FOLIAR NUTRIENT RESORPTION AND LITTERFALL PRODUCTION WITH STAND AGE, OVERSTORY COMPOSITION, AND DISTURBANCE ORIGIN IN BOREAL FORESTS

By

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ABSTRACT

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Keywords: *Betula papyrifera*; boreal forest; logging; nutrient resorption; plant nutrition; *Populus tremuloides*; productivity; soil fertility; stand development; wildfire.

Nutrient resorption (NuR) prior to developmental senescence allows for nutrient conservation in plants, driven primarily by genetics, development stage, climate and soil fertility, and litterfall is the vector for the influx of nutrients to the soil. Despite their importance, changes in NuR and litterfall through stand development, under different overstory compositions, and following different disturbance scenarios in boreal forests are not fully understood. My objectives were to examine the effects of time since stand-replacing fire, overstory composition and disturbance origin on leaf NuR efficiency (NuRE) and litterfall production in a boreal forest.

I used an age chronosequence with 7 to 209 years since fire to examine the effects of stand age and overstory composition (broadleaf or mixed with conifer) on the resorption efficiency of nitrogen (NRE), phosphorus (PRE) and potassium (KRE) in the leaves of trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*). I then compared NRE, PRE and KRE between stands of three disturbance origins (fire alone, full-tree logging alone, or full-tree logging followed by fire) in 7-year-old *Populus tremuloides* in pure stands or mixed with jack pine (*Pinus banksiana*). A similar age chronosequence was used to study the effects of stand age and overstory composition (broadleaf, mixedwood, and conifer) on litterfall production. Within this chronosequence, I examined how litterfall production varies with disturbance origin (fire and logging) for 7, 15 and 33 years since disturbance.

In *Populus tremuloides* and *Betula papyrifera*, PRE and KRE decreased with increasing stand age. No overstory effects were found for *Betula papyrifera*, but PRE and KRE were lower in *Populus tremuloides* when mixed with conifer trees. Full-tree logging followed by fire resulted in a marginally lower PRE in *Populus tremuloides* in mixedwood stands when compared with fire and full-tree logging alone. Total, foliar and other litterfall production increased to 33 years since fire then reached a steady rate. Total and foliar litterfall were higher in broadleaf stands than conifer and mixedwood stands. Arboreal epiphytic lichen fall was highest in the 209-year-old conifer stands and 146-year-old mixedwood stands. Total and foliar litterfall peaked in October, other litter peaked in June and October, and epiphyte fall reached its maximum in June. Litterfall production did not vary significantly between fire and logging origin.

The results of this study suggest that NuR in trees can be influenced by stand development stage since fire and that species composition in the overstory can play an interactive role. This study also indicates that, although fire and logging can result in variable effects on the soil environment, NuR is mostly conserved shortly after disturbance. Although it has been shown that overall forest productivity declines with age, this study demonstrates that litterfall can be maintained over time in boreal forests, regardless of tree species composition, but that broadleaf stands produce more litterfall than conifer and mixedwood stands. Disturbance origin may not be a significant driver in litter production. The implications of this study can fit into a larger framework of research on productivity and nutrient flux in northern boreal environments.

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NOTE TO THE READER

There is some overlap of definitions of terms, study area description and sample design description among chapters 2, 3 and 4. Each chapter has been prepared as a separate manuscript for submission to publication. Chapter 1 has been invited for submission to *Critical Reviews in Plant Sciences*. Chapters 2, 3 and 4 are in preparation for submission.

CHAPTER ONE: GENERAL INTRODUCTION

The boreal region of Canada is characterized by shallow acidic soils, cool temperatures, and restricted nutrient availability (Bonan and Shugart, 1989). Wildfire is the most common natural stand-replacing disturbance in boreal forests (Senici *et al.*, 2010), driving species replacement patterns that result in the mosaic of coniferous and deciduous trees in the landscape (Oliver, 1981). Throughout stand development post-fire, forests undergo a series of changes in the soil environment, the understory tree and vegetation layer, and the overstory tree layer. Time since fire allows for the accumulation of organic material onto the forest floor and increased shading and cooling of mineral soil, changing the microclimate of the stand through time.

Nutrient resorption (NuR) prior to tissue senescence in plants varies among species and can depend on soil nutrient availability (Killingbeck, 1996). A review on this topic is found in chapter 1. The stoichiometric balance of nutrients in forests changes throughout development (Yang and Luo, 2011), largely due to changes in nutrient demands for growth and the shifts in availability in the soil (Lambers *et al.*, 2008). Therefore, NuR may vary among boreal species under different stand development stages, which will be addressed in chapter 2. Logging typically results in varying degrees of soil erosion (Fuller *et al.*, 1988) and soil compaction (Brais and Camire, 1998) on-site, directly affecting the thickness of the forest floor. The effects of fire, logging and logging plus fire on nutrient resorption (NuR) will be addressed in chapter 3.

Net primary production (NPP) was originally defined as the amount of carbon biomass fixed via photosynthesis that is available to the first trophic level in an ecosystem (Lindeman, 1942). In boreal ecosystems, temperature and AET affect primary productivity in coniferous trees differently than deciduous trees (Berg and Meentemeyer, 2001; Kljun *et al.*, 2006).

While forest productivity is mainly driven by regional climate (Rosenzweig, 1968; Cleveland *et al.*, 2011; Weiskittel *et al.*, 2011), local factors such as intraspecific competition (Cavard *et al.*, 2011), nutrient availability (Trap *et al.*, 2009), and type and severity of disturbance (Weber, 1987) can result in variation in productivity. An age-related decline in productivity has been suggested for forests worldwide (Gower *et al.*, 1996; Ryan *et al.*, 1997), so litterfall production may vary with stand age, addressed in chapter 4. Full-tree logging practices have been increasing since the mid-1980's, raising concerns for the maintenance of productivity on-site (Boyle *et al.*, 1973; Turner and Lambert, 1986).. The effects of fire and logging on litterfall production are understudied and will be addressed in chapter 4.

CHAPTER TWO: PATTERNS AND MECHANISMS OF NUTRIENT RESORPTION IN PLANTS

Introduction

The mobilization and use of nutrients by plant communities have captivated researchers for almost a century (Combes, 1926; Williams, 1955; Vitousek, 1982; Attiwill and Adams, 1993). Nutrient resorption (NuR) allows for the conservation of nutrients that may be otherwise lost to soils via litterfall following senescence (Aerts and Chapin, 2000). It has been demonstrated that when the NuR process is artificially prevented, plant fitness traits such as biomass increment growth, stem growth, and fruit production are adversely affected (May and Killingbeck, 1992). Improving the knowledge of this process can provide a great deal of information regarding nutrient use strategy. The most recent global estimate for average percentage of nutrients that are resorbed back into live plant tissues are 62.1% for N and 64.9% for P (Vergutz *et al.*, 2012) (Figure 2.1).

The first two reviews on the topic placed emphases on the physiological mobility of given nutrients and the transport of these nutrients throughout the phloem tissues (Loneragan *et al.*, 1976; Hill, 1980). At this time, interest in NuR was more on physiological constraints (Chapin, 1980), but it was not until the review by Aerts (1996) that the effects of soil fertility and interspecific variation on NuR were addressed. In this review, Aerts (1996) found no evidence for a connection between soil fertility and NuR, and argued that NuR is not reflected in green leaf nutrient concentrations. Since then, many studies have provided positive evidence for both of these claims (Eckstein *et al.*, 1999; Diehl *et al.*, 2003; Yuan *et al.*, 2005b; Yuan and Chen, 2009a), supported by increased effort with global syntheses and updated methods (Vergutz *et al.*, 2012). Building on previously published concepts, Aerts and Chapin (2000) presented a review

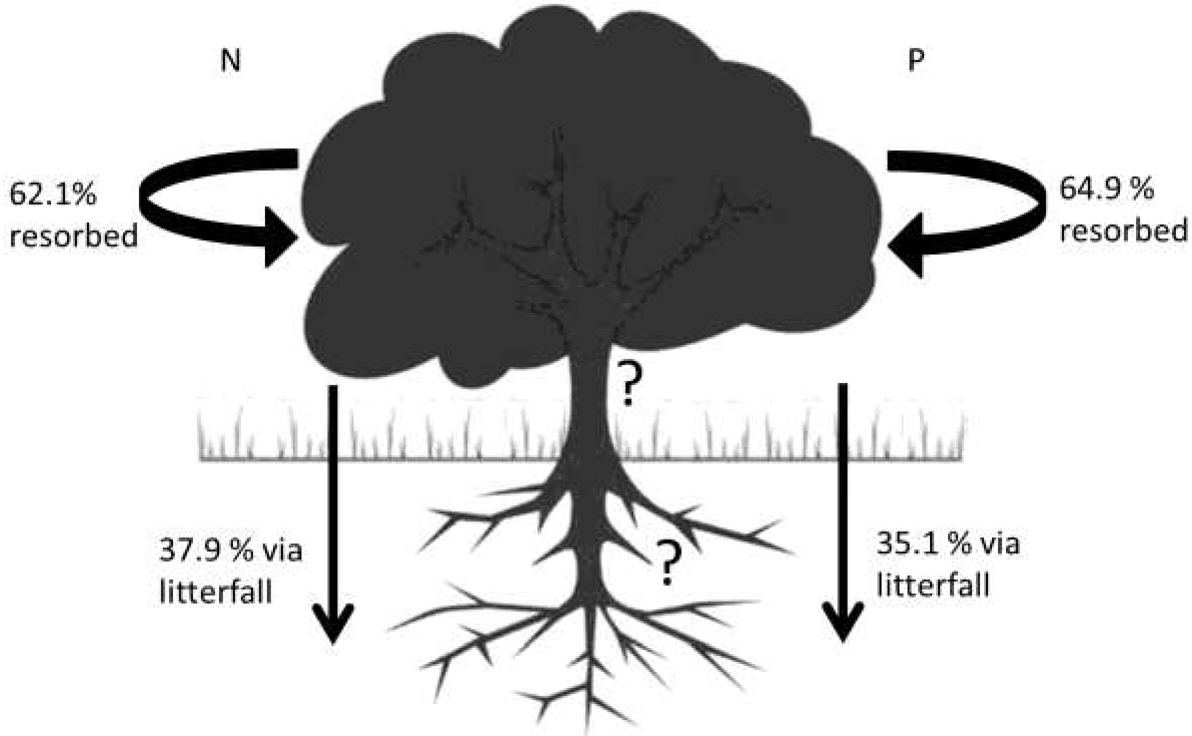

Figure 2.1 Percentage of nitrogen (N) and phosphorus (P) resorbed back into live tissues and inputs into the soil via litterfall during leaf senescence from global estimates (Vergutz *et al.*, 2012). Question marks are for plant tissues with no global estimate.

of NuR in the context of variation across plant functional types and soil fertility, but focused mainly on the variation of plant strategies with mineral nutrition, nutrient use and cycling.

Despite increased focus on plant functional traits and their effects on NuR and cycling (Killingbeck and Tainsh, 2002; Escudero and Mediavilla, 2003; Wright and Westoby, 2003; Ordonez *et al.*, 2009; Fujita *et al.*, 2013; Zhang *et al.*, 2013), there has been no critical review since Aerts and Chapin (2000) that addresses the effects of soil and growth forms on NR. Furthermore, there has also been no critical review for the effects of climate and developmental stage on NuR for observations among non-leaf plant tissues, which is a new parameter of this field of study.

The way that perennial plants retranslocate nutrients back into living tissues is influenced by leaf habit (Aerts, 1995; Lal *et al.*, 2001), development stage (Milla *et al.*, 2005; Yuan and Chen, 2010a; Ye *et al.*, 2012; Tully *et al.*, 2013), soil fertility status (Yuan *et al.*, 2006; Drenovsky *et al.*, 2013), and climatic factors (Oleksyn *et al.*, 2003; Yuan and Chen, 2009a). While these studies have made advances toward understanding of plant nutrients, specifically with nutrient recycling in plants, questions still remain as to addressing how NuR may differ among plant tissues and how genetic variability, development, and environment of plants control NuR. In this review, we develop a general conceptual framework of how NuR is influenced by

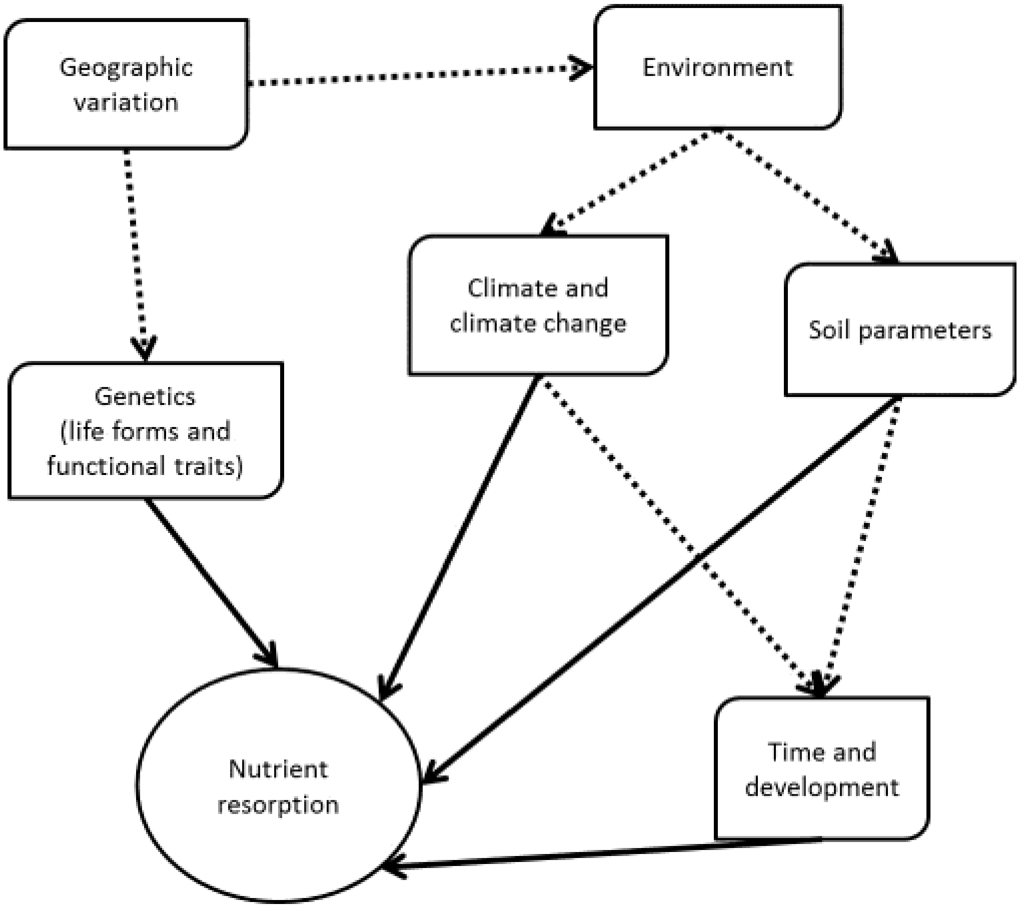

Figure 2.2 Conceptual model of controls of nutrient resorption in plants (solid arrows) and interactions between the controls (dashed arrows).

genetic variability, development, and environment (Figure 2.2). We begin with a description of plant nutrient use and NuR as a strategy for nutrient conservation. We then discuss the structural controls on NuR, specifically the observations in different plant tissues. The variation in the genetic expression of NuR in the context of plant life forms and leaf habit is further examined. We then examine how NuR changes with plant development at both the plant and ecosystem levels. Finally, we address the environmental controls that drive the variation in NuR in plants.

