INVESTIGATING PRODUCTIVITY AND FOLIAR NUTRIENT STATUS IN SECOND GROWTH WHITE SPRUCE (*Picea glauca*) AND TREMBLING ASPEN (*Populus tremuloides*).

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ABSTRACT

Neufeld, B.A. 2011. Investigating productivity and foliar nutrient status in second growth white spruce (*Picea glauca*) and trembling aspen (*Populus tremuloides*).

Keywords: Boreal mixedwoods, Hegyi‟s competition index, facilitation, foliar nutrient status, periodic basal area increment, productivity, trembling aspen, white spruce.

This thesis synthesizes two related papers investigating competitive interactions of second growth white spruce (*Picea glauca* [Moench] Voss) and trembling aspen (*Populus tremuloides* Michx.) at the Fallingsnow Ecosystem Project sites near Thunder Bay, Ontario. In the first paper, biweekly white spruce foliar concentrations and ratios of N, P, K, Ca, Mg and micronutrients were analyzed for 12 trees of varying mixture proportion, throughout the 2010 growing season. Results were analyzed with repeated measures design to determine patterns in foliar nutrient concentrations, including seasonal stability and the effect of mixture proportion on the timing of these relationships. Seasonal trends were evident in concentrations of N, P, K and Ca, as well as in many nutrient ratios (Ca/N, Mg/N, Mn/N and Zn/N). Significantly lower foliar P, K and P/N and higher Ca, Ca/N, Mn/N and Zn/N were observed in foliage from spruce trees in spruce dominated stands. The presence of aspen appeared to influence the amount and duration of nutrient uptake. These results suggest that it is important to differentiate between mixed- and mono-cultures for foliar nutrient research in plantation white spruce.

The second paper investigated mixedwood productivity, white spruce and trembling aspen growth rates and white spruce nutrient status along a range in density and mixture at these same sites. Growth rates, in the form of periodic basal area increment (PBAI), were measured from the cores of 39 white spruce trees and 44 trembling aspen. Core tree-rings were measured using WinDENDRO software. The 39 sample spruce trees were analyzed for several foliar macro- and micro-nutrient concentrations. Foliar nutrient contents were estimated using an allometric equation for foliar biomass of plantation grown white spruce. Nutrient use efficiencies were determined as the relative amount of nutrient invested per unit growth. PBAIs were scaled to compare site productivity. The relationships between spruce and aspen growth rates, spruce nutrient status and productivity with mixture proportion and density were analyzed as response surface designs. Mixture proportion and density adequately predicted aspen PBAI ($p = 0.02$), white spruce foliar concentrations of P, K and Ca/N ($p = 0.053$, 0.060 and 0.031, respectively), as well as mixedwood productivity ($p = 0.001$). Results suggest that 20 year old plantation spruce-aspen mixedwoods experience decreased intra-specific competition than do monocultures of either species. A facilitative relationship is expected to exist between these species where nutrients are limiting growth.

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1.0 THESIS INTRODUCTION

1.1 THESIS RATIONALE AND OVERVIEW

Mixedwood competition can be described and measured in many ways including belowground competition for soil resources (i.e. nutrients, water) and aboveground competition for light and physical growing space. There are species-specific requirements for resources (including water, light and nutrients) to attain optimal growth. Species interactions can be complimentary, detrimental or neutral to one or both when grown together as opposed to in monocultures. The factors that determine whether species will be antagonistic or beneficial in mixture, are numerous and species-specific. Density, for one, can strongly influence competitive outcomes. High density stands are expected to experience greater competition, resulting in lower individual tree growth rates than those found in stands with lower densities. However, in combination, species may be able to tolerate moderate densities due to beneficial combining ability, resulting in greater overall productivity. Due to the ever changing dynamics in a stand‟s development, it is important to focus on recent productivity as opposed to whole tree biomass to investigate current competitive interactions. Furthermore, variation in annual growth may vary due to climatic extremes, e.g. a drought year vs. an ideal growing season. For these reasons, average growth rates of the last 5 years (periodic basal area increment; PBAI) may best represent the effect of species interaction and density on tree growth and site productivity. Furthermore, where there is improved productivity there may an improvement in site nutrient status as a result of mixed v. single species conditions (facilitation). Where greater productivity exists in mixedwoods compared to conifer monocultures, we may expect to find increased forest products per hectare. This may reduce the amount of managed land and vegetation control and thus, the associated financial, social and environmental costs. In this thesis, competition between (inter-specific) and within species (intra-specific) is assessed at a white spruce (*Picea glauca* [Moench] Voss) and trembling aspen (*Populus tremuloides* Michx.) second growth research site.

To understand how the presence of aspen may influence white spruce growing conditions, Chapter 2 investigates the effect of species mixture on seasonal variation in white spruce foliar nutrient concentrations and ratios. If the presence of aspen is beneficial to white spruce growing conditions, an improvement in white spruce foliar nutrient status should exist where aspen is present. This chapter investigates white spruce foliar nutrient stability (when foliar nutrients are physiologically stable, i.e. translocation at its minimum) for ideal sampling time as well as the effect of mixture proportion on these nutrient values and timings of stability. Since density also plays a significant role in species interactions, Chapter 3 investigates how density and the presence of aspen influence white spruce and trembling aspen growth rates (PBAI) and site productivity (PBAI •ha^{-1}). If white spruce growth rates and increased productivity occur at optimal densities and mixtures compared to spruce monoculture, facilitation from aspen may be occurring. To investigate this relationship, white spruce foliar nutrient status was measured along mixture and density gradients.

The final chapter discusses the implications of managing these mixed, second-growth spruce-aspen plantations in northwestern Ontario.

1.2 LITERATURE REVIEW

1.2.1 Mixedwood competition

Competition between species occurs when two or more species are adapted to capturing the same growth resources either above- or below-ground (José *et al*. 2006). However, species in a mixedwood system may have different resource needs, both in terms of timing and amounts, as well as different structural means of obtaining them, leading to mutually beneficial stratification. Without these differences in resource use and acquisition, more intense competition may occur, resulting in decreased uptake per individual (Begon *et al.* 1996). Mixtures that include both coniferous and deciduous species have some of the best combining abilities (Kelty 1992). These species have different crown shapes, light optima, and leaf-off periods where more light can reach the understory.

Mixtures of trembling aspen and white spruce in particular, with differing rooting, nutrient accumulation and distribution strategies may utilize and replenish soil resources differently (Man and Lieffers 1999). Furthermore, having aspen in a stand is expected to increase the amount of nutrients available from the soil (Wang *et al.* 1995). Aspen litter can improve forest floor conditions by increasing decomposition, reducing acidification and thus increasing nutrient turnover compared to spruce monoculture. Furthermore, aspen‟s low leaf area allows more light to reach the forest floor, creating improved growing conditions for shrub and herb species which may further enrich belowground growing conditions for white spruce.

Another beneficial trait of these spruce-aspen mixtures comes from the difference in the species‟ life cycles; aspen tends to dominate for 50 to 60 years until they reach their pathological rotation, at which point spruce dominance increases. Since spruce foliage becomes light saturated at a lower light level than aspen does, spruce is an ideal species for understory growth.

Where beneficial combining characteristics exist, mixed-species systems may be able to better capture limited resources, resulting in greater total biomass than the same species grown as monocultures (Cannell *et al.* 1996; Kelty 2006). Mixtures are expected to be more productive when they include a fast growing, shade intolerant hardwood in the overstory, such as trembling aspen, and a slow growing, more shade tolerant conifer, like white spruce, in the understory (Man and Lieffers 1999). Mixtures with trembling aspen in particular are said to increase productivity of northern conifers compared to single species stands (Peterson 1988). For example, a range of aspen basal area was added to black spruce stands without affecting spruce volume (Legaré *et al.* 2005). Furthermore, greater overall biomass and periodic annual increments were evident in aspen stands with understory white spruce compared to pure aspen conditions (MacPherson *et al.* 2001). Among the possible numerous mechanisms responsible for these increases are; i) exploitation of greater volumes of soil resources (Wang *et al.* 1995), ii) temporal separation of resource use and/or iii) enhanced nutrient cycling (Man and Lieffers 1999).

1.2.2 Competition indices

Competition indices, based on any one or a combination of tree and/or plot characteristics, are used to quantify for the purpose of comparison, the amount of competition that a tree is experiencing due to neighbouring trees. In a review of several competition indices and comparison studies, it was found that the simple size ratio indices are just as good as the more complex (Holmes and Reed 1991). In particular, indices that incorporate diameter at breast height (DBH) were found to be more reliable than indices that include crown dimensions or calculated influence zone overlaps or area potentially available. Hegyi‟s competition index (HCI) [1] is a simple size ratio, distance dependant index that was found to be both reliable and consistent over time, regardless of species (Holmes and Reed 1991).

$$HCI = \sum_{c=1}^{n} \left(\frac{DBH_c}{DBH_s} x \frac{1}{DIST_{cs}} \right) \qquad [1]$$

where, *DBH* is the diameter at breast height (cm) of the subject tree *s* and competitor tree *c*, and *DISTcs* is the distance (m) between the subject tree *s* and competitor tree *c*.

Higher HCI values are associated with competitor trees (*C*) that are larger than (diameter at breast height or DBH), and closer to the subject tree (*S*) compared to smaller and/or more distanced competitors (Table 1.1). Understandably, a larger and closer competitor tree is expected to have a greater influence on local growth resources.

Table 1.1. An example of the numerical evaluation of competition as measured by Hegyi‟s competition index demonstrating how this index accounts for the size and distance away of four competitor (*C*) trees in relation to the subject tree (*S*).

		DBH	
		$C > S$	$C < S$
DIST_{CS}	Far	1	0.5
	Near	1.5	1

When calculating competition, it is also necessary to determine the size of the search radius. Competition indices based on the idea of influence zone (such as distance dependant indices like Hegyi‟s) assume that the majority of competition for resources occurs closest to the tree where a tree and its neighbours‟ growth “zones” overlap (Holmes and Reed 1991). Therefore, it is common to use a search radius that is slightly wider than the longest crown radius of the largest species. Others have suggested doubling the radius of the widest horizontal crown to ensure that the majority of the competing vegetation is captured (Barbour *et al.* 1987). The original HCI study used a 3 metre search radius, however, it was noted that the size is not critical with this index as the output values are strongly affected by the distance between the sample and competitor trees (Hegyi 1974). As the search radius extends further, the individual HCI value for distant competitors becomes minimal.

1.2.3 Density and realized productivity

Density has been controlled to increase conifer yield in forest management for many years. However, the optimal density for highest yield may be different depending on the species, mixture proportion and age. It has been suggested that for white spruce and trembling aspen, productivity will vary depending on mixture and density (Man and Lieffers 1999). At high densities, the two species are likely to be stunted due to limited resources. Competition is anticipated to be minimal in low densities where interactions between individuals are limited. Theoretically, at optimal densities, competition would be sufficient to encourage positive interactions for certain species combinations. Although the optimal density may change over time, the greater influence of density is expected to occur in juvenile stands, before canopy closure. As a stand nears canopy closure, optimal density may become relatively stable until the stand reaches maturity. This period of stability, however, may occur at different stands ages for the varying mixture proportions due to differences in canopy structure.

In competitive interactions, shading may be just as important as crowding depending on a species" tolerance to either (Canham *et al*. 2004). Deciduous species can have a competitive advantage over conifers through fast growth after disturbance and tolerance of crowding.

Productivity is also affected by a tree"s nutrient status. Nutrient deficiencies affecting photosynthetic rates will immediately reduce growth. However, a tree under optimal conditions of soil moisture and nutrients, light and space (all influenced by density to some degree), will have optimal photosynthetic rates. Photosynthetic rates depend heavily on nitrogen for metabolic processes, for deciduous species in particular (Waring and Schlesinger 1985). Conifers, on the other hand, have a slower reaction to increased levels of available N and are more likely to respond with an increase in leaf biomass rather than higher photosynthetic rates (Waring and Schlesinger 1985).

1.2.4 Foliar nutrition

Most macro- and micronutrients have known roles in plant growth and maintenance. The vital role of N in plant growth is often used as an indicator of plant nutrient status. However, N cannot function alone. Another key nutrient in plant metabolic processes is P and a deficiency in either (P or N) would reduce growth. Phosphorus is required for the synthesis of ATP, the main form of plant energy. Adequate levels (> 0.16%) of P are needed for proper partitioning of the products of photosynthesis, without which, these products would get backed up in the chloroplast, reducing the efficiency of N (Lambers *et al.* 2008). Therefore, a deficiency in P may inhibit the utilization of N. For this reason it is also useful to study nutrient ratios. Ratios of P/N < 0.06 are considered deficient whereas P/N >0.16 means P deficiency is unlikely (Ballard and Carter 1986). Intermediate ranges of P/N of 0.06 to 0.16 have the potential for becoming deficient if relatively more N is acquired than P.

