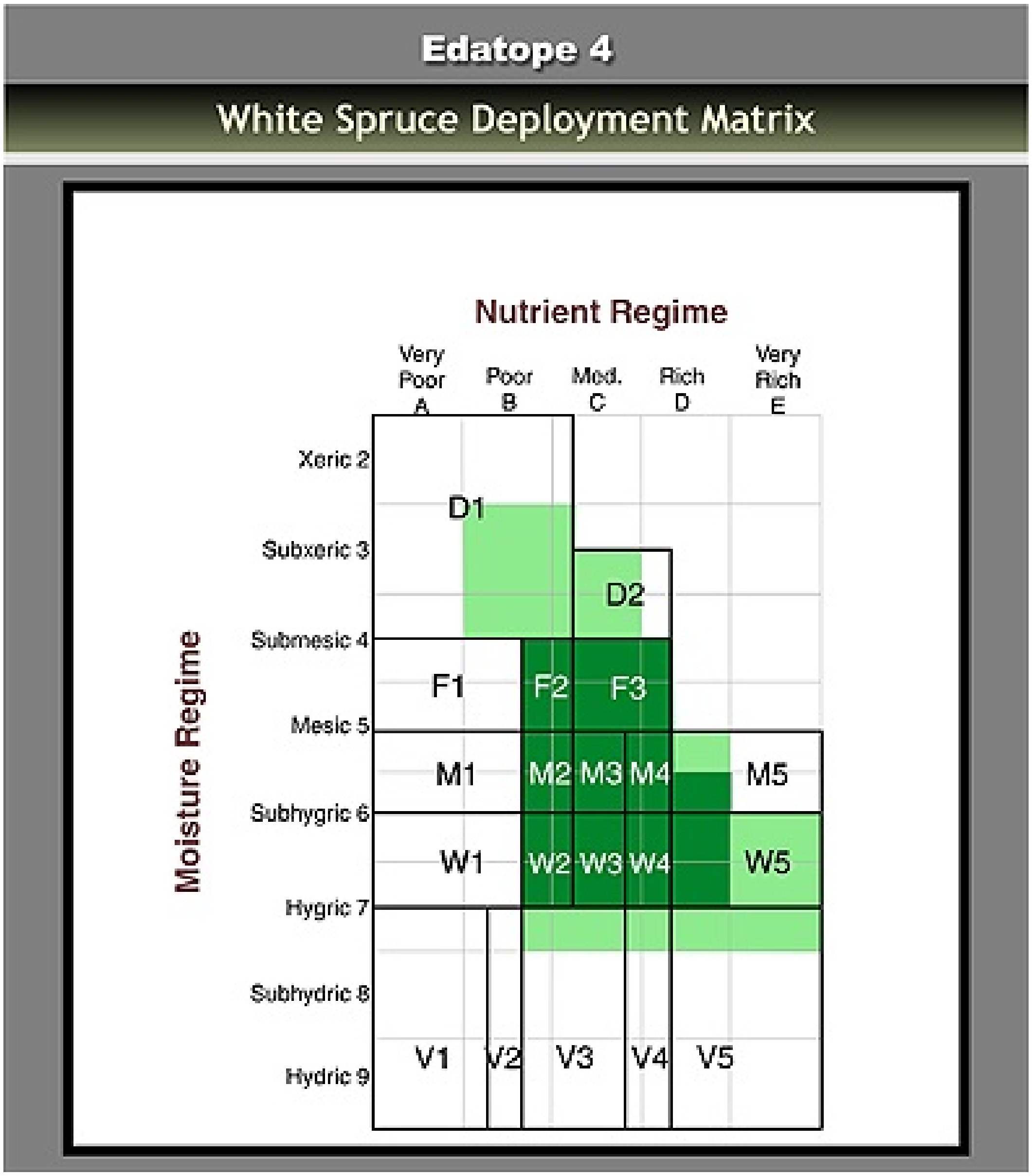

Figure 4.3. Edatope indicating deployment considerations for white spruce. Darker shading indicates preferred deployment position.

This relationship is particularly complex during the earliest phases of plant community development as aspen's use of incident light tends to reach maximum levels sometime around age 20, at which time light levels below the aspen canopy are at minimum (Lieffers 2005). This condition is popularly referred to as "the light bottleneck". That is, the point at which light is least available to white spruce under the young aspen canopy, during which white spruce growth is most reduced, and risk of competition-induced mortality is quite high. Prior to this stage of community development white spruce seedlings are most at risk of winter desiccation and frost damage. Comeau (2007 pers. Comm.) suggested that for small seedlings, the light bottleneck actually begins at about age 2 or 3 due to combined effects of aspen, herbs and grasses. Light levels below 10% can be encountered in the second growing season after clearcutting as a result of effects of both aspen (light levels of about 20 to 40%) and herbaceous vegetation.

