INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

ProQuest Information and Learning
300 North Zeeb Road, Ann Arbor, MI 48106-1346 USA
800-521-0600

UMI®

University of Alberta

Is growth of trembling aspen affected by white spruce understories in Alberta's boreal mixedwood forests?

by

Daniel N. MacPherson

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

Department of Renewable Resources

Edmonton, Alberta

Fall 2000

0-612-59839-X

University of Alberta

Library Release Form

Name of Author: Daniel Neil MacPherson

Title of Thesis: Is growth of trembling aspen affected by white spruce under-stories in Alberta's boreal mixedwood forest?

Degree: Masters of Science

Year this Degree Granted: 2000

AUGUST 15, 2000

7219- 91st Avenue,
Edmonton
Alberta
T6B 0R7

Abstract

Mixedwood management of white spruce (*Picea glauca (*Moench) Voss) and trembling aspen (*Populus tremuloides* Michx.) is hypothesized to have benefits over the management of either species in pure stands. Experimental plantings of aspen and spruce have been made to test this hypothesis, but it will be several decades before the results are known. Therefore a survey of natural stands was undertaken to determine the productivity of pure aspen and mixtures of spruce and aspen. A total of 29 aspen stands were surveyed, each having areas with spruce understories, as well as areas without such an understory. In each stand, three plots in the pure aspen portion of the stand were paired with three corresponding plots having a spruce understory. Standing biomass and periodic annual increment (PAI) over the last 5 years were determined for both the aspen overstory and the spruce understory. Plots with white spruce and aspen carried 23.2% greater basal area, 10% more total biomass and 12.5% more PAI than pure aspen plots. Additionally, biomass, basal area and PAI of aspen were less in the mixed aspen plots than in the pure plots, with the reduction in aspen productivity being only weakly correlated with the amount of spruce. In conclusion, mixtures of aspen and spruce had greater total productivity but less aspen productivity than pure aspen plots.

University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled Is growth of trembling aspen affected by white spruce understories in Alberta's boreal mixedwood forests? Submitted by Daniel Neil MacPherson in partial fulfillment of the requirements for the degree Master of Science.

Victor Lieffers

Dr V. J. Lieffers

Dr P. Blenis

E. W. Bork

Dr. E. Bork

Dr. P. Comeau

Acknowledgments

I would like to acknowledge the invaluable guidance of Dr. Victor Lieffers and Dr. Peter Blenis. Their experience, insight into mixedwood boreal forests, and scientific investigative skills taught me volumes. The commitment of time and patience they have made has been much appreciated. I would like to thank Simon Landhäusser for his time, technical expertise and valued advise, Ken Stadt for his time and patience with old dog questions, Vashty Thompson for her assistance in the field work, Sarah Lieffers for her assistance in field work and months of patience, reading increment cores. Generous funding by Alberta Pacific Forest Industries made this work possible. Lastly I would like to acknowledge that research more than any other area of work that I am familiar with is a team effort. In many cases the work of researchers is used by individuals and groups that follow to gain advancements in scientific exploration. I salute the many brilliant researchers that are cited in this paper for their hard work and dedication.

Dedication

I would like to dedicate this work to Kerry Frances MacPherson, for her many sacrifices and words of encouragement, and to my sons Benjamin, Mitchell and Thomas for giving up a piece of dad while he was away chasing his youth in academia.

Table of Contents

List of Tables Page

List of Figures

Page

Chapter 1

Dynamics of mixed species forests

1.1 Introduction

The boreal mixedwood zone of Alberta covers approximately 256,000 sq. km. of productive forest land representing the largest and most productive forested ecological area in Alberta (McDougall 1988). Optimal management of these lands is imperative to Alberta's forest economy as this zone contributes more fiber, employment and gross revenue than any other.

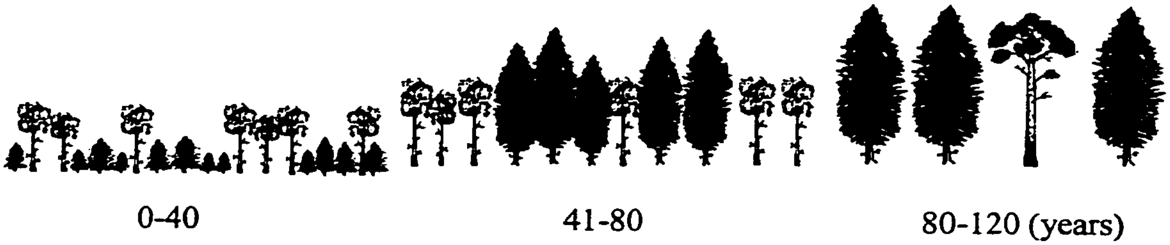
White spruce understories in trembling aspen stands typically occur in one of two ways. Either spruce can become established immediately following harvesting or stand replacing natural disturbances, such as fire and wind events, or alternatively it can take up to several decades, slowly establishing under aspen. The naturally occurring white spruce in the understory of aspen is a resource that forest managers can manipulate to increase forest productivity, reduce silviculture costs, increase site revegetation and enhance aesthetics.

Many foresters and scientists are concluding that natural forest succession may provide the best example of how to manage aspen-spruce associations in the future. In contrast, past management of these sites has focused on removing the aspen to establish single species conifer plantations. The biggest problem associated with removing the mixture has been the high reforestation cost of trying to achieve pure spruce stands immediately following harvesting (Navratil et al., 1991). Despite the high costs, establishment and performance of pure spruce plantations has only been partly successful. Smith et al., (1997), typifies Alberta's mixedwood experience with the general statement, "Under favorable site conditions it is often difficult, expensive, or even impossible to maintain purity of stand composition, so it may be prudent to work at least partly with natural tendencies rather than row upstream against them". This introductory chapter provides a review of the current literature and discusses the important interaction between aspen and understory spruce.

1.2 Pathways of development in aspen-spruce mixedwoods

In aspen-spruce stands, two successional pathways are most common. In the first, aspen and spruce establish simultaneously at the stand initiation stage following disturbances, as described by Oliver (1981), provided an abundant spruce seed source exists and appropriate mineral soil seedbeds are available.

Figure 1.1 Development stages of co-dominant mixedwood stands.



In this instance the faster growing aspen initially dominates the site, suppressing spruce height growth. These stands eventually become '**co-dominant mixedwoods**'. Spruce under-stories are often well developed and uniform in height and age. I believe that the competition that develops between spruce and aspen may contribute to the early demise of the aspen. At 80 years of age or older, these co-dominant mixedwoods are mostly referred to, in traditional forest inventories, as conifer leading mixedwoods (CD) or pure conifer (C) stands.

In a second pathway following disturbance, spruce recruitment may be delayed because of inadequate seed sources or seedbeds. A pure aspen stand develops that lacks significant spruce in the understory for several decades. These stands, low in spruce composition or with an uneven-aged spruce population, are '**successional mixedwoods**'.

Figure 1.2 Development stages of successional mixedwood stands.

Unless a spruce seed source is present, aspen stands may complete a full growth cycle as pure aspen stands. If a spruce seed source becomes available it can lead to the eventual development of understory spruce within the aspen stand. Understory development begins when snags fall down or self-thinning produces downed logs, which become suitable recruitment sites for spruce regeneration (Rowe, 1955). Increasing light levels in the understory, as the aspen stands age and self-thin, likely play an important role at this time (Lieffers and Stadt, 1994). At 80 years or older these stands are likely to be considered deciduous leading mixedwoods (DC) or pure deciduous (D) stands in traditional forest inventories.

Successional mixedwoods appear chronologically first and in subsequent rotations can lead to co-dominant mixedwoods following disturbance and stand initiation. Knowing the density, height and age of dominant spruce in the understory will allow workers to differentiate between co-dominant and successional mixedwoods and predict their development trajectory from an early stand age. The protected conditions found under an aspen canopy will allow a lower density understory of 400-800 spruce stems per hectare to develop into a high volume co-dominant mixedwood. I believe that this is the stand condition silviculture should replicate, to maximize forest growth and economic return on investment.

1.3 Understory communities of developing aspen-spruce stands

The development pattern of stands following disturbance has been described by numerous authors (Whitmore 1975, 1989; Hartshorn 1980; Oliver 1981, 1992; and Oliver and Larson, 1990).

Factors affecting understory development are light levels, canopy tree leaf litter, soil nutrients, reproductive ecology of understory species, microhabitat gradients, precipitation, coarse woody debris, herbivory and evolutionary strategies. In boreal spruce-aspen communities, nutrients and light levels are the dominant factors. Light levels under mixed stands of aspen and spruce range between 14 and 40% of the incoming light (Lieffers and Stadt, 1994) and support a wide diversity of vascular plant species (Uemura 1993). In contrast, pure spruce stands attenuate levels of incoming light, allowing only 5 to 11% to reach the forest floor (Lieffers and Stadt, 1994). Zavitkovski

(1976) found ground level light conditions are positively correlated to understory biomass.

1.3.1 Stand initiation

Following stand disturbance, revegetation is prolific and diverse. Plant species that may appear eliminated from the site will reappear from seed storage in the soil or seed bank (Simmons and Buckley 1992). These species can effectively take advantage of high light, nutrients and moisture levels to capture a significant growing space. In some instances these fast growing species can dominate a site, slowing tree initiation (Rowe 1955; Eis 1981). During the stand initiation phase it is common to see numerous layers of understory vegetation develop. In young aspen dominated forests, understory development of spruce can be slowed (Tappeiner and Alaback, 1988). The clonal nature of aspen allows this species to regenerate vigorously following natural or man-caused disturbances. Regeneration of aspen can be so vigorous as to completely dominate some sites. In a codominant stand trajectory, spruce may assume the role of a dominant understory species. An understanding of the site specific characteristics which lead to spruce regeneration in the understory in some areas and not others is lacking. In a successional stand trajectory, deciduous shrubs and herbs dominate the understory.

1.3.2 Stem exclusion

Once a forest stand has developed to full canopy, and the leaf area index has reached maximum, further growing space becomes available only through the loss of existing stems in the stand (Oliver 1981). During this period in stand development, light levels are at there lowest in both aspen and spruce stands (Lieffers and Stadt, 1993). At these light levels the taller shrubs, which may have dominated at stand initiation, lose their dominance and give way to deciduous and small wintergreen-evergreen herbs, which can tolerate lower light levels (Landhäusser et al., 1997). Spruce has the ability to persist in the understory during this period of stand development.

1.3.3 Understory re-initiation

In later stand succession, the stand density and leaf area index of aspen drops, allowing increased light levels to reach the ground. Understories may redevelop or, alternatively, persistent understory spruce may respond to this increased light with rapid height growth and dominate the understory. Spruce understory height growth allows the spruce to eventually reach the aspen canopy. Aspen is able to maintain only a temporary height dominance through physically suppressing spruce leader growth, a process referred to as leader whipping. Eventually the spruce emerges through the canopy and surpasses the aspen by 5 or more meters.

In later conifer stand succession, it is not until the canopy in pure conifer forest develops spatial heterogeneity, through the mortality of larger stems, that is it possible for increased understory development (Tappeiner and Alaback, 1988). In conifer forests, a majority of vascular plants are long-lived perennials with clonal growth and high persistence that use a foraging strategy to locate nutrients and light regimes favorable for growth (Eriksson 1989). Similarly, perennial leaved plants predominate in intensely shaded habitats whereas annual-leaved plants are more abundant in less shaded habitats (Uemura 1993). Species richness in understories was higher in mixed forest understories than in oligophotic forests of spruce-fir (Uemura 1993) primarily because of the abundance of the light resource.

1.4 Purpose of this study

A mixedwood approach to forest management has many aesthetic and bio-diversity benefits in addition to the potential growth and yield benefits, the later which is typically the focus of fiber-oriented managers. This study is narrowly focused on the growth and yield of aspen-spruce stands. Of the many potential benefits of promoting mixed species stands, growth and yield benefits may prove to be the strongest in promoting a widespread shift to mixedwood management. For this reason a focused study to estimate the growth and yield effects of white spruce understories on trembling aspen was deemed timely.

1.5 Productivity of mixed species stands

Mixedwood stands of aspen and white spruce are believed to be more productive than single species stands, due to greater utilization of natural resources (Kabzems and Senyk, 1967; Opper 1981). Kelty (1992) reviewed the reasons why mixed stands may be more productive than single species stands. It may be several decades before experimental data from mixed plantings of aspen and spruce can be used to provide a rigorous test of the hypothesis. However, qualitative evidence from studies of species with similar characteristics to aspen and spruce suggests that species mixtures are more productive than single species (Man and Lieffers, 1998). Competition reduction and facilitation (Vandermeer, 1989) are two important concepts that help to explain the benefits of forest tree mixtures on productivity (Man and Lieffers, 1998).