Potassium, another key element for plant growth, is required for stomatal conductance (Lambers *et al.* 2008). Pumping K ions in and out of guard cells regulates the aperture of the stomata, thus influencing the rate of water loss and gaseous exchange in the leaf. Another important role of K is in regulating sapwood hydraulic conductivity which is also sensitive to transpiration rates (Zwieniecki *et al.* 2001). Calcium aids in reducing toxicity of other cations (including Fe and Al). Without sufficient levels of Ca, cell walls would weaken and moisture stress would increase (Kimmins 1987). However, too much calcium can cause high pH within the leaf which can lead to a deficiency in P. Chlorophyll, the photon receptor for a leaf (or any green tissue), is synthesized in part using Fe and Mg.

Nutrients involved in plant growth and function are interconnected and inter-dependent. Furthermore, fluctuations of stored carbohydrates in the leaves during the growing season make it best to use nutrient ratios for comparisons as opposed to concentration alone (Linder 1995). Nutrients expressed as a per cent of nitrogen by weight were found to be more valid than optimal or target concentrations for Norway spruce (Linder 1995) which may be the case for white spruce as well.

The mobility of nutrients like N, P and K also plays a role in avoiding deficiency through redistribution. Immobile nutrients including Ca, B, Mn and Al cannot be re-translocated and thus are lost when leaves are shed. Since these nutrients must be obtained anew for new growth, deficiencies of immobile nutrients are most evident in new growth (Kimmins 1987). If aspen foliage, shed annually, improves local soil conditions through faster turnover and greater nutrient availability, immobile nutrients would have a faster cycle and be less likely to get tied up in the forest floor. This is another potential benefit of the white spruce/trembling aspen mixture dynamic or any mixture that includes both coniferous and deciduous species.

Some studies have measured the response of conifer foliar nutrient levels to the presence of deciduous trees in mixture compared to pure stands. No difference in nutrient status was evident for Norway spruce growing with European beech (Rothe *et al.* 2003) while an overall improvement in nutrient status for Norway spruce was evident in mixed stands with beech, birch or oak (Thelin *et al.* 2002). The improved nutrient status for Norway spruce included higher concentrations of N, K, P and Zn, higher K/N, P/N and Zn/N. If these increases were associated with improved tree health or growth rates, it would suggest a facilitative relationship between the species in question.

The concentration of nutrients in spruce needles at any point may vary by needle age and position in the crown (Kimmins 1987). Specifically, concentrations of N, P and K in white spruce foliage have been shown to decline with age (Wang and Klinka 1997). Furthermore, nutrient levels vary throughout the growing season but are expected to become stable in late summer and fall (Fernandez *et al.* 1990). Another factor to consider for the sampling of spruce foliage is that exposure to sunlight creates denser needles than those found in the shade (sun v. shade leaves). This effect is most evident in conifers known to self shade (Waring and Schlesinger 1985). All of these factors make it important to be consistent in sampling location on the tree, timing of sampling and needle age cohort collected.

1.2.5 Nutrient content

Although useful as simple indicators, nutrient concentrations and ratios are not the whole story. A nutrient concentration may appear to be declining when in fact the amount of the nutrient has not changed but the size of the leaves has increased. This is known as dilution effect. For this reason, nutrient contents are a better assessment of a tree‟s nutrient status. Contents can be estimated using allometric equations when destructive sampling for foliar biomass measurement is not an option. For example, Trees A, B and C of the same species have the same concentration of a foliar nutrient but Tree C has a higher total foliar biomass and thus has a greater nutrient content that would be contributing to tree growth (Table1.2). On the other hand, Trees 1, 2 and 3 have similar foliar biomass values but Tree 1 has a higher concentration of foliar nutrients and thus higher content. Comparing between sets, even though Tree C has the largest foliar biomass, it has lower nutrient content than Tree 1 due to its lower concentration. The question then becomes: Is it better to have more foliage with lower nutrient levels, or less foliage with higher levels? Will greater nutrient content result in a more productive tree? Nutrient use efficiency (NUE) brings these two questions together as it is a measure of the amount of growth per gram of nutrient. Using nitrogen for example, a higher NUE would suggest a more efficient tree, having more growth associated with the same unit of nitrogen (mg, g, kg). White spruce foliar nutrient concentrations, contents and NUEs have never been reported for second growth spruce and aspen in mixture across a range in species proportion and density.

Table 1.2. Varying nutrient concentration and foliar biomass: An example of the importance of nutrient content.

Tree	Concentration %	Biomass	Content kg tree^{-1}
A	0.5	20	10
B	0.5	30	15
C	0.5	40	20
1	0.75	30	22.5
2	0.5	30	15
3	0.25	30	7.5

1.3 THESIS OBJECTIVES

The general purpose of this thesis was to investigate the competitive interactions of second growth white spruce and trembling aspen across a range in proportional mixtures and density. Specifically, it was of interest to determine if facilitation is occurring between these species, resulting in greater PBAI, white spruce nutrient status and/or stand-level productivity, which may only be evident at specific mixture proportion/density combinations. We expected to see increased productivity and spruce growth in mixture as opposed to monoculture and for white spruce foliar nutrient status to be an indicator for these optimal conditions. In order to confirm ideal foliar sampling time for white spruce in northwestern Ontario, it was also of interest to determine the seasonal variation and period of nutrient stability of white spruce foliage as well as the influence of aspen on these patterns. We expected to see a significant relationship between the presence of aspen and white spruce foliar nutrient levels.

2.0 SEASONAL FOLIAR NUTRIENT VARIATION IN PLANTATION WHITE SPRUCE GROWING IN MIXTURE WITH VARYING LEVELS OF TREMBLING ASPEN COMPETITION

2.1 INTRODUCTION

White spruce (*Picea glauca* [Moench] Voss) and trembling aspen (*Populus tremuloides* Michx.) are commercially and ecologically important species with their overlapping ranges found across Canada and the upper United States. White spruce is relatively slow growing, moderately shade-tolerant, and tends to dominate in intermediate and late successional stages (Nienstaedt and Zasada 1990). In contrast, trembling aspen is a fast growing, shade-intolerant, pioneer species with vigorous vegetative growth that allows it to quickly occupy a site after disturbance (Perala 1990). Aspen has been shown to be a nurse/shelter species for young white spruce where it benefits from reduced intensity of solar radiation, wind, frost and pests (Brace Forest Services 1992; Comeau 1996; Groot and Carlson 1996; Pritchard and Comeau 2004). Improved conditions in such mixedwoods may be a result of differences in use and/or replenishing of soil resources including improved soil decomposition and turnover, lower likelihood of acidification and greater nutrient availability (Wang *et al.* 1995; Man and Lieffers 1999; Thelin *et al.* 2002) due to faster turnover of aspen foliage and/or a greater amount of nutrients in aspen foliage compared to spruce. An improvement in soil nutrients should be evident in foliar chemistry (Iyer and Wilde 1974; Ballard and Carter 1986; Kimmins 1987) when comparing spruce trees grown with varying levels of aspen competition.

Aspen canopies have less leaf area than white spruce, allowing greater light penetration (particularly in spring and fall) and resulting in more desirable microclimate conditions (Constabel and Lieffers 1996; Voicu and Comeau 2006). Furthermore, if aspen and spruce in mixture can stratify roots, both species may have more space for root growth improving their ability to capture soil resources (Man and Lieffers 1999) possibly leading to prolonged nutrient uptake during the growing season in mixtures when compared to pure stands.

White spruce foliar nutrient concentrations in current needles have been shown to be positively correlated with soil available nutrients including N, P, K, Mg, and S (Wang and Klinka 1997); however, it is unclear how these foliar nutrients are influenced by the relative amount of trembling aspen in mixed stands. We expect white spruce foliar nutrient concentrations and ratios to vary with different levels of aspen present in the immediate neighbourhood of the tree. Similar studies have described seasonal trends for red spruce (*Picea rubens* Sarg.) (Fernandez *et al.* 1990) and compared pure and mixed Norway spruce (*Picea abies* [L.] Karst.) stands (Thelin *et al.* 2002). Limited data exists for optimal nutrient status and sampling time (when nutrients are relatively physiologically stable) for plantation white spruce.

Nutrient concentrations in spruce needles vary by age of the foliage and position in the crown (Kimmins 1987) making it important to be consistent with needle age and sampling location on the tree. Concentrations of N, P and K tend to decline with needle age (annual cohorts), while Ca increases for white spruce (Wang and Klinka 1997). Variation in nutrient concentrations and ratios also occurs with different stand types. Current growth of Norway spruce growing in mixed stands was shown to have higher concentrations of P, K and Zn and higher P/N, K/N and Zn/N ratios than pure stands

(Thelin *et al.* 2002). We expect to see similar results for various nutrients in white spruce foliage over time where aspen is present.

To ensure that results are comparable, studies of foliar nutrient dynamics in forest systems rely on the use of consistent and standardized measures. For example, between species and even individual age cohorts of coniferous foliage, foliar nutrient levels fluctuate with time of year and soil nutrient availability (Fernandez *et al.* 1990; Wang and Klinka 1997). As well, nutrient levels in newly flushed foliage differ from those in leaves entering senescence due to differences in physiological development, nutrient requirements at different life stages, and nutrient mobility within the leaf. Nutrient levels in seedlings grown in greenhouses differ from those grown in the forest (Wang and Klinka 1997). Species that hold foliage for more than one season present additional complexity as do those that re-translocate nutrients prior to leaf fall. Given the possible range in nutrient levels and the potential errors associated with scaling up from individual trees to the stand level, it is necessary to understand nutrient fluctuation patterns and choose an appropriate sampling time. To that end, we investigated the effects of sampling time and stand composition on the concentration of N, P, K, Ca, Mg, and several micro-nutrients in the foliage of white spruce (*Picea glauca* [Moench] Voss) growing with and without trembling aspen (*Populus tremuloides* Michx.) in a twenty-year old stand near Thunder Bay, Ontario. We suspect that due to differences in physiology and rooting pattern, the point in time when nutrient concentrations become stable during the growing season may differ depending on the amount of aspen present. Once nutrient concentrations stabilize, we expect our samples to be consistent and our foliar nutrient results comparable to other white spruce nutrient concentration studies.

2.2 METHODS

This study was conducted within the Fallingsnow Ecosystem Project (FEP), which consists of three cut blocks (named 2, 3 and 4) situated between 89˚49-53‟W and 48˚8-13‟N, 60 kilometres southwest of Thunder Bay, Ontario. Before harvest, these blocks were aspen-spruce mixedwoods and were planted primarily with white spruce at 1,700 stems •ha^{-1}, approximately 20 years prior to this study (Bell *et al.* 1997). As part of the original study in 1993, the sites underwent four vegetation management treatments including herbicide (Vision® and Release®), thinning (brushsaw and Silvana), and no treatment (control), which led to a range in densities of even-aged white spruce and trembling aspen mixtures (Pitt and Bell 2005).

In 2008, 45-150m^2 permanent sample plots were established across the FEP cut blocks; these were stem mapped in 2009. Mixture was measured as the level of competition experienced by individual trees was measured using Hegyi‟s competition index (HCI). The HCI is a distance-dependent, size-ratio, competition index measured at the tree level (Hegyi 1974). We are not aware of any studies that have used a similar method for describing plot mixture. We consider this approach better than using density or basal area alone since the latter do not assess the „importance‟ of each competing tree relative to the subject tree. This method accounts for differences in distance away and size (competitor relative to subject tree) but not species. The HCI has been shown to be reliable and consistent across a range of species and over time (Holmes and Reed 1991) and is plot size independent (Hegyi 1974). In general, in even-aged, single canopy stands it is accepted that most competition for above- and below-ground resources occurs between a tree and its nearest neighbours. In the HCI method the assessor decides what constitutes a “nearest neighbour”. Some have suggested that most competition for any individual occurs within or just beyond the lateral extent of the crown (Weiner 1984). We chose a plot size of 3 m, double the average spruce crown radius, which extended beyond the maximum crown radius and included all competitor trees in the immediate vicinity of the subject tree.

Using the 150 m^2-fixed plot stem map database, the level of competition for each eligible subject white spruce (crown in the canopy, and with only white spruce and trembling aspen neighbours; Figure 2.1) was calculated individually for HCI [1] using azimuths and distances from centre for a 3-m-radius plot.