Plant Nutrient Use and Resorption

Plant Nutrient Use and Stoichiometry

The importance of nutrient use and cycling in plant ecosystems cannot be underestimated, given that plants often do have sufficient amounts of biologically available nutrients to support growth, survival, and reproduction. Essential nutrients for plant functioning include carbon (C), nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), among others. Nutrients are first introduced to the soil from either biological or parent material sources (Aerts and Chapin, 2000). Primary influxes of N derive from the atmosphere through deposition, while P derives from rock weathering (Aerts and Chapin, 2000). Once in the soil, nutrients are taken up by plants, facilitated by mycorrhizae and/or nitrogen-fixing bacteria found within the soil environment (Aerts and Chapin, 2000). At the cellular level, N is primarily used by plants for enzymatic activity and photosynthetic capacity (Evans, 1989), while also playing an essential role in the mobilization and storage of other key nutrients (Canton *et al.*, 2005). Phosphorus is used for energy transfer (Aerts and Chapin, 2000) and metabolism (Vance *et al.*, 2003).

A fundamental focus of plant nutrient research is limitation – a metric classically recognized as the requirement of a given nutrient for plant growth, reproduction and survival (Chapin, 1980). Many studies on nutrient limitation divide land forms between terrestrial and marine environments (Vitousek and Howarth, 1991), but all concentrate on either single elements (Aber *et al.*, 1998; de Campos *et al.*, 2013) or ratios between elements (Koerselman and Meuleman, 1996; Güsewell, 2004). N and P are the two macronutrients that have received the most attention in plant nutrient studies, primarily for their close relationship with plant productivity (Attiwill and Adams, 1993; Aerts and Chapin, 2000) and are therefore the most limiting in terrestrial environments (Chapin, 1980). The differences in influx between the two macronutrients explain the variation in nutrient limitation among biomes. Net primary production of all photosynthetic organisms is limited by N (Vitousek and Howarth, 1991) in both aboveground (LeBauer and Treseder, 2008) and belowground (Yuan and Chen, 2012d) environments. It is widely accepted that P-limitation is more apparent in the tropics than other biomes (Yuan and Chen, 2012d). The irreversible binding of P with clay soils without weathering, renders it unavailable for plant mobilization (Vitousek, 1984). Growth in boreal and temperate plants, however, tends to be more N-limited, because of N losses due to leaching and denitrification into the atmosphere from frequent fire events and lower temperatures (Bonan and Shugart, 1989).

Interest in nutrient limitations of plant communities has shifted from single nutrient use (Williams, 1955; Vitousek, 1982) to factors affecting nutrient co-limitation on large spatial scales (Harpole *et al.*, 2011; Fisher *et al.*, 2012; Yuan and Chen, 2012d) as well as long temporal scales (Menge *et al.*, 2012). Nutrient stoichiometry in biological communities was first introduced by Alfred C. Redfield in the early 1930's, who developed and published a set of chemical constraints of C, N, and P on the biomass production of planktonic organisms in marine environments (Redfield, 1934). Since then, C:N:P ratios at sea have been translated for applications in terrestrial environments (McGroddy *et al.*, 2004). The updated C:N:P ratio for plant foliage by mass using Redfield numbers is 1212:28:1, while the ratio for plant litter is 3007:45:1 (McGroddy *et al.*, 2004), and that for plant fine roots (<2 mm in diameter) is 906:15:1 (Yuan *et al.*, 2011). Stoichiometry is becoming a more important aspect of plant nutrition because of the inherent relationships between essential elements and growth rate (Elser *et al.*, 2003), making Liebig's classical Law of the Minimum practically obsolete (Danger *et al.*, 2008). A main focus of research in plant nutrient dynamics today is the flexibility of stoichiometric relationships in terrestrial environments (Yuan *et al.*, 2011; Ågren and Weih, 2012; Sistla and Schimel, 2012) due to the increasing interest in global ecosystem change (Aerts *et al.*, 2012; Austin and Vitousek, 2012; Sardans and Penuelas, 2012).

Resorption as a Nutrient Conservation Strategy

Nutrient resorption plays a significant role in maintaining a balance in the stoichiometry of plant organisms (Reed *et al.*, 2012). Classically named "backmigration" (Fries, 1952), "redistribution" (Williams, 1955), "retranslocation" (Chapin, 1980), "remobilization" (Hill, 1980), or "reabsorption" (Jonasson, 1989), among others, NuR is defined most succinctly as the movement of nutrients from senescing tissues back to surviving tissues in photosynthetic organisms (Killingbeck, 1986). Killingbeck (1996) used a large database to develop the concept of nutrient resorption proficiency, the terminal concentration of a given nutrient in senesced tissue, as a proxy for resorption potential (complete, intermediate, and incomplete). The definition has since been widened to include the transfer from old plant tissues to new sink tissues such as plant stems or current-year foliar growth (Nambiar and Fife, 1991; Freschet *et al.*, 2010; Mao *et al.*, 2013). Interest in NuR within the field of plant biology has been growing since the early 20th century with the increased occupation with fertilization and nutrient cycling experiments (Combes, 1926; McHargue and Roy, 1932). NuR is being studied today most commonly in the context of its response to fertilization (Goodman *et al.*, 2014; Mayor *et al.*, 2014; Wang *et al.*, 2014a) and nutrient limitation (Han *et al.*, 2013).

Nutrient resorption is much different from the leaching of materials from one plant organ to another, which is a passive process (Hagen-Thorn *et al.*, 2006). Resorbed nutrients are actively transported via the phloem in plants (Williams, 1955; Chapin, 1980; Hill, 1980) through the abscission zone, activated by the protein kinetin (Dela Fuente and Leopold, 1968) and recycled for the biosynthesis of lignin required, along with carbon, for the growth of new tissues (Canton *et al.*, 2005). Passive leaching of nutrients allows escape to the atmosphere or into an aqueous body in which the organ is submerged; heavy rainfall can also induce leaching (Long *et al.*, 1956; Tukey Jr, 1970). The most important difference between these two processes is that leaching results in a net loss of nutrients from the plant, while NuR is a form of recycling. It is the active nature of the process of NuR that qualifies it as an adaptation and not just a passive process (Freschet *et al.*, 2010; Menge *et al.*, 2011). The adaptive nature of NuR elicits a degree of variation in expression between different plant species, thus prompting research into this topic.

Plants resorb relatively more of a nutrient if it is more limiting to its growth (Han *et al.*, 2013). Still unknown, however, is the energetic costs of nutrient uptake, versus nutrient resorption in plants. While there have been advances in recent years for the mechanisms of NuR with limitation status, this area of research can be broadened to include components of nutrients themselves (organic and inorganic), as well as lesser-studied micronutrients such as K, Ca, and

Mg, and how the ratios between these and N and P may vary with limitation status and competitive ability of plant communities.

Nutrient Resorption among Plant Tissues

The remobilization of nutrients to different parts of plant anatomy is important to measure in order to estimate the nutrient economy of an individual plant or plant community. Senescence of plant tissues has generally focused on leaves (Dela Fuente and Leopold, 1968; Smart, 1994; Zhang *et al.*, 2013). Senescence can be considered as a form of programmed cell death (PCD) (Humbeck, 2014), and occurs in all areas of the plant anatomy, but the most relevant step in this process is the movement of nutrients within the plant and out of the plant into the soil environment. The use of a whole plant system in the context of nutrient resorption is important for describing the nutrient economy of plant communities. Huang *et al.* (2012) estimated resorption patterns using both plant- and leaf-level measurements and found different results between the two methods. Furthermore, Yuan *et al.* (2005a) argued that other above-ground tissues are as important as leaves for accurate estimates of resorption.

The physical structure of the plant determines the allocation of nutrients to different tissues. For example, woody plants use and allocate nutrients differently from grasses, forbs and ferns. Most studies dealing with woody plants do not measure resorption patterns in other plant tissues apart from foliage because of the difficulty in sampling root, bark and stem tissues throughout the annual cycle of woody plants and non-woody species have been easier logistically to use for studying non-foliar plant tissues (Mao *et al.*, 2013). In the following section of the review, we first examine the allocation of nutrients to different plant tissues and then compare NuR among plant tissues. Leaves, stems (or culms: supporting structures similar to woody plant stems found in graminoid species) and fine roots will serve as the three most basic plant components for this review, as they represent the only plant features measured for NuR.

Leaves

Leaves represent a low fraction of aboveground biomass in woody plants, exact ranges for percent of total depends on age, species, and turnover rates (Poorter *et al.*, 2012), but are integral to the carbon assimilation and photosynthetic capacities within the plant's anatomy (Wright *et al.*, 2004). Carbon gain is maximized only if sufficient N is allocated to leaves depending on an optimal level of irradiance (Hikosaka, 2005). There is often a trade-off between nutrient investment and leaf longevity (Wood *et al.*, 2011), which is closely related to the trade-off between mean residence time (MRT) of nutrients and nutrient productivity (deAldana and Berendse, 1997; Yuan *et al.*, 2008). For example, the mean residence time of N is longer than leaf longevity in most species (Aerts and Chapin, 2000; Marty *et al.*, 2009) because of the resorption process which allows for continual cycling of N in the canopy (Eckstein *et al.*, 1999).

The resorption of nutrients occurs within leaf tissues in two ways: from senescing leaves to stems and/or roots, and from senescing leaves to new leaves. The distribution of leaf N varied throughout the canopy of a stand of *Quercus serrata* trees in a study conducted by Ueda (2012), depending on light differentiation with vertical structure. Nutrients are translocated from older, shaded leaves in the lower canopy to newer, sunlit leaves (Smart, 1994; Saur *et al.*, 2000; Hirose and Oikawa, 2012). Siebrecht *et al.* (2003) found that it was primarily the increased xylem sap flow rate (activated by nutrient demands from newer shoots) between these tissues that allowed the transfer of nutrients from older to newer leaves. In evergreen deciduous trees of a Mediterranean environment, resorption occurs from young leaves to other tissues six months after leaf initiation, then from mature leaves after two years, and finally from dying leaves prior to senescence and leaf fall (Fife *et al.*, 2008). These nutrients from all three leaf stages were translocated to new shoots which, in turn, support new leaf production (Fife *et al.*, 2008). For evergreen temperate coniferous species, nutrients are also translocated from old to new foliage, as well as from senescing foliage (Nambiar and Fife, 1991). Coniferous trees remobilize nutrients from old needles to facilitate growth in sink tissues such as stemwood, resulting in a positive increase in basal area increment with increased resorption of N and P from needles throughout the crown of *Pinus radiate* (Nambiar and Fife, 1991). This remobilization occurs after the growing season during senescence for over-winter storage, then is retranslocated in the spring to support new growth (Helmisaari, 1992).

Global data for leaf NuR is ubiquitous, however there have only been a few studies that have included sampling of non-leaf plant tissues along with leaves (Table 2.1). In these studies for each life-form, nitrogen resorption efficiency (NRE, the proportion of nitrogen resorbed back to live tissues prior to senescence) is generally higher in leaves than in stems/culms or roots (Table 2.1). By contrast, phosphorus resorption efficency (PRE) is nearly identical among all tissues (Table 2.1). Lü *et al.* (2012) measured NRE and found a similar decreasing trend from leaf to stems/culm tissues A new avenue for study may include the mechanisms that drive NuR in leaves, in the context of relative nutrient resorption (N, P and others), as well as among plant tissues. As previously mentioned, the cost of leaf production may justify the higher NRE, but this has also yet to be demonstrated.

Stems

In both woody and non-woody plants, stems are the conduits between the roots, soil and the photosynthetic tissues of the plant. For trees, the mass of stems increases linearly with whole plant (Enquist and Niklas, 2002); however stemwood is generally lower in nutrient

Table 2.1 Nitrogen resoption efficiency (NRE) and phosphrous resorption efficiency (PRE) in leaves, stems/culms and roots by plant life form. Values are mean ± s.e.m. The number of observations is in parantheses.

Plant life form	NRE (%)			PRE (%)			Source
	Leaves	Stems/culms	Roots	Leaves	Stems/culms	Roots	
Woody deciduous	70.2 ± 3.9 (12)	35.2 ± 4.5 (12)	19.3 ± 16.2 (2)	59.0 ± 6.6 (12)	44.9 ± 5.3 (12)	61.8 ± 2.7 (2)	Freschet et al. (2010)
Woody evergreen	62.7 ± 4.4 (4)	23.3 ± 5.7 (4)	13.3 ± 10.3 (2)	65.7 ± 3.4 (4)	44.1 ± 5.0 (4)	48.1 ± 16 (2)	Freschet et al. (2010)
Graminoids	69.8 ± 2.9 (10)	52.9 ± 6.3 (10)	75.2 (1)	74.5 ± 3.1 (6)	66.8 ± 5.3 (1)	79.8 (1)	Aerts and de Caluwe (1989a), Freschet *et al.* (2010), Lü *et al.* (2012), and Mao *et al.* (2013)
Forbs	63.2 ± 5.9 (15)	55.9 ± 4.4 (15)	28.1 ± 9.8 (4)	58.7 ± 6.9 (15)	65.7 ± 5.4 (15)	59.1 ± 5.9 (4)	Freschet *et al.* (2010)
Ferns	57.8 ± 18.0 (4)	66.4 ± 9.3 (15)	22.1 ± 13.6 (2)	78.3 ± 3.4 (4)	54.1 ± 17.9 (15)	44.4 ± 26.4 (2)	Freschet et al. (2010)
Overall	**65.8 ± 2.8**	**47.1 ± 3.0**	**27.0 ± 6.8**	**63.3 ± 3.4**	**55.7 ± 3.4**	**56.8 ± 5.5**	

concentrations than the rest of the components of tree aboveground biomass such as leaves, flowers, and fruits (Woodwell *et al.*, 1975). Within tree stems, there are two broad categories of tissues: stembark and stemwood (further divided into sapwood and heartwood). Generally, stembark has higher nutrient concentrations than stemwood (Ponette *et al.*, 2001; Boucher and Côté, 2002; Hagen-Thorn *et al.*, 2004), but their sizes and growth rates are substantially different. For example, biomass production in the stemwood of *Eucalyptus* trees is ten times higher than the stembark, but, the demands for P, Ca, and Mg are similar between the tissues (Laclau *et al.*, 2003), suggesting that the demand of these nutrients for growth is different between these tissues. Sapwood has higher concentrations of N, P, and K than heartwood using a database for 22 gymnosperm and 71 angiosperm trees (Meerts, 2002), but no clear distinction was found for Ca or Mg between the wood tissues. Andrews and Siccama (1995) found higher concentrations of Ca and Mg in the sapwood of Atlantic white cedar (*Chamaecyparis thyoides* L.), but no patterns currently exist for the resorption of Ca and Mg in stemwood.