1.5.1 Competition reduction

Competition reduction occurs when two species use resources differently, thereby reducing competition relative to situations in which two species use similar strategies to capture the same resource. Four modes of differential utilization of resource in the aspen-spruce association are: differential use of light, phenological separation, successional separation, and root competition reduction.

In differential light utilization, shade intolerant aspen occupy a dominant canopy position above shade tolerant spruce (Lieffers and Stadt, 1994). The lower canopy layer of spruce is able to grow using the light not captured by the aspen. These shaded conditions would be fatal to, or greatly suppress, the growth of aspen (Landhäusser, unpublished).

Phenological separation is the ability of spruce to experience an extended growing season by starting photosynthesis in early spring, before the canopy of aspen develops and by extending photosynthesis in late autumn after leaf fall (Man and Lieffers, 1997;Constabel and Lieffers, 1996). In deciduous stands, seasonal changes in light conditions can have a significant influence on understory development (Jurik 1986; Lieffers and Stadt, 1994; Constabel and Lieffers, 1996; Man and Lieffers, 1998). Aspen stands typically complete bud flush by early May to the middle of June. Growing conditions however are favorable starting in late April or early May. During this period many understory species react quickly, expanding their leaf area and producing considerable photosynthate under the high light conditions. The fall canopy leaf-off period offers the same opportunity, although it is not as dramatic as in the spring.

Successional separation describes the early leaf area development in shade intolerant species such as aspen (Peterson and Peterson, 1992, 1996). After disturbance and new stand initiation, aspen rapidly regenerates suckers and leaf area. The amount of leaf area in aspen is maximum between 5 and 15 years (Peterson and Peterson, 1992). Spruce, in contrast, can take many decades to obtain maximum leaf area (Strong and La Roi, 1983). This temporal consideration, where aspen leaf area is gradually replaced by spruce leaf area, may ultimately prove to be the biggest factor responsible for any productivity increases in aspen-spruce associations (Brace and Bella, 1988).

Root competition reduction occurs due to differential rooting depths and structures between aspen and spruce (Strong and La Roi 1983). Aspen fine roots can be located at much greater depths than spruce roots; spruce roots are usually less than 50 centimeters deep while aspen roots may grow to a depth of up to 100 centimeters. The deeper rooting horizon of aspen and the clonal nature of the species, may be an adaptive mechanism allowing aspen to survive fire events.

1.5.2 Facilitative Production

Facilitative production is the improved growth of one species due to the presence of a second species (Vandermeer 1989). Aspen may benefit white spruce by increasing nutrients (Kelty 1992), creating sheltered conditions, reducing pest attacks (Montagnini et al., 1995), and providing protection from wind (Navratil 1995).

Nutritional benefits are mediated by an increase in decomposition of litter and faster nutrient cycling (Brown 1992, Kelty 1992, Gordon 1983). In the boreal mixedwood zone, trembling aspen and white spruce are found in associations on mesic sites within a moderate to rich nutrient regime. Domination by conifers through late succession reduces nutrient availability and concentrations in litterfall (Gosz 1981), decreases soil respiration (Flanagan and Van. Cleve, 1983), reduces availability of macro and micro-nutrients (Bormann and Silde, 1990), increases the carbon to nitrogen ratio of litter (Borman and Silde, 1990), increases forest floor biomass (Gosz 1981) and reduces seasonal soil temperature (Van Cleve and Yarie, 1986). In mixedwoods, these conditions are often ameliorated through processes initiated by the increase of light found on the forest floor.

Shelter from nurse trees reduces frost occurrence and over-heating in seedlings and increases humidity in the understory (Keenan et al. 1995, Montagnini et al. 1995). Reduction of pest attacks, most notably the white pine terminal weevil (*Pissodes strobi* Peck), occurs when spruce is overtopped by aspen (Stiell and Berry 1985, Alfaro 1996). Mixed stands of trees may also disperse insects in ways that reduce attack intensity (Maclean 1996).

1.5.3 Nutrient dynamics of mixed aspen-spruce stands

Aspen, being a rapid colonizer of recently disturbed sites and having a clonal root system, can effectively capture vast quantities of nutrients made available by fire or other disturbances (Man and Lieffers, 1998). White spruce, regenerating from seed, is not able to take advantage of the nutrient flush during stand initiation. Spruce, being much slower in juvenile growth, reaches its highest nutrient requirements in pure stands once canopy closure is complete, often several decades after stand disturbance.

The general trend of aspen-spruce stands is that input and uptake of nutrients increases with an increasing hardwood component (Gordon 1983). In later stages of aspen growth, once canopy structure has developed, aspen nutrient demands are considerably reduced as internal recycling increases. Storage of nutrients by aspen in the long-lived clonal root system is an important adaptation for nutrient recycling and the ability to regenerate itself after disturbance (Tew 1968). Conifer litter holds nutrients for much longer periods of time than aspen owing to higher C:N ratios, lower foliar nutrient content, lower pH, and higher lignin content of the needles (Chabot and Hicks, 1982; Simmons and Buckley 1992). As a result of poor litter quality and slow decomposition, the forest floor litter layer increases with time in conifer dominated stands.

Deep conifer litter layers, which can hold a significant quantity of the nutrient pool unavailable for growth, can have a dramatic effect on soil pH. For example, over a 231 year chronosequence, soil pH dropped from 5.5 to 3.65 (Brais, et al. 1995). A soil pH of 3.65 severely reduced the uptake of some required nutrients and increased the uptake of harmful heavy metals (Schier and McQuattie, 1995).

Soil temperature can be severely reduced by the presence of a deep litter layer that can delay and reduce soil warming. Aspen root growth is inhibited by cold soil temperatures (Landhäusser and Lieffers, 1998); aspen may require a minimum of 15° to 18° C for active root growth and subsequent nutrient uptake. In contrast, white spruce needs a minimum of 5° C (Landhäusser and Lieffers, 1998) or 10°C (Binder 1989) for active root growth. White spruce is capable of continuous growth within extreme/harsh environmental conditions, such as low soil temperature, low pH and lower nutrient availability, that are promoted by its heavy canopy. In contrast, aspen is intolerant of these same conditions. Conversely, conditions under aspen are often thought to be favorable for the growth of white spruce; nutrient rich foliage discarded and recycled every year by aspen and associated understory species offers a rich environment for spruce growth.

Decomposition is closely linked with soil temperature, microbial biomass and activity, soil carbon and soil pH. Aspen's rapid nutrient cycling ability, especially of nitrogen, phosphorous and base cations, maintains a more favorable environment for decomposing organisms. Aspen stands, as compared to pure spruce stands, enjoy a much faster rate of decomposition and subsequent nutrient cycling (Peterson and Peterson, 1992). Decomposition rates are increased in mixedwood stands as compared to pure conifer stands, due to increased pH, increased surface temperature, and the increased nutrient content of litter. The higher levels of nutrients found in the leaf litter of aspen contributes in several ways to accelerated decomposition. Higher nitrogen content benefits numerous fungi, which attack the structural components of the leaf (Flanagan and Van Cleve, 1983). Insect communities also thrive on the annual flush of aspen foliage and respond very quickly to available carbon (Jackson et al., 1997). Spruce litter is much slower to decompose than aspen litter. It is suspected that the mixing of aspen and spruce litter in mixedwoods increases the decomposition of spruce litter.

There is more nitrogen in aspen stands than in spruce stands due to the presence of nitrogen fixing legumes and understory species in the genera *Alnus* and *Sheperdia*. Although understory vegetation accounted for only 19% of the annual above ground litter fall it contributed 36% of the litter nitrogen, 40% of the litter phosphorous and 59% of the litter potassium (Perela and Alban, 1982). Nitrogen fixation by understory species can contribute between 20-85 kg/ha/year (Binkley 1992). In coastal stands most studied, red alder was the primary nitrogen fixing species. In boreal mixedwood spruce-aspen associations, nitrogen fixation is primarily due to shrubs and legumes. Although lower rates of nitrogen fixation would be expected in the boreal mixedwood than in coastal forests, the accumulation of nitrogen, over a 40-60 year period is likely very significant. Mixed species stands contain more nitrogen fixing understory species than pure spruce stands, which limit understory vegetation by reducing light (Lieffers and Stadt, 1994; Landhäusser et al., 1997).

1.6 Specific hypotheses

This study examined aspen and spruce productivity in pure aspen plots paired with mixedwood plots having a white spruce component ranging from 'Successional mixedwood' to 'Co-dominant mixedwood'. Two indices of productivity were used: total biomass to date and average annual biomass increment over the last 5 years excluding foliage.

For both these productivity indices, the following specific hypotheses were tested:

1. Total aspen and spruce productivity in the mixedwood plots exceeded productivity in the pure aspen plots.
2. Aspen productivity in the mixedwood plots was as great as aspen productivity in the pure aspen plots.
3. In the event that the second hypothesis was rejected in favor of the alternative hypothesis, (that aspen productivity reduced in the mixedwood plots), then the amount of reduction would be positively correlated with the amount of spruce in the mixed plots.

1.7 Literature cited

Alfaro, R.I., 1996. Role of genetic resistance in managing ecosystems susceptible to white pine weevil. For. Chron. **72**:374-380.

Bergeron, Y., and B. Harvey, 1997. Basing silviculture on natural ecosystem dynamics: an approach applied to the southern boreal mixedwood forest of Quebec. For. Ecol. Manage., **92**:235-242.

Binder, W.D., 1989. Ecophysiology: post-planting physiological results and their implications for growing spruce. *In*: B.A. Scrivener and J.A. MacKinnon (eds.). Learning from the past, looking to the future. pp. 33-35. For. Can. and B.C. Min. For., Victoria, B.C. FRDA Report 030.

Binkley, D., 1992. Mixtures of nitrogen$_2$ fixing and non-nitrogen$_2$ fixing tree species. *In* M.G.R. Cannell, D.C. Malcolm and P.A. Robertson (eds.). The ecology of mixed-species stands of trees. pp. 125-150. Blackwell Scientific Publications. Oxford. 312 p.

Bormann, F.H., and R.C. Silde, 1990. Changes in productivity and distribution of nutrient in a chronosequence at Glacier Bay National Park, Alaska. J. Ecol., **78**:561-578.

Brace, L.G. and I.E. Bella, 1988. Understanding the understory: Dilemma and opportunity. *In* J.K.Samoil (ed.). Management and Utilization of Northern Mixedwoods. Symp. Proc. April 11-14, 1988. Edmonton. Alberta. pp. 69-86. Can. For. Serv., Northern For. Cent., Edmonton, AB. Info. Rep. NOR-X-296. 163p.

Brais, S., Camiré, C., Bergeron, Y., and D. Paré, 1995. Changes in nutrient availability and forest floor characteristics in relation to stand age and forest composition in the southern part of the boreal forest of northwestern Quebec. For. Ecol. Manage., **76**:181-189.

Brown, A.H.F., 1992. Functioning of mixed-species stands at Gisburn, N.W. England. *In* M.G.R. Cannell, D.C. Malcolm and P.A. Robertson (eds.). The ecology of mixed-species stands of trees. pp. 125-150. Blackwell Scientific Publications. Oxford. 312 p.

Chabot, B.F., and D.J. Hicks, 1982. The ecology of leaf life spans. Ann. Rev. Ecol. Syst. **13**:229-59.

Constabel, A.J., and V.J. Lieffers, 1996. Seasonal patterns of light transmission through boreal mixedwood canopies. Can. J. For. Res., **26**:1008-1014.

Eis, S., 1981. Effects of vegetative competition on regeneration of white spruce. Can. J. For. Res., **11**:1-8.

Eriksson, O., 1989. Seedling dynamics and life histories in clonal plants. Oikos **55**:231-238.

Flanagan, P.W. and Van Cleve, K., 1983. Nutrient cycling in relation to decomposition and organic-matter quality in taiga ecosystems. Can. J. For. Res., **13**:795-817.

Gordon, A.G., 1983. Nutrient cycling dynamics in differing spruce and mixedwood ecosystems in Ontario and the effects of nutrient removals through harvesting. *In* R.W. Wein, R.R. Riewe and I.R. Methven (eds.). Resource and dynamics of boreal zone. Proc. Conf. August 1982, Thunder Bay, Ont. pp. 97-118. Assoc. Can. Univ. North. Stud., Ottawa, Ont. 544 p.