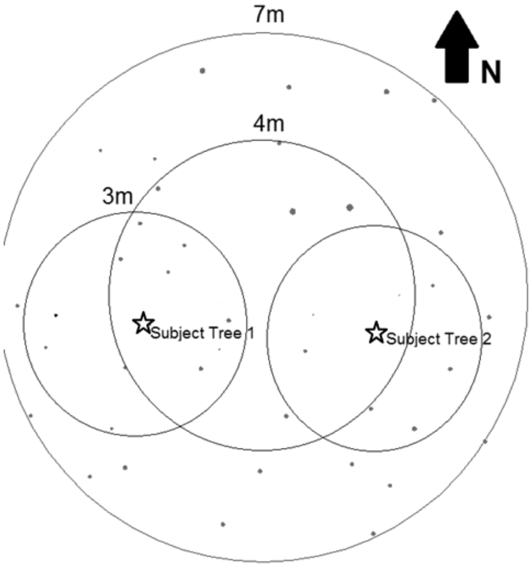


Figure 2.1. A search radius example for eligible subject trees within a 150m^2 fixed area pure spruce plot located at the Fallingsnow Ecosystem Project.

A total HCI value was determined for each tree-centred plot (3m) as well as a proportion by species. These proportions were used to assign the mixture class at the tree level denoted as Sw100, Sw75, Sw50 and Sw25 based on level of aspen competition (from least to most). Each mixture class represents the mid-point of the class, e.g., a 50-50 mixture indicates spruce competition accounted for 37.5 to 62.5% of total HCI and was classified as Sw50. Density was calculated from the number of trees in the 3-m-radius plot. Of the entire pool of eligible trees (n =140, within 4 m radius of centre), 12 white spruce trees surrounded by total densities between 2,500 and 5,700 stem •ha^{-1} were selected for biweekly foliage sampling (3 trees from each mixture group).

For the 12 sample trees, current year‟s foliage, a reflection of existing forest floor conditions, was collected every two weeks from mid-April to mid-October from south facing branches in mid-crown. Samples were bagged for transport to the lab where they were oven-dried at 70°C for 24 hrs and ground using a Wiley Mill with a 40-mesh screen. Foliage was analyzed for N (LECO CNS), P, K, Ca, Mg, Al, B, Cu, Fe, Mn, and Zn concentrations (digestion followed by ICP-AES; Munter and Grande 1981). Blanks and quality control samples were used to ensure quality data. Foliar moisture contents were measured in the lab after 2 hrs at 105˚C. Sample weights were adjusted to reflect oven dry weight. Although sampling began in April, adequate (approximately 4 g per tree) oven dry, ground foliage for analyses was not available until the end of May. Repeated measures design (SPSS 17.0) was used to determine the period of stability for each nutrient concentration and ratio overall and by mixture. Duncan‟s post hoc test determined differences between mixtures.

2.3 RESULTS AND DISCUSSION

The 12 selected spruce trees were similar in age and size, as well as plot density and basal area (Table 2.1) regardless of mixture classification. Shapiro Wilk test for normality and Levene‟s test of homogeneity of variance of residuals were performed for each nutrient model. Residuals were normally distributed with homogenous variance.

Table 2.1. Attributes of white spruce trees sampled for foliar nutrient analysis.

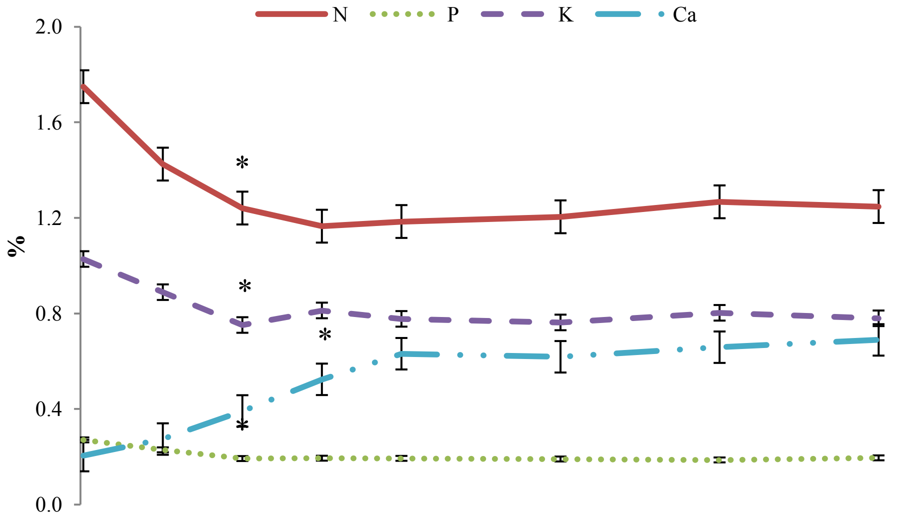
Attribute	**Mean** (n =12)	**Standard deviation**	**Min.**	**Max.**	**p-value**
Diameter at breast height (cm)	10.2	1.5	7.4	12.0	0.70
Total height (m)	6.9	1.1	5.0	8.5	0.38
Vertical live crown (m)	5.5	1.0	3.8	7.0	0.24
Total density (stems ha^{-1})	3,500	204	2829	5659	0.17
Basal area in (m^2 ha^{-1})	20	3	0.05	0.10	0.15

2.3.1 Seasonal nutrient variability: Concentration and ratios

For all nutrients in all trees, the greatest change occurred in the first four to six weeks (late June and mid-July) with levels of N, P, and K declining and Ca increasing (Figures 2.2a and 2.3; Appendix I). These trends were similar to those observed in Norway spruce (Linder 1995). However, a seasonal trend in Mg was not apparent in this study, which differed from the early season decline observed for Norway spruce. Declines in P between the initial (0.27%), second (0.23%), and third (0.19%) measurements appeared slight but were statistically significant. Concentration of N declined from 1.7 to 1.2% while K declined from just above 1 to 0.75% over the first four weeks. At the same time, Ca doubled from approximately 0.2 to just over 0.4%. Levels of all four nutrients were stable for the remainder of the season. In contrast, foliar concentrations of N, P, and K for red spruce in the northeastern United States did not become stable until late summer (Fernandez *et al.* 1990), likely due to the warmer and more variable coastal climate. Furthermore, red spruce Ca values did not stabilize over time but rather continued to increase throughout the season.

Increasing ratios of Zn/N, Mn/N, Mg/N, and Ca/N (Figures 2.2b and 2.4) were evident at the beginning of the growing season, attaining stability by Week 6 (mid-July). Additional upwards shifts in these ratios near the end of the sampling season (mid- to late-September) may suggest that nutrient re-translocation was beginning as the trees entered the dormant season. No seasonal trend was evident for Mg, Al/N, B/N, Cu/N, Fe/N, K/N, Mg/N, or P/N.

a) Concentrations



b) Ratios

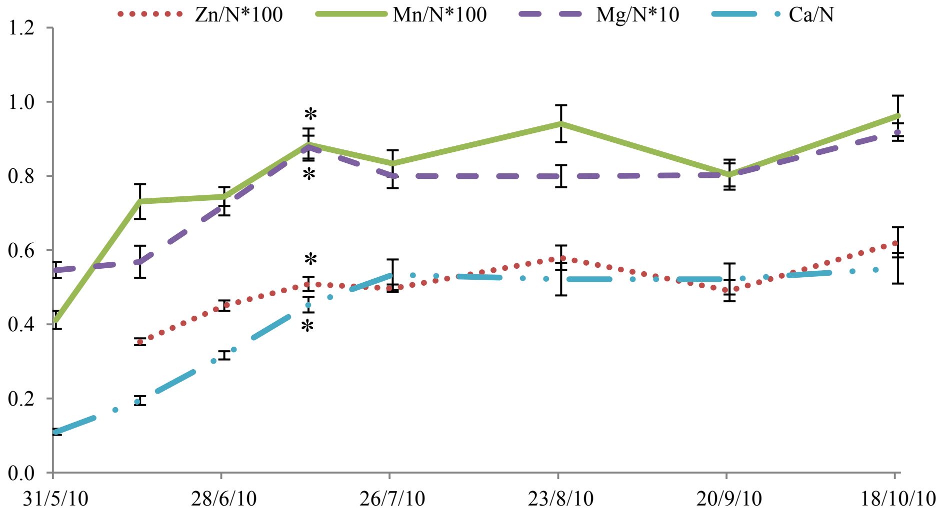


Figure 2.2. Seasonal patterns with standard error bars for (a) foliar concentrations of N, P, K and Ca and (b) foliar ratios of Zn, Mn, Mg and Ca to N concentrations for white spruce in 2010 at Fallingsnow Ecosystem Project. The symbol "*" denotes onset of nutrient stability.

2.3.2 Seasonal nutrient variability by mixture

When separated by mixture, significant differences were evident in the foliar concentration of P, Ca, and K, and in the P/N, Ca/N, Zn/N, and Mn/N ratios (Table 2.2).

Several patterns emerged when foliar concentrations were plotted by species mixture. First, lack of aspen competitors led to significantly lower foliar P (a mobile nutrient) concentration and P/N relative to that found in trees with more competition from aspen (Figures 2.3b and Figure 2.4a, respectively). As P/N declines, the chances of P deficiency increase. The opposite trend was found for Ca, a non-mobile element, where the presence of aspen (Sw25) led to significantly lower concentrations while a lack of aspen (Sw100) led to higher concentrations after June 28 (Figure 2.3d). The lower foliar P concentrations associated with greater spruce presence may be a result of more acidic soils, expected under conifer-dominated canopies, where P can get locked up with Al or Fe making it unavailable for uptake (Brady 1990).

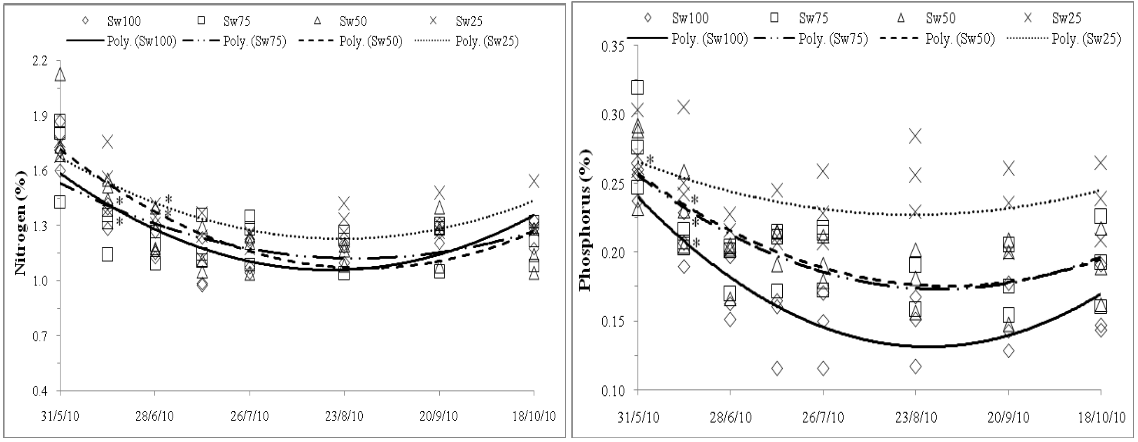
Table 2.2 Mean foliar nutrient concentrations and ratios during their periods of stability for white spruce (Sw) mixtures, from least (Sw100) to most (Sw25) trembling aspen competition.

Nutrient concentrations and ratios	Mixture			
	Sw100	Sw75	Sw50	Sw25
N (%)	1.27^{a}	1.27^{a}	1.31^{a}	1.40^{a}
P (%)	0.17^{a}	0.20^{ab}	0.21^{ab}	0.24^{b}
K (%)	0.75^{a}	0.74^{a}	0.89^{b}	0.92^{b}
Ca (%)	0.59^{a}	0.50^{ab}	0.50^{ab}	0.41^{b}
P/N	0.14^{a}	0.16^{ab}	0.16^{ab}	0.17^{b}
Ca/N	0.48^{a}	0.41^{a}	0.41^{a}	0.30^{b}
Mn/N*100	0.90^{a}	0.80^{b}	0.77^{b}	0.68^{c}
Zn/N*100	0.56^{a}	0.52^{a}	0.49^{ab}	0.42^{b}

Notes: Different letters within rows denote significant differences at $p < 0.05$.
Values derived from Duncan‟s post hoc test, which displays the means for the period of stability (groups in homogeneous subsets).