The relationship between white spruce and aspen becomes less equivocal when seedlings become saplings as aspen rubbing or whipping significantly damages white spruce saplings.

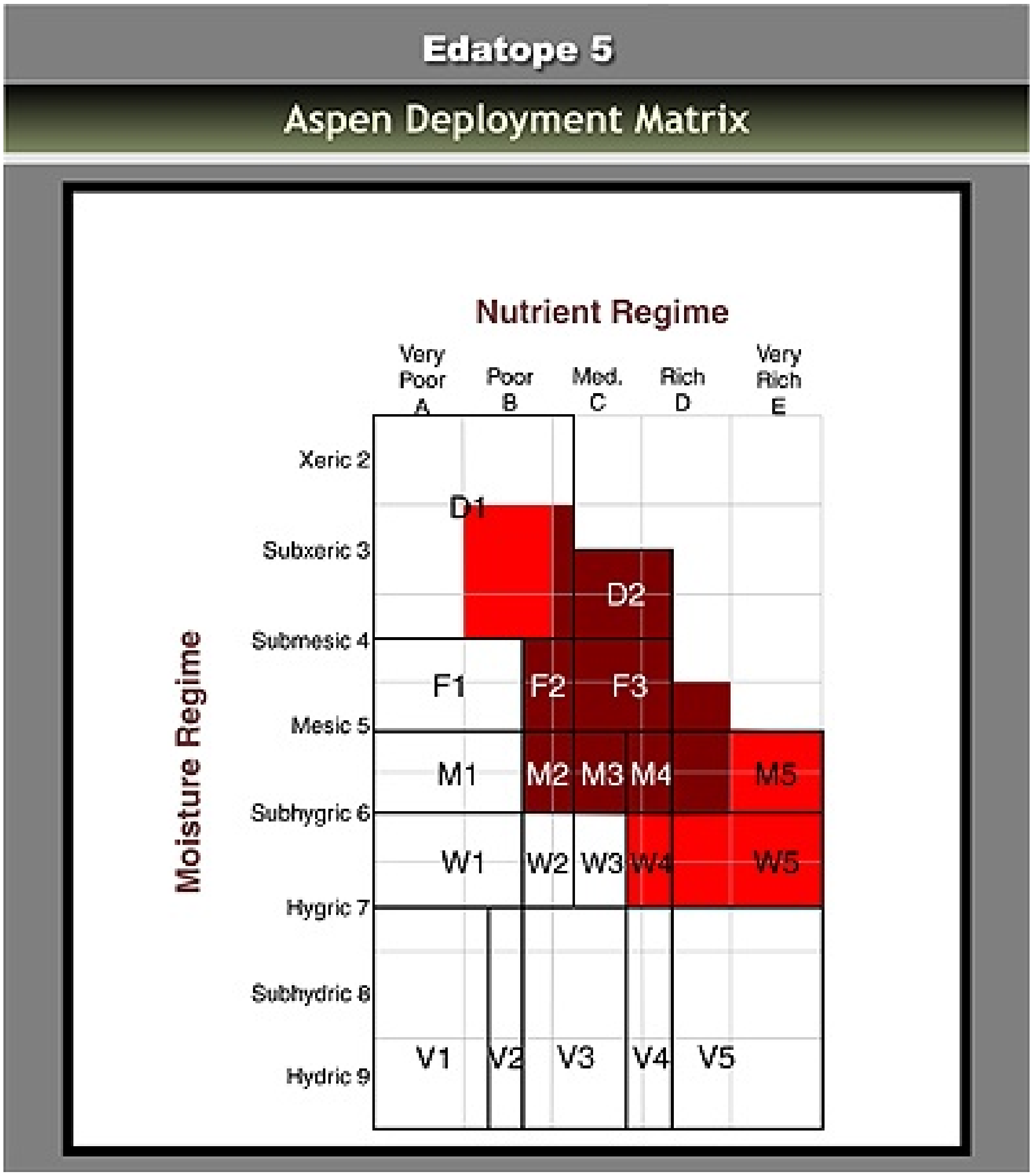

Figure 4.4. Edatope indicating deployment considerations for aspen. Darker shading indicates preferred deployment position.