Gosz, J.R., 1981. Nitrogen cycling in conifer ecosystems. Ecol. Bull. (Stockholm), **33**:405-426.

Hartshorn, G. S., 1980. Neotropical forest dynamics. Biotropica **12**(suppl.):23-30

Jackson, R. B., Mooney, H.A., and E. D. Schulze, 1997. A global budget for fine root biomass, surface area, and nutrient contents. Proc. Natl. Acad. Sc. USA. **94**:7362-7366.

Jurik, T. W., 1986. Seasonal patterns of photosynthetic capacity in successional northern hardwood tree species. Amer. J. Bot., **73**(1):131-138.

Kabzems, A., and J.P. Senyk, 1967. A comparison of actual and potential forest land production in Saskatchewan. For. Chron., **43**:257-264.

Keenan, R., Lamd, D., and G. Sexton, 1995. Experience with mixed species rainforest plantations in North Queensland. Commonwealth Forestry Review **74**:315-321.

Kelty, M. J., 1992. Comparative productivity of monocultures and mixed species stands. *In* M. J. Kelty, B. C. Larson and C. D. Oliver (eds.). The ecology and silviculture of mixed-species forests. pp. 125-141. Kluwer Academic Publishers, Dordrecht, 287 p.

Kerr, G., Nixon C. J., and R.W. Matthews, 1992. Silviculture and yield of mixed-species stands: *In* M.G.R. Cannell, D.C. Malcolm and P.A. Robertson (eds.). The ecology of mixed-species stands of trees. pp. 125-150. Blackwell Scientific Publications. Oxford. 312 p.

Landhäusser, S. M., 1999. Unpublished.

Landhäusser, S. M. and V. J. Lieffers, 1998. Growth of Populus tremuloides in association with Calamagrostis canadensis. Can. J. For. Res., **28**:396-401

Landhäusser, S. M., Stadt K. J., and V. J. Lieffers, 1997. Seasonal changes in photosynthetic rates of understory deciduous and evergreen herbs. Oecologia (Berl.), **112**:173-178.

Lieffers, V. J., and K. J. Stadt, 1994. Growth of understory Picea glauca and Epilobium angustifolium in relation to overstory light. Can. J. For. Res. **24**:1193-1198.

MacLean, D. A., 1996. Forest management strategies to reduce spruce budworm damage in the Fundy Model Forest. For. Chron. **72**:399-405.

Man, R., and V. J. Lieffers, 1997. Seasonal photosynthetic responses to light and temperature in white spruce (*Picea glauca*) seedlings planted under an aspen (*Populus tremuloides*) canopy and in the open. Tree Physiol. **15**:437-444.

Man, R. and V. J. Lieffers, 1998. Are mixtures of aspen and white spruce more Productive than single species stands? For. Chron. **75**:505-513.

McDougall, F. W., 1988. Management of boreal mixedwood forests. *In* J.K. Samoil, (ed.). Management and utilization of northern mixedwoods. Symp. Proc., April 11-14, 1988, Edmonton, Alberta. pp. 3-4. Can. For. Serv., North. For. Cent., Edmonton, AB. Inf. Rep. Nor-X-296. 163 p.

Montagnini, F., González, E., Porras C., and R. Rheingans, 1995. Mixed and pure forest plantations in the humid neotropics:a comparison of early growth, pest damage and establishment costs. Commonwealth For. Review **74**:306-314.

Navratil, S., Branter K., and J. Zasada, 1991. Regeneration in the mixedwoods. Pp. 32-48. *In* A. Shortried, (ed.). Northern mixed-wood '89. Proc. Symp., Sept. 12-14, 1989. Fort St. John, B.C. Pacific Forestry Centre, Victoria, B.C. FRDA Rep. 164.

Navratil, S., 1995. Minimizing wind damage in alternative silvicultural systems in boreal mixedwoods. Nat. Res. Can., Can. For. Serv., North. For. Cent., Edmonton, Alberta, and Alberta Environ. Prot., Land For. Serv., Edmonton, Alberta. Canada-

Alberta Partnership Agreement in Forestry Report.

Oliver, C. D., 1981. Forest development in North America following major disturbances. For. Ecol. Manage. **3**:153-158.

Oliver, C. D., 1992. Similarities of stand structures and stand processes throughout the world-some evidence and applications to silviculture through adaptive management. *In* M. J. Kelty, B. C. Larson and C. D. Oliver (eds.). The Ecology and Silviculture of Mixed-Species Forests. pp. 11-28. Kluwer Academic Publishers, Boston.

Oliver, C. D., and B. C. Larson, 1990. Forest stand dynamics. McGraw-Hill, Inc., New York.

Opper, M. A., 1981. Present utilization of species in the boreal mixedwood forests in Ontario: Industrial perspective. *In* R. D. Whitney and K. M. McClain (eds.). Boreal mixedwood symposium. Proc., Sept. 16-18, 1980. Thunder Bay, Ont. Pp. 97-103. Environ. Can., Can. For. Serv., Great Lakes For. Res. Cent., Sault Ste. Marie, Ont. COJFRC Symp. Proc. O-P-9. 278 p.

Perela, D. A. and D. H. Alban, 1982. Biomass, nutrient distribution and litterfall in *Populus, Pinus and Picea* stands on two different soils in Minnesota. Plant Soil **64**:177-192.

Peterson, E. B. and N. M. Peterson, 1992. Ecology, management and use of aspen and balsam poplar in the prairie provinces. For. Can., Northwest Reg., North. For. Cent., Edmonton, Alberta. Spec. Rep.1.

Peterson, E. B., and N.M. Peterson, 1996. Ecology and silviculture of trembling aspen. *In* P.G. Comeau, G.J. Harper, M.E. Blache, J.O. Boateng and K.D. Thomas (eds.). Ecology and management of B.C. hardwoods. Workshop Proc., Dec. 1-2, 1993, Richmond B.C. pp. 31-51. Canada-B.C. Partnership Agreement on For. Res. Devel.: FRDA Report 244. 246 p.

Rowe, J. S., 1955. Factors influencing white spruce reproduction in Manitoba and Saskatchewan. Tech. Note No. 3. Can. Dep. of North. Affairs and Nat. Res., Forest Research Div., Ottawa, Ont.

Schier, G. A., and C. J. McQuattie, 1995. Effects of aluminum on the growth, anatomy, and nutrient content of ectomycorrhizal eastern white pine seedlings. Can. J. For. Res.. **25**:1252-1262.

Simmons, E. A., and G. P. Buckley, 1992. Ground vegetation under planted mixtures of trees. M.G.R. Cannell, D.C. Malcolm and P.A. Robertson (eds.). The ecology of mixed-species stands of trees. pp. 211-232. Blackwell Scientific Publications. Oxford, 312 p.

Smith D. M., Larson B. C., Kelty M. J., and P. M. S. Ashton, 1997. The Practice of Silviculture: Applied Forest Ecology. 9th Ed. John Wiley and Sons Inc. 537 p.

Stiell, W. M., and A. B. Berry, 1985. Limiting white pine weevil attacks by side shade. For. Chron. **61**:5-9.

Strong, W. L., and G. H. La Roi, 1983. Root-system morphology of common boreal forest trees in Alberta, Canada. Can. J. For. Res. **13**:1164-1173.

Tappeiner, J. C. II. and P. B. Alaback, 1988. Early establishment and vegetative growth of understory species in the western hemlock-sitka spruce forests of southeast Alaska. Can. J. Bot. **67**:318-326.

Tew, R. K., 1968. Properties of soil under aspen and herb-shrub cover. U.S. Dept. Agric., For. Serv., Intermt. For. Range Exp. Stn., Ogden, Utah. Res. Note INT-78.

Uemura, S., 1993. Patterns of leaf phenology in forest understory. Can. J. Bot. **72**:409-414.

Vandermeer, J., 1989. The Ecology of Intercropping. pp. 15-64. Cambridge University Press. p. 237.

Van Cleve, K., and J. Yarie, 1986. Interactions of temperature, moisture and soil chemistry in controlling nutrient cycling and ecosystem development in the taiga of Alaska. *In*: K. Van Cleve, F.S. Chapin III, P.W. Flannigan, L.A. Viereck and C.T. Dryness (eds.). Forest Ecosystems in the Alaska Taiga. A Synthesis of Structure and Function. Ecological Studies 57. Springer, New York, pp. 160-189.

Whitmore, T. C., 1975. Tropical Rain Forests of the Far East. Clarendon Press Oxford. 282 pp.

Whitmore, T. C., 1989. Canopy gaps and the two major groups of forest trees. Ecology **70**(3):536-538.

Zavitovski, J., 1976. Ground vegetation biomass production, and efficiency of energy utilization in some northern Wisconsin forest ecosystems. Ecology **57**:694-706.

Chapter 2

Is growth of aspen affected by white spruce under-stories in Alberta's boreal mixedwood forests?

2.1 Introduction

Trembling aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* (Moench) Voss) in pure or mixed stands occupy the largest ecological association in Alberta, covering approximately 25 million hectares (McDougall 1988). Optimal management of these lands is imperative to Alberta's forest economy and forest sustainability. Experience in the last four decades has shown that problems exist in managing mixedwood aspen-spruce forests (Navratil et al., 1991). Out of date administrative pressures to create pure species stands, coupled with high forest renewal costs, have forced forest manager to re-evaluate present management practices. This re-evaluation has focussed on an ecological theme, examining nature's way of forest regeneration and renewal.

The boreal mixedwood ecological area of Alberta is dominated by aspen and white spruce in various stages of successional change. In the early stages of succession, these stand types are either pure aspen or aspen dominated stands underlain with white spruce. Over time these stands develop into either maturing pure aspen or co-dominant mixedwood stands, varying in densities of aspen and white spruce. Later in the successional process, pure aspen stands can become uneven aged aspen-spruce stands if a spruce seed source and seedbed are present, or remain as pure aspen stands. Mixedwood aspen stands later become spruce stands that persist for up to 200 years or longer before stand disturbances, such as fire or wind, open the stands for regeneration to start anew.

Based upon ecological theory, there is growing evidence that mixed aspen-spruce stands are more productive than pure aspen stands. Through the process of facilitative production or competition reduction, the average productivity of two species grown together can exceed their average productivity where they are grown apart (Vandermeer 1989; Man and Lieffers, 1999). Kelty (1992), identifies this process of increased productivity as ecological combining ability.

Logically, aspen and white spruce mixtures should have greater total productivity in mixture than in single species stands (Man and Lieffers, 1999). There has been little work, however, that actually verifies this conjecture except for some FORECAST models (Wang et al., 1995), that suggest mixed stands carry more biomass than single species stands. More recently in western Canada, the Western Boreal Growth and Yield

Cooperative (WESTBOGY), has established growth trials to determine aspen and spruce productivity in mixtures, but the long term results are still many years away. For this reason an in-situ, interpretive study of natural stands was undertaken to gain an immediate indication of the productivity of these mixed systems.

This study surveyed natural stands dominated by aspen that have patches of white spruce growing as an understory species. A paired plot design was used in which plots in locations with no spruce understory were paired with nearby plots in areas with understory white spruce. Paired plot establishment occurred where adjacent topography and site conditions were similar. Based on the assumption that the only difference between the plot pairs was the understory spruce, this study was the equivalent of an additive experiment where understory spruce was added to the aspen. Kelty (1992) used a similar approach but only examined two pairs of stands, compared to 29 pairs in this study.

The overall objective was to understand the productivity of pure aspen stands compared to aspen stands with a spruce understory. The specific hypotheses tested were:

1. Total aspen and spruce productivity in the mixedwood plots exceeded productivity in the pure aspen plots.
2. Aspen productivity in the mixedwood plots was as great as aspen productivity in the pure aspen plots.
3. In the event that the second hypothesis was rejected in favor of the alternative hypothesis, (that aspen productivity was reduced in the mixedwood plots), then the amount of reduction would be positively correlated with the amount of spruce in the mixed plots.

2.2 Methods

A total of 29 study sites were selected from trembling aspen stands in the boreal forest, near Athabasca(6), Calling Lake(7), Wandering River(8) and north of Lac La Biche lake(8), Alberta. All stands were in either the Central or Dry Mixedwood Natural Subregions (Beckingham and Archibald, 1996).