The second pattern among mixtures was with concentrations of K which followed one of two paths (Figure 2.3c): lower concentrations where aspen presence was scarce (Sw75, Sw100) or higher concentrations where aspen were abundant (Sw50, Sw25). This is likely an effect of greater availability in the soil due to increased aspen foliage on the forest floor.

a) Nitrogen b) Phosphorus



c) Potassium d) Calcium

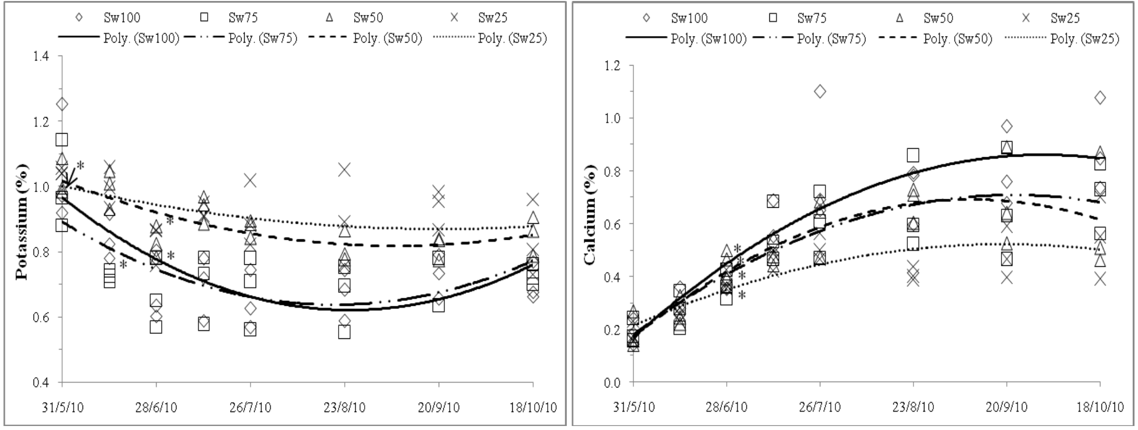
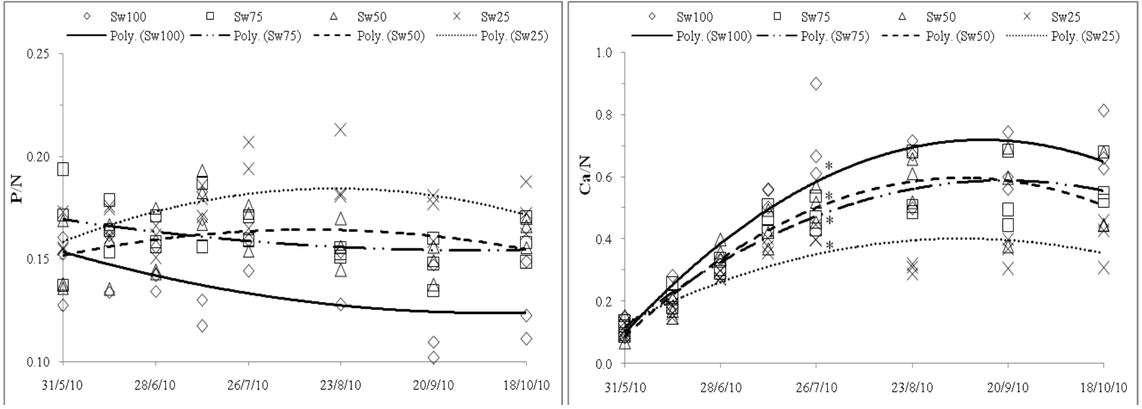


Figure 2.3. Seasonal foliar concentration (%) of (a) nitrogen, (b) phosphorus, (c) potassium, and (d) calcium for white spruce in 2010 at the Fallingsnow Ecosystem Project by spruce-aspen mixture. The symbol "*" denotes onset of nutrient stability.

The third trend showed the Sw25 mixture had significantly lower ($p < 0.05$) Ca/N and Zn/N than other mixtures (Figures 2.4b and c). And finally, spruce trees with the most aspen competition (Sw25) had significantly lower Mn/N values than those with the least aspen (Sw100) (Figure 2.4d). Mn/N values for both high and low aspen competition levels differed significantly ($p = 0.05$) from those found in trees with moderate (Sw75, Sw50) aspen competition. Nitrogen concentration, on the other hand, did not differ significantly ($p = 0.10$) among mixtures (Figure 2.3a). This was also the case for several other nutrients and ratios (Mg, Al/N, B/N, Cu/N, Fe/N, K/N, and Mg/N). Current growth of Norway spruce growing in mixed stands with various broadleaf species in Sweden also showed higher concentrations of P (1.7 v. 1.5, $p < 0.05$) and K (6.4 v. 5.0, $p < 0.0001$) and higher P/N (12.1 v. 11.8, $p < 0.1$) and Zn/N (0.27 v. 0.22, $p < 0.1$) ratios than pure stands as well as no difference for N (Thelin et al. 2002).[1]


a) Phosphorus/nitrogen ratio

b) Calcium/nitrogen ratio

c) Zinc/nitrogen ratio

d) Magnesium/nitrogen ratio

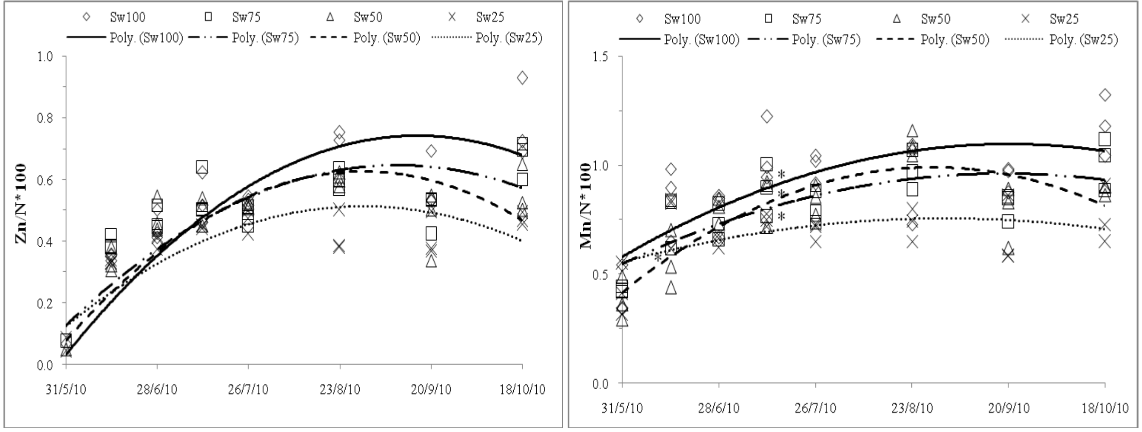


Figure 2.4. Seasonal foliar (a) P/N, (b) Ca/N, (c)Zn/N, and (d) Mn/N for white spruce in 2010 at the Fallingsnow Ecosystem Project by spruce-aspen mixture. The symbol "*" denotes onset of nutrient stability.

Differences were apparent in the onset of nutrient stability by mixture. Mixtures with more aspen became stable earlier for P, Ca, K, Ca/N, and Mn/N and later for N than

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[1] Nutrient concentration values given are means while nutrient ratios are approximate medians

mixtures with little to no aspen (see Figure 2.3 and 2.4). Based on these findings, the presence of aspen does appear to influence the timing of white spruce foliar nutrient stability.

2.3.3 White spruce nutrient standards

Nutrient status during the period of stability (mean value of homogenous subset as assessed by Duncan‟s post hoc test; Appendix II) was determined based on standards for white spruce foliar concentrations (Ballard and Carter 1986; Table 2.3). Using these criteria, Sw25 and Sw50 mixtures had slight/moderate (1.30 to 1.54%) N deficiency while-spruce dominated mixtures had severe deficiencies (1.05 to 1.29%). Given that the N in aspen-dominated plots stabilizes later, it is possible that this is due to more available N and thus a longer acquisition time. Regardless of species mixture, all trees had adequate levels of P (>0.16%), K (>0.50%) and Ca (>0.20%) but slight/moderate Mg deficiency (0.06 to 0.10%).

Foliar N, P, K, Ca, and Mg concentrations in this study, overall and by mixture, during the period of stability were comparable to results from other unfertilized white spruce field studies (Wang and Klinka 1997; McKinnon and Quiring 1998). Target nutrient levels for white spruce are based primarily on a greenhouse study of 26-week-old white spruce seedlings, which evaluated foliage nutrient levels required for optimal growth (Swan 1971). Using these standards, a study of 102 white spruce stands ranging from 32 to 128 years old in British Columbia, Canada found all stands were N deficient to some degree (Wang and Klinka 1997). More interestingly, their results showed that N, P, and K are negatively correlated with stand age and suggest that because of this relationship, it is likely that although white spruce can grow faster with higher N levels, seedling N, P, and K requirements are higher than those for older trees. Wang and

Klinka (1997) proposed that optimal ranges of these nutrients need to vary to account for physiological differences by age.

Table 2.3 Mean white spruce foliar macronutrient concentrations during their periods of stability and deficiency status (relative to adequate levels documented in literature) by spruce-aspen mixture from least (Sw100) to most (Sw25) trembling aspen competition.

Nutrient/ Species mixture	Mean (%)[2]	Deficiency status[3]
N (>1.55%)[1]		
Sw100	1.27	Severe
Sw75	1.27	Severe
Sw50	1.31	Slight/Moderate
Sw25	1.40	Slight/Moderate
P (>0.16%)		
Sw100	0.17^{a}	None
Sw75	0.20^{ab}	None
Sw50	0.21^{ab}	None
Sw25	0.24^{b}	None
K (>0.50%)		
Sw100	0.75^{a}	None
Sw75	0.74^{a}	None
Sw50	0.89^{b}	None
Sw25	0.92^{b}	None
Ca (>0.20%)		
Sw100	0.59^{a}	None
Sw75	0.50^{ab}	None
Sw50	0.50^{ab}	None
Sw25	0.41^{b}	None
Mg (>0.12%)		
Sw100	0.09	Slight/Moderate
Sw75	0.09	Slight/Moderate
Sw50	0.10	Slight/Moderate
Sw25	0.10	Slight/Moderate

[1] Adequate level as described in Ballard and Carter (1986)

[2] Mean values during the periods of stability attained from Duncan"s post hoc test

[3] As interpreted for nursery grown white spruce seedlings (26 weeks old) (Ballard and Carter 1986)

We studied young, plantation-grown, white spruce about 20 years of age, for which no published foliar nutrient concentration studies were found. As expected, our nutrient concentrations were within the range between those of Swan (1971) and Wang and Klinka (1997). Our N and P concentrations for all mixtures were lower than seedling optimal levels (2 to 2.6% and 0.3%, respectively) while at the higher range or similar to naturally occurring, mature stands (0.8 to 1.4% and 0.1 to 0.3%, respectively). The concentrations of K in our trees of all mixtures were similar to seedling ranges (0.7 to 1.0), which are higher than values given for mature stands (0.4 to 0.7). Finally, for Ca and Mg concentrations, we found our values for all mixtures to be similar to predominant white spruce studies for seedlings and mature stands.

Although critical value approaches with respect to foliar concentrations are often used to assess tree health, nutrient ratios in the foliage are more accurate indicators (Ingestad 1987) as ratios account for variation in carbohydrates stored in the leaf at any given time (Linder 1995). Ratios of P to N across all mixtures showed no change throughout the growing season (Figure 2.4a). As both of these nutrients are needed at relatively the same rate for consistent metabolic processes, this finding may suggest that neither is limiting or they are equally limiting throughout the growing season. According to P/N standards[2] (not species-specific), all trees combined, as well as each mixture, had ideal P/N values (≥ 0.08), meaning they were not P deficient (Ballard and Carter 1986). However, according to these standards, P deficiency could occur if N increased relative to P (P/N values 0.08 to 0.16) in pure spruce plots (0.14), Sw75 (0.16) and Sw50 (0.16), whereas Sw25 (0.17) is unlikely to become P deficient even with an increase in N (P/N

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[2] Described in Ballard and Carter (1986) as N/P

values > 0.16). This suggests that the greater aspen presence and the associated improvement in nutrient turnover may reduce the possibility of P deficiency.

Nutrient concentrations (K, Ca) and ratios (B/N, K/N) were consistent with those of new growth of fertilized Norway spruce in mixed and pure stands (Thelin *et al.* 2002). Our N and P results appeared lower than those for Norway spruce, except for Sw25 (N) and all mixtures except pure spruce (P). However, we did find that all ratios with N (P/N, K/N, Ca/N, Mg/N, Zn/N and B/N) were similar to target levels for Norway spruce.