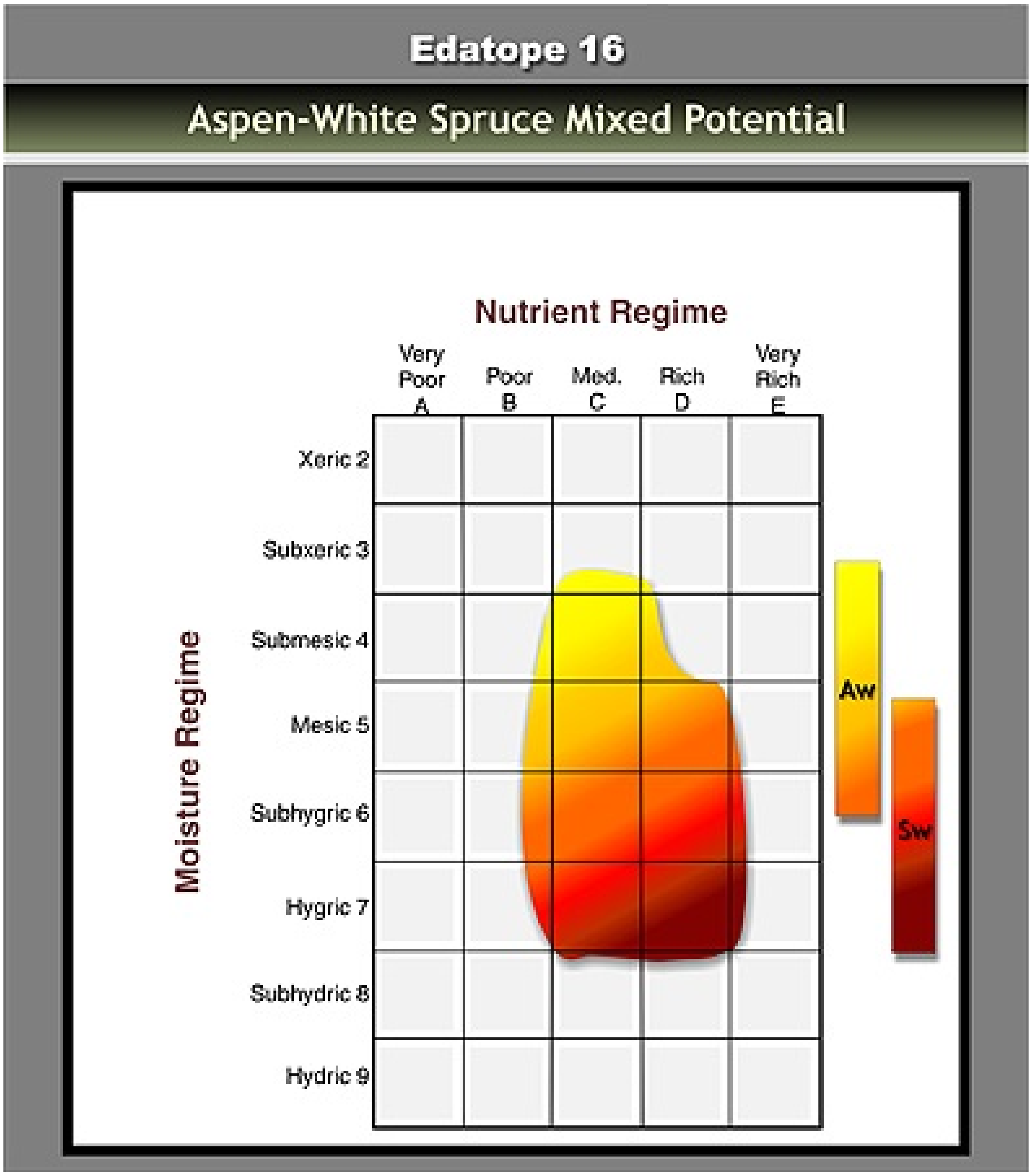

Figure 4.5. Edatope indicating mixed deployment and or management opportunity for white spruce and aspen.

Silviculturists need to be aware that, when prescribing management regimes to achieve specific light levels, thought should be given to recovery of the plant community. That is, regardless of treatment method, the plant community will "rebound" from treatment resulting in a reduction in light level within a few years of treatment. Later sections (Section 7) discuss treatment durability. the silviculturist should consider durability when making prescriptions to ensure that the desired light levels are maintained long enough to provide the "nudge" necessary to shift the plant community in the desired direction.

This relationship is also challenged by the essentially subtractive relationship between most silvicultural treatments and aspen. That is, current aspen silviculture relies on aspen root regeneration – ensuring harvesting activities do not jeopardize aspen suckering potential, then relying on abundant sucker regeneration to establish the deciduous component of the new plant community.