2.2.1 Ecological site and stand selection criteria

To reduce variability, stands initially were selected to meet several criteria. The overstory aspen was even aged, at least 40 years old and with greater than 75% canopy closure. Each stand had areas of spruce understory in close association with areas lacking spruce understories. Stands were at least 500 m apart and did not exceed 5 % slope. All stands belonged to one of three plant community types within the ecosites: d1.2 (Aw/saskatoon-pin cherry), d1.3 (Aw-beaked hazelnut) and d2.2 (Aw-Sw beaked hazelnut) (Beckingham and Archibald, 1996). These were the most abundant ecosites within the natural subregions. All of these ecosites had a similar component of saskatoon (*Amelanchier alnifolia* Nutt.) as an indicator species, allowing efficient site identification.

Further selection criteria were applied in the field. The stands had to; a) be healthy and free from significant mortality of dominant aspen; b) have uniform stem distribution with no large canopy gaps; c) have no anthropogenic disturbances such as grazing, harvesting, pollution or mechanical disturbances; and, d) have no natural disturbances (such as wind throw) for the past five years. Soil texture was also checked in 38 plots to ensure significant textural differences did not consistently occur (Table 2). In addition, a plant list was checked at each plot to ensure that species representation in the sample plot matched the ecosites (Table 3).

2.2.2 Plot location selection

In each of the 29 different stands, 6-83.3m^2 fixed area circular plots where randomly established (Fig. 2.1), three in the pure aspen portion of the stand (pure plots), and three in the white spruce understory portion (mixed plots). The first plot was established in the spruce understory. The paired plot was established in pure aspen, 30 - 40 paces away. This process was repeated until all six plots had been located. A buffer, approximately 1.5 times the height of the tallest understory spruce was present around each plot, in higher density spruce understories. This was done to ensure the plot was not located on the edge of the spruce understory.

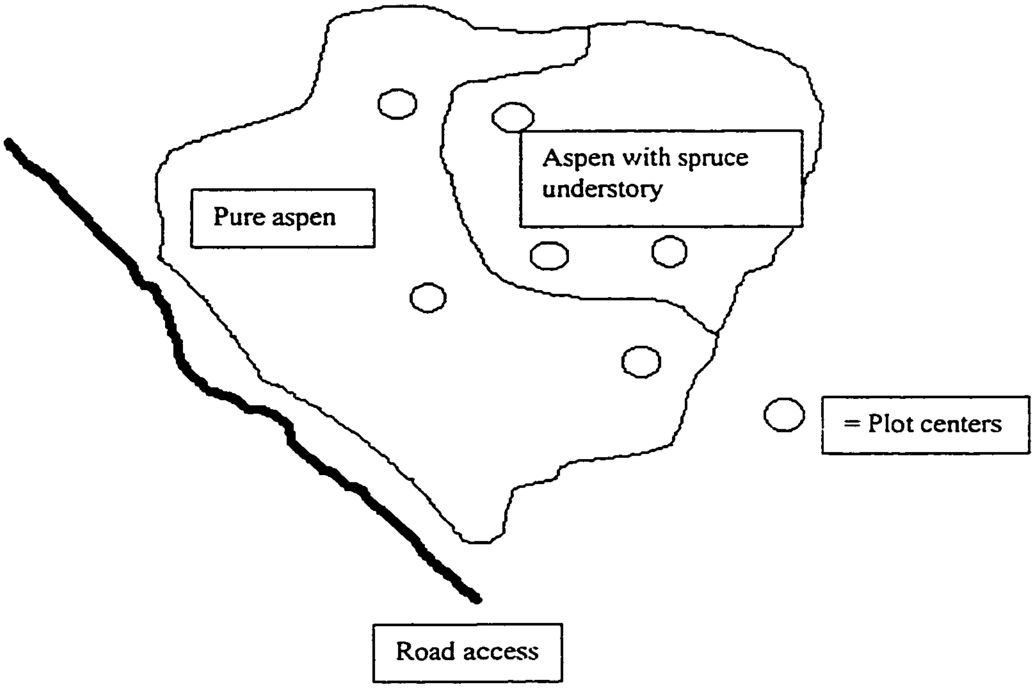


Figure 2.1 Treatment plot layout

2.3 Treatment Layout and Measurement

The diameter at breast height (1.3m, DBH) was recorded on all trees in all plots. In the pure aspen plots, four sample trees were chosen, covering the range of diameter sizes from smallest to largest. The heights of these trees were determined with a clinometer and increment cores were taken at DBH from two directions, at right angles, on the bole of each sample tree. Increment cores were stored in plastic straws and frozen within 48 hours of collection. The increment cores were oriented as in the tree bole, and the top surface was shaved with a razor blade. Chalk dust was then applied to the prepared surface to enhance visibility of the annual rings which were counted using a dissecting microscope. The radial increment for the last five years was measured with a manual Parker micrometer and the two radial increments for each sample tree were averaged. Aging of all plots was not possible due to rot or the core not hitting the pith. However, after accounting for these missing rings, maximum aspen ages in the six plots per stand typically varied by less than 5 years. In the mixed aspen plots the same procedure was followed, sampling four trees each of aspen and white spruce.

Spruce canopies were measured to determine if there was a relationship between the amount of spruce within the mixed aspen plots, and the difference in productivity between mixed aspen and pure aspen. Forty nine spruce crowns were measured in twelve randomly selected stands, with a maximum of five trees per stand. Measurements included DBH, total tree height, crown radius average and height to live crown average.

Soil texturing was carried out to ensure systemic differences between pure and mixed plots was not occurring (Table 2).

2.4 Data Compilation

2.4.1 Diameter increment regression estimation

Determination of diameter increment followed the double sampling procedure outlined in Lieffers and Campbell, (1983). Simple linear regression was used to predict diameter increment over the last 5 years as a function of current diameter. Eighty seven separate equations were developed, for aspen in the pure plots, aspen in mixed plots and spruce in mixed plots in each of the 29 stands.

2.4.2 Diameter height regression estimation

The development of a height to diameter relationship was required before biomass calculations could be completed. The height-diameter model used was from Huang et. al., (1994);

$$H=1.3+a(1-e^{-bDBH})^{c}, \qquad \text{Equation 1}$$

Coefficients a, b, and c were fitted, using nonlinear regression PROC NLIN of SAS (Stokes et al., 1995). Calculating 87 separate regression equations, as had been done to determine the diameter to increment relationship, was not satisfactory, as sample sizes of 12 to 15 trees often did not establish a significant height-diameter relationship. Therefore data from the 29 stands were combined to develop three equations, one each for pure aspen, mixed aspen and understory spruce. Because there was significant overlap of the 95% confidence intervals for the a, b, and c coefficients for pure and mixed aspen, those data were combined and new values of a, b and c calculated. The final equation for predicting aspen height was:

$H = 1.3 + 25.24809*(1\text{-}\exp(-0.09048*DBH))^{*1.2975988}$ Equation 2 (Fig. 2.2)

and the equivalent equation for spruce was:

$H = 1.3 + 52.64295*(1\text{-}\exp(-0.017904*DBH))^{*1.0608138}$ Equation 3 (Fig. 2.3).

2.4.3 Biomass calculations

The present and past biomass of all trees in all plots was calculated using the direct measurements of DBH and the modeled increments and heights. The current height of each tree in each plot was calculated on the basis of the height to diameter relationship. The diameter 5 years previous was estimated by subtracting the radial increment (calculated on the basis of the increment to diameter relationship) from the current diameter. Once the current and past heights and diameters were determined, current and past plot biomass was calculated using biomass prediction equations which estimated individual tree biomass. The equation used for aspen (Singh 1982) was as follows:

$\text{Weight (kg)} = 0.34961 + 0.01916(DBH)^2H$ Equation 4

The equation for spruce was:

$\text{Weight (kg)} = 6.09159 + 0.01499(DBH)^2H$ Equation 5

These equations took into consideration the total living tree above ground without foliage. Each plot biomass was calculated by summing the values of the individual trees. By subtracting the past plot biomass from the present plot biomass, a 5 year biomass increment was determined. This 5 year increment was then divided by 5 to determine a Periodic Annual Increment (PAI). The three $83.3m^2$ plots, were scaled up to a hectare basis by multiplying by 40.

2.4.4 Statistical Analysis

Two methods were used to compare the productivity between pure and mixed plots within stands: paired t-tests to determine if differences in mean productivity were significant, and exact chi-square tests for frequency analysis (SAS 1995). Regression analysis was used to determine if the reduction in aspen productivity in the mixed plots increased with increasing spruce competition. The following measures of spruce competition were used: total stand biomass, periodic annual increment, spruce crown area, spruce crown volume, and spruce basal area. The best 1-, 2-, 3-, and 4-variable models were examined.

2.5 Results

2.5.1 Stand ages

Aspen stand ages, taken in pure and mixed plots, confirmed that paired stands had the same date of origin. Among all the stands however, stand ages ranged from 48 to 105 years at 1.3 meters height (Table 1). Dominant spruce understory ages varied from 4 to 64 years at breast height. The average age difference between dominant understory spruce and overstory aspen was 22.9 years at breast height. No age-biomass relationship (Figure 2.4) or age-PAI relationship (Figure. 2.5) was evident.

2.5.2 Stand densities

Stand densities per hectare were determined for pure aspen, mixed aspen and spruce understories (Table 1). The objective of the study required aspen densities to be the same in the mixed and pure plots within stands. For the 29 stands, the mean stem density of pure aspen was 1458 stems/ha, essentially the same as the mean density of 1462 stems/ha for the aspen in mixed stands (Table 1). Among the 29 stands however, there was up to a 41% difference in the aspen density between the paired stands. The mean density of spruce understories in the 29 stands was 1056 stems/ha. Spruce density was sampled across a wide range of values from, 200 to 2920 stems per hectare, to vary competitive effects on aspen.

2.5.3 Basal area

Mixed plots of spruce and aspen carried 23.2% more basal area of aspen and spruce combined than pure plots of aspen ($P<0.0001$), (47.3 m^2/ha compared to 38.4 m^2/ha for pure aspen stands) (Table 1). However, pure plots carried 11.0% greater aspen basal area than mixed plots ($P=0.0028$) (38.4 m^2/ha compared to 34.6 m^2/ha). On average, spruce represented 26.9% of the basal area of mixed plots. The average height to diameter ratio for the spruce sample trees in all plots was 0.843:1, indicating the majority of spruce had growth characteristics of trees grown in protected, low light understory conditions. For this reason, comparison of spruce basal areas to open grown plantation spruce is invalid as open grown trees would tend to have higher basal area or larger diameters per individual tree.

2.5.4 Total stand biomass

Mean stand biomass for aspen in the mixed plots was 178 Mg/ha (Table 1) whereas mean stand biomass of aspen in the pure plots was 201 Mg/ha. Mean biomass of spruce in the mixed plots was 43 Mg/ha. Thus there was 12.9% (23.0 Mg/ha, 95% C.I. ± 13.9) greater aspen biomass within pure plots than in the mixed plots ($P=0.0011$). Nineteen of the stands had greater aspen biomass in the pure plots than in the mixed plots, compared to only ten stands with greater biomass in the pure plots ($P=0.068$). When spruce was added to aspen biomass, the mixed plots had 10.0% (20.1 Mg/ha, 95% C.I. ± 15.6) more total biomass than pure plots ($P=0.0067$). Twenty of the stands had greater total biomass in the mixed than in the pure plots, compared to only nine stands having greater total biomass in the pure plots ($P=0.030$). In the mixed stands, spruce ranged in biomass from 10 Mg/ha to 119 Mg/ha.

For each stand, the biomass of the aspen in the mixed plots was subtracted from the biomass in the pure aspen plots. This reduction in aspen biomass in the mixed plots was weakly correlated with spruce PAI ($P=0.045$, $R^2=0.141$) (Figure 2.6), spruce basal area ($P=0.053$, $R^2=0.131$, Figure 2.7) and spruce biomass ($P=0.081$, $R^2=0.108$). However the procedure of examining the best 1-, 2-, 3-, and 4-variable models may have overstated the significance of a correlation with spruce PAI. None of the models with two or more variables were better than the single variable models. The other indicators of spruce competition, spruce crown area and spruce crown volume, were not significantly associated with the reduction in aspen biomass in the mixed plots.