Translocation of N, P, and K occurs during the senescence of sapwood to new heartwood formation (Meerts, 2002), which challenged the viewpoint of Eckstein *et al.* (1999), who first stated that there is “probably no resorption from woody stems […]”. An important distinction between stems and other plant tissues is that the rate of senescence is much lower in these structures, while leaves and roots senesce annually (Yuan and Chen, 2010b, 2012c). PRE in stems or culms is similar to that of leaves for all life forms, whereas NRE is lower for stems than leaves, especially for woody plants as shown by Freschet *et al.* (2010) (Table 2.1). One possible reason for this lower NRE may be a higher priority allocation of P to new stem growth, whereas N uptake from the soil may be sufficient for woody plants to facilitate new stem growth. On the other hand, P-limitation may create a higher degree of PRE in stems, simply due to low availability in the soil.

Fine Roots

The study of nutrient dynamics within fine roots is always progressing in terms of available technology for use in experimentation. Root turnover patterns drive nutrient cycling (Aerts *et al.*, 1992) and fine live root mass production (Vogt *et al.*, 1986; Yuan and Chen, 2010b) in plants and this turnover frequency is highly influenced by temperature (Gill and Jackson, 2000). The relationship between fine root biomass and resource availability governs the growth response in these tissues. Yuan and Chen (2012a) found that the production of fine roots is influenced by available soil N and P. For instance, northern *Pinus sylvestris* individuals allocate more N to their roots than those of the same species in southern, more fertile environments because of increased competition for soil resources in cooler, northern environments (Merilä *et al.*, 2014), but variation in climate may play a factor.

Nutrient resorption in senescing fine roots was originally thought to be negligible compared to that of foliage and other tissues (Gill and Jackson, 2000; Gordon and Jackson, 2000). However, Kunkle *et al.* (2009) found an overall 20% decrease in N concentration following senescence in roots of four deciduous trees after correcting for mass loss. This finding confirms the need to apply mass loss correction factors (Vergutz *et al.*, 2012) even with non-leaf structures. Kunkle *et al.* (2009) also concluded that the N concentration of dead roots is almost always lower than live roots, providing supportive evidence that roots do retranslocate nutrients before senescence. Values for NRE in the roots of previous studies range from -8.4% (increase after root death) in a *Fagus sylvatica* L. stand (Van Praag *et al.*, 1988) to 48% in a *Picea abies* stand (Ahlström *et al.*, 1988), after mass loss was corrected by Kunkle *et al.* (2009). Freschet *et* *al.* (2010) found that NuR in the senescing fine roots of subarctic perennial plants can be also be substantial; up to 75.2% NRE and 79.8% PRE was measured in the graminoid *Carex rostrata* (Table 2.1).

It has been suggested by several authors that nutrient concentrations measured in different plant tissues, and thereby NuR, is largely dependent on environmental plasticity (Freschet *et al.*, 2013; Zhang *et al.*, 2014; Zhou *et al.*, 2014). Environmental controls will be discussed further on in this review, but it is important to note that differentiation of NuR among plant tissues has some bearing on differences in both the allocation and use of nutrients that become available in the soil. This topic may be of particular interest in future studies dealing with whole-plant nutrient economy.

Controls of Genetic Variability

Like most plant strategies, NuR is variable among plant species (Vitousek, 1982). Plants express traits to maximize overall fitness (Aerts and Chapin, 2000), promote growth, reproduction, dispersal, establishment and/or persistence as a response to abiotic and biotic environments (Kattge *et al.*, 2011). Traits that facilitate nutrient mobility are becoming more recognized for their role in biogeochemical cycles (Wright *et al.*, 2004; Ordonez *et al.*, 2009). In this section, we differentiate NuR among plant life-forms and leaf habits.

Variation Among Plant Life-Forms: Woody Plants

Competitive ability among plant functional types is strongly correlated with nutrient acquisition and use, depending on the environment (Hebert *et al.*, 2011; Menge *et al.*, 2011). Within a given species, Chapin and Kedrowski (1983) and Pugnaire and Chapin (1993) have claimed that NuR in nutrient-poor soils is not adaptive, but can be described as a phenotypic reaction to changes in nutrient availability in the soil, much like the passive adjustment of water uptake and use in variable moisture conditions. The variation of NuR between plant species and between functional groups of plants is, however, believed to be adaptive and non-random. Woody plants are the functional group for which there is the most published data on nutrient resorption, but there has been an increased focus on graminoids and forbs (Soudzilovskaia *et al.*, 2007; Lü *et al.*, 2011; Lü *et al.*, 2012).

Growth in woody plants depends on relatively higher carbon assimilation than in non-woody plants and plant nutritonal investments strongly correlate with biomass production (McGroddy *et al.*, 2004). Wood production is costly (Ryan *et al.*, 1996), and there is a higher mean residence time of C in the fine roots of trees than in the fine roots of grasses (Solly *et al.*, 2013), which suggests a higher degree of storage capabilities, recycling, and cellulose formation in woody plants. The leaves of woody plants also typically have a lower leaf N and P concentrations than non-woody species (Ordonez *et al.*, 2010; Sardans and Penuelas, 2013). These observations suggest that the investment of energy and resource acquisition for biomass production in roots of woody plants is higher than that for non-woody plants, as structural support demands higher allocations of energy in this group.

As previously mentioned, NRE is typically higher for leaves than other tissues in woody plants and the resorption of N in stems and roots in this functional group are lower than in non-woody plants, as demonstrated by Freschet *et al.* (2010) (Table 2.1). The longer residence time of nutrients in the stems and roots of woody plants likely reduces the need for NuR, compared with non-woody plants whose stems and roots were routinely shed.

Variation Among Plant Life-Forms: Graminoids and Other Non-Woody Plants

One of the first studies to address NuR in graminoids was that of Aerts and de Caluwe (1989b) who, by separating the plant parts following Berendse *et al.* (1987), found that N and P in *Molina caerulea* are resorbed from senescing leaves and culm structures into the basal internodes for over-winter storage. The root mass fraction is higher in grasslands than other biomes (Poorter *et al.*, 2012), and these below-ground tissues serve as reservoirs for future growth. Green leaf N concentration tends to be higher in forbs than graminoids, as demonstrated by Lü and Han (2010). However, leaf NRE of graminoids is higher (58.5%) than the NRE for forbs (41.4%) and evergreen woody plants (46.7%), and the PRE of graminoids is higher (71.5%) than forbs (42.4%) and both evergreen (54.4%) and deciduous (50.4%) woody plants, as shown by Aerts (1996). Differences in both biomass and nutrient allocation to leaves and overall plant productivity levels may explain the higher NuR in graminoids (Aerts and Berendse, 1989), because leaf mass loss is similar between graminoids (8-28%) (Güsewell, 2005) and woody plants (3-37%) (van Heerwaarden *et al.*, 2003). Tissue longevity and storage may be the primary contributors to variation in NuR among plant life-forms.

Ferns tend to have a similar nitrogen resorption proficiency to other non-woody plants, but phosphorus resorption proficiency appears to be lower (Killingbeck *et al.*, 2002), indicating that ferns contribute more nutrients back to the soil, being less proficient at resorbing nutrients back to the plant prior to senescence. Both NRE and PRE are similar between the ferns, *Dennstaedtia punctilobula* (winter-deciduous) and *Polystichum acrostichoides* (wintergreen) (Minoletti and Boerner, 1993; Killingbeck *et al.*, 2002). The similarity in NuR between these species that have distinctly different leaf habits suggests that functional form has a stronger role in NuR than leaf longevity in this plant functional group. PRE in the winter-deciduous fern, *Athyrium distentifolium*, was higher than NRE under ambient conditions in a fertilization experiment (Holub and Tuma, 2010). These studies represent very few that examine resorption patterns in ferns; more research is needed for this functional group to discern any broader trends on nutrient resorption.

Role of Leaf Habit

Plant nutrient use and NuR are variable across seasons (McHargue and Roy, 1932; Chapin *et al.*, 1980; Milla *et al.*, 2005; Niinemets and Tamm, 2005), leaf longevity (Jonasson, 1989; Escudero *et al.*, 1992; Eckstein *et al.*, 1999), and length of leaf abscission period (del Arco *et al.*, 1991). Evergreens are highly specialized plants, likely an adaptive strategy to nutrient-poor soil conditions, where an extended leaf lifespan allows for minimized nutrient losses that occur during senescence and shedding (Aerts, 1995). Evergreens occupy areas that are relatively colder and less fertile than those that support deciduous plants (Reich *et al.*, 1992). An extended leaf lifespan in evergreens leads to a maximized growth rate (Reich *et al.*, 1997b), while deciduous species exhibit higher levels of leaf production, which shed annually (Aerts and Berendse, 1989; Reich *et al.*, 1997a).

In deciduous plants, NuR occurs from live foliage to woody tissues prior to abscission from the tree, whereas in evergreen foliage, NuR occurs from older to younger shoots (Chapin and Kedrowski, 1983; Nambiar and Fife, 1991). Deciduous plants tend to allocate higher quantities of nutrients to facilitate faster growth for a competitive advantage during the shorter growing season in temperate environments, whereas evergreens are slow-growing, tolerant to harsh conditions, and have a longer leaf life span. Although informative, the measurement of absolute concentrations on a per mass basis in these life-forms can be misleading. Comparing absolute concentrations prior to and following senescence in deciduous trees is meaningless when compared with that of evergreens, because nutrient-use varies widely between the two groups. Deciduous fitness depends on NuR since a great deal of energy is invested into the process with a high investment in green leaf nutrients over the growing season. These nutrients must be returned to storage tissues following senescence, or the entire nutrient economy is compromised. For example, when resorption was prevented in *Quercus ilicifolia*, stem and foliar growth declined (May and Killingbeck, 1992).

More recently, Tang *et al.* (2013) reached conclusions consistent with others that deciduous broadleaves have a higher NRE than evergreens, but only a slightly higher PRE. More importantly, their findings suggest that plant functional type contributes more to the variation in NRE and nitrogen resorption proficiency than climate and soil, while climate and soil contribute more to the variation in PRE and phosphorus resorption proficiency (Tang *et al.*, 2013). Evergreens also have a higher phosphorus resorption proficiency than deciduous plants (Killingbeck, 1996; Yuan and Chen, 2009b), suggesting that species with this leaf habit are more P-limited. This leads to a further discussion on how plants with evergreen and deciduous leaf habits obtain and use both N and P. Sardans and Penuelas (2013) found a higher leaf N concentration in evergreen tree species compared with deciduous species growing in a similar Mediterranean climate on a similar soil type. Additionally, evergreens had higher aboveground biomass (Sardans and Penuelas, 2013), contrary to results reached by Gower *et al.* (2001) for boreal ecosystems. From these studies, evergreens appear to conserve high N concentrations for longer periods in the foliage, while deciduous plants contain relatively less N during the growing season and retranslocate more prior to senescence.

While it may seem that leaf N is consistently higher for evergreens, longevity plays a strong role in the residence time of N. The cumulative leaf N allocation in a deciduous tree throughout its lifetime is likely much greater than that of an evergreen. The study of cumulative nutrient use and NuR throughout the lifetimes of both evergreens and deciduous plants may provide more information than observations within a year or one growing season.

Controls of Plant Development

The establishment and persistence of plants through ecosystem succession influences soil properties, which in turn facilitates continued growth and plant community nutrition (Jenny, 1941). Soil profile development provides for nutrient storage capacity, however, secondary succession can result in subsequent nutrient losses from soil. As a result, natural systems experience fluctuations of nutrient capital associated with disturbance (Vitousek and Reiners, 1975a). Leaf litter concentrations of N and P decreases in woody plants of New Zealand along a soil chronsequence, with age ranging from 60 to 120,000 years, and therefore resorption proficiency of N and P increase with older, infertile soil (Richardson *et al.*, 2005).

As perennial plants age, a number of processes govern both the allocation and use of resources for growth. The shoot:root ratio for biomass allocation increases in non-woody perennial plants as they age (Wilson, 1988), but decreases in woody plants (Poorter *et al.*, 2012; Costa *et al.*, 2014). For trees at the individual level, aboveground net primary productivity (ANPP) increases with age, but reaches a threshold level and then decreases (Gower *et al.*, 1996; Ryan *et al.*, 1997), as does fine root production (Yuan and Chen, 2012c). The nutrient allocation to plant tissues shifts from foliage to woody tissues as trees age (Vitousek and Reiners, 1975a) where trees can allocate substantially more biomass to stemwood as tree size increases (Stephenson *et al.*, 2014). This change in biomass allocation and, consequently, energy allocation ultimately puts pressure on the plant's nutrient demands.

The first empirical study that reported the effect of stand age on patterns of leaf NuR of *Populus tremuloides* was performed by Yuan and Chen (2010a), who compared stands with ages 7, 25, 72 and 139 years since fire. Their results showed that both leaf N and litter N concentration increased with age, and that NRE significantly decreased with age, from 68.5% NRE in 7-year-old stands to 58.4% NRE in 139-year-old stands. However, mass loss was not corrected for in this study. A contrasting trend was found by Yang and Luo (2011), where the C:N ratio in plant tissues (especially coniferous trees) increased with stand age, but remained constant in litter. These results, paired with those of Yuan and Chen (2010a), suggest that younger trees are more N-limited if NuR increases with nutrient limitation (Kobe *et al.*, 2005). Since then, similar results have been reached by Li *et al.* (2013b) for *Caragana microphylla* and Ye *et al.* (2012) for *Casuarina equisetifolia*. However, these studies all found significantly negative relationships between soil available N and P and NRE and PRE with age. Therefore, both soil fertility and plant growth rates associated with time since disturbance can play roles in plant NR.

One of the primary drivers for differential allocation of resources is reproduction, which explains the trends observed for stand age and NuR patterns. Zhang *et al.* (2014) found that production of reproductive tissues in the aquatic plant, *Sagittaria graminea*, increases as soil availability of both N and P increases, with soil N having a higher influence on the production of flowers after N and P fertilization. Although nutrient-dependent reproduction in plants is not a new concept (Harper, 1967; Harper and Ogden, 1970; Van Andel and Vera, 1977), it does inspire questions about nutrient resorption patterns with reproductive stage. Many authors suggest that in low-nutrient soil conditions, plants allocate more energy and resources into growth and less into reproductive effort (Liu *et al.*, 2009; Zhang *et al.*, 2014), although in some cases, stress can induce flowering and fruit production (Pigliucci and Schlichting, 1995).

The nutrients required for reproduction in plants derive from three basic sources: uptake from soil, retranslocation from living but older structures, and following resorption from senescing tissues (Chapin *et al.*, 1990; Ashman, 1994). Reproductive efforts can put different demands on nutrient uptake and use. Ågren (1988) found that both N and P decreased in the leaves, stems, petioles, and rhizomes prior to fruit set in a dioecious perennial herb, *Rubus chamaemorus*. When nutrient resorption was prevented in *Quercus ilicifolia*, reproductive effort, measured by acorn production, declined (May and Killingbeck, 1992). Similar findings have been reached by Karlsson (1994) for branch N in *Rhododendron lapponicum*, leaf N in *Mangifera indica* (Urban *et al.*, 2004), and leaf K and stem P in *Dryobalanops aromatica* (Ichie and Nakagawa, 2013). All authors suggested that the nutrients were translocated to reproductive structures during these stages, causing nutrient decline in non-reproductive structures. The most recent study to address the role of NuR in reproductive effort was Tully *et al.* (2013) who found that leaf PRE is highest at intermediate seed counts in intermediate soil fertility in *Pentaclethra macroloba* of Costa Rica, a finding that suggests that reproductive effort, which interacts with soil fertility, can explain the variation in NuR patterns. This introduces a new dimension to the measurement of plant NuR that has been overlooked in the past, where biological events can play significant roles in nutrient dynamics parallel to edaphic conditions.