Given the complex interaction of these species, it may be prudent to manage for mixtures of aspen and spruce using a risk reduction strategy. This will depend on the level of risk inherent to the area being managed and on other management objectives. Vegetation management techniques are available to release individual white spruce seedlings/saplings from aspen competition while maintaining a mixture of both species. This is of particular importance when managing for both white spruce and aspen crops on the same operational management unit in an intimate mixture.

The following tables (Table 4.2a and Table 4.2b) summarize the facilitative and competitive interactions discussed. The tables are derived from a tool developed for the first version of the mixedwood guide and include comments from the expert review panel members. The temporal scale of the interactions presented in the tables is nominal and will vary with risk factors inherent to the site, aspen density, and condition/performance of aspen and white spruce over time.

Table 4.2a. Aspen-white spruce facilitative interactions.

Temporal Interval	Facilitative Interaction	Comment
T5 – Treatment Community Initiation	Shade from sunscald	Sunscald potential is highest on south facing dry slopes. This equates to areas of high evapotranspiration potential.
	Inhibition of reedgrass[1.]	Aspen cover limits reedgrass emergence on mesic and slightly moister sites.
	Reduce risk of winter desiccation	Aspen reduces wind exposure both directly and through snow trapping.
	Reduce risk of late spring frost damage	Aspen shifts the thermal boundary layer for frost events up from young white spruce seedlings.
T6-Treatment to 4 years Community Establishment	Inhibition of reedgrass[2.]	Aspen cover limits reedgrass expansion on mesic and slightly moister sites.
	Reduce risk of late spring frost damage	Aspen shifts the thermal boundary layer for frost events up from young white spruce seedlings.
	Reduce risk of winter desiccation	Aspen reduces wind exposure both directly and through snow trapping.
T7 – 4 to 12 years Composition to Performance	Inhibition of reedgrass[2.]	Aspen cover limits reedgrass dominance on mesic and slightly moister sites.
	Reduce risk of late spring frost damage	Aspen shifts the thermal boundary layer for frost events up from young white spruce seedlings.
	Reduce risk of white pine weevil strike	White pine weevil identifies target saplings visually from above – therefore overtopped trees are less likely to be struck.

[1] Particularly important in the absence of site adjustment treatments and on mesic to sub-hygric sites

[2] Particularly important when stand tending with herbicides will not be employed.

Table4.2b. Aspen-white spruce competitive interactions.

Temporal Interval	Competitive Interactions	Comment
T5 – Treatment Community Initiation	Competition for light	Young white spruce seedlings have limited root egress from planning plugs – insulating them from competition for moisture and providing them nutrients from the plug.
	Smothering of germinated seed	Germinated seed is at risk of smothering for the first year following germination.
T6-Treatment to 4 years Community Establishment	Competition for light	Aspen suckers will significantly overtop white spruce seedlings.
	Competition for moisture	As white spruce roots emerge from the planting plug they must directly compete with other vegetation for moisture.
	Cover for herbivores.	Aspen provides hiding cover for both girdling and browsing rodents from both terrestrial and aerial predators.
T7 – 4 to 12 years Composition and Performance	Competition for light	Aspen suckers will significantly overtop white spruce seedlings.
	Competition for moisture	At this point white spruce and aspen share the same rooting zone so compete directly for all three critical life factors – light, moisture and nutrients.
	Competition for nutrients	At this point white spruce and aspen share the same rooting zone so compete directly for all three critical life factors – light, moisture and nutrients.
	Mechanical damage	As white spruce saplings move into the mid-crown zone of the aspen canopy in lightly tended or untended stands they are susceptible to whipping damage by aspen stems moving in the wind.
	Cover for herbivores.	Aspen provides hiding cover for both girdling and browsing rodents from both terrestrial and aerial predators.

4.3.2 ASPEN – WHITE SPRUCE AND REEDGRASS

The disclimax autecology of reedgrass following harvesting can be characterized as a massive invasion of harvested sites by reedgrass due to reedgrass' invasive building potential via rhizome development in aging stands. High levels of reedgrass in pre-harvest stands result in reedgrass invasion of harvested areas from rhizomes, not from seed. Thus, reedgrass poses a challenge to establishment of both aspen and white spruce on sites to which it is best adapted (Landhäusser and Lieffers 1997, Newton and Cole 1999, Collins 2001).