2.5.5 Periodic annual increment (PAI)

Mean plot PAI for aspen in the mixed plots was 3.9 Mg/ha (Table 1) whereas mean plot PAI of aspen in the pure plots was 4.8 Mg/ha. Mean PAI of the spruce in the mixed plots was 1.5 Mg/ha. Thus, there was 25.2% (0.97 Mg/ha/year, 95% C.I. ± 0.37) greater PAI for the aspen in the pure plots than in the mixed plots ($P<0.001$). Twenty-five of the stands had greater aspen PAI in the pure plots, compared to only four stands with greater PAI in the mixed plots ($P<0.001$). When spruce was added to aspen PAI however, these mixed plots had 12.5% (0.52 Mg/ha/year, 95% C.I. ± 0.44) more PAI than pure plots ($P=0.0118$). Nineteen of the stands had greater total PAI in mixed plots, compared to ten stands having greater total PAI in the pure plots ($P=0.0680$).

For each stand pair, the PAI of aspen in the mixed plots was subtracted from the PAI in the pure aspen plots. The difference in aspen PAI between pure and mixed stands was not significantly correlated with spruce basal area (R^2=0.041), spruce biomass (R^2=0.021), spruce PAI (R^2=0.027), spruce crown area (R^2=0.024) or spruce crown volume (R^2=0.033).

2.6 Discussion

Because of the high cost and low success of establishing pure spruce stands, the possibility of growing mixtures of aspen and spruce is becoming increasingly attractive. The feasibility of mixedwood management will depend in large part on the ability of mixedwood stands to produce aspen and spruce fiber. The most accurate way to assess production would be to plant aspen and spruce together in all combinations and determine production over time. Indeed the WESBOGY experiment, which examines different planting densities of aspen and spruce will eventually yield these types of data. Yield comparisons can also be made through the use of growth and yield tables (Man and Lieffers, 1999) or through modeling (Wang et. al., 1995). The present study attempts to obtain these results much earlier than the experimental approach, through examining natural stands, but suffers from several criticisms.

1. Kelty (1992) points out, 'The spatial arrangement of trees of different species must be fine-grained (i.e., trees must be adjacent to trees of different species) in order for reduction of competition to occur.' In natural stands, trees have clumped or random distribution, and thus this objective is impossible to achieve.
2. The lack of control over organic substrate and clonal variation of the aspen likely increased the variability of productivity among and within stands.
3. Shrub biomass was not measured. Thus, an important component of productivity was not considered in the analysis.
4. A conscious attempt was made to sample over a range of aspen stand ages and levels of spruce competition. The increases in PAI and biomass of 12.5 % and 10.0 %, respectively, in the mixed plots, are averages over that range of ages and spruce competition. In normally developing stands, any such increases in productivity would likely vary with stand age and understory competition.

The three hypotheses in this study involved an examination of mixed and pure plots on the basis of 1) the combined productivity of aspen and spruce, 2) the difference in aspen productivity and 3) explanations for any differences in aspen productivity between pure and mixed plots.

Mixed plots sampled in this study carried 10.0% more total biomass than pure aspen plots. This finding is consistent with the theory that mixed stands are more productive than single specie stands (Vandermeer, 1989). Similarly, Kelty (1989), also found shade intolerant hardwoods growing over more shade tolerant hardwoods were more productive than the single cohort of shade intolerant hardwoods alone. Mixed plot PAI was 12.5% greater than pure plot PAI. The greater total stand biomass and PAI in the mixedwood plots leads to the acceptance of the first hypothesis, 'Mixed stands of aspen and white spruce were more productive than stands of pure aspen'. Given that many of the mixed stands had very low stocking of understory spruce (Table 1), the productivity differences reported above would likely have been greater if understory spruce stocking had been consistently high.

The theory of ecological combining ability (Harper 1977;Man and Lieffers, 1999) identifies the potential of spruce in an understory to utilize resources that are not completely captured by the overstory. The concept of facilitation refers to the potential for overstory aspen to improve site growing characteristics for white spruce by increasing nutrients, creating sheltered conditions, reducing pest attacks and providing protection from wind. Unfortunately in this study we are not able to identify which factors are most important.

The comparison of productivity of aspen alone, in mixed and pure stands, shows a different trend. Pure aspen plots carried 12.9% more biomass than the aspen component in the mixed plots. Pure plots were also 25.2% more productive in PAI than the aspen in mixed plots. These results indicate that aspen in mixed plots were less productive compared to pure aspen plots, disproving hypothesis #2 in which we stated, 'Aspen productivity in mixedwood plots was as great as aspen productive in the pure aspen plots'. The larger difference in current productivity (5 year based PAI) of 25.2%, compared to the 12.9% difference in aspen total cumulative stand biomass indicates the productivity difference is a more recent phenomenon. This is possibly due to the spruce gaining in stature and competitive position in recent years and displacing the aspen.

The third hypothesis, i.e. 'The reduction in aspen productivity in mixed plots is correlated with the amount of spruce in those plots', seems to be weakly refuted based upon the PAI data or supported based upon the biomass data (figures 2.6 and 2.7 below). We could not find a significant correlation between the reduction in aspen PAI in the mixed stands and the abundance of spruce, even though there was a wide range in spruce biomass in mixed plots (10 to 119 Mg/ha). Thus it cannot be concluded that spruce caused the reduction of aspen productivity in the mixed stands. There are a number of possible explanations why there was less aspen in the mixed plots than the pure plots, even if this difference could not be easily accounted for by the indices of spruce competition.

1) Spruce recruitment is highly dependent upon forest floor conditions at the time of establishment. Mineral soil seedbeds are considered ideal for spruce establishment (Stewart et al., 2000). Fires can be highly irregular in the amount of forest floor material they consume within a small space (Johnson 1992). Thus, it is likely that the mixed wood plots could have had greater forest floor removal (and nutrient losses), than the adjacent pure aspen plots. This could explain the greater growth in immediately adjacent pure aspen sample plots.
2) There are large differences in productivity among clones of aspen (Lehn and Higginbotham, 1982). More productive clones may have carried more leaf area in their juvenile state than less productive clones. Productive clones may therefore, have transmitted insufficient light to allow survival of spruce. Thus, the pure aspen plots may have had greater productivity due to genetic characteristics. Although this phenomenon would explain why there was greater aspen productivity in pure than mixed plots, it would be expected to result in a stronger correlation between spruce productivity and the reduction in aspen productivity, which occurred, but was generally weak.
3) In general, the pure aspen plots had a greater shrub layer than the mixed plots. This added an uncontrolled component to the plot comparisons and partially contributed to the lack of evidence identifying spruce as the cause for the difference in aspen PAI. Why then, would there be a reduction in aspen productivity in the mixed plots, even though there was little correlation between

this reduction and spruce competition? It is possible that in those stands with high spruce basal area, the competitive effect of the spruce would have greatly exceeded the competitive effect of the deciduous plants in the pure plots.

4) Ten thousand data sets were simulated using the observed values of spruce biomass and the slope and error from the relationship between spruce biomass and the reduction in aspen biomass in the mixed plots. In 42 % of the data sets, the t-test showed a significant reduction in biomass between pure and mixed stands with no significant association between spruce biomass and the reduction in aspen biomass. This suggests that even if increasing spruce was associated with a decrease in aspen production, it would be possible that the regression would not be significant even if the t-test was.

In conclusion, there was an increase in total biomass and PAI in the mixedwood plots, confirming the superior productivity of mixedwood stands. Because the surveyed stands included young stands and stands with little spruce, it is possible that the increases of 12.5 % and 10.0 % in PAI and biomass, respectively, may be an underestimate of the increase that could be realized under mixedwood management. The expectation that the difference in aspen productivity, between mixed and pure plots, could be accounted for by spruce competition was not strongly supported by the data. However, it is still possible that spruce did lead to a reduction in aspen biomass, that was not detected because of the relatively small sample size and extreme variability, especially in the deciduous understory in the pure plots.

There was no relationship found between total stand biomass, or PAI, and aspen age. This is somewhat surprising as in the older aspen stands the age of the spruce understory increased. This lack of an age-biomass relationship in aspen suggests that aspen stand productivity reached its maximum previous to the minimum age of stands surveyed.

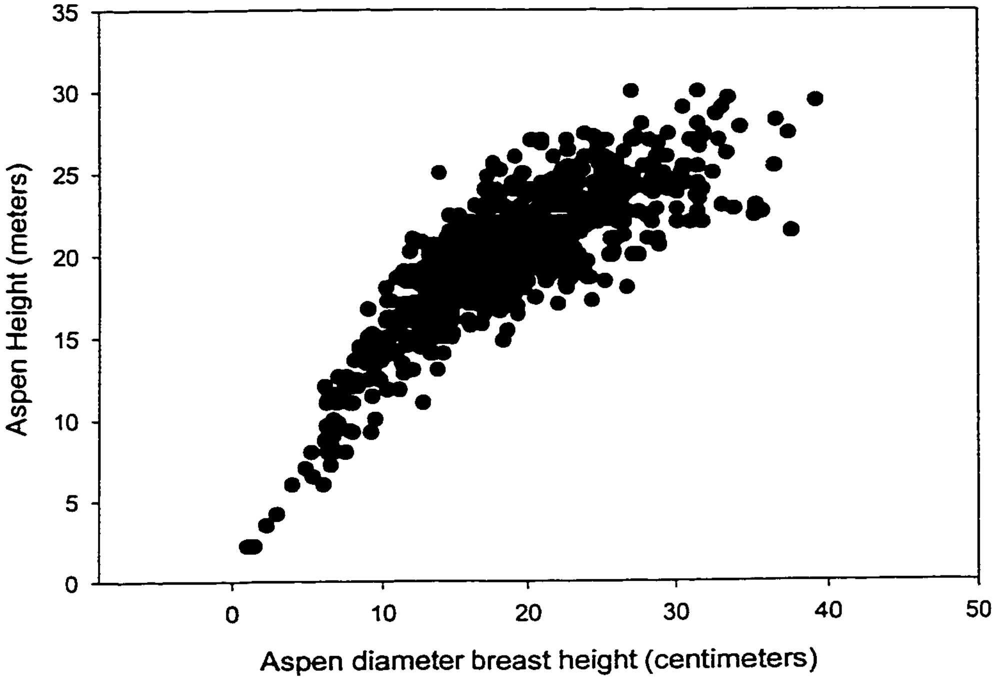


Figure 2.2 Height versus diameter curve for trembling aspen (n=690). Aspen in mixed and pure stands were combined to produce a single height versus diameter curve. $H=1.3+25.248095*(1-\exp(-0.090486*DBH))^{*1.2975988}$

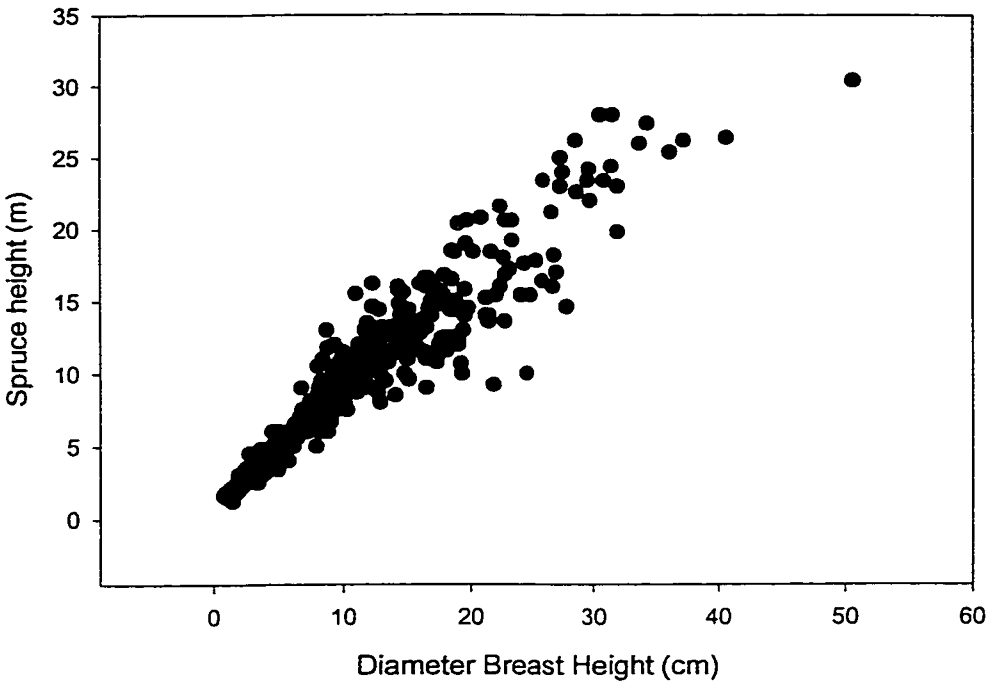


Figure 2.3 Height versus diameter curve for understory white spruce (n=342). $H=1.3+52.64295*(1-\exp(-0.017904*DBH))^{*1.0608138}$