Environmental Controls

The environment influences NuR, in some cases more so than genetic makeup (Ågren and Weih, 2012). Foliar nutrient information has guided researchers in determining the overall nutritional status of an ecosystem for over four decades now (Van den Driessche, 1974).

However, it has only been in recent years that interest has shifted from using plant foliage to assess ecosystem quality to estimating the relative influence of the environment on foliage. In this section, we divide environmental controls between climate and soil.

Climate

Latitude is commonly used as a predictor variable for plant nutrient cycling patterns and productivity. Oleksyn *et al.* (2003) found a positive relationship between latitude and N and P resorption as well as green needle N and P in *Pinus sylvestris* communities living between 48° and 60° N latitude. Using five dominant plant groups (coniferous trees, deciduous trees, grasses, herbs, and shrubs), Reich and Oleksyn (2004) found that leaf N and P increases with latitude, with P increasing with a higher magnitude than N, attributing this pattern to temperature-controlled restrictions on plant and soil biochemistry as well as the differences in the limitation status of both N and P in different geological zones. Similarly, Lovelock *et al.* (2007) reported that PRE and P photosynthetic use efficiency (units of P used to perform photosynthesis) decreases with latitude in mangroves with increasing latitude, suggesting that plants living in the tropics have evolved for historically low P availability. On a smaller scale, Tang *et al.* (2013) found a general increase in NRE and decrease in PRE with latitude in eastern China for different functional plant groups. Between tropical and temperate forests, N limitation is comparable (LeBauer and Treseder, 2008), however the relatively higher abundance of N fixers in the tropics than temperate forests makes this limitation more complicated (Hedin *et al.*, 2009). Along a global latitudinal gradient, N limitation for productivity appears to increase from low to high latitudes (Yuan and Chen, 2012d), but it is more often P limitation that differentiates the tropics from temperate ecosystems, due to the increasing soil age and decreasing P deposition from lack of glaciation at lower latitudes (Elser *et al.*, 2007).

Climate parameters have been identified as primary drivers in NuR. Using a meta-analysis with a global database, Yuan and Chen (2009a), determined the relationship between climate variables (MAT and MAP) and resorption efficiency (NRE + PRE). Within four plant groups (trees, shrubs, conifers and broadleaves), NRE decreased with MAT and MAP, confirming the results found by Oleksyn *et al.* (2003). In contrast, PRE increased with MAT and MAP (Yuan and Chen, 2009a), strengthening the argument of N-limitation in colder climates and P-limitation in warmer ones (Yuan and Chen, 2012d). However, Vergutz *et al.* (2012) found that both NRE and PRE decreased with MAT and MAP and increased with latitude, contrary to the previous results (Yuan and Chen, 2009a). This inconsistency with PRE warrants some further examination. Both studies used the meta-analysis approach with a global dataset. While Vergutz *et al.* (2012) used senesced data collected from litter traps, Yuan and Chen (2009a) opted to use only freshly-abscised leaves, which reduces the sample size but may maintain a higher level of reliability, given that leaching can lead to underestimation of litter concentration by up to 8% for N and 10% for P (Boerner, 1984). An underestimation of litter nutrient concentration would lead to an overestimation of resorption efficiency, which does explain lower PRE for climates with higher MAP found by Vergutz *et al.* (2012), given that rainfall is the main driver of nutrient leaching from leaves in low latitudes. NRE between the two studies was consistent, however.

It is thought that plants with broad ecological amplitudes may be able to buffer against climate change events such as: increased CO_2 deposition, global warming, drought, N eutrophication, and species invasions (Sardans and Penuelas, 2012). The pathways for adaptation to climate change, however, are still unknown and have been a principle focus of climate change research for the past decade because of the importance of plant ecosystems for our sustenance

(Tubiello *et al.*, 2007), clean air (Nowak *et al.*, 2006), and provisions for wildlife (Doiron *et al.*, 2014).

There is a lot of evidence that supports the idea that climate change affects the nutritional stoichiometry of the global plant community (Dijk *et al.*, 2012; Dijkstra *et al.*, 2012; Sardans *et al.*, 2012). Northern environments, which tend to be N-limited, are especially susceptible to this N restriction under elevated CO_2 since enhanced plant growth increases mineral nutrient requirements (Norby *et al.*, 2010). Nitrogen is used in plant tissues and also stored in organic matter in the soil following CO_2 sequestration. However, the progressive nitrogen limitation (PNL) hypothesis (Luo *et al.*, 2004) states that N from biological and atmospheric sources cannot keep up with sources of CO_2 for plant uptake and use (Hungate *et al.*, 2003; Körner *et al.*, 2005; Reich *et al.*, 2006; Norby *et al.*, 2010). Variation in N metabolization and remetabolization among plant species may result in variable responses of plants to CO_2 enrichment (Bassirirad, 2000). It has also been suggested that increased aridity in global drylands due to climate change will decrease the availability of N in the soil and increase the availability of P, driving changes in the soil environment and plant communities (Delgado-Baquerizo *et al.*, 2013). In other areas of the world, particularly in northern temperate environments that are experiencing increased levels of nitrogen deposition due to human activities, an increase in the N:P ratio is occurring, creating a shift from N-limitation to P-limitation in plants (Penuelas *et al.*, 2013).

The effect of elevated CO_2 conditions on NuR was first addressed in an experiment performed by Norby *et al.* (2000) with *Acer* trees using open-top chambers. Litter N was lower, (i.e., high nitrogen resorption proficiency) in the elevated CO_2 chambers, but NRE was unaffected (Norby *et al.*, 2000). There was a brief mention of a decrease in the N:P ratio between green and senesced leaves in graminoid species under warming and CO_2-elevated treatments by

Dijkstra *et al.* (2012), implying that greater PRE was observed in these species. Aerts *et al.* (2007) found no effect of summer warming on the NRE of *Betula* and *Rubus* species residing in a bog.

The availability of water is a major factor in NuR, as pointed out by Killingbeck (1993). Changes in the hydrological cycle can change nutrient availability, thereby altering the ability of plants to utilize nutrients in the soil (Tomer and Schilling, 2009). Housman *et al.* (2012) presented a study in which the NRE and PRE of desert plants were only responsive to elevated CO_2 concentration in a dry year, suggesting that drought may be a more determinant factor in the variation of NuR than atmospheric effects. Drought-tolerant desert plants, for example, tend to be more plastic in their ability to retranslocate nutrients, as demonstrated in ocotillo, *Fouquieria splendens*, a drought-deciduous shrub which was inefficient in resorbing N (11%) in 1986 (Killingbeck, 1992a), but in 1989 resorbed up to six times the amount of N (72%) (Killingbeck, 1993). Drought-deciduous shrubs such as these are adapted to low water environments by way of multiple foliar production cycles in one growing season, induced by intermittent rain periods (Killingbeck, 1992b). More recently for temperate plants, Stewart *et al.* (2008) found a decrease in NRE in both N-fixing and non-N-fixing plants growing in Illinois, U.S.A. over one year, which coincides with a 7.2% increase in precipitation from August to November. However, Khasanova *et al.* (2013) found a lower NRE during drought conditions in plants adapted to drier environments, but a higher resorption proficiency of N under drought conditions in this same group of species. Drenovsky *et al.* (2010) found no direct relationship between annual precipitation and NuR, but argued that greenhouse studies may be useful to study NuR under differential moisture conditions. Resorption has been identified as a key mechanism in the delay of desertification in plants during reduced nutrient capitals of soils (Killingbeck, 1993; Li *et al.*, 2014), but there is still no evidence to support this theory.

While there is extensive research on long-term climate change, it is more realistic to consider NuR in parallel with ecosystem change in the context of changes in the frequency of extreme weather events along with the gradual long-term effects of climate change. A classic study published by Killingbeck (1988) used a rare opportunity to study the effect of a hurricane on NuR in ramets of *Populus tremuloides* in Rhode Island, USA, with data collected both before and after the hurricane. Phosphorus resorption efficiency decreased significantly after the hurricane event, and there was an actual increase of N in the senesced litter (Killingbeck, 1988). This study suggests that large-scale, short-term disturbances such as hurricanes may cause damage to ecosystem function, even in the absence of more obvious mechanical damage. Research into the effects of extreme weather events on NuR can improve the knowledge base for climate change modelling (Thompson *et al.*, 2013) in terms of droughts, floods, and other environmental disasters. Although the focus continues to be on individual elements – N-limitation vs. P-limitation – the most stressed consequence of climate change on plant nutrition is in the relative ratios of the nutrients and how they interact with other biotic or biochemical events in the ecosystem. Sistla *et al.* (2014) recently presented the Stoichiometrically Coupled, Acclimating Microbe-Plant-Soil model (SCAMPS) to address the issues surrounding co-limiting nutrient dynamics under ecosystem change. The incorporation of stoichiometric relationships between nutrients and between life-forms is crucial for understanding the impacts of climate change on plants.

Soil Fertility

Plant growth is nutrient-limited, and therefore a nutrient-conserving strategy is selected for plants occupying infertile soils (Aerts and Vanderpeijl, 1993). In a classic experiment performed by Small (1972), it was postulated that the higher NuR patterns observed in evergreens residing in bogs, compared with those residing in nutrient-rich ecosystems, is a result of plant adaptation to low nutrient availability. However, there is still an ongoing debate as to whether NuR is directly related to soil fertility, especially for plants adapted to low-nutrient soil conditions.

In one of the first reviews on plant mineral nutrition, Chapin (1980) states that the amount of NuR depends on plant nutrient concentration in the environment. Soil fertility has been used interchangeably with green leaf nutrient concentration when describing NuR. Both Chapin (1980) and Aerts (1996) originally found no relationship between green leaf nutrient concentration and resorption efficiency. Upon further experimentation and review, the concept of soil-NuR relationships was re-assessed by Aerts and Chapin (2000), where it was stated that 32% of the experiments analyzed in the paper published by Aerts (1996) resulted in a decrease in NRE (and 35% for PRE) with increased nutrient availability in the soil. At that time, it was concluded that because 63% of studies supported the null response of NRE (and 57% of PRE) to soil nutrient concentration, the debate was temporarily put aside (Aerts and Chapin, 2000). More recently, Kobe *et al.* (2005), using a global dataset, found evidence to support that there is a negative relationship between NRE and green leaf N and P, which was later corroborated by Vergutz *et al.* (2012).

It remains important to use natural gradients of nutrient availability to understand the relationship between NuR and nutrient availability, particularly for large, long-lived plants such as trees (Drenovsky *et al.*, 2013; Tully *et al.*, 2013; Campo *et al.*, 2014). Fertilization experiments, on the other hand, provide direct tests for the effects of nutrient availability on NuR in natural environments (Lü *et al.*, 2013; Mao *et al.*, 2013; Mayor *et al.*, 2014; Wang *et al.*, 2014a) and greenhouse experiments (de Campos *et al.*, 2013). Experimental studies can also examine whether the influences of multiple factors on NuR are additive (Holub and Tuma, 2010). Furthermore, the addition of N, P and other macronutrients in different ratios alters NuR in plants, as demonstrated by Wang *et al.* (2014a) and the addition of N can cause a decline in green leaf P and K (Goodman *et al.*, 2014), emphasizing the importance of stoichiometric relationships between nutrients in the soil (Ågren and Weih, 2012).

The relative costs associated with resorbing materials back into live tissues from senescing ones compared with nutrient uptake from the soil is currently unknown, as pointed out by Kobe *et al.* (2005). However, both Field (1983) and Chapin *et al.* (1990) have made cases for the optimization of NuR relative to leaf longevity and nutrient storage, respectively. Yuan *et al.* (2006) found that the N response efficiency (biomass production per unit N in the soil) increases as a response to decreasing N availability in the soil, which is closely tied to N uptake efficiency. This gap in the knowledge base for how NuR relates to soil nutrient capital as a function of energy optimization could serve as one of many future research efforts.

Summary and Future Perspectives

1. Nutrient resorption is the remobilization of nutrients from senescing or older tissues to storage structures or newer tissues in plants. Global estimates for leaf NRE and PRE are 62% and 65%, respectively.

2. Nutrient resorption also occurs in stems, culms and roots, but to a lesser degree than leaves. NuR from senescing roots can be greater than that for leaves, but empirical evidence in non-leaf tissues is scarce.
3. Genetic variability among plants affects NuR. Nutrient resorption efficiency in woody plants is typically lower in senescing stems and roots than non-woody plants. Non-woody plants are more plastic in their expression of NuR along a soil fertility gradient.
4. Evergreen species, due to their long leaf lifespan, have lower nutrient resorption efficiency than deciduous plants. Nutrient residence time is higher in evergreens than deciduous species whose nutrient cycling is more dependent on the NuR.
5. Along a soil chronosequence at the large temporal scale (thousands of years), NuR increases to accommodate older, infertile soils. With stand development in trees, resorption efficiency decreases, attributable to less demand for nutrients with less growth in older trees, but this observation can be often confounded with increasing soil fertility over time. Nutrient resorption increases during periods of high production of reproductive structures due to high nutrient demands.
6. Along the global geographic variation in climate and substrate, phosphorus resorption efficiency increases and nitrogen resorption efficiency decreases with increasing temperature and precipitation, although there are discrepancies within the literature. Nutrient availability variation between differing substrates along latitudinal gradients can explain this trend.
7. Short-term extreme weather events such as drought, floods, and hurricanes can significantly influence NuR. Evidence for the effect of long-term climate change (CO_2 enrichment and warming) on NuR are limited.

8. Increasing soil fertility tends to decrease NuR, but latitudinal patterns reflect the influences of several coupling factors such as genetic variation, climate, soil, and disturbance history.

Plant response to environmental change involves regulatory pathways that we are only beginning to understand. Unravelling the mechanisms for NuR in plant communities is important to understanding ecosystem function, health and resilience to change. Much more information is needed for non-leaf tissues in order to understand NuR at the entire plant and ecosystem levels. This topic may be of particular interest in future studies dealing with whole-plant nutrient economy. The variation in NuR among leaf habits also raises questions as to how nutrient cycling is affected by compositional shifts in vegetation resulting from succession in plant communities. Future research efforts on how NuR changes with leaf habit can aid in forecasting global changes in nutrient ecosystem economy.

The influence of plant age on NuR, especially in trees, is under-studied. Future research could include patterns of NuR in old-growth forests as well as grasslands, which comprise a large portion of the global vegetative cover. Older plant communities may serve as either a nutrient reservoir for future generations or may be under stress of nutrient limitation. In addition to ecosystem age, the incorporation of reproductive stage in NuR measurement can also improve accuracy of the estimates, given that it contributes a great deal of variation in terms of energy allocation.