Based on our study, in which samples were collected from 20-year-old white spruce foliage between mid-April and mid-October, to capture N, P, K, and Ca and their ratios during their common period of stability, it is best to sample between mid-July and mid-September. This is when nutrient levels were stable.

2.4 CONCLUSIONS

The relative presence of trembling aspen as a neighbouring competitor appears to influence white spruce foliar nutrient concentrations and timing of nutrient stability in the leaf. Overall, white spruce foliar N, P, and K concentrations decreased and Ca increased rapidly at the beginning of the growing season, becoming stable in summer. Furthermore, higher aspen competition resulted in higher P and K values and lower Ca than those in pure spruce. Another consequence of greater aspen competition was earlier (P, K, Ca, Ca/N, Mn/N) or later (N) nutrient stability than found in the spruce-dominated plots. Diagnosing nutrient status by species mixture revealed likely N deficiencies in all cases. However, white spruce foliar N concentrations in Sw50 and Sw25 mixtures, classified as having slight/moderate deficiency, were higher than those in spruce-dominated plots where deficiencies may be severe. This may be the result of a positive relationship between available N and the amount of aspen litter (facilitation), with a longer nutrient acquisition period where aspen is present. Foliar concentrations were similar to those found by others in field studies of mature and young stands but age-specific optimal nutrient ranges are lacking for white spruce. Overall, it is evident that the presence of aspen (>25% of HCI competition) influenced foliar nutrient content, likely in part due to improved soil nutrient status.

3.0 INVESTIGATING HOW INTER- AND INTRA- SPECIFIC COMPETITION AND DENSITY INFLUENCE WHITE SPRUCE AND TREMBLING ASPEN GROWTH RATES, WHITE SPRUCE NUTRIENT STATUS AND MIXEDWOOD PRODUCTIVITY

3.1 INTRODUCTION

For forest managers, aside from the many ecological benefits of mixedwoods such as enhanced diversity, habitat and resistance to pests (Kelty et al. 1992), creating mixedwood conditions may result in greater overall productivity, even at higher densities. Specifically, the presence of trembling aspen has been shown to increase production of northern conifers (Peterson 1988), resulting in greater overall biomass and periodic annual increments (PAI) when grown with understory white spruce (MacPherson et al. 2001).

The extent to which a tree can influence its neighbours by modifying local growth resources depends on the species in question as well as the relative size and distance away of those neighbours. Some species are known to act as facilitators by improving the growing conditions of another, such as N-fixing shrubs like alder which increase available N in the soil (Binkley 1983). Similarly, inter-specific competition may alleviate intra-specific competition, resulting in competitive reduction, where one or both species experience reduced competition for growth resources (Kelty 2006). It has been suggested that naturally occurring coniferous/deciduous mixedwoods, such as white spruce (*Picea glauca* [Moench] Voss) and trembling aspen (*Populus tremuloides* Michx.), are well suited for the benefits of mixed culture (Man and Leiffers 1999).

White spruce is a moderately shade tolerant boreal species that tends to dominate in mid- to late successional stages whereas trembling aspen is a shade intolerant, pioneer species (Nienstaedt and Zasala 1990; Perala 1990). Aspen is a nurse tree for white spruce where the aspen canopy can reduce the effect of weather extremes and the occurrence of disturbance (Groot and Carlson 1996). Furthermore, the combination of white spruce‟s lower photosynthetic capacity (i.e. saturates at a light level lower than full sunlight) and aspen‟s low leaf area, means aspen has much less of a shading effect on spruce than would other spruce trees (or by comparison, the effect of spruce on aspen) and is not believed to decrease spruce photosynthetic rates (Pritchard and Comeau 2004). White spruce may also be able to take advantage of aspen‟s leaf off period in the spring and fall, reducing the amount of competition for above- and below-ground resources that would occur in a monoculture during these times. A combination of these benefits are expected to, in part, result in greater growth rates where these species are growing in mixture as opposed to monocultures. Growth rates of plantation grown conifers are influenced by density because competition between trees, regardless of species, increases with density. Increased spacing between trees through planting and thinning practices has resulted in greater yields in managed stands. However, these increased yields will likely vary depending on the relative presence of neighbouring species, herein described using the relative size and distance of neighbours (via Hegyi‟s competition index; HCI) and the density of those neighbours.

If these beneficial processes occur, white spruce foliar nutrient status would be greater where aspen is present, but only at an ideal density. If optimal growth and improved nutrient status occur at similar species proportions and densities, then white spruce foliar nutrient status could be used to model white spruce growth response to planned stand species/density manipulations.

Nutrient concentrations alone are no longer viewed as sufficient to explain a tree"s nutrient status. Nutrient ratios in relation to N are considered a more accurate assessment because ratios negate the differences in carbohydrates stored in the leaves (Linder 1995). Furthermore, nutrient contents (based on foliar biomass at the tree level) may further improve nutrient assessment as this variable accounts for the total of each nutrient that is available for growth and resource acquisition. This can be taken a step further to compare tree nutrient use efficiencies (NUE) describing growth increment (cm^2) per unit of nutrient. A higher NUE suggests a more efficient tree, where more growth is acquired per unit nutrient. To that end, we investigated the relationship between site productivity ($m^2 \cdot ha^{-1} \cdot yr^{-1}$), white spruce and trembling aspen growth rates and white spruce nutrient status along species proportion and density gradients in a 20 year old plantation in northwestern Ontario. We expected to see improved productivity and growth rates at some moderate density and mixture proportion compared to pure stands of white spruce. Furthermore, we expected white spruce foliar nutrient status to be greater where spruce growth and productivity were higher, helping explain this phenomenon and making spruce nutrient status an indicator for site productivity and spruce growth.

3.2 METHODS

This study was conducted at the Fallingsnow Ecosystem Project (FEP) as described in section 2.2. A mensurational and stem map database exists for all trees within the FEP"s 45 permanent sample plots of $150m^2$. Due to variation in density and species proportion throughout the sites, we decided to implement this study at the tree level using this established database. The levels of competition and mixture were controlled and measured for 3-m-radius, tree-level plots using Hegyi‟s competition index (HCI) (Hegyi 1974; Equation1) as described in section 2.2. Using this database, 39 white spruce and 44 trembling aspen subject trees were selected for sampling.

Current year‟s foliage was collected from the south facing branches, mid-crown from the 39 subject white spruce trees in late-August 2009 using a pole pruner. Samples were prepped and analyzed for concentrations of N, P, K, Ca, Mg, Al, B, Fe and Zn, as described in section 2.2.

Total foliar biomass (Y in kg •tree^{-1}) was calculated using an allometric equation [2] (Harding and Grigal 1985) for plantation-grown white spruce trees, aged 19-43 years. Nutrient content estimates were calculated by multiplying foliar biomass by the concentrations for each nutrient. Although current year foliar biomass estimates would be a more accurate measure, these equations have not been developed for white spruce.

$$Y\ (\text{kg} \bullet \text{tree}^{-1}) = 0.0498(\text{DBH})^{3.835}\ \text{X}\ \text{Height}^{(-)2.260} \qquad [2]$$[3]

Two cores at breast height (1.3 m) were collected from each subject spruce (39) and aspen (44) tree in April/May 2010 and stored in plastic straws as described by Cole (1977). In preparation for analysis, the cores were glued into wooden blocks with grooves designed for this purpose and sanded with a table sander. The cores were then scanned and analyzed using WinDENDRO software and corrected to actual DBH measurements for data accuracy as described by Clark et al. (2007). Basal area growth, in cm^2, was calculated for the last five years and averaged on a per year basis (PBAI). NUE (cm^2 •yr^{-1} •g^{-1}) was then calculated as PBAI by nutrient content.

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[3] n=115, R^2 =0.78

To determine productivity of mixtures at the per hectare scale using the 39 spruce and 44 aspen centred plots (n = 83), regression equations were developed for white spruce and aspen (Figure 3.1) separately using total competition (HCI) as the independent variable. These species-specific equations for PBAI were multiplied by species density (stems per hectare, sph) for each plot to determine total productivity. For example, in spruce centred plots that also had aspen present, the aspen growth was estimated using the regression equation for aspen and multiplied by aspen density to obtain aspen productivity. Spruce growth was already known for that plot, and multiplied by density to obtain spruce productivity.

Response surface equations were created using Design-Expert 7b1.1 to determine how the proportion of aspen presence (% HCI) and total density (sph) influenced spruce and aspen PBAI, white spruce nutrient status and site productivity.

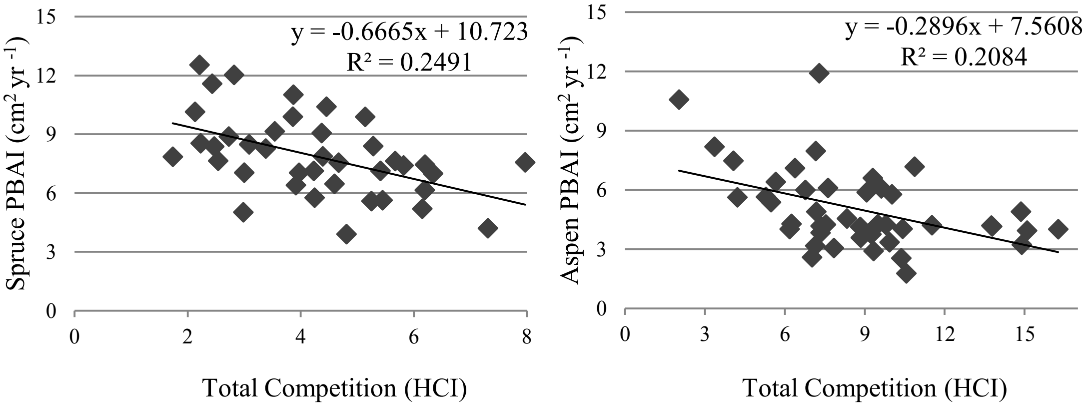

Figure 3.1 Regression equation and linear trend line for (a) white spruce and (b) trembling aspen periodic basal area increments (cm^2 •yr^{-1}) relative to total Hegyi‟s competition index.

3.3 RESULTS AND DISCUSSION

Spruce PBAI, at the tree-level, was not significantly (p= 0.294) driven by a combination of density and aspen presence. This is likely a result of a high tolerance of aspen presence by white spruce (intra- > inter-specific competition) as was shown for black spruce where spruce volume remained stable regardless of the amount of aspen in the canopy (Newton and Jolliffe 1998). Furthermore, if intra-specific competition is relatively more negatively influential on white spruce, the wide spacing of the planted spruce trees (1700 sph) might mean that this type of competition is avoided at this site resulting in similar growth rates regardless of mixture and density.

On the other hand, aspen PBAI was predicted [3] to be the greatest in low density, high spruce conditions ($p = 0.02$; Figure 3.2). This is likely due in part to aspen‟s shade intolerance and the reduced intra-specific competition experienced in mixed stand canopies versus aspen-dominated stands. As the aspen are taller than spruce at the FEP (as is common in most/all spruce-aspen mixtures, natural or plantation), they would experience most competition for aboveground resources from other aspen trees. However, the best growth at low density may suggest that aspen cannot compete as well with spruce and/or aspen at higher densities, likely for other resources as well.