Reedgrass causes physical damage and changes in microclimate, and increasing small rodent predation of seedlings and suckers. Physical damage occurs in early winter when cured reedgrass stems bridge together under snow loading, resulting in white spruce seedlings being flattened and literally crushed by the snow pack. This phenomenon, called “vegetation press” or “snow press”, is the major limitation to white spruce seedlings in the northwestern areas of the boreal forest (Comeau 1996, Day 1994 pers. Comm.). In addition, decaying reedgrass stems form a grass thatch at the soil surface, which reduces soil temperature by two to four degrees © during the growing season. Reduced soil temperature effectively shortens the growing season due to delayed soil thawing and earlier soil freezing. The delay in soil thawing is particularly limiting to white spruce survival and growth. Reductions in soil temperature caused by reedgrass thatch also reduce aspen suckering. Small mammals (mice and voles) eat reedgrass seed and shelter in reedgrass thatch; in the winter when supplies of grass seed diminish they girdle seedlings and suckers by eating bark.

Lieffers et al. (1993) suggest reedgrass root and rhizome structure (which comprise 85 percent of reedgrass total biomass) may pose physical limitations on white spruce and aspen root occupancy in the soil. This is of particular concern given the shallow nature of many boreal soils.

Man et al 2008 described some of the mechanisms of competition between aspen, reedgrass and spruce. They were able to ascertain that in an untreated recently reforested area reedgrass posed a competitive challenge to both aspen and spruce. While aspen is competitive with spruce it is less so than reedgrass. In fact, they demonstrated that selective removal of the aspen resulted in significant increase in reedgrass competitive effect on spruce. In large part, this was due to the effectiveness of reedgrass in capturing soil moisture and nutrients. From this work, there did not appear to be an upper limit on nitrogen use by reedgrass; meaning as more nitrogen becomes available reedgrass simply grows more rapidly and uses whatever nitrogen is available (luxury use).

Management of reedgrass must control and prevent the interaction of vegetation press and soil temperature reduction. When planting spruce, the easiest solution is to select white spruce seedlings sufficiently sturdy to resist vegetation press and sufficiently tall to stand up through the reedgrass thatch. This strategy is a successful first step but it does not address soil temperature reduction caused by the reedgrass thatch. This must be addressed by using raised micro-site planting spots. Finally, timely tending allows coniferous seedlings a longer interval (approximately two to three more growing seasons) without direct interaction with reedgrass.

Reedgrass management is the most striking boreal example of the need for integration of vegetation management treatments. Unfortunately, the tending techniques that adequately control reedgrass after seedling establishment drastically reduce aspen (and other deciduous tree species’) density in treated areas. Thus, managing for both white spruce and aspen in areas with heavy reedgrass competition is daunting. In particular management for intimate mixtures of aspen and spruce in the face of reedgrass composition will likely require either selective site preparation or selective tending, and in both cases, will likely require use an herbicide since only herbicide treatments are effective in providing long-term control of reedgrass root systems.

4.3.3 ASPEN – ASPEN INTRA-SPECIFIC COMPETITION

Aspen relies on large numbers of suckers or (very rarely) seedlings to rapidly colonize secondary disturbances. Aspen densities approaching (or even exceeding) 100,000 stems ha-1 are frequently encountered when vigorous, thrifty aspen are harvested on favorable sites. Clearly mature aspen and mixedwood stands carry far fewer stems. Perala (1990) indicates self-thinning in aspen begins at age 7 to 10 years and rises to a peak near age 15 (similar to the light bottleneck identified by Lieffers (2005)) at which time self-thinning diminishes quickly.

Operational observations by the author do not dispute this but suggest that self-thinning may not be the only mechanism of aspen density reduction. The following mechanisms are suggested as other factors in the "Natural Reduction of Aspen Density":

- Browsing by large ungulates, particularly moose (*Alces alces*), is likely to pre-dispose some individuals to other mechanisms of density reduction.
- Insect outbreaks of forest tent caterpillar (*Malacosma distria*), large aspen tortrix (*Choristoneura conflictana*), and bruce spanworm (*Operophtera bruceata*), if repeated over a two or three-year period, can reduce density of young aspen either directly or through physical damage by bears stripping the insect larvae from the young trees.
- Disease attack, in particular shepherd's crook (*Venturia macularis*), can reduce aspen thrift during wet years, substantially increasing the susceptibility of young trees to other mechanisms of thinning.

It is suggested that these factors likely contribute to the phenomenon labeled self-thinning. That is, pre-disposition by an external stressor may impose a stochastic component on self-thinning of aspen that results in different rates (and possibly extents) of aspen density changes. This, in turn, would have implications for both aspen and spruce components of mixedwood stands.

Unfortunately, quantitative guidance on these factors cannot be offered, but the silviculturist should consider these factors, especially previous outbreaks of insects or disease, when considering compositional objectives.

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