While the findings of the effect of climate change (specifically CO_2 enrichment and warming) on NuR are currently inconsistent, abrupt changes in weather patterns can reveal interesting patterns in plant responses. The incorporation of stoichiometric relationships between nutrients and between life forms is crucial for the study of climate change mitigation and monitoring. While much is known about the capabilities of plants to retranslocate materials to living parts in the prevention of nutrient losses, a great deal of information has yet to be explored. Under a changing climate, plant communities on the global scale experience changes that are difficult to accurately predict. Improving the understanding of how plants express NuR can supplement global climate change models, especially those concerning biogeochemical parameters.

CHAPTER THREE: EFFECTS OF STAND DEVELOPMENT AND OVERSTORY COMPOSITION ON FOLIAR NUTRIENT RESORPTION IN TREMBLING ASPEN (*POPULUS TREMULOIDES*) AND WHITE BIRCH (*BETULA PAPYRIFERA*) IN A BOREAL FOREST

Introduction

The remobilization of nutrients is a key process in tree metabolism, growth and survival (Aerts and Chapin, 2000). Nutrient resorption (NuR) in foliage is a key nutrient conservation strategy in plants (Chapin, 1980; Aerts, 1996; Killingbeck, 1996), which takes place at three general stages in a plant's life cycle: from older foliage to newer foliage prior to the growing season (Nambiar and Fife, 1991; Saur *et al.*, 2000; Hirose and Oikawa, 2012; Ueda, 2012), to sink organs for overwinter storage (Chapin and Kedrowski, 1983; Millard and Grelet, 2010), and prior to senescence and abscission as litterfall (Killingbeck, 1996). Nitrogen (N) and phosphorus (P) are most frequently studied nutrients for resorption. A primary reason for this is their close relationship with primary production (Attiwill and Adams, 1993; Aerts and Chapin, 2000) as they are thought to be most limiting for terrestrial plant growth (Harpole *et al.*, 2011; Fisher *et al.*, 2012). Few have studied resorption of potassium (K), which is surprising given the role of K in plant growth through osmoregulation, carbohydrate translocation, and enzymatic activity (Ericsson and Kahr, 1993). K is highly mobile (Vergutz *et al.*, 2012), and some studies have reported significant losses through leaching in canopy throughfall (Hagen-Thorn *et al.*, 2006). However, K uptake by plants is highly selective (Marschner and Marschner, 2012), and may provide as much information about nutritional balances in plants as N or P.

Nutrient resorption is variable among plant species (Vitousek, 1982; Koerselman and Meuleman, 1996; Güsewell, 2004; Davidson and Howarth, 2007; Vergutz *et al.*, 2012). The reason for this may or may not be the soil, as the relationship between soil fertility and NuR has been debated among researchers (Aerts, 1996; Eckstein *et al.*, 1999; Aerts and Chapin, 2000; Kobe *et al.*, 2005; Lü *et al.*, 2011). Studies have found both negative (Kobe *et al.*, 2005; Vergutz *et al.*, 2012) and positive (Diehl *et al.*, 2003; Wang *et al.*, 2014b) relationships between NuR and green leaf nutrient concentration, but the relationship between soil nutrient availability and green leaf nutrient concentration varies among species due to phylogenetic differences in nutrient allocation and leaf life span among life forms (Mayor *et al.*, 2014). For this reason, the use of a variety of plant species in the study of NuR can provide a wealth of information about the nutritional balance of an ecosystem.

Wildfire is the most common natural stand-replacing disturbance in boreal forests (Senici *et al.*, 2010). Nutrient use and allocation can change as a result of increased mortality and wood biomass nutritional sinks with the decline in stand productivity over time since fire (McMurtrie *et al.*, 1995; Murty, 1996; Xu *et al.*, 2012). Resorption of N and P in trees tends to decrease with stand age (Killingbeck *et al.*, 1990; Nambiar and Fife, 1991; Yuan and Chen, 2010a; Ye *et al.*, 2012; Li *et al.*, 2013b), coinciding with an increase in leaf and litter N concentration (Donaldson *et al.*, 2006; Yuan and Chen, 2010a; Ye *et al.*, 2012; Li *et al.*, 2013a), despite high variability among species and elements (Wang *et al.*, 2014b). Although a decrease in NuR has been found with stand age, it is unknown how NuR changes throughout the entire successional chronosequence, or accounting for stand composition of tree species.

Interspecific interactions between tree species drives forest succession, which influences the availability of sunlight, water and soil nutrients and therefore tree growth and survival (Chen and Popadiouk, 2002). Competition for soil resources connotes a struggle for acquisition of soil nutrients, but it can also result in beneficial changes in foliar chemistry and litterfall influxes from trees, where proximity to neighbouring trees of different species can affect foliar nutrition (Richards *et al.*, 2010), mostly where broadleaves improve the soil for conifers. Mixes with broadleaf trees have been associated with an increase in NuR in neighbouring conifer trees (Primicia *et al.*, 2014), but it is unknown how NuR in broadleaf trees can change when found in either pure stands or stands mixed with conifer trees.

The purpose of this study was to examine the effects of forest stand development (stand age) and interspecific interactions on NuRE (N, P, K) in two deciduous broadleaf species. First, we examined the effects of time since fire and overstory composition on NuRE. Secondly, we assessed how NuRE changes with soil and green leaf nutrient concentration. We also examined the effects of independent variables (stand age, overstory, and disturbance type) on soil attributes, and the effects of soil and green leaf nutrient concentration on NuRE. Given that nutrient demands for growth tend to peak at the juvenile stage, we predicted that NuRE in the leaves of broadleaf species should decrease with stand age. Our second hypothesis was that, due to facilitative nutritional benefits in mixedwood forests, NuRE is highest in broadleaf-dominated stands for broadleaf species. We also predicted that nutrient NuRE varies with soil but that green leaf nutrient concentration more significantly predicts NuRE in these tree species than soil nutrient concentration.

Methods

Study Area

The study was conducted in the mixedwood boreal forest located west of Lake Nipigon, 150 km north of Thunder Bay, Ontario, Canada in the Upper English River (B. 11) Forest Region (Rowe, 1972), between 49°22’ N to 49°45’ N and 89°10’ W to 89°56’ W, 400 m in elevation. This region has short summers with a moderately dry, cool climate. The mean annual temperature is -0.4 °C with a mean annual precipitation of 716 mm, recorded at the closest meteorological station in Armstrong, Ontario (50º18′ N, 89º55′ W) (Environment Canada 2012-2013). Dominant soil orders in the region are sandy loam dystric brunisols, which occur under forest vegetation and often lack a developed mineral-organic surface horizon (SoilClassificationWorkingGroup, 1998). Occurring with dominance in the overstory are trembling aspen (*Populus tremuloides* Michx), paper birch (*Betula papyifera* Marsh.), jack pine *(Pinus banksiana* Lamb.), white spruce (*Picea glauca* [Moench] Voss), and balsam fir (*Abies balsamea* (L.) Mill.). Understory plant species common in the area are mountain maple (*Acer spicatum* Lam.), green alder (*Alnus viridis*), willow (*Salix sp.*) and beaked hazel (*Corylus cornuta* Marsh.) (Hart and Chen, 2008).

Sample Design

To test the effect of stand age on NuRE, sampling plots were selected within forest stands following a chronosequence with six development stages outlined by Chen and Popadiouk (2002): early stand initiation, stem exclusion stage, early canopy transition, late canopy transition and gap dynamics stage, representing 7, 33, 98, 146, and 209 years since fire, respectively. The chronosequence method is commonly used to describe the successional trajectories that would otherwise be time-ineffective to study (Walker *et al.*, 2010). The sampling plots in this study were selected within stands that followed successional patterns over a multi-decadal time scale (Walker *et al.*, 2010). To determine TSF for stands <70 years old, detailed provincial fire records were used. For stands >70 years old, tree ages were used to estimate TSF (Senici *et al.*, 2010).

Two overstory compositions were identified to represent the species composition with broadleaf- or mixedwood dominance within mesic sites in the south end of the North American

Table 3.1 Species composition for the 30 plots sampled in the study area.

Age	Overstory*	*n*	Mean stand density** (stems ha^{-1}, ± s.e.m.) or basal area (m^2 ha^{-1}± s.e.m.)	Stand composition (% abundance** or % basal area of total)					
				Populus tremuloides	*Betula papyrifera*	*Pinus banksiana*	*Picea glauca*	*Abies balsamea*	Others†
7	B	3	11533 (4173)	87 (5)	4 (4)	5 (5)			4 (1)
	M	3	9200 (1301)	52 (9)	12 (6)	29 (4)			7 (3)
33	B	3	25.6 (0.7)	93 (4)	4 (4)	1 (1)			2 (1)
	M	3	16.8 (3.4)	45 (14)		49 (17)	6 (6)		
98	B	3	49.2 (7.2)	94 (1)	2 (2)		2 (2)	1 (1)	1 (1)
	M	3	41.3 (5.2)	42 (12)	15 (13)	10 (6)	15 (8)	18 (3)	
146	B	3	56.7 (7.0)	86 (4)	8 (4)		4 (2)	1 (1)	2 (2)
	M	3	35.0 (2.1)	45 (9)	21 (10)		10 (4)	23 (6)	2 (2)
209	B	3	39.4 (3.3)	56 (23)	24 (18)		10 (6)	10 (5)	
	M	3	46.0 (3.3)	11 (4)	39 (6)	5 (3)	38 (7)	7 (3)	

Notes: *B=broadleaf, M=mixedwood. **Stand density/% abundance for 7-15 years since fire. †Includes *Salix sp.*, *Acer spicatum*, *Populus balsamifera*, *Alnus viridis*, *Sorbus decora*, *Corylus cornuta*, *Prunus pensylvanica* and Amelanchier sp.

boreal forest (Bonan and Shugart, 1989): 1) pure broadleaf dominance including *Populus tremuloides* and *Betula papyrifera*, and 2) mixedwood, which can include either of the two broadleaf species, coexisting with *Pinus banksiana*, *Picea glauca* or *Abies balsamea* (Table 3.1). For both species compositions, stands with ages 7 to 209 years since fire were used to sample *Populus tremuloides*, while *Betula papyrifera* was sampled in stands with ages 98 to 209 years since fire. Although not widely accepted as a late successional species, *Betula papyrifera* was identified as having higher importance than *Populus tremuloides* later in stage development, while *Populus tremuloides* was identified as an early successional species with decreasing dominance later in succession. A total of 30 plots were sampled with 3 replicates per age and overstory combination.

In order to minimize the confounding effects of soil characteristics on nutrient resorption, sampling plots were located on mesic sites positioned on flat midslope positions (<5 % slope) on well-drained moraine soils >50 cm in thickness. Plots were selected within stands that were visually homogenous for at least 1 ha in size. Efforts were made to minimize spatial auto-relationship (Legendre and Legendre, 2012) by allowing for at least 100 m between each selected stand. Individual plots were also established at least 50 m from a roadway to avoid edge effects.

Foliar and Soil Sampling

Green foliage was collected in the canopies of the two broadleaf species, *Populus tremuloides* and *Betula papyrifera* in late August to represent the end of the growing season just prior to entering senescence. From trees in old stands (≥33 years since fire), foliage was collected using a 12-gauge shotgun from both the sunlit and shaded areas of the canopy to account for nutrient concentration variations and movement (Verry and Timmons, 1976; Hirose and Oikawa, 2012; Ueda, 2012). In young plots (7 years since fire), foliage from *Populus tremuloides* was harvested by hand or with the use of a pole pruner. A total of 40 leaves were collected from 4 canopy-dominant trees within each plot. Senesced foliage was collected in October of the same year from the ground. Collections of foliage as litterfall in resorption studies is known to affect resorption estimates due to mass loss through leaching on the ground (Hagen-Thorn *et al.*, 2006). For this reason, foliage was collected following a recent snowfall to guarantee recent shedding and minimal decomposition or leaching.

All foliar samples were placed into paper bags and placed in a freezer (-18°C) on-site until processing. The samples were then oven-dried at 60°C for 48 hours and individual leaves were weighed for the calculation of mass loss during senescence. The samples were then grinded in a Wiley-Mill to a fine powder (No. 40 sieve) in preparation for chemical analyses.

To measure soil characteristics in the sampling plots, ten cores were randomly taken per plot as a composite and placed in bags for analysis for soil pH and concentrations of carbon (C) as well as macronutrients: nitrogen (N), phosphorus (P) and potassium (K). The ten cores were divided into four depths: forest floor (<5 cm), mineral layer 1: 0-15 cm, mineral layer 2: 15-30 cm, and mineral layer 3: 30-50 cm. Often, mineral layer 3 was not accessible, due to shallow soils which are common in the region.

Soil core samples were air-dried to constant weight and sieved (2-mm mesh size). The sieved soil was then analyzed for pH using the distilled water method. Soil C and total soil N as well as foliar C and N concentrations were determined with high temperature combustion with thermal conductivity detection (LECO) following Horneck and Miller (1998), and soil total P and K as well as foliar P and K concentrations were measured using acid wet digestion followed by ICP-AES (Munter and Grande, 1981; Miller, 1998). All chemical analyses were performed by the Forest Resources & Soils Testing (FoReST) Laboratory, located at Lakehead University, Thunder Bay, Ontario, Canada. All concentrations were calculated as mg nutrient per g of soil.

Calculations

Nutrient resorption efficiency (NuRE) was calculated using the following equation, after Vergutz *et al.* (2012):

$$NuRE = (1 - ((Nu_s \div Nu_g) \times MLCF)) \times 100$$

where: NuRE is percentage of nutrients resorbed prior to senescence, Nu_s is nutrient concentration in senesced foliage (mg per g leaf), Nu_g is nutrient concentration in green foliage (mg per g leaf), and MLCF = mass correction factor (Vergutz *et al.*, 2012), which accounts for loss in mass during senescence of foliage (van Heerwaarden *et al.*, 2003).

The MLCF was calculated as follows on a plot basis:

$$MLCF = m_s \div m_g$$

where MLCF = mass correction factor, $m_s \div m_g$ = fraction of the average mass of senesced leaves over the average mass of the green leaves in a plot (*n*=all intact leaves per plot sample, ~20). Unique MLCF values were used on a plot basis for calculations of NuRE, having weighed the exact number of leaves used in chemical analysis.

Statistical Analyses

To determine the effects of stand age (7, 33, 98, 146, 209 years) and overstory composition (broadleaf and mixedwood or conifer and mixedwood) on NuRE, the following model was used:

$$Y_{ijk} = \mu + A_i + C_j + AC_{ij} + \varepsilon_{(ij)k} \qquad (1)$$

where: Y_{ijk} is NuRE (%), μ = overall mean, A_i = fixed effect of ith stand age class (i= 1, 2,3…5), C_j = fixed effect of the jth overstory composition (j=1, 2), $\varepsilon_{(ij)k}$ = random error from random replication with k=3 replicates.

An analysis of variance (ANOVA) was conducted for the effects of stand age and overstory on NuRE. Overstory composition can be either: broadleaf or mixedwood (2 levels). The assumption of data normality was examined with Q-Q plots, histograms and the Shapiro-Wilk test. The assumption of data homogeneity was examined using Bartlett's test. All sets of data confirmed both assumptions.