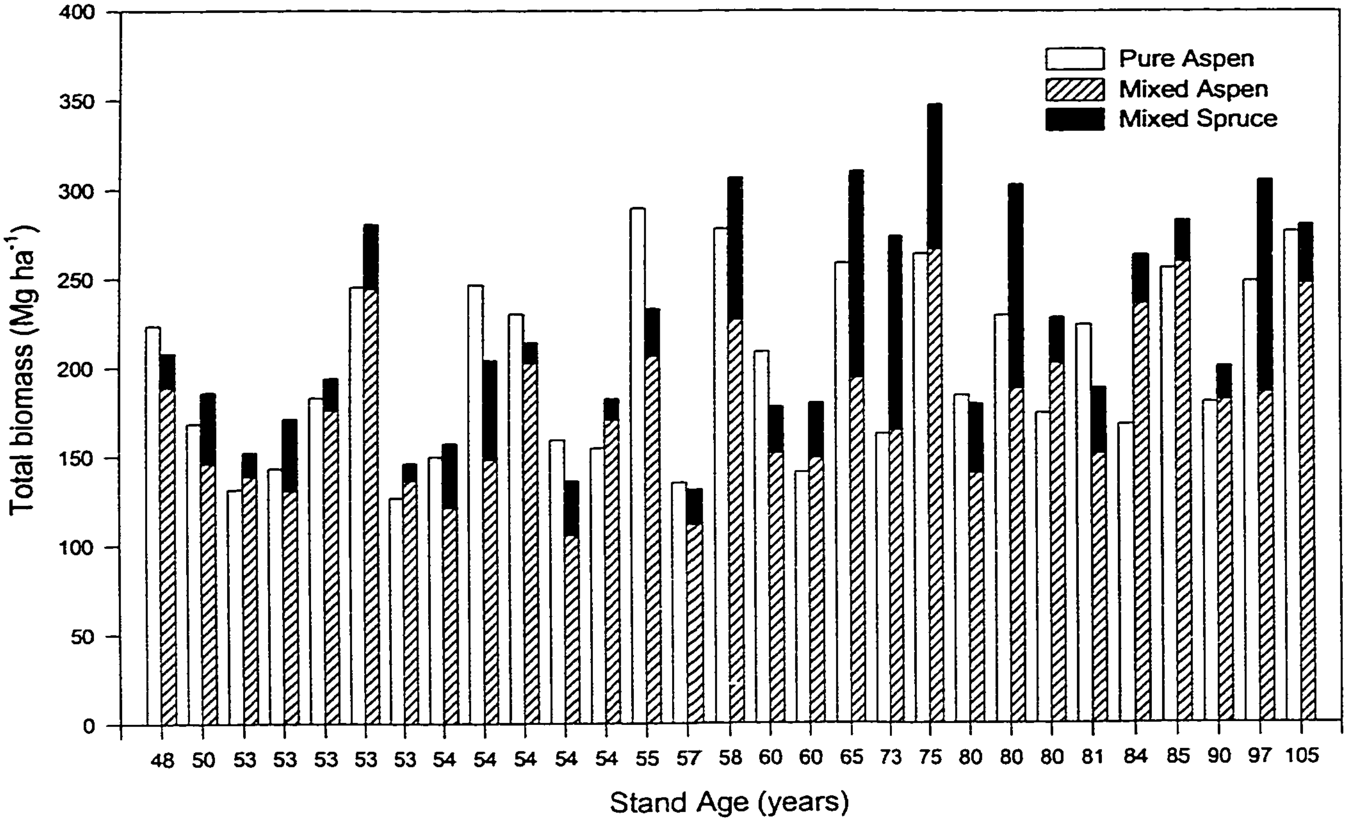


Figure 2.4 Total biomass of pure and mixed plots. The 29 paired aspen plots are arranged from youngest to oldest to demonstrate that no relationship existed between age and biomass.

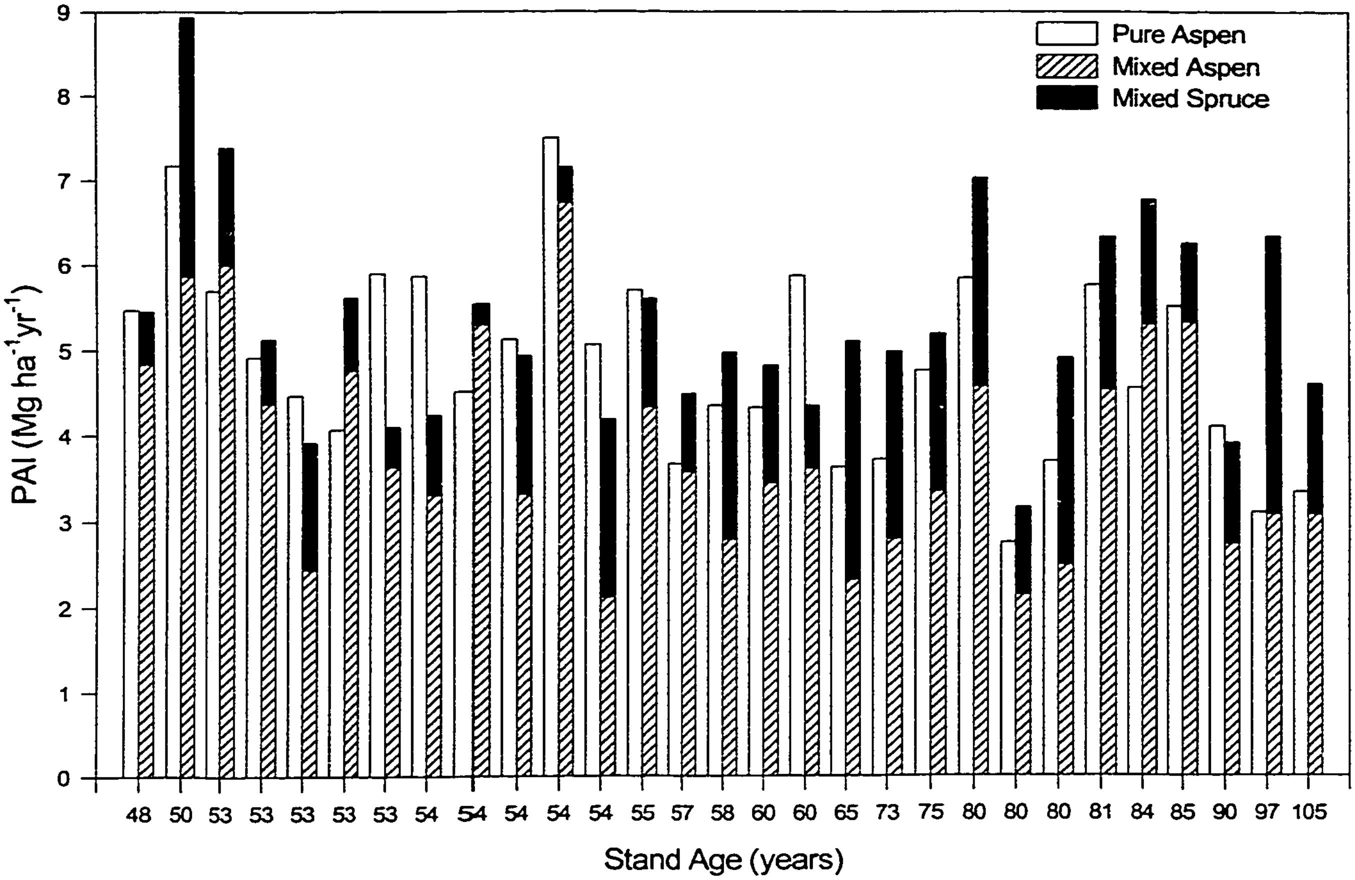


Figure 2.5 Periodic annual increment (5 year) of pure and mixed plots. The 29 paired aspen plots are arranged from youngest to oldest to demonstrate that no relationship existed between age and PAI.

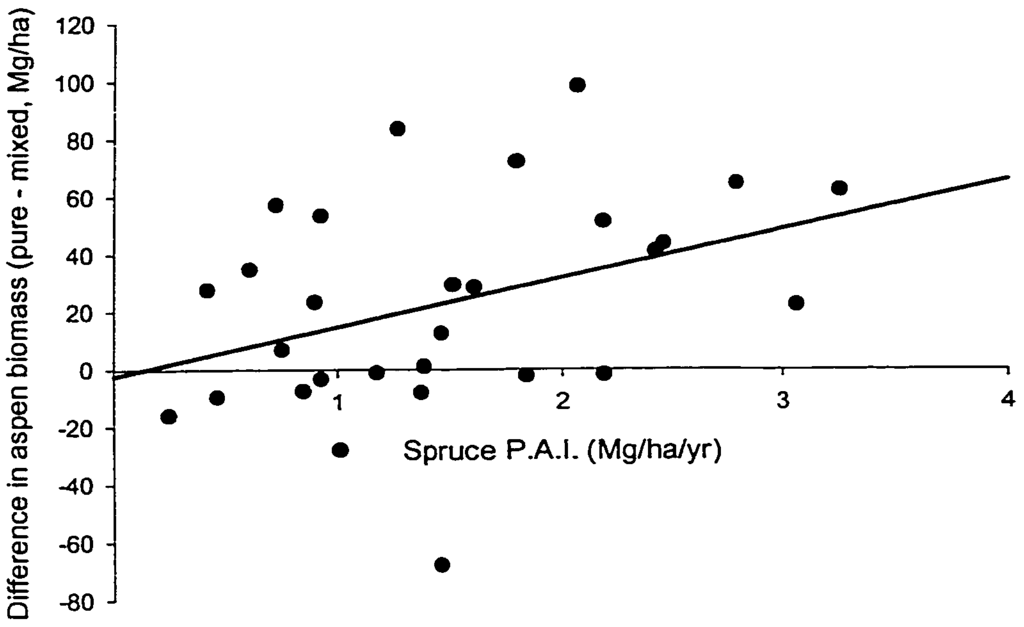


Figure 2.6 Difference in aspen biomass (biomass from pure aspen plots minus biomass from aspen in mixed plots) versus understory white spruce PAI from the mixed plots. $D=16.528*S - 1.911$, $R^2=0.141$, $P=0.045$

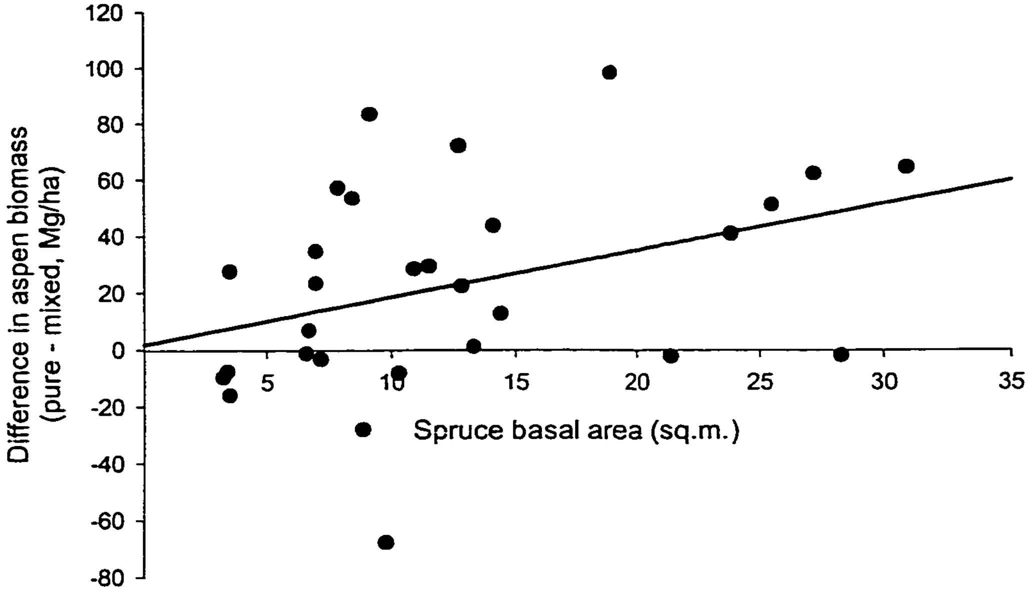


Figure 2.7 Difference in aspen biomass (biomass from pure aspen plots minus biomass from aspen in the mixed plots) versus understory white spruce basal area in the mixed plots. D=1.668*S + 1.774, R^2=0.131, P=0.053.