Response surface analysis for several nutrient concentrations and ratios as well as all nutrient contents and NUEs were not significant ($p \geq 0.01$). The lack in significance for foliar nutrient contents and NUEs may in part be the result of a need for more specialized foliar biomass estimation equations. Although the allometric equation used was for plantation white spruce of similar age, the true biomass values are likely influenced by density and mixture proportion. Further accuracy of nutrient relationships could be achieved by determining only current year‟s foliar biomass as it is the younger foliage that is most actively contributing to growth. In retrospect, destructive sampling to determine current year foliar biomass by mixture and density would have validated this research model.

$$Aspen\ PBAI\ (cm^2 \bullet yr^{-1}) = 4.5 + 1.7A + 2.1D + 2.0AD + 3.7D^2 - 3.5AD^2 - 6.0D^3 \qquad [3]$$

where A is aspen presence in %HCI, D is density in sph

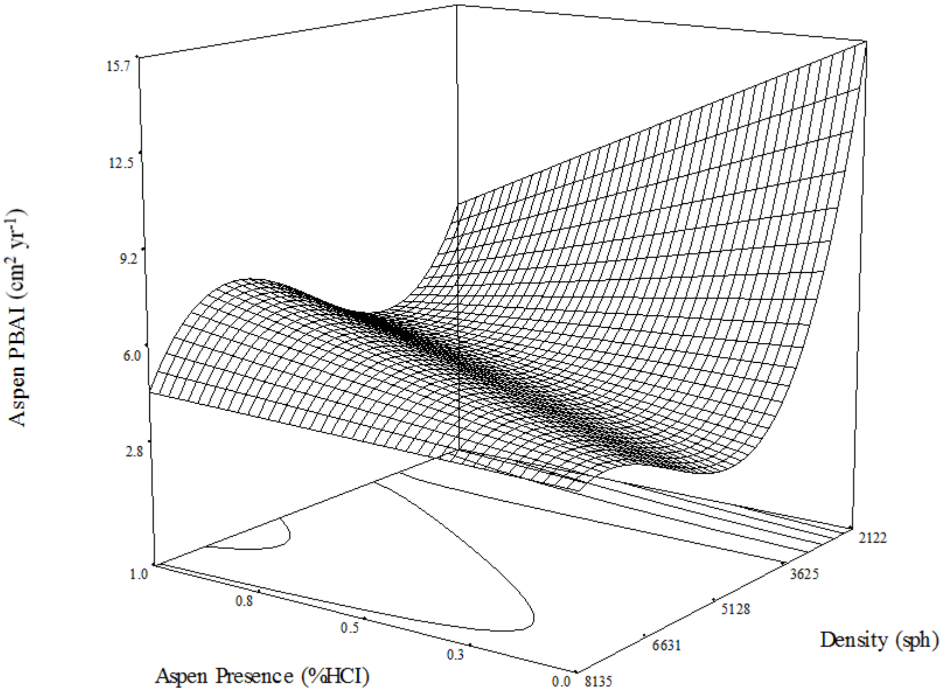

Figure 3.2 Aspen growth (cm^2 •yr^{-1}) at the tree-level predicted based on total density (sph) and proportion of aspen presence (%Hegyi"s competition index).

Significant relationships did occur between stem density, proportion of aspen in the stand and white spruce foliar concentrations of P [4] and K [5] and the ratio of Ca/N [6]. Concentrations of K (p =0.060; Figure 3.3) showed negative linear relationships with density and positive relationships with aspen presence while foliar P (p =0.053; Figure 3.4) was largely a function of aspen presence. Phosphorus and potassium are important nutrients for growth where P is involved in the synthesis of ATP, the primary form of plant energy, and K controls stomatal apertures and thus the rate of gaseous exchange, water use efficiency and hydraulic conductivity. The higher P and K concentrations where aspen presence is greatest may suggest; 1) aspen is a facilitator for white spruce by improving litter and soil conditions and/or 2) white spruce is more positively affected by inter-specific competition than intra-specific conditions due to physical separation of roots and crowns resulting in more access to and more efficient use of resources. As to why the concentrations of P and K are greatest at lower densities, both facilitation and reduced intra-specific competition may be at play. In lower density conditions, intra-specific competition would be reduced, making more resources available spatially, meanwhile aspen may be improving soil nutrient status where there is relatively less spruce presence competing for the extra resources. However, since growth rates of white spruce were not significantly different along the mixture and density gradient, these higher nutrient levels in mixture is not direct evidence of facilitation. This may, however, suggest that at poorer nutrient sites, the presence of aspen would significantly improve spruce growth rates.

$$P\ (\%) = 0.22 + 0.014A - 0.00086D \qquad [4]$$

where A is aspen presence in %HCI, D is density in sph

$$K\ (\%) = 1.01 + 0.05A + 0.038D$$

where A is aspen presence in %HCI, D is density in sph [5]

$$\frac{Ca}{N} = 0.48 - 0.068A - 0.016D - 0.097A^2$$

where A is aspen presence in %HCI, D is density in sph [6]

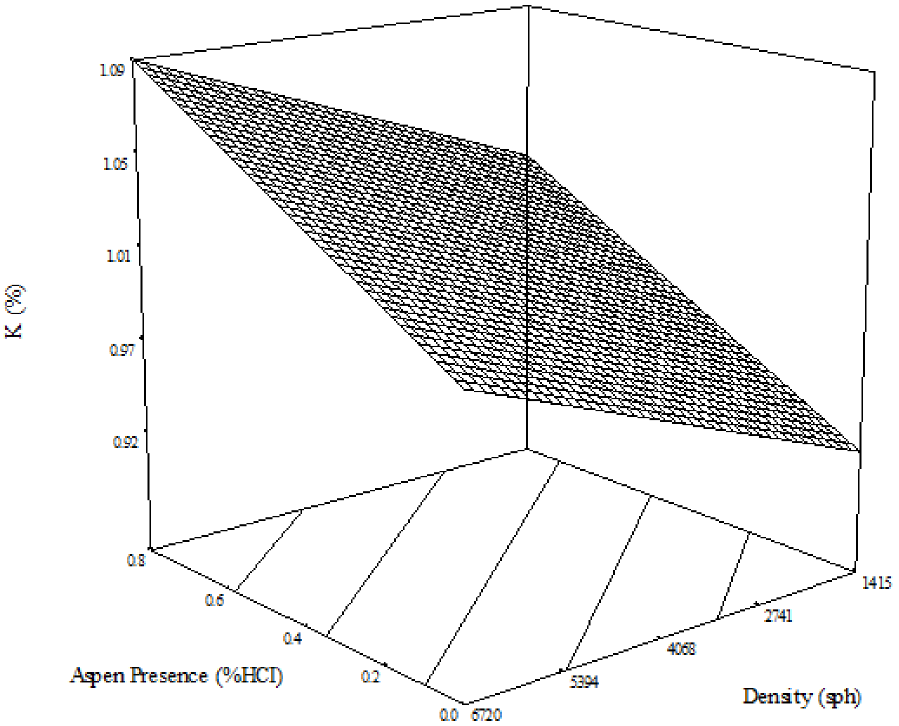

Figure 3.3 White spruce foliar K concentration (%) predicted based on total density (sph) and proportion of aspen presence (%Hegyi‟s competition index).

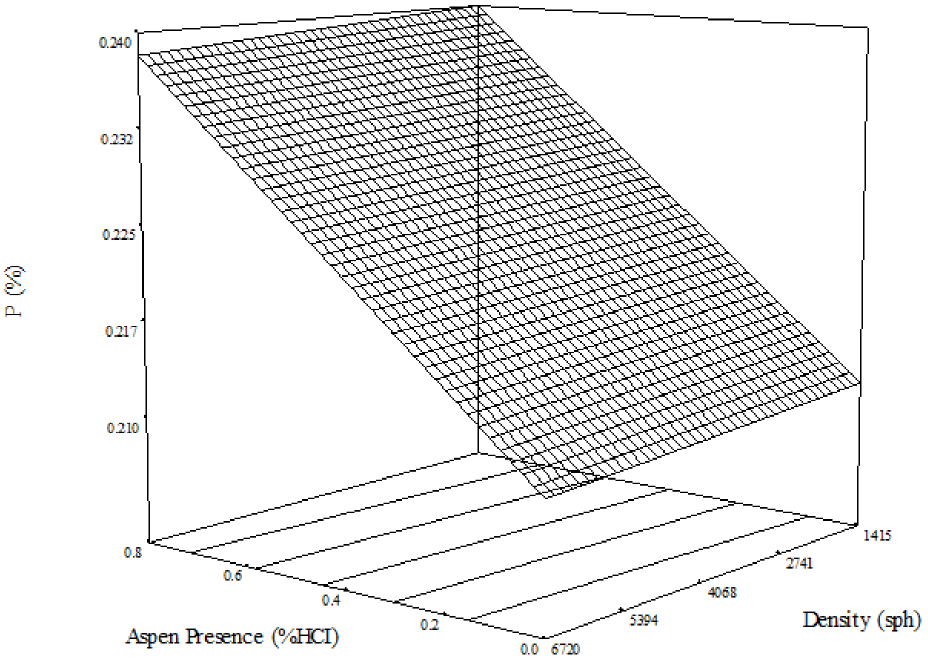

Figure 3.4 White spruce foliar P concentration (%) predicted based on total density (sph) and proportion of aspen presence (%Hegyi‟s competition index).

The relative concentration of Ca to N in spruce foliage increased as aspen presence increased until the percent of aspen HCI reached approximately 30%, at which point Ca/N declined again ($p = 0.031$; Figure 3.5). Density however, appeared to have less of an impact, showing spruce foliar Ca/N increasing only slightly as density decreased. Calcium is important for cell wall structure and avoiding toxicity of other elements like Fe and Al. As no signs of toxicity were noticed for sample trees, it is unlikely that the range of Ca values by mixture significantly contributed to this cause. Not only could aspen in mixture be improving decomposition rates and thus making more Ca values available, but also, the differences in species acquisition methods may contribute to higher Ca values. If trees in intra-specific conditions compete in the same soil strata, for the same length of time every day, while also requiring the same relative amount of each resource, then lower Ca values may be expected. If Ca is too low (< 0.1 %), which was not present in this study, cell walls can become weak, resulting in water stress. Water stress could be expected more where the intra-specific competition is greatest for the above reasons.

When PBAIs for each species were scaled up, there was an effect of density and aspen presence on productivity ($m^2 \cdot ha^{-1} \cdot yr^{-1}$) ($p < 0.0001$; Figure 3.6). Productivity was predicted to be the greatest at high density and high aspen presence [7]. However, as density drops, the presence of aspen becomes less influential on total productivity. At low and moderate densities, pure spruce and mixedwood conditions are predicted to be most productive, respectively. This increase in overall productivity with increasing aspen presence is counter to an aspen productivity study in Alberta which found the greatest total biomass and periodic annual increments of growth to be in mixtures as opposed to pure aspen (MacPherson *et al.* 2001). However, the Alberta aspen study was focused on mature aspen stands with spruce understory and did not have pure spruce conditions for comparison, nor did they account for the variation in plot density. Our response surface model does show greater productivity in mixture, but only at intermediate densities. This is likely a result of the shade tolerance of spruce, which can tolerate a lot of aspen added to the canopy with little effect on growth (MacPherson *et al.* 2001) making mixtures more productive than spruce monocultures.

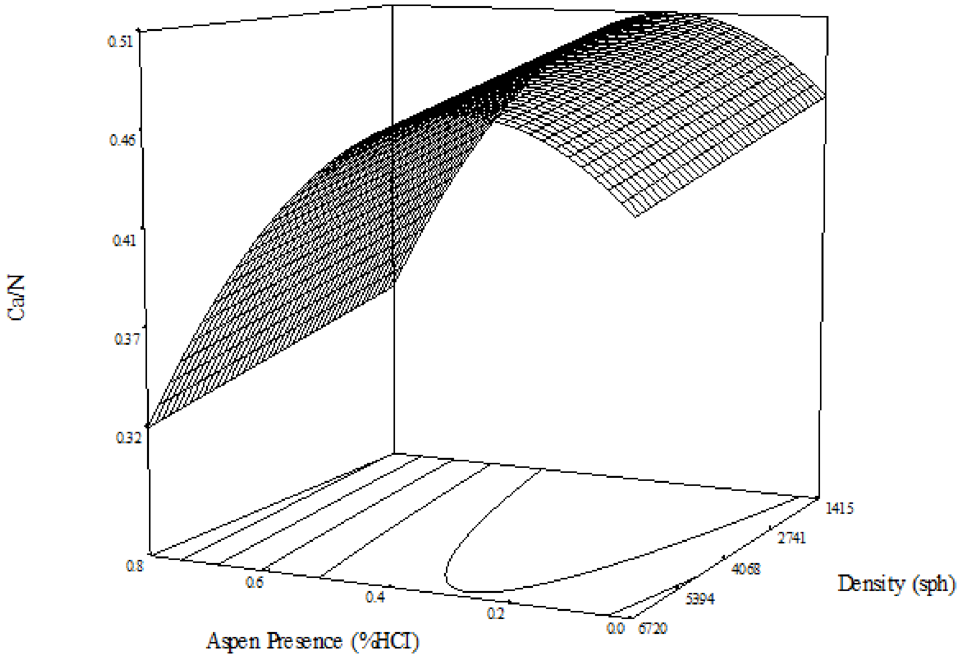

Figure 3.5 White spruce foliar Ca/N predicted based on total density (sph) and proportion of aspen presence (%HCI).

$$Y = 2.64 + 1.59A + 0.06D + 0.93AD$$

where A is aspen presence in %HCI, D is density in sph [7]