Soil C:nutrient ratios used in lieu of total nutrient concentrations in the soil can provide a better indication of nurtient availability (Sterner and Elser, 2002; Sistla and Schimel, 2012). The effects of stand age and overstory composition on soil attributes (dependent variables: pH, C:N, C:P, C:K) were also tested. Two linear regressions was performed to predict NuRE with soil nutrient concentration, as a ratio with carbon, and green leaf concentration using the *lm()* function in the base R, using all observations per species. All statistical analyses were conducted using R version 2.15.2. Statistical significance for ANOVA (*Anova* function in the *car* package) was based on α=0.05. Tukey-HSD multiple comparisons were performed following all ANOVAs using the *glht()* function in the *multicomp* package when significant main effects or interaction effects were found.

Results

Effects of Stand Age and Overstory Composition

In *Populus tremuloides*, the overall mean NRE was 61 ± 2 %, mean PRE was 58 ± 4 %, and mean KRE was 74 ± 3 %. NRE was not significantly affected by age or overstory

Table 3.2 Summary of P values and coefficient of determination (R^2) from ANOVA for the effects of stand age and overstory (broadleaf and mixedwood) on resorption efficiency (%) of (NRE), P (PRE), and K (KRE). Available stand ages varied among *Populus tremuloides* (age = 7, 33, 98, 146, 209 years) and *Betula papyrifera* (age = 98, 146, 209 years). Values in bold are significant at 0.05.

Variable	Species	Age	Overstory	Age x Overstory	Model R^2
		P-value	P-value	P-value	
NRE	*Populus tremuloides*	0.820	0.337	0.960	0.147
	Betula papyrifera	**0.030**	0.632	0.579	0.532
PRE	*Populus tremuloides*	**0.003**	0.141	**0.019**	0.688
	Betula papyrifera	**<0.001**	0.895	0.374	0.787
KRE	*Populus tremuloides*	**<0.001**	0.827	**0.019**	0.816
	Betula papyrifera	**0.013**	0.810	0.805	0.591

Notes: In *Populus tremuloides*, *n*=3 for all except 209 broadleaf (*n*=2) and mixedwood (*n*=2). In *Betula papyrifera*, *n*=3 for all except 98 broadleaf (*n*=2) and 146 mixedwood (*n*=2).

composition (Table 3.2; Figure 3.1A). There was a significant interaction between stand age and overstory on PRE (Table 3.2), where PRE in the leaves of 209-year-old mixedwood stands was significantly lower than in 7- to 98-year old stands, with no age effect in broadleaf stands (Figure 3.1B). KRE was also significantly affected by the interaction between stand age and overstory (Table 3.2), where KRE was significantly lower in the leaves of 209-year-old mixedwood stands than in the 7- to 146 year-old stands, whereas KRE in broadleaf stands did not vary with stand age (Figure 3.1C).

In *Betula papyrifera*, mean NRE was 61 ± 2 %, mean PRE was 46 ± 6 %, and mean KRE was 52 ± 7 %. NRE was significantly affected by stand age (Table 3.2); with 146-year-old stands having higher NRE than 98- and 209-year-old stands (Figure 3.1D). PRE was also significantly affected by stand age for this species (Table 3.2), where 209-year-old stands have lower PRE than 98- and 146-year-old stands (Figure 3.1E). There was also a significant stand age effect on

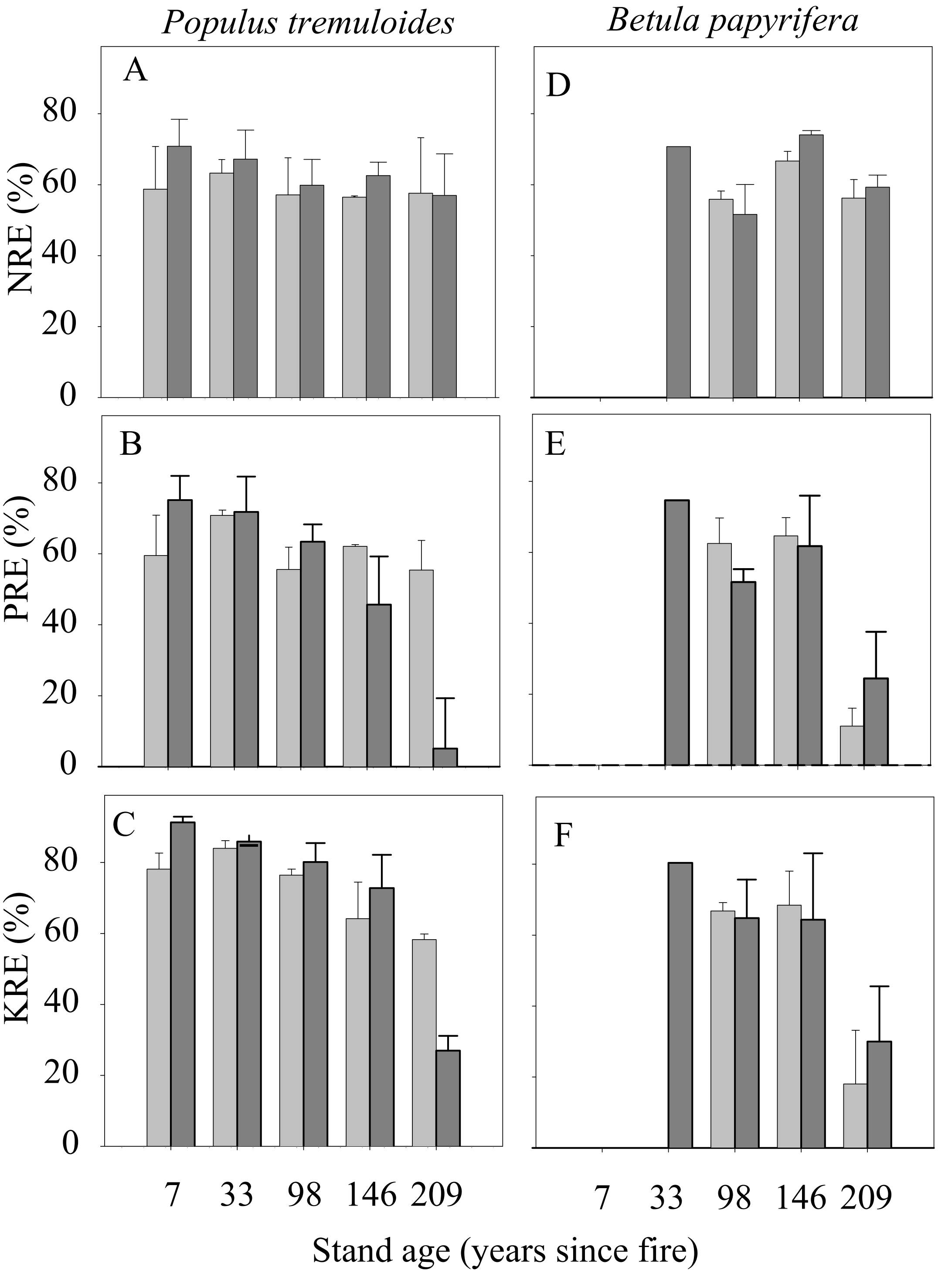

Figure 3.1 Resorption efficiency (%) of nitrogen (NRE), phosphorus (PRE), and potassium (KRE) with stand age for *Populus tremuloides* and *Betula papyrifera* sampled in broadleaf and mixedwood stands. Open bars are for broadleaf stands, filled bars for mixedwood stands.

KRE (Table 3.2), with 209-year-old stands having lower KRE than 98- and 146-year-old stands (Figure 3.1D-F). No overstory effects were found for this species (Table 3.2).

Effects of Soil and Green Leaf Nutrient concentration

Mineral soil P and K and forest floor N, P, K and C increased with stand age, having the highest concentrations in the 209-year-old stands and the lowest in 7-year-old stands (Table 3.3). However, soil nutrient concentrations were not significantly different after 98 years since fire (Table 3.3). There was an interaction with overstory for forest floor P, but no significant comparisons were found among stand ages (Table 3.3). Mineral soil C:N and C:K decreased with stand age, while forest floor C:N, C:P and C:K increased with stand age (Table 3.4). In *Populus tremuloides*, only KRE increased significantly with increasing soil C:K (b=0.4; Figure 3.2C). In *Betula papyrifera*, PRE increased with increasing soil C:P (b=0.5; Figure 3.3B), and KRE increased with increasing C:K (b=0.6; Figure 3.3C). No relationships were found between green leaf nutrient concentration and NuRE for either species (Figures 3.2 and 2.3). See supplementary materials for results of ANOVA.

Discussion

Interspecific Variation in Nutrient Resorption

In both species, mean NRE, PRE and KRE were positive, indicating that nutrients were resorbed back to live tissues prior to leaf abscission. Their NRE values are consistent with those reported by other studies for broadleaf species (Kobe *et al.*, 2005; Vergutz *et al.*, 2012). The low PRE in these species (58% for *Populus tremuloides* and 46% for *Betula papyrifera*) is consistent with the lower P-limitation in the boreal region due to the high influx from rock weathering (Aerts and Chapin, 2000). In *Populus tremuloides*, K was resorbed more than N or P (74%

Table 3.3 Mean soil pH and total nutrient concentrations (mg g^{-1}) (± s.e.m.) with stand age and overstory (B= broadleaf, M=mixedwood).

		Mineral soil					Forest floor			
Stand age	Over-story	pH*	N	P	K	C	N	P	K	C
7	B	5.2 (0.1)	1.02 (0.13)	0.28 (0.03)^{b}	0.21 (0.01)^{b}	16.0 (1.6)	2.5 (0.1)^{b}	0.30 (0.01)^{bc}	0.30 (0.02)^{b}	35 (2)^{b}
	M	5.0 (0.1)	0.86 (0.14)	0.24 (0.02)^{b}	0.25 (0.03)^{b}	13.0 (2.1)	1.0 (0.2)^{b}	0.17 (0.01)^{c}	0.26 (0.04)^{b}	14 (4)^{b}
33	B	4.9 (0.1)	1.03 (0.18)	0.22 (0.01)^{b}	0.21 (0.01)^{b}	13.2 (2.5)	17.9 (2.4)^{a}	1.06 (0.19)^{a}	0.97 (0.15)^{a}	338 (100)^{a}
	M	5.2 (0.2)	1.17 (0.23)	0.36 (0.03)^{b}	0.28 (0.01)^{b}	15.6 (4.5)	9.9 (3.1)^{a}	0.58 (0.11)^{ac}	0.53 (0.10)^{a}	235 (89)^{a}
98	B	5.4 (0.1)	1.58 (0.05)	0.54 (0.07)^{a}	0.75 (0.08)^{a}	21.4 (1.2)	11.6 (4.2)^{a}	0.83 (0.15)^{ab}	0.92 (0.08)^{a}	222 (93)^{ab}
	M	5.1 (0.1)	1.37 (0.30)	0.42 (0.06)^{a}	0.59 (0.16)^{a}	21.3 (5.9)	5.6 (1.5)^{a}	0.44 (0.01)^{ac}	0.63 (0.14)^{a}	158 (54)^{ab}
146	B	5.2 (0.1)	1.63 (0.25)	0.38 (0.05)^{ab}	0.63 (0.07)^{a}	22.7 (3.2)	8.0 (2.0)^{a}	0.67 (0.15)^{ac}	0.81 (0.13)^{a}	165 (31)^{a}
	M	5.2 (0.1)	1.47 (0.26)	0.44 (0.03)^{ab}	0.55 (0.11)^{a}	25.2 (6.1)	10.5 (1.5)^{a}	0.88 (0.23)^{ab}	1.09 (0.14)^{a}	246 (62)^{a}
209	B	5.1 (0.03)	1.04 (0.08)	0.50 (0.04)^{a}	0.74 (0.10)^{a}	11.5 (0.8)	12.9 (1.3)^{a}	0.90 (0.06)^{ab}	0.90 (0.07)^{a}	304 (35)^{a}
	M	5.2 (0.1)	1.27 (0.32)	0.45 (0.06)^{a}	0.74 (0.10)^{a}	16.7 (5.1)	15.4 (1.5)^{a}	1.04 (0.05)^{a}	1.20 (0.05)^{a}	306 (37)^{a}

Notes: Different letters indicate significant ($p<0.05$) differences in soil attributes among treatments (Tukey HSD test) following two-way ANOVA (see Appendix for F-test details).

*Forest floor layer + mineral soil (0-50 cm) for pH.

Table 3.4 Mean soil carbon to nutrient ratios (± s.e.m.) across stand age and overstory (B= broadleaf, M=mixedwood).

		Mineral soil			Forest floor		
Stand age	Overstory	C:N	C:P	C:K	C:N	C:P	C:K
7	B	15.7 (0.5)^{a}	58.0 (4.6)	74.4 (4.9)^{a}	14 (1)^{b}	118 (7)^{b}	117 (2)^{b}
	M	15.2 (0.4)^{a}	54.5 (5.7)	56.5 (16.4)^{a}	13 (1)^{b}	81 (19)^{b}	62 (28)^{b}
33	B	12.7 (0.2)^{ab}	62.0 (16.0)	61.7 (9.8)^{a}	18 (3)^{ab}	311 (40)^{a}	340 (50)^{a}
	M	15.2 (2.2)^{ab}	69.8 (26.3)	66.6 (14.3)^{a}	22 (3)^{ab}	392 (146)^{a}	414 (131)^{a}
98	B	13.6 (1.1)^{ab}	43.2 (8.5)	30.4 (2.9)^{ab}	18 (1)^{a}	248 (73)^{ab}	230 (80)^{ab}
	M	15.3 (1.4)^{ab}	52.6 (16.6)	44.8 (16.9)^{ab}	28 (2)^{a}	361 (127)^{ab}	288 (152)^{ab}
146	B	13.7 (0.4)^{ab}	55.5 (12.4)	33.3 (5.8)^{b}	22 (5)^{a}	253 (16)^{ab}	204 (27)^{ab}
	M	14.7 (1.6)^{ab}	39.0 (8.2)	33.7 (10.1)^{b}	23 (3)^{a}	291 (44)^{ab}	223 (45)^{ab}
209	B	11.0 (0.2)^{b}	22.5 (2.5)	16.0 (2.1)^{b}	23 (1)^{a}	334 (22)^{a}	337 (23)^{a}
	M	12.9 (0.7)^{b}	38.6 (12.2)	26.1 (10.2)^{b}	20 (1)^{a}	296 (38)^{a}	254 (28)^{a}

Notes: Different letters indicate significant ($p<0.05$) differences in soil attributes among treatments (Tukey HSD test) following two-way ANOVA (see Appendix for F-test details).