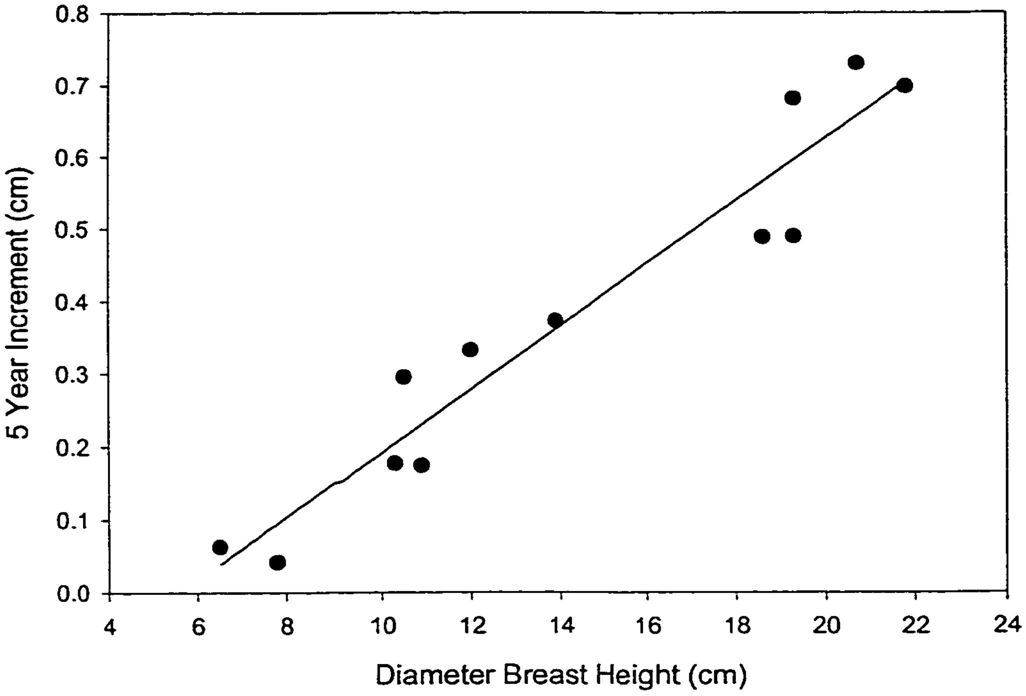


Figure 2.8 Diameter-Increment regression estimation for Stand 27 pure aspen. I=0.0435*D – 0.2437, R^2=0.9269, P=0.0001.

2.7 Literature cited

Beckingham, J. D., and J. H. Archibald, 1996. Field Guide to Ecosites of Northern Alberta. Special Report 5. Can. For. Serv., North. For. Cent., Edmonton Alberta.

Harper, J. L., 1977. Population biology of plants. Academic Press London. 892 p.

Huang, S., Titus, S. J., Lakusta, T. W. and R. J. Held, 1994. Ecologically Based Individual Tree Height-Diameter Models for Major Alberta Tree Species. Alberta Lands and Forest, internal document.

Johnson, E. A., 1992. Fire and vegetation dynamics-studies from the North American boreal forest. Cambridge Studies in Ecology. Cambridge University Press. Cambridge. 129p.

Kelty, M. J., 1989. Productivity of New England hemlock/hardwood stands as affected by species composition and canopy structure. For. Ecol. Manage. **28**:237-257.

Kelty, M. J., 1992. Comparative productivity of monocultures and mixed species stands. *In* M.J. Kelty, B.C. Larson and C.D. Oliver (eds.). The ecology and silviculture of mixed-species forests. pp.125-141. Kluwer Academic Publishers, Dordrecht, 287p.

Lehn, G. A., and K. O. Higginbotham, 1982. Natural variation in merchantable stem biomass and volume among clones of *Populus tremuloides* Michx. Can J. For. Res. **12**:83-89.

Lieffers, V. J., and J. S. Campbell, 1984. Biomass and growth of *Populus tremuloides* in northeastern Alberta: estimates using hierarchy in tree size. Can J. For. Res. **14**:610-616.

Man, R., and V.J. Lieffers, 1999. Are mixtures of aspen and white spruce more productive than single species stands? For. Chron. May/June 1999, V. 75, No. 3.

McDougall, F. W., 1988. Management of boreal mixedwood forests. *In* J.K. Samoil, (ed.). Management and utilization of northern mixedwoods. Symp. Proc., April 11-14, 1988, Edmonton, Alberta. pp. 3-4. Can. For. Serv., North. For. Cent., Edmonton, AB. Inf. Rep. Nor-X-296. 163 p.

Navratil, S., Branter K., and J. Zasada, 1991. Regeneration in the mixedwoods. pp. 32-48. *In* A. Shortried, Editor. Northern mixed-wood '89. Proc. Symp., Sept. 12-14, 1989. Fort St. John, B.C. Pacific Forestry Centre, Victoria, B.C. FRDA Rep. 164.

SAS Institute Inc., 1989. SAS/Stat Users Guide, Version 6, Vol. 2. 4th Ed. Cary, NC. 846 pp.

Singh, T., 1982. Biomass Equations for Ten Major Tree Species of the Prairie Provinces. Info. Rep. NOR-X-242, Nor. For. Res. Cent. Can. For. Serv., Edmonton Alberta.

Stewart, J. D., Hogg, E. H., Hurdle, P. A., Stadt, K. J., Tollestrup. P., and V.J. Lieffers, 1998. Dispersal of white spruce seed in mature aspen stands. Can. J. Bot. **76**:181-188.

Stokes, Maura E., Davis, Charles S., and Koch, Gary G., 1995. Categorical Data Analysis Using the SAS System, Cary, NC. SAS Institute Inc., 499 pp.

Vandermeer, J., 1989. The Ecology of Intercropping. pp. 15-64. Cambridge University Press. p. 237.

Wang, J. R., Comeau, P., and J. P. Kimmins, 1995. Simulation of mixedwood management of aspen and white spruce in northeastern British Columbia. Water, Air and Soil Pollution **82**:171-178.

Chapter 3

Questions from the understory, now what?

3.1 Introduction

This study of mixedwood aspen and spruce productivity was conducted to determine if these species, when grown in association, had greater total biomass or P.A.I. than aspen grown in pure stands. The significance of this study indicates that white spruce understories, in association with trembling aspen overstories, increase total stand P.A.I. and biomass by 12.5% and 10% respectively, over pure aspen stands. Total stand basal area is similarly increased in mixed wood stands by 23.2% over pure stands. This clear evidence shows that spruce-aspen associations have a distinct productivity benefit over pure aspen stands and has been suggested on the basis of theoretical considerations (Man and Lieffers, 1999). Yet the strongest evidence supporting the claim of greater productivity, could only be attained through establishment of trials of controlled densities of different species mixtures. The Western Boreal Growth and Yield Co-op have established growth trials, but it will be many decades before the results from these trials will be available for mid-rotation stands. Therefore a survey of natural stands was deemed the quickest and potentially the easiest way to determine if a productivity trend exists.

3.2 Study weakness and potential corrective measures

This study had several inherent weaknesses, which may have been the reason for failure to develop a strong link between the difference in aspen productivity and increasing spruce basal area, total biomass and P.A.I. Only a weak correlation was observed between the difference in aspen biomass (pure minus mixed) and spruce P.A.I. The failure to detect a strong relationship between aspen productivity and increasing spruce in the understory is reviewed in Chapter 2 (see Discussion). Factors attributing to the lack of a relationship between aspen productivity and spruce understory are thought to be the clonal nature of aspen and its high genetic variability. The lack of controls over tree spacing and organic/inorganic substrate in wild stands. The uncontrolled and variable shrub biomass (in pure aspen stands) and their competitive effects. Lastly the sampling was over too broad a range of aspen stand ages, densities and spruce understory levels.

3.2.1 Sampling in aspen

There are three possibilities in sampling to determine productivity differences between pure aspen and aspen with spruce understories. These include, sampling exclusively within a single clone, sampling a heterogeneous stand with few dominant clones or ignoring the clonal nature of aspen and sampling on a larger scale. The advantage of sampling within the individual clone would be the elimination of genetic variability, excluding vegetative mutation. The difficulty here would be in finding significant numbers of clones of aspen in which an understory spruce was present in part of the stand and missing in another portion of the stand. Alternatively, sampling in a heterogeneous stand with a large number of clones would be preferred, providing the opportunity to examine a wide genetic spectrum within a small unit. The difficulty would be the identification of such a stand and determining that a single clone is not dominant. Finally, ignoring the clonal nature of aspen and increasing the number of paired plots sampled was the technique used and most applicable to industry needs.

As aspen stands age there is usually continual mortality beyond what is typically observed in self-thinning stands. Thus, due to reducing stand densities, the uniformity of fixed area plots decreases as the age of the stand increases. As a result older stands with wide spacing need to be sampled using a larger plot. In this study a fixed area plot was used in all stands regardless of density or age. This, coupled with non-uniform understory spruce distribution, probably added considerable variability to the results obtained from the plots. Sample size should be standardized in the future but sample plot area adjusted with density of stand. Spruce understory spacing must also be controlled in future studies, if the objective is to determine the maximum productivity of aspen stands with spruce understory. Overly dense spruce has several negative impacts, which would tend to reduce the estimate of productivity that might be obtained in mixtures. The growing of high density spruce understories reduce aspen productivity by limiting moisture, slowing the nutrient cycling, and eliminating understory shrubs, herbs and legumes which may be nitrogen fixing. Also the removal of other nutrients, by large volumes of spruce foliage and moisture interception or usage, could limit aspen growth.

3.2.2 Organic substrate

Two problems present themselves when dealing with the issue of organic substrate. The condition of the organic substrate at the time of stand establishment almost certainly affected whether or not spruce seedlings established. If fire is assumed to be the stand initiating event in stand sampled, then two questions can be asked. Firstly, did the removal of organic substrate by fire influence the establishment of spruce? Secondly, did fire have an effect on nutrient availability and growth of the stand in the following decades? If these are true then the paired plot comparison is weakened in validity because there really are two different stands even if fire dissected a single aspen clone. A study of spruce seeded on a fire burned site with vigorous aspen regeneration may increase the understanding of what has happened in these natural occurring understories. Aspen's vigorous re-growth, through suckering, has been the cause of mortality in spruce plantations yet numerous young aspen stands can be found that support spruce in the understory.

The difference between pure and mixed aspen productivity is likely a combination of competitive effects from white spruce in mixed plots and secondly competition from deciduous shrubs, herbs and grasses in the pure aspen plots. In the mixed plots, spruce effectively eliminated or prevented shrubs from getting established, or becoming dominant in the understory. The difference in understory composition highlights two important points. In the spruce understory, the elimination of shrub competition allowed direct use of site resources by both commercial species. In the pure aspen stand the shrub understory would present some competition to the aspen, reducing productivity. This would decrease tree site productivity. Alternatively, some of the shrub or herb species could have improved site conditions for the aspen by such activities as stimulating nitrogen fixation, thus increasing a limiting element on the site and increasing productivity. The deciduous understory would also increase nutrient cycling over what occurred within the spruce understory plots.

3.2.3 Aspen age and decline

In co-dominant mixedwood stands, spruce understories in this study, were approximately the same age as the aspen overstory. Determining if aspen productivity declines in later years was due to stand age or spruce competition is an unanswered question. In this study, we did not see a decline in aspen productivity with age in the pure stands. The approach in this study sampled a range of stands over a 60-year time span. For this approach to be sound, however, the plots should be evenly spaced on the age axis. A difference in productivity between pure and mixedwood plots should be determined for each decade of a stands development. This would allow the forest manager to identify which decade to under-plant spruce in pure aspen stands and for how long they can be grown under aspen, without the competitive effects of spruce reducing aspen productivity.

3.2.4 Spruce basal area

This study examined mixedwood plots with spruce basal area ranging from $3.2m^2$ to $30.9m^2$/hectare. This range was chosen to determine if aspen decline in productivity as the amount of understory spruce is increased. This range of variation in the understory spruce, however, did cloud interpretation of the possibilities for increased total yield in mixtures. An alternative approach would be to sample stands of similar spruce density but uniformly increase basal area of spruce within each decade of aspen stand age. Uniformity in density and relative height of the spruce understory would be desirable characteristics to use in identifying understories for sampling. Although the results of this study did not show the inflection point of critical level of spruce understory (measured by biomass, basal area or age) when productivity of aspen is negatively affected, I believe that such a point exists. Initially when spruce are very small, their competitive effects on aspen is negligible. At some point in the development of spruce understories, the competitive effect they exert on the overstory aspen exceeds the background competitive effects of understory shrub competition. Once spruce understories pass this critical biomass or age or basal area, a reduction in aspen productivity occurs. A study focussing on finding this critical point of competition would be useful to forest managers wishing to grow spruce under aspen for as long as possible without sacrificing aspen growth. The obvious benefit of this would be to keep the basal area on the site as high as possible and therefore maintain continuously high productivity.