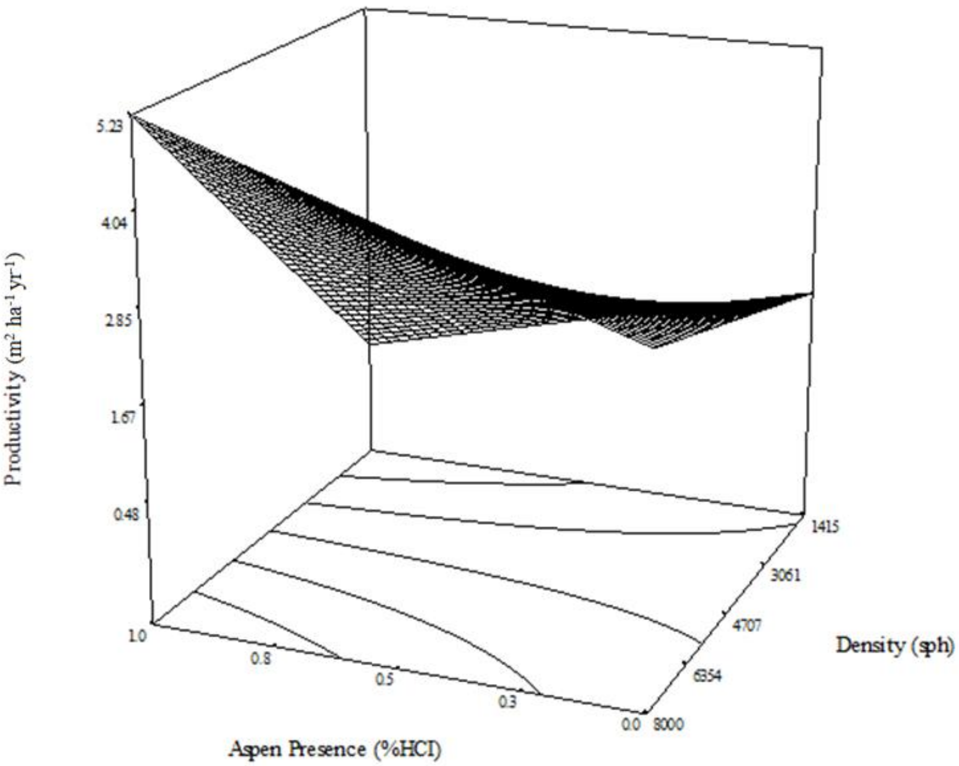

Figure 3.6 White spruce and trembling aspen productivity (m^2 •ha^{-1} •yr^{-1}) predicted based on total density (sph) and aspen presence (%Hegyi‟s competition index).

It is evident that for 20-year-old plantation spruce/aspen stands, an optimal density for total productivity depends on species mixture. It is therefore important for forest managers to consider both of these variables when considering the benefits of mixedwood productivity.

3.4 CONCLUSIONS

Mixtures of 20-year-old plantation white spruce and trembling aspen appear to experience reduced intra-specific competition and the potential for facilitation, depending on the range in density. Where density was low, aspen tended to have the greatest PBAI values where intra-specific competition was also low. Thus it may be concluded that intra-specific competition is more severe in aspen for aboveground resources, whereas spruce is more sensitive to intra-specific competition for belowground resources.

Overall site productivity response varied depending on density. Pure aspen conditions at high densities tended to have higher productivity in this 20-year-old stand, which is in accordance with the vigorous growth expected of this species at this stage of stand development. However, as density decreased, productivity in high aspen conditions dropped off, likely due to the larger aspen on site out-competing their smaller neighbours. At moderate and low densities, mixtures and high spruce conditions were the most productive, respectively. This is likely due to the beneficial combining characteristics of these species where aspen can be added to the canopy with little effect on spruce growth. If greater overall productivity of second growth spruce forests is desired, it appears beneficial to allow a moderate amount of aspen to regenerate on site with white spruce. Since spruce growth does not appear to vary across the range in density and mixture for this study, this increased productivity in mixture may be suggesting that a certain amount of aspen can be added to the canopy with no loss in spruce growth.

4.0 SUMMARY

White spruce and aspen appear to have a certain amount of combining ability depending on the species proportion and total density. Where density was controlled, differences in white spruce foliar nutrient status and the onset of stability between mixtures were evident. When nutrients were studied over a wider range of densities and mixture, few relationships were evident. Specifically, response surface models for concentrations of P and K showed a positive relationship with increased aspen presence and density. These results are comparable to P and K concentrations in chapter 2 where greater values were present in mixtures with more aspen. The effect of density, however, was not evaluated in that part of this study. White spruce foliar Ca/N did not appear to be influenced by density, showing greatest Ca/N values in mixture opposed to monocultures, regardless of density. The variation of foliar nutrient concentrations over time, as well as by mixture and density, suggest that researchers should be mindful of these factors when studying foliar nutrients in mixtures.

4.1 MANAGEMENT IMPLICATION

Mixed culture of white spruce and trembling aspen can increase biodiversity, site quality and productivity compared to spruce monocultures. For efficient and effective mixedwood management, a shift in forest practices is required when compared to the management of monocultures. Furthermore, where spruce-aspen mixedwoods are more productive, management would be more cost-effective. Not only would wood volume increase per unit land base (by following a two-step harvest), but white spruce volume (more commercially valuable species) should not decrease significantly where the ideal mixture and density exists, resulting in greater revenue per unit area. In addition to this increase in revenue, reducing the required land base for the same volume of wood would result in a reduced “managed” footprint across Ontario‟s boreal forest. As well, a reduction in vegetation management would lower costs and improve the public perception of forest management.

4.2 LIMITATIONS AND FUTURE RESEARCH

The greatest limitation of this study was time. As the density/mixture proportion relationship will change over time, a long term study of productivity and nutrient status would result in a better understanding of competitive interactions between these species. With more time, this study could have been improved with the addition of aspen foliar nutrient status and plot-specific soil nutrient status for more in-depth comparisons. Furthermore, for more accurate white spruce foliar contents and nutrient use efficiencies, foliar biomass values for plantation white spruce, that also incorporate species mixture and density, that are specific to the active portion of the crown, are needed.

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APPENDICES

APPENDIX I

WHITE SPRUCE FOLIAR NUTRIENT CONCENTRATIONS AND RATIOS REPEATED MEASURES

Nutrient or Ratio	Mixture Sw:At	Dependent Variable	Mean	Std. Error	95% Confidence Interval Lower Bound.	95% Confidence Interval Upper Bound.
Ca	Combined	T1	0.20	0.02	0.15	0.26
		T2	0.27	0.02	0.24	0.31
		T3	0.39	0.01	0.36	0.42
		T4	0.52	0.02	0.47	0.58
		T5	0.63	0.04	0.53	0.73
		T6	0.62	0.03	0.55	0.69
		T7	0.66	0.05	0.55	0.77
		T8	0.69	0.05	0.57	0.81
	25:75	T1	0.19	0.05	0.08	0.30
		T2	0.26	0.03	0.18	0.33
		T3	0.38	0.03	0.32	0.44
		T4	0.47	0.05	0.36	0.58
		T5	0.51	0.09	0.31	0.71
		T6	0.41	0.06	0.26	0.56
		T7	0.49	0.10	0.26	0.71
		T8	0.55	0.10	0.31	0.78
	50:50	T1	0.21	0.05	0.10	0.32
		T2	0.26	0.03	0.19	0.34
		T3	0.45	0.03	0.40	0.51
		T4	0.49	0.05	0.38	0.60
		T5	0.60	0.09	0.40	0.80
		T6	0.68	0.06	0.53	0.83
		T7	0.69	0.10	0.46	0.91
		T8	0.62	0.10	0.38	0.85
	75:25	T1	0.19	0.05	0.08	0.30
		T2	0.28	0.03	0.21	0.35
		T3	0.37	0.03	0.31	0.42
		T4	0.56	0.05	0.45	0.67
		T5	0.60	0.09	0.40	0.80
		T6	0.66	0.06	0.51	0.81
		T7	0.66	0.10	0.44	0.89
		T8	0.71	0.10	0.47	0.94
	100:00	T1	0.23	0.05	0.12	0.34
		T2	0.30	0.03	0.23	0.37
		T3	0.37	0.03	0.31	0.42
		T4	0.58	0.05	0.47	0.69
		T5	0.82	0.09	0.61	1.02
		T6	0.73	0.06	0.58	0.87
		T7	0.80	0.10	0.58	1.03
		T8	0.89	0.10	0.65	1.12

Nutrient or Ratio	Mixture Sw:At	Dependent Variable	Mean	Std. Error	95% Confidence Interval	
					Lower Bound.	Upper Bound.
Ca/N	Combined	T1	0.11	0.01	0.09	0.13
		T2	0.19	0.01	0.17	0.22
		T3	0.32	0.01	0.30	0.33
		T4	0.45	0.01	0.42	0.48
		T5	0.53	0.03	0.48	0.59
		T6	0.52	0.03	0.46	0.58
		T7	0.52	0.03	0.45	0.60
		T8	0.55	0.03	0.48	0.62
	25:75	T1	0.11	0.02	0.07	0.15
		T2	0.16	0.02	0.11	0.22
		T3	0.28	0.02	0.25	0.32
		T4	0.38	0.03	0.32	0.44
		T5	0.41	0.05	0.30	0.53
		T6	0.31	0.05	0.19	0.42
		T7	0.36	0.07	0.20	0.51
		T8	0.40	0.06	0.26	0.53
	50:50	T1	0.11	0.02	0.06	0.15
		T2	0.18	0.02	0.12	0.23
		T3	0.36	0.02	0.33	0.40
		T4	0.43	0.03	0.37	0.49
		T5	0.51	0.05	0.40	0.63
		T6	0.60	0.05	0.48	0.71
		T7	0.56	0.07	0.40	0.71
		T8	0.52	0.06	0.39	0.66
	75:25	T1	0.11	0.02	0.07	0.16
		T2	0.22	0.02	0.17	0.27
		T3	0.31	0.02	0.27	0.34
		T4	0.46	0.03	0.41	0.52
		T5	0.48	0.05	0.36	0.60
		T6	0.56	0.05	0.44	0.67
		T7	0.54	0.07	0.39	0.69
		T8	0.58	0.06	0.45	0.72
	100:00	T1	0.11	0.02	0.07	0.16
		T2	0.22	0.02	0.17	0.27
		T3	0.31	0.02	0.28	0.35
		T4	0.54	0.03	0.48	0.60
		T5	0.73	0.05	0.61	0.84
		T6	0.63	0.05	0.51	0.74
		T7	0.64	0.07	0.48	0.79
		T8	0.70	0.06	0.56	0.84

Nutrient or Ratio	Mixture Sw:At	Dependent Variable	Mean	Std. Error	95% Confidence Interval Lower Bound.	Upper Bound.
K	Combined	T1	1.03	0.03	0.95	1.10
		T2	0.89	0.02	0.85	0.93
		T3	0.75	0.03	0.69	0.81
		T4	0.81	0.02	0.76	0.86
		T5	0.78	0.03	0.72	0.84
		T6	0.76	0.03	0.70	0.83
		T7	0.80	0.02	0.76	0.85
		T8	0.78	0.02	0.73	0.83
	25:75	T1	1.04	0.07	0.89	1.20
		T2	1.00	0.03	0.92	1.07
		T3	0.83	0.05	0.72	0.94
		T4	0.92	0.04	0.82	1.02
		T5	0.91	0.05	0.79	1.02
		T6	0.90	0.06	0.76	1.03
		T7	0.94	0.04	0.85	1.02
		T8	0.83	0.04	0.74	0.93
	50:50	T1	1.02	0.07	0.87	1.18
		T2	1.00	0.03	0.92	1.07
		T3	0.83	0.05	0.71	0.94
		T4	0.93	0.04	0.83	1.04
		T5	0.87	0.05	0.76	0.99
		T6	0.81	0.06	0.68	0.95
		T7	0.82	0.04	0.73	0.90
		T8	0.85	0.04	0.76	0.95
	75:25	T1	1.00	0.07	0.84	1.15
		T2	0.73	0.03	0.65	0.80
		T3	0.67	0.05	0.55	0.78
		T4	0.70	0.04	0.60	0.80
		T5	0.68	0.05	0.57	0.80
		T6	0.67	0.06	0.53	0.80
		T7	0.73	0.04	0.65	0.82
		T8	0.73	0.04	0.63	0.83
	100:00	T1	1.05	0.07	0.89	1.20
		T2	0.84	0.03	0.77	0.92
		T3	0.68	0.05	0.57	0.80
		T4	0.70	0.04	0.59	0.80
		T5	0.65	0.05	0.53	0.76
		T6	0.67	0.06	0.54	0.81
		T7	0.73	0.04	0.64	0.81
		T8	0.70	0.04	0.61	0.80