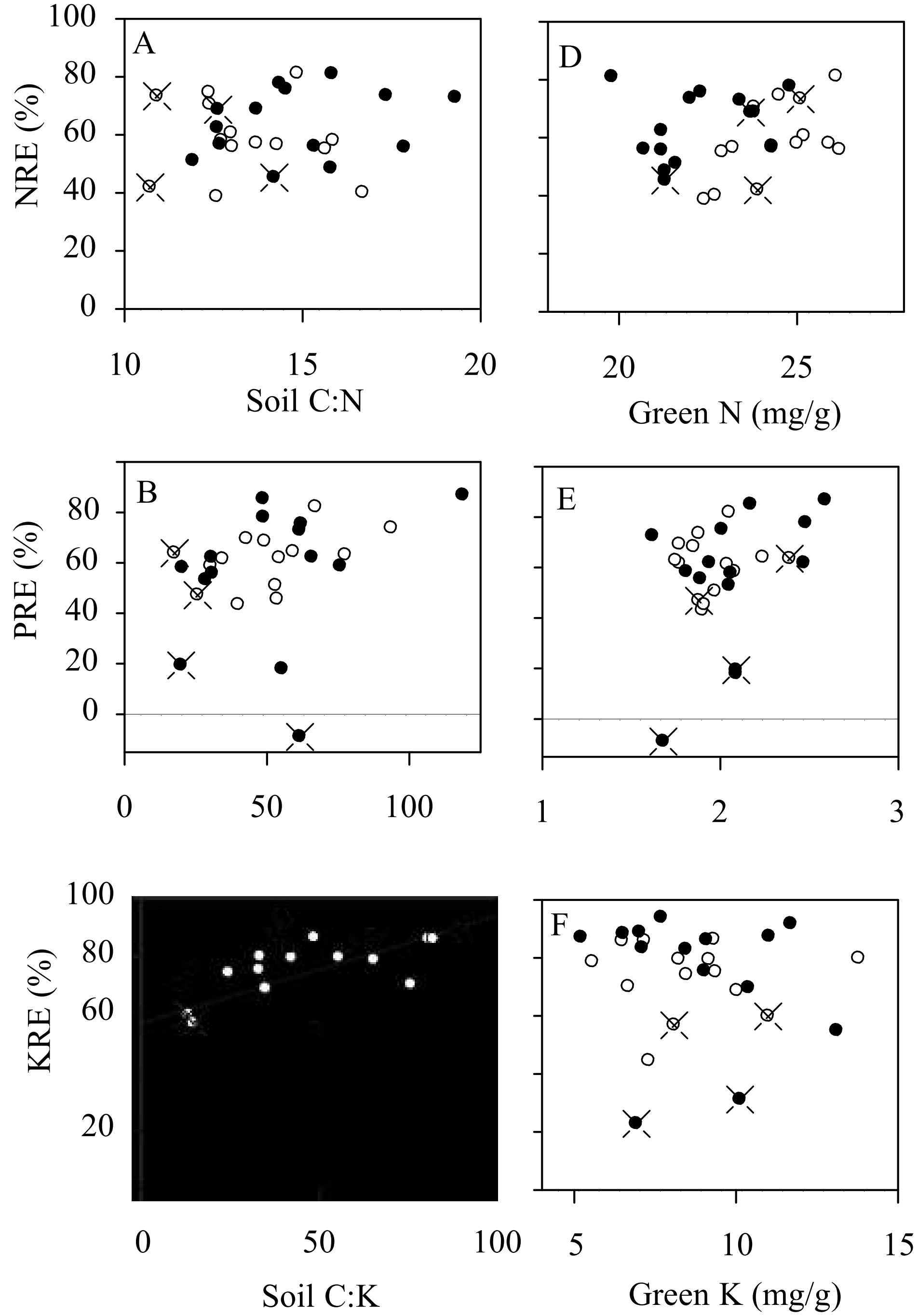

Figure 3.2 Linear regression of resorption efficiency (%) of N (NRE), P (PRE), and K (KRE) of *Populus tremuloides* (*n*=28) with respect to total nutrient concentrations in the mineral soil as carbon ratios and green leaf nutrient concentration. Observations below dashed lines indicate nutrient accretion in foliage between collection periods. Open circles = broadleaf stands, filled circles = mixedwood stands, X = 209-year-old stands.

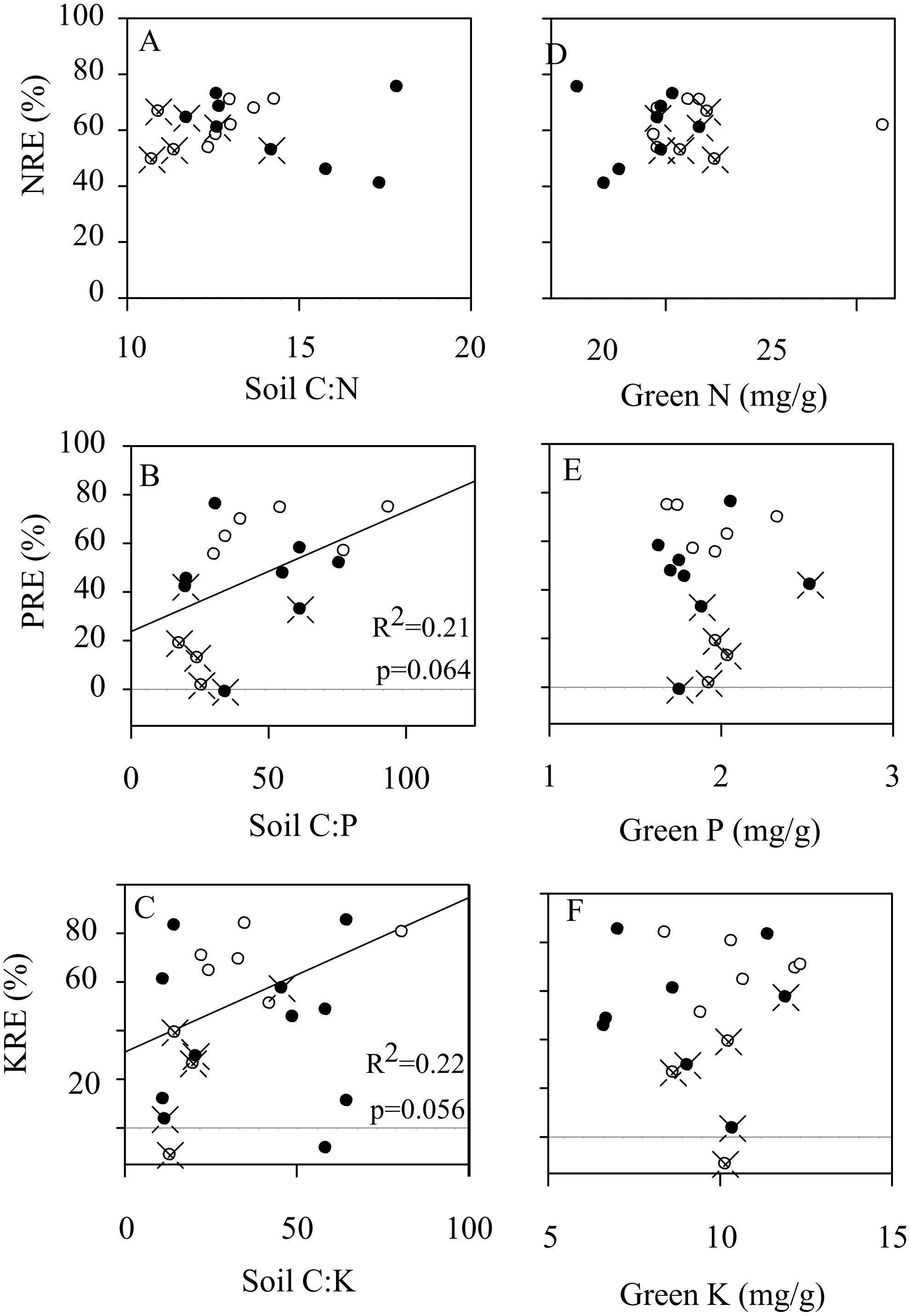

Figure 3.3 Linear regression of resorption efficiency (%) of N (NRE), P (PRE), and K (KRE) of *Betula papyrifera* (*n*=17), with respect to total nutrient concentrations in the mineral soil as carbon ratios and green leaf nutrient concentration. Observations below dashed line indicate nutrient accretion in foliage between collection periods. Open circles = broadleaf stands, filled circles = mixedwood stands, X = 209-year-old stands.

efficiency), an expected result given its high mobility in trees (Wang *et al.*, 2014b). In *Betula papyrifera*, however, KRE was intermediate between NRE and PRE. The differences between these two species may be largely from genetic variability (Smith *et al.*, 2011) that affects both green leaf nutrients (Lindroth and Hwang, 1996) and litter nutrient quality (Madritch *et al.*, 2006).

Effects of Stand Age on Nutrient Resorption

In *Betula papyrifera*, NRE peaked at 146 years since fire when compared with 98-year-old stands, coinciding with dynamics of aboveground primary production in broadleaf trees (Gower *et al.*, 1996). PRE and KRE in both species decreased with stand age, similar to the observations by Alban (1985), in young *Populus tremuloides* stands where the proportion of foliar N, P and K to total aboveground tissues decreases by nearly half from year 20 (46, 27 and 21%, respectively) to year 40 (24, 19 and 16%, respectively) to year 40 since fire. This suggests that with increasing stand age, NuRE in *Populus tremuloides* should increase due to the increased demand for nutrients in non-foliar tissues. However, our study found a positive relationship between green leaf nutrient concentration and NuRE, which contradicts the relationships reported by Kobe *et al.* (2005) for the same species but is consistent with those of Diehl *et al.* (2003).

Another explanation for the reduction in PRE and KRE with age could be physical restrictions on the mobility of nutrients as trees age. We measured the tallest trees with the widest DBH to capture the oldest age cohort in the stands. Older, larger ramets of the same *Populus tremuloides* clone has been shown to resorb less N than younger, smaller ones (Killingbeck *et al.*, 1990). Although C:total nutrient ratios are higher in the 209-year-old stands, it is highly likely that the trees sampled within these stands are less capable of accessing and using these nutrients (Vitousek and Reiners, 1975b). These findings in addition to our own suggest that this species uses and stores nutrients differently as they age, likely due to physical restrictions on nutrient mobility and transfer.

Effects of Overstory Composition on Nutrient Resorption

In the present study, no overstory effects were found for NuRE in *Betula papyrifera*. NRE in *Populus tremuloides* was also not affected by overstory type. However, declines in PRE and KRE from the stand age of 146 to 209 years since fire were steeper for *Populus tremuloides* sampled in mixedwood stands than in broadleaf stands. Within the 209-year-old stands, a low sample size (*n*=2) may have prevented statistically significant differences in overstory types for either PRE or KRE, but our results suggest that there are overstory effects on *Populus tremuloides* which are apparent only later in the successional timeline. The presence of conifers in the mixedwood stands clearly has an influence on NuRE in this species, but explanations for this are complex. Firstly, if green leaf P and PRE are relatively lower in the mixedwood 209-year-old stands, effects from conifers may be non-beneficial. Soil nutrient concentrations did not change with overstory type for any given stand age. Therefore, explanations for overstory composition must be drawn from non-soil influences. Annual growth rate of *Populus tremuloides* is initially higher when mixed with conifers early in stand development, but later in the successional timeline, growth is increasingly inhibited by conifer neighbours from 50 to 90 years since fire, especially when mixed with both *Pinus banksiana* and *Picea mariana* (Cavard *et al.*, 2011). However, growth largely depends on soil fertility, which was unaffected by overstory composition in this study.

The basal area of *Betula papyrifera* doubled from the 146-year-old to the 209-year-old mixedwood stands, equal to that of *Pinus banksiana* in the 209-year-old stands. However, the basal area of *Populus tremuloides* was reduced by a third in mixedwoods between these two stand ages. The same age increase in broadleaf stands also reduced this species by half, but *Populus tremuloides* was maintained as the most common species in the stand, with many neighbours of the same species. This transition of species is a result of interaction and succession between the two broadleaf species, which may explain the lower NuRE in *Populus tremuloides* in mixedwood stands. Nutrients can be retranslocated from younger to older clonal ramets of the same organism in *Populus tremuloides* (Pinno and Wilson, 2014), so the distance from younger ramets in mixedwood stands with *Populus tremuloides* may explain the lower PRE and KRE for this species.

Conclusions

This study used the chronosequence approach to examine the variation NuRE in tree species commonly found in the boreal forest. Mean NRE was 61% and mean PRE was 52% for both species, but KRE was much higher in *Populus tremuloides* with 74%, compared with 52% in *Betula papyrifera*. We found that stand age decreases NuRE 209 years after fire, during which time gap and successional dynamics may play a role in nutrient use and conservation. PRE and KRE in *Populus tremuloides* were lower when sampled in mixedwood stands, indicating that interaction from conifers reduced the green leaf nutrient concentrations of *Betula papyrifera* and *Populus tremuloides*. In the former species, this reduction may have been caused by increased mortality in the older stands, exasperated by the co-existing conifer species.

CHAPTER FOUR: IMPACTS OF DISTURBANCE AND INTERSPECIFIC INTERACTIONS ON FOLIAR NUTRIENT RESORPTION IN TREMBLING ASPEN (POPULUS TREMULOIDES) IN A BOREAL FOREST

Introduction

The remobilization of nutrients is a key process in tree metabolism, growth and survival (Aerts and Chapin, 2000). Nutrient resorption (NuR) in foliage is a key nutrient conservation strategy in plants (Chapin, 1980; Aerts, 1996; Killingbeck, 1996), which takes place at three general stages in a plant's life cycle: from older foliage to newer foliage prior to the growing season (Nambiar and Fife, 1991; Saur *et al.*, 2000; Hirose and Oikawa, 2012; Ueda, 2012), to sink organs for overwinter storage (Chapin and Kedrowski, 1983; Millard and Grelet, 2010), and prior to senescence and abscission as litterfall (Killingbeck, 1996).

Wildfire is the most common natural stand-replacing disturbance in boreal forests (Senici *et al.*, 2010), with logging a close second. Full-tree logging (FT) is the removal of most branches and foliage as a source of bioenergy and has become an important disturbance in boreal forests. FT raises concerns for nutrient budgets of the forest ecosystem (Boyle *et al.*, 1973; Turner and Lambert, 1986; Fahey *et al.*, 1988; Hendrickson *et al.*, 1989; Proe *et al.*, 2001), especially in the boreal region, relative to its temperate and tropical counterparts, because of the restriction of nutrient availability by low soil temperatures (Bonan and Shugart, 1989). In the short-term, logging (conventional logging, full-tree logging, removal of organic layer) can affect foliar chemistry (Piatek and Allen, 2000; Ponder *et al.*, 2012), despite its lesser impact than that of fire (Li *et al.*, 2013b). Salvage logging in boreal forests after fire has been suggested to promote total N concentration in the soil (Poirier *et al.*, 2014). It has been suggested that NuR in understory plants does not change after fire or logging or the combination of the two (Huang and

Boerner, 2007), while others have suggested an increase in NuR recently following logging (Covelo *et al.*, 2008). It is not known how disturbance regimes, logging or fire or their combinations, affect tree NuR that typically decreases after any disturbance (Li *et al.*, 2013b), especially in boreal tree species. Fire and logging with and without silviculture result in differences in the regeneration of the understory layer (Hart and Chen, 2008). Species interactions affect NuR in conifer trees (Primicia *et al.*, 2014), but it is unknown how species mixtures after different disturbance scenarios affect NuR in young broadleaf trees.