Strong light and complete exposure to strong winds may adversely affect white spruce. High light and wind stresses force an individual tree to grow more in diameter and less in height. In contrast, spruce in an understory grow taller (excluding leader whipping) and with smaller diameters. Therefore, basal area comparisons between the open grown spruce and protected understory spruce stands do not accurately represent the future potential growth of each stand. A given basal area of understory spruce usually represents a stand with higher stem density and taller spruce trees than would be found for a similar stand of open-grown spruce. With a gradual release of understory spruce from aspen overstories, these spruce are in a position to respond quickly to improved growing conditions and take on a dominant position in the stand.

3.3 Future mixedwood productivity assessments

The present work has answered the question about mixedwood aspen and spruce stand productivity, indicating mixedwoods are more productive in the stands studied. The next study could focus on identifying how much **more** productive, mixed aspen and spruce stands could be by sampling optimal density mixedwood stands. Future sampling of spruce understories could focus on identifying stands with approximately 6 to 8 m^2 basal area in the understory. The understory density of 800-1000 well-spaced spruce trees, less than 10 meters in height, would be similar to planted understories at 30 years of age or natural stands presently being managed through shelterwood harvesting methods. The location of plots could be carried out using the same methodology as before whereby the spruce understory is located first and then a comparison pure aspen plot within the stand is subsequently located.

This study focussed on comparing mixedwood aspen and spruce productivity to pure aspen stands. This productivity comparison should now be made comparing mixedwood aspen and spruce productivity to pure spruce stand production. The argument against growing mixedwoods could identify that yes, mixedwoods are more productive in total biomass, but they are not more productive at growing conifers, which represent a higher value in the market place. The cost/benefit analysis however, also needs to take into consideration coniferous establishment costs, which will not show pure conifer management to be the best economic opportunity. A different approach will need to be made, as pure 40 year-old conifer stands currently are very rare.

The focus of another study could be the determination of how much spruce can be grown under aspen before the competition from spruce exceeds the normal competition exerted by deciduous herb, grass, and shrub understories, that are so well developed under pure aspen stands. The question could also be asked in reverse, first defining the competitive effect of a deciduous shrub understory and substituting it with a spruce understory.

3.4 Conclusions

Clear evidence supporting increases in basal areas, total biomass and P.A.I. of mixedwood aspen and spruce stands, over pure aspen stands, has been found in this survey. The lack of a stronger relationship between spruce biomass and the difference between pure and mixed aspen biomass, support for the most part the observation that great variability exists in nature and that any survey of natural stands, which has not been controlled experimentally, will contain natural variation. The stands chosen for sampling in this study only crudely mirror the stand composition that would be created by deliberate mixedwood management, but support the critical argument of improved growth and yield in mixedwoods compared to pure stands.

3.5 Literature cited

Man, R. and V.J. Lieffers, 1999. Are mixtures of aspen and white spruce more Productive than single species stands? The Forestry Chronicle. May/June 1999, V. 75, No. 3.

Vandermeer, J., 1989. The Ecology of Intercropping. pp. 15-64. Cambridge University Press. p. 237.

Table 1. Summary of characteristics for 29 paired, pure aspen and mixed (aspen and spruce) stands.

Stand	Age	Density (stems/ha)			Basal Area (m^2/ha)			Total Biomass (Mg/ha)			P.A.I. (Mg/ha/yr)			Spruce	Crown
		Pure	Mixed		Pure	Mixed	Mixed	Pure	Mixed	Mixed	Pure	Mixed	Mixed	surface area	volume
Number	Aw[1]	Aw	Aw	Sw	Aw	Aw	Sw	Aw	Aw+Sw[3]	Aw	Aw	Aw+Sw	Aw	(m^2/ha)	(m^3/ha)
1	80	1680	1320	1320	35.4	29.7	14.1	184	179	140	5.84	7.02	4.57	2344	21518
2	50	1200	1320	720	33.6	28.9	12.8	168	186	146	7.17	8.93	5.87	3196	25146
3	53	1640	1120	1640	45.1	47.3	13.3	245	281	244	5.69	7.39	6.00	3306	32463
4	80	920	640	760	30.9	36.5	8.9	174	227	202	2.74	3.15	2.14	2236	19873
5	84	1480	1400	1120	33.2	44.8	9.8	167	263	235	4.55	6.77	5.30	2456	23331
6	57	1680	1720	960	29.3	25.9	7.0	135	131	111	3.67	4.48	3.58	1756	17590
7	90	880	960	780	32.3	30.9	6.6	180	200	181	4.10	3.90	2.73	1096	10270
8	54	2960	2960	2920	36.1	25.7	8.5	159	136	105	5.87	4.23	3.31	2139	26579
9	54	1640	1480	1000	31.1	34.6	3.5	154	182	170	4.51	5.54	5.29	880	10425
10	53	2600	2400	800	42.4	39.2	6.7	183	194	176	4.92	5.13	4.37	1677	16547
11	81	1440	1640	1400	43.7	30.4	12.7	223	188	151	5.75	6.33	4.53	3217	29802
12	60	1760	1680	840	30.3	31.8	10.3	140	179	149	4.32	4.82	3.44	2666	23186
13	105	920	1240	920	51.0	42.6	11.5	276	280	247	3.33	4.59	3.07	2870	25245
14	53	2080	1880	1240	31.3	29.4	14.4	143	171	131	4.47	3.91	2.44	3595	32146
15	54	1520	1840	640	31.8	26.6	10.9	149	157	121	5.12	4.93	3.32	2786	21760
16	55	1560	1840	560	55.4	40.6	9.2	290	233	206	5.70	5.60	4.33	2301	19140
17	85	1400	1680	1760	39.7	47.6	7.2	255	282	259	5.51	6.25	5.32	1823	20206
18	54	2840	2400	1000	47.9	42.0	3.5	230	214	202	7.50	7.15	6.73	861	10418
19	48	1280	1760	760	44.2	34.2	7.0	223	208	189	5.47	5.45	4.84	1664	15574
20	60	1520	1600	2600	39.9	31.4	7.9	208	177	151	5.87	4.34	3.61	1680	20849
21	65	1160	1040	1200	45.9	36.5	30.9	258	310	194	3.63	5.10	2.32	7713	52622
22	58	680	960	1440	48.6	38.8	25.5	278	307	227	4.35	4.97	2.78	6574	52541
23	54	1160	1440	560	46.7	29.7	18.9	246	204	148	5.06	4.18	2.11	3927	27453
24	53	1280	1360	680	26.0	28.7	3.4	131	152	139	4.07	5.61	4.76	862	7712
25	73	760	680	1240	29.1	25.7	28.3	162	273	164	3.72	4.98	2.79	7155	49525
26	75	800	720	560	44.9	45.8	21.4	264	347	266	4.75	5.18	3.34	5356	35043
27	53	1880	1800	200	26.4	29.8	3.2	126	146	136	5.90	4.10	3.64	808	6524
28	80	600	600	320	38.7	32.4	23.9	229	302	188	3.69	4.90	2.48	5961	31966
29	97	1080	800	680	43.0	36.0	27.2	248	305	185	3.10	6.34	3.08	6794	40042
Mean	**66.1**	**1462**	**1458**	**1056**	**38.4**	**34.6**	**12.7**	**201**	**221**	**178**	**4.8**	**5.4**	**3.9**	**3093**	**25017**

Aw[1] Trembling Aspen Sw[2] White Spruce Aw+Sw[3] Aspen and Spruce volumes

Table 2. Soil textures of 38 mixed and pure aspen plots

Stand Plot Number	Effective Texture Class	Texture Code	Texture	Duff Depth cm	Mottling
3A	3	SiL	silt loam	2.00	no
3B	3	SiL	silt loam	4.00	no
3C	3	L	loam	2.25	no
3D	3	SiL	silt loam	4.00	no
3E	1	S	sand	2.00	no
3F	3	L	loam	4.00	no
4A	3	L	loam	1.75	no
4B	2	SL	sandy loam	2.00	no
4C	1	S	sand	2.00	no
4D	3	L	loam	3.75	no
7A	3	SiL	silt loam	3.50	no
7B	2	SiS	silty sand	2.50	no
7C	3	SiL	silt loam	1.75	no
7D	2	SiS	silty sand	3.00	no
7E	3	SiL	silt loam	2.50	no
7F	3	SiL	silt loam	2.75	no
8A	3	L	loam	2.50	no
8B	2	SiS	silty sand	2.50	no
8C	2	SiS	silty sand	2.25	no
8D	2	SiS	silty sand	1.75	no
8E	2	SiS	silty sand	1.75	no
8F	3	L	loam	2.00	no
9A	1	S	sand	3.00	no
9B	1	S	sand	2.25	no
9C	1	S	sand	3.00	no
9D	1	S	sand	2.75	no
9E	1	S	sand	2.00	no
9F	1	S	sand	3.00	no
14A	4	SiCL	silty clayloam	1.50	no
14B	2	SL	sandy loam	3.00	no
14C	2	SiS	silty sand	2.50	no
14F	2	SiS	silty sand	3.00	no
16A	3	L	loam	2.25	no
16B	3	L	loam	5	no
16C	3	SiL	silt loam	2.5	no
16D	4	SiCL	silty clayloam	3.75	no
16E	4	SiCL	silty clayloam	2	no
16F	4	SiCL	silty clayloam	3.75	no

Table 3. Plant community occurance[1] rating in 22 Trembling aspen stands

	STAND NUMBER																					
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
T. aspen	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6
W. spruce	5	6	6	6	6	6	6	6	6	6	6	5	5	6	6	6	6	6	6	6	6	6
B. spruce		4			4			1		1		1		2	3							
W. birch	5	6	3	3	6	6	2	1	4	1	3	1		6	5	6			1	4	2	2
B. poplar	1	2	3	1	1	5	6	2	2	6	6	4	3	2	4	3	5	6	6	6	1	5
B. fir	1	1	1					1														
B. hazelnut		1																		6		
P. Rose	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6
HB. Cranberry	5	5	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6
Buffalo berry	1	3	2	3		1	4	4		1	6		2		4	1	5	3			6	5
alder sp.				1						6	6	1			2						2	2
willow sp.	4	6	6	6	6	6	6	6	6	6	6	3	1	4	6	6	6	6	5	4	6	3
Twin-flower	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6
Saskatoon	4	4	1	Y[3]	2	3	5	1	6	6	X	2	3	3	3	5	6	6	6	6	3	4
Pin cherry			1		2								1									
Sarsaparillo	X[2]	4	X	5	6	5	5	2	5	6	6	6	5	6	6	6	6	6	6	6	2	6
Bunchberry	6	5	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	5	6	6	6	6
Bishop's cap	4	4	2	4	5	1	5	6	6	6	6	6	6	6	6	5	6	6	6	6	6	6
Fireweed	1	3	6	6	6	6	6	6	6	6	6	5	6	6	6	6	6	6	5	6	5	3
Dewberry	2	6	1	3	X	X	6	6	6	6	6	6	5	6	6	5	6	6	6	6	6	6
Strawberry	3	6	6	6	6	6	6	6	6	6	6	4	4	6	6	6	6	6	6	5	5	6
Wintergreen	6	6	6	4	6	6	6	5	4	4	6	2	3	6	5	4	6	5	5	5	6	6
Coltsfoot	5	6	4	3	6	6	4	5	3	6	6	6	6	6	6	6	6	6	6	6	6	6
M. Reed grass	6	6	6	6	6	6	6	6	6	6	6	6	5	6	6	6	6	6	6	6	6	5
Hairy Wild rye	2	X	X	X	X	X	1	6	6	6	6	6	5	6	6	5	6	6	6	6	6	6
Stairstep moss	6	6	6	5	6	6	6	6	6	6	6	6	5	6	6	6	6	6	6	6	6	6

occurance[1] = rating reflected the number of plots in a stand in which species was found. Total n=6.

X[2] = early spring sampling made identification of plant difficult as species had not emerged.

Y[3] = not found in plots but in surrounding stand.