Nutrient or Ratio	Mixture Sw:At	Dependent Variable	Mean	Std. Error	95% Confidence Interval	
					Lower Bound.	Upper Bound.
Mg/N	Combined	T1	0.055	0.003	0.049	0.060
		T2	0.057	0.004	0.047	0.067
		T3	0.072	0.002	0.067	0.077
		T4	0.088	0.003	0.080	0.095
		T5	0.080	0.003	0.073	0.088
		T6	0.080	0.002	0.074	0.085
		T7	0.080	0.003	0.074	0.086
		T8	0.092	0.003	0.086	0.098
	25:75	T1	0.053	0.005	0.042	0.065
		T2	0.044	0.009	0.024	0.064
		T3	0.065	0.005	0.055	0.075
		T4	0.084	0.007	0.069	0.099
		T5	0.082	0.007	0.067	0.097
		T6	0.077	0.005	0.066	0.088
		T7	0.079	0.005	0.066	0.091
		T8	0.089	0.005	0.077	0.102
	50:50	T1	0.055	0.005	0.043	0.066
		T2	0.060	0.009	0.041	0.080
		T3	0.081	0.005	0.071	0.092
		T4	0.094	0.007	0.079	0.110
		T5	0.089	0.007	0.074	0.104
		T6	0.091	0.005	0.080	0.102
		T7	0.092	0.005	0.079	0.104
		T8	0.094	0.005	0.082	0.106
	75:25	T1	0.055	0.005	0.043	0.066
		T2	0.063	0.009	0.043	0.083
		T3	0.071	0.005	0.060	0.081
		T4	0.088	0.007	0.073	0.103
		T5	0.076	0.007	0.061	0.091
		T6	0.080	0.005	0.068	0.091
		T7	0.078	0.005	0.066	0.091
		T8	0.093	0.005	0.081	0.106
	100:00	T1	0.056	0.005	0.044	0.067
		T2	0.060	0.009	0.040	0.080
		T3	0.071	0.005	0.060	0.081
		T4	0.084	0.007	0.069	0.100
		T5	0.072	0.007	0.057	0.087
		T6	0.072	0.005	0.061	0.083
		T7	0.072	0.005	0.060	0.085
		T8	0.091	0.005	0.078	0.103

Nutrient or Ratio	Mixture Sw:At	Dependent Variable	Mean	Std. Error	95% Confidence Interval Lower Bound.	Upper Bound.
Mn/N	Combined	T1	0.41	0.03	0.35	0.48
		T2	0.73	0.04	0.64	0.82
		T3	0.74	0.02	0.69	0.79
		T4	0.88	0.03	0.81	0.96
		T5	0.83	0.02	0.79	0.88
		T6	0.94	0.04	0.86	1.02
		T7	0.80	0.03	0.73	0.88
		T8	0.96	0.03	0.89	1.04
	25:75	T1	0.43	0.06	0.30	0.55
		T2	0.76	0.08	0.57	0.95
		T3	0.65	0.04	0.55	0.75
		T4	0.75	0.07	0.60	0.90
		T5	0.70	0.04	0.61	0.78
		T6	0.73	0.07	0.57	0.89
		T7	0.68	0.07	0.52	0.83
		T8	0.76	0.07	0.61	0.91
	50:50	T1	0.38	0.06	0.25	0.51
		T2	0.56	0.08	0.37	0.75
		T3	0.80	0.04	0.70	0.90
		T4	0.85	0.07	0.70	1.00
		T5	0.85	0.04	0.76	0.93
		T6	1.10	0.07	0.94	1.26
		T7	0.78	0.07	0.63	0.93
		T8	0.89	0.07	0.74	1.04
	75:25	T1	0.43	0.06	0.30	0.56
		T2	0.76	0.08	0.58	0.95
		T3	0.74	0.04	0.64	0.84
		T4	0.89	0.07	0.74	1.04
		T5	0.80	0.04	0.71	0.88
		T6	0.97	0.07	0.81	1.14
		T7	0.81	0.07	0.66	0.97
		T8	1.01	0.07	0.86	1.17
	100:00	T1	0.41	0.06	0.28	0.54
		T2	0.84	0.08	0.65	1.03
		T3	0.79	0.04	0.69	0.89
		T4	1.05	0.07	0.90	1.20
		T5	0.99	0.04	0.91	1.08
		T6	0.96	0.07	0.80	1.12
		T7	0.94	0.07	0.79	1.10
		T8	1.18	0.07	1.03	1.33

Nutrient or Ratio	Mixture Sw:At	Dependent Variable	Mean	Std. Error	95% Confidence Interval Lower Bound.	Upper Bound.
P	Combined	T1	0.270	0.008	0.252	0.289
		T2	0.229	0.007	0.212	0.245
		T3	0.192	0.006	0.179	0.205
		T4	0.194	0.006	0.179	0.208
		T5	0.193	0.007	0.177	0.209
		T6	0.190	0.007	0.174	0.206
		T7	0.186	0.008	0.167	0.206
		T8	0.195	0.008	0.176	0.214
	25:75	T1	0.278	0.016	0.240	0.315
		T2	0.266	0.014	0.234	0.298
		T3	0.215	0.011	0.189	0.241
		T4	0.221	0.013	0.192	0.250
		T5	0.231	0.014	0.199	0.263
		T6	0.256	0.014	0.225	0.288
		T7	0.232	0.017	0.194	0.270
		T8	0.237	0.017	0.199	0.276
	50:50	T1	0.271	0.016	0.233	0.308
		T2	0.231	0.014	0.199	0.263
		T3	0.191	0.011	0.165	0.218
		T4	0.207	0.013	0.178	0.236
		T5	0.194	0.014	0.162	0.226
		T6	0.180	0.014	0.148	0.211
		T7	0.186	0.017	0.147	0.224
		T8	0.189	0.017	0.151	0.228
	75:25	T1	0.281	0.016	0.244	0.319
		T2	0.209	0.014	0.176	0.241
		T3	0.191	0.011	0.165	0.218
		T4	0.199	0.013	0.170	0.228
		T5	0.202	0.014	0.169	0.234
		T6	0.180	0.014	0.148	0.211
		T7	0.178	0.017	0.140	0.217
		T8	0.193	0.017	0.154	0.231
	100:00	T1	0.251	0.016	0.214	0.289
		T2	0.209	0.014	0.176	0.241
		T3	0.170	0.011	0.144	0.197
		T4	0.147	0.013	0.118	0.176
		T5	0.145	0.014	0.113	0.177
		T6	0.145	0.014	0.114	0.177
		T7	0.150	0.017	0.111	0.188
		T8	0.160	0.017	0.122	0.199

Nutrient or Ratio	Mixture Sw:At	Dependent Variable	Mean	Std. Error	95% Confidence Interval Lower Bound.	Upper Bound.
P/N	Combined	T1	0.156	0.006	0.142	0.169
		T2	0.161	0.004	0.151	0.170
		T3	0.155	0.003	0.147	0.163
		T4	0.166	0.005	0.154	0.178
		T5	0.163	0.006	0.149	0.177
		T6	0.157	0.005	0.145	0.169
		T7	0.147	0.005	0.136	0.157
		T8	0.156	0.004	0.147	0.165
	25:75	T1	0.161	0.011	0.134	0.187
		T2	0.170	0.008	0.151	0.189
		T3	0.159	0.007	0.143	0.175
		T4	0.178	0.010	0.154	0.202
		T5	0.189	0.012	0.160	0.217
		T6	0.192	0.010	0.168	0.215
		T7	0.172	0.009	0.151	0.193
		T8	0.174	0.008	0.156	0.192
	50:50	T1	0.147	0.011	0.121	0.174
		T2	0.154	0.008	0.135	0.172
		T3	0.154	0.007	0.138	0.170
		T4	0.181	0.010	0.157	0.205
		T5	0.167	0.012	0.139	0.196
		T6	0.157	0.010	0.133	0.180
		T7	0.148	0.009	0.127	0.168
		T8	0.164	0.008	0.146	0.182
	75:25	T1	0.167	0.011	0.141	0.194
		T2	0.165	0.008	0.147	0.184
		T3	0.162	0.007	0.146	0.178
		T4	0.166	0.010	0.142	0.190
		T5	0.163	0.012	0.134	0.191
		T6	0.153	0.010	0.129	0.177
		T7	0.147	0.009	0.127	0.168
		T8	0.159	0.008	0.141	0.177
	100:00	T1	0.147	0.011	0.121	0.173
		T2	0.153	0.008	0.135	0.172
		T3	0.144	0.007	0.128	0.160
		T4	0.139	0.010	0.115	0.163
		T5	0.132	0.012	0.104	0.161
		T6	0.126	0.010	0.103	0.150
		T7	0.120	0.009	0.099	0.140
		T8	0.127	0.008	0.109	0.145

Nutrient or Ratio	Mixture Sw:At	Dependent Variable	Mean	Std. Error	95% Confidence Interval Lower Bound.	Upper Bound.
Zn/N	Combined	T1	35.3	0.7	33.7	36.8
		T2	45.0	1.3	42.1	47.9
		T3	50.8	1.8	46.7	54.9
		T4	49.7	0.7	48.0	51.4
		T5	57.9	1.7	54.1	61.8
		T6	49.0	2.5	43.3	54.8
		T7	62.1	2.4	56.6	67.6
	25:75	T1	33.3	1.3	30.2	36.4
		T2	40.2	2.5	34.4	46.1
		T3	44.8	3.6	36.6	53.0
		T4	46.4	1.5	43.0	49.9
		T5	42.3	3.3	34.6	50.0
		T6	41.5	5.0	29.9	53.0
		T7	47.2	4.8	36.2	58.2
	50:50	T1	33.6	1.3	30.5	36.7
		T2	48.0	2.5	42.2	53.9
		T3	50.2	3.6	42.0	58.4
		T4	51.4	1.5	47.9	54.8
		T5	59.9	3.3	52.3	67.6
		T6	46.3	5.0	34.7	57.8
		T7	55.9	4.8	44.9	66.9
	75:25	T1	39.3	1.3	36.2	42.4
		T2	47.0	2.5	41.1	52.8
		T3	55.0	3.6	46.8	63.2
		T4	47.9	1.5	44.5	51.3
		T5	60.2	3.3	52.5	67.9
		T6	49.8	5.0	38.3	61.4
		T7	67.1	4.8	56.1	78.1
	100:00	T1	34.9	1.3	31.9	38.0
		T2	44.8	2.5	38.9	50.6
		T3	53.3	3.6	45.1	61.5
		T4	53.1	1.5	49.6	56.5
		T5	69.4	3.3	61.7	77.0
		T6	58.6	5.0	47.0	70.2
		T7	78.1	4.8	67.1	89.1

APPENDIX II

DUNCAN‟S POST HOC TESTS FOR FOLIAR NUTRIENT CONCENTRATIONS AND RATIOS BY MIXTURE

Nutrient	Mixture	N	Subset		
or Ratio	Sw:At		1	2	3
Ca	25:75	3	0.405		
	50:50	3	0.499	0.499	
	75:25	3	0.503	0.503	
	100:0	3		0.588	
	Sig.		0.17	0.21	
Ca/N	25:75	3	0.301		
	50:50	3		0.408	
	75:25	3		0.408	
	100:0	3		0.484	
	Sig.		1.00	0.07	
K	25:75	3	0.920		
	50:50	3	0.891		
	75:25	3		0.737	
	100:0	3		0.751	
	Sig.		0.52	0.74	
Mg/N	25:75	3	0.072		
	50:50	3	0.082		
	75:25	3	0.075		
	100:0	3	0.072		
	Sig.		0.11		
Mn/N	25:75	3	0.682		
	50:50	3		0.774	
	75:25	3		0.802	
	100:0	3			0.897
	Sig.		1.00	0.49	1.00
N	25:75	3	1.396		
	50:50	3	1.307		
	75:25	3	1.273		
	100:0	3	1.265		
	Sig.		0.10		
P	25:75	3	0.242		
	50:50	3	0.206	0.206	
	75:25	3	0.204	0.204	
	100:0	3		0.172	
	Sig.		0.07	0.10	
P/N	25:75	3	0.174		
	50:50	3	0.159	0.159	
	75:25	3	0.160	0.160	
	100:0	3		0.136	
	Sig.		0.19	0.05	
Zn/N	25:75	3	42.24		
	50:50	3	49.32	49.32	
	75:25	3		52.32	
	100:0	3		56.02	
	Sig.		0.06	0.08	