The purpose of this study was to examine the effects of interspecific interactions and origin of disturbance on nutrient resorption efficiency (N, P, K) in trembling aspen, a broadleaf boreal tree species, *Populus tremuloides*. First, I examined the effects of overstory composition and origin of disturbance on NuRE. Secondly, I assessed how NuRE changes with soil and green leaf nutrient concentration. I also examined the effects of independent variables (stand age, overstory, and disturbance type) on soil attributes, and the effects of soil and green leaf nutrient concentration on NuRE. Firstly, I predicted that nutrient NuRE varies with origin of disturbance (lowest in full-tree logging followed by fire), with two caveats: 1) NuRE depends on soil fertility and 2) origin of disturbance influences soil fertility. Given the theorized facilitative nutritional benefits of tree species found in mixedwood stands, I also predicted that NuRE in *Populus tremuloides* is highest in broadleaf-dominated stands, regardless of disturbance origin. I also predicted that nutrient NuRE varies with soil but that green leaf nutrient concentration more significantly predicts NuRE in these tree species than soil nutrient concentration.

Methods

Study Area

The study was conducted in the mixedwood boreal forest located west of Lake Nipigon, 150 km north of Thunder Bay, Ontario, Canada in the Upper English River (B. 11) Forest Region (Rowe, 1972), between 49°22’ N to 49°45’ N and 89°10’ W to 89°56’ W, 400 m in elevation. This region has short summers with a moderately dry, cool climate. The mean annual temperature is -0.4 °C with a mean annual precipitation of 716 mm, recorded at the closest meteorological station in Armstrong, Ontario (50º18′ N, 89º55′ W) (Environment Canada 2012-2013). Dominant soil orders in the region are sandy loam dystric brunisols, which occur under forest vegetation and often lack a developed mineral-organic surface horizon (SoilClassificationWorkingGroup, 1998). Occurring with dominance in the overstory are jack pine *(Pinus banksiana* Lamb.), white spruce (*Picea glauca* [Moench] Voss), trembling aspen (*Populus tremuloides* Michx), paper birch (*Betula papyifera* Marsh.), and balsam fir (*Abies balsamea* (L.) Mill.). Understory plant species common in the area are mountain maple (*Acer spicatum* Lam.), green alder (*Alnus viridis*), willow (*Salix sp.*) and beaked hazel (*Corylus cornuta* Marsh.) (Hart and Chen, 2008).

Commercial logging began in the early 1970’s with successive operations occurring throughout the study area. Methods of logging have shifted from conventional, stem-only harvesting in the 1970’s to full-tree logging (FT) in recent years (Paul Poschmann, *pers. comm.*). Newly-developed stands are dominated by *Populus tremuloides* and *Pinus banksiana* in either pure or mixed stands depending on the type of stand-replacing disturbance and silviculture. For stands originated after FT, *Populus tremuloides* are typically left to regenerate naturally, while stands with mixes of *Populus tremuloides* and jack pine (*Pinus banksiana*) were planted when herbicide treatment was not used. Fire is a common stand-replacing disturbance in the region, with an estimated average fire return interval of 100 years (Senici *et al.*, 2010). Some overlap between the two disturbance types has occurred in the region, where stands developing after logging in 2002 were burned in a natural fire in 2006, creating 7-year-old stands compounded by both disturbance types.

Sample Design

Two overstory compositions were identified to represent mesic sites including aspen *Populus tremuloides* in the south end of the North American boreal forest (Bonan and Shugart, 1989): 1) >60% dominance by *Populus tremuloides* and 2) mixedwoods of *Populus tremuloides* and *Pinus banksiana* in equal dominance, with less than 60 % dominance of either species (Table 4.1).

The interspersion of the three identified disturbance types (F = fire, FT = full-tree logging and FT + F = full-tree logging plus fire) allowed an opportunity for a completely randomized sampling design for comparison between stands originated by different disturbance types for the two overstory compositions (broadleaf and mixedwood). Harvesting records were obtained to assist with plot selection. A total of 6 FT plots (logged in 2006) and 6 FT + F (logged in 2002, burned in 2006) plots were established, along with 6 F plots (burned in 2006), and two overstory compositions (broadleaf and mixedwood). In order to minimize the confounding effects of soil characteristics on nutrient resorption, sampling plots were located on mesic sites positioned on flat midslope positions (<5 % slope) on well-drained moraine soils >50 cm in thickness. Plots were selected within stands that were visually homogenous for at least 1 ha in size. Efforts were made to minimize spatial auto-relationship (Legendre and Legendre, 2012) by allowing for at least 100 m between each selected stand. Individual plots were also established at least 50 m

Table 4.1 Tree species composition for the 18 plots sampled in the study area.

Origin	Overstory*	*n*	Mean stand density (stems ha^{-1} ± s.e.m.)	Stand composition (% abundance per species of total)					
				Populus tremuloides	*Betula papyrifera*	*Pinus banksiana*	*Picea glauca*	*Abies balsamea*	Others†
Fire	B	3	11533 (4173)	87 (5)	4 (4)	5 (5)			4 (1)
	M	3	9200 (1301)	52 (9)	12 (6)	29 (4)			7 (3)
Full-tree logging	B	3	6333 (769)	63 (13)	7 (2)	3 (3)	1 (1)		27 (9)
	M	3	11200 (577)	50 (10)	3 (3)	40 (9)	3 (2)		4 (1)
Full-tree logging + fire	B	3	7667 (1272)	77 (3)	5 (2)	2 (2)	8 (3)	1 (1)	7 (1)
	M	3	2333 (437)	30 (11)	15 (8)	48 (24)			6 (6)

Notes: *B=broadleaf, C=conifer, M=mixedwood. Trees/shrubs ≥1.3 m. †Includes *Salix sp.*, *Acer spicatum*, *Alnus viridis*, *Sorbus decora*, *Corylus cornuta*, *Amelanchier*, *Prunus pensylvanica*, and *Larix laricina.*

from a roadway to avoid edge effects.

Foliar and Soil Sampling

Green foliage was collected in the canopies in late August to represent the end of the growing season just prior to entering senescence. From each tree, foliage was collected by hand or with the use of a pole pruner. A total of 40 leaves were collected from 4 tallest trees within each plot. Senesced foliage was collected in October of the same year from the ground. Collections of foliage as litterfall in resorption studies is known to affect resorption estimates due to mass loss through leaching on the ground (Hagen-Thorn *et al.*, 2006). For this reason, foliage was collected following a recent snowfall to guarantee recent shedding and minimal decomposition or leaching.

All foliar samples were placed into paper bags and placed in a freezer (-18°C) on-site until processing. The samples were then oven-dried at 60°C for 48 hours and individual leaves were weighed for the calculation of mass loss during senescence. The samples were then grinded in a Wiley-Mill to a fine powder (No. 40 sieve) in preparation for chemical analyses.

To measure soil characteristics in the sampling plots, ten cores were randomly taken per plot as a composite and placed in bags for analysis for soil pH and concentrations of carbon (C) as well as macronutrients: nitrogen (N), phosphorus (P) and potassium (K). The ten cores were divided into four depths: forest floor (<5 cm), mineral layer 1: 0-15 cm, mineral layer 2: 15-30 cm, and mineral layer 3: 30-50 cm. Often, mineral layer 3 was not accessible, due to shallow soils which are common in the region.

Soil core samples were air-dried to constant weight and sieved (2-mm mesh size). The sieved soil was then analyzed for pH using the distilled water method. Soil C and total soil N as well as foliar C and N concentrations were determined with high temperature combustion with thermal conductivity detection (LECO) following Horneck and Miller (1998), and soil total P and K as well as foliar P and K concentrations were measured using acid wet digestion followed by ICP-AES (Munter and Grande, 1981; Miller, 1998). All chemical analyses were performed by the Forest Resources & Soils Testing (FoReST) Laboratory, located at Lakehead University, Thunder Bay, Ontario, Canada. All nutrient concentrations were reported as mg g^{-1} of air-dried soil.

Calculations

Nutrient resorption efficiency (NuRE) was calculated using the following equation, after Vergutz *et al.* (2012):

$$NuRE = (1 - ((Nu_s \div Nu_g) \times MLCF)) \times 100$$

where: NuRE is percentage of nutrients transferred over a period of time, Nu_s is nutrient concentration in senesced foliage (mg per g leaf), Nu_g is nutrient concentration in green foliage (mg per g leaf), and MLCF = mass correction factor (Vergutz *et al.*, 2012), which accounts for loss in mass during senescence of foliage (van Heerwaarden *et al.*, 2003).

The MLCF was calculated as follows on a plot basis:

$$MLCF = m_s \div m_g$$

where MLCF = mass correction factor, $m_s \div m_g$ = fraction of the average mass of senesced leaves over the average mass of the green leaves in a plot (*n*=all intact leaves per plot sample, ~20). Unique MLCF values were used on a plot basis for calculations of NuRE, having weighed the exact number of leaves used in chemical analysis.

Statistical Analyses

To test the effects of overstory composition (broadleaf and mixedwood) and disturbance origin (F, FT, FT + F) on nutrient resorption in *Populus tremuloides*, the following general linear model was used:

$$Y_{ijk} = \mu + C_i + D_j + CD_{ij} + \varepsilon_{(ij)k}$$

where: Y_{ijkl}, μ, C_j, = eq. 1; C*i* is fixed effect of the *i*th overstory composition (*i*=1, 2) D_j is fixed effect of the *j*th disturbance origin type (*j*=1, 2, 3), $\varepsilon_{(ij)k}$ = random error from random replication with *k*=3 replicates.

An analysis of variance (ANOVA) was conducted for the effects of overstory and disturbance origin on NuRE in *Populus tremuloides*. Overstory composition can be either: broadleaf or mixedwood (2 levels). The assumption of data normality was examined with Q-Q plots, histograms and the Shapiro-Wilk test. The assumption of data homogeneity was examined using Bartlett's test. All sets of data confirmed both assumptions.

Soil C:nutrient ratios used in lieu of total nutrient concentrations in the soil can provide a better indication of nurtient availability (Sterner and Elser, 2002; Sistla and Schimel, 2012). The effects of overstory composition and disturbance type on soil attributes (dependent variables: pH, C:N, C:P, C:K) were also tested using the same general linear model with soil attribute as the response variable. Two linear regressions was performed to predict NuRE with soil nutrient concentration, as a ratio with carbon, and green leaf concentration using the *lm()* function in the base R, using all observations. All statistical analyses were conducted using R version 2.15.2. Statistical significance for ANOVA (*Anova* function in the *car* package) was based on α=0.05. Tukey-HSD multiple comparisons were performed following all ANOVAs using the *glht()*

function in the *multicomp* package when significant main effects or interaction effects were found.

Results

Effects of Disturbance Type With and Without Conifer Interaction

In the leaves of *Populus tremuloides*, there were no significant effects of overstory or disturbance type on NRE (Table 4.2; Figure 4.1A). There was, however, a significant interaction between overstory and disturbance type on PRE (Table 4.2), with PRE in mixedwood FT + F stands lower than in the mixedwood stands of FT disturbance (Figure 4.1B), but no significant differences were found among broadleaf stands. There was a significant main effect of overstory on KRE in the leaves of *Populus tremuloides* (Table 4.2), with KRE was significantly lower in the broadleaf stands when compared with mixedwood (Figure 4.1C).

Table 4.2 The effects of overstory (broadleaf and mixedwood) and disturbance (fire, fire + full-tree logging, full-tree logging) on resorption efficiency (%) of N (NRE), P (PRE), and K (KRE) in 7-year-old *Populus tremuloides*. Values in bold are significant at 0.05.

Variable	Overstory	Disturbance	Overstory x Disturbance	Model R^2
NRE	0.943	0.189	0.239	0.371
PRE	0.640	0.736	**0.005**	0.595
KRE	**<0.001**	0.273	0.060	0.720

Notes: *n*=3 for all.

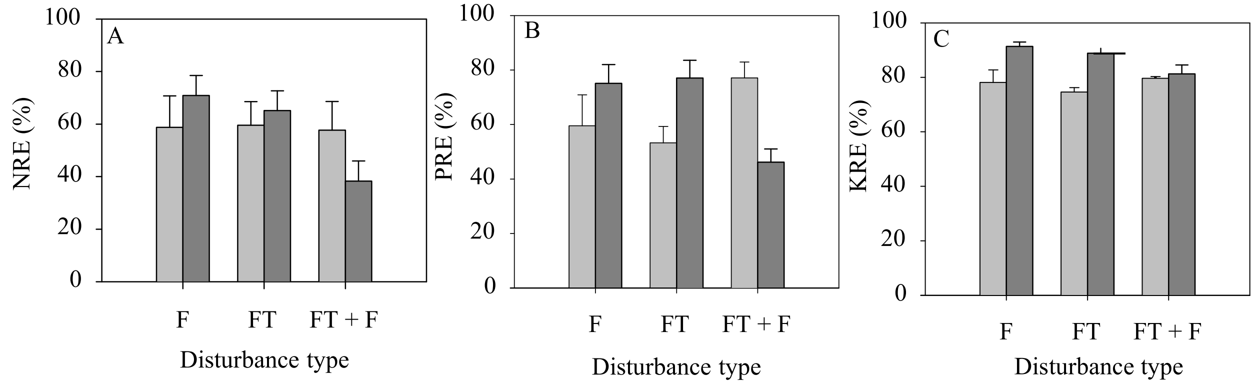

Figure 4.1 Resorption efficiency (%) of N (NRE), P (PRE), and K (KRE) with disturbance type (F=fire, FT = full-tree logging, FT + F = full-tree logging + fire) for *Populus tremuloides*. Open bars are for broadleaf stands, filled bars for mixedwood.

Effects of Soil and Green Leaf Nutrient concentration

Following FT + F disturbance, total nutrient concentrations were higher than F disturbance, their carbon to nutrient ratios being lower (Table 4.3). Soil N only varied as a ratio with C in both the mineral soil and forest floor (Table 4.3). Nutrient concentrations following FT disturbance were generally intermediate between F and FT + F disturbance (Table 4.3). NRE and PRE of *Populus tremuloides* in mixedwood stands increased significantly with increasing mineral soil C:N (b=6.8; Figure 4.2D) and mineral soil C:P (b=0.6; Figure 4.2E). NRE and PRE increased with increasing green leaf N (b=3.8; Figure 4.3A) and P concentration (b=14.3; Figure 4.3B) in broadleaf stands. In mixedwood stands, PRE increased with increasing green leaf P concentration (b=24.8; Figure 4.3E). See supplementary materials for results of ANOVA.

Table 4.3 Mean soil pH, total nutrient and carbon concentrations (mg g^{-1}) (± s.e.m.), and nutrient ratios with carbon with overstory and disturbance treatments.

Horizon		Fire		Full-tree logging		Full-tree logging + fire	
		Broadleaf	Mixedwood	Broadleaf	Mixedwood	Broadleaf	Mixedwood
FF + M	pH	5.2 (0.1)	5.0 (0.1)	5.2 (0.3)	4.9 (0.1)	5.4 (0.2)	5.4 (0.2)
Mineral	N	1.02 (0.13)	0.86 (0.14)	1.08 (0.13)	1.19 (0.11)	1.01 (0.19)	0.73 (0.03)
	P	0.28 (0.03)^{b}	0.24 (0.02)^{b}	0.33 (0.003)^{ab}	0.29 (0.01)^{ab}	0.42 (0.08)^{a}	0.42 (0.06)^{a}
	K	0.21 (0.01)^{c}	0.25 (0.03)^{c}	0.41 (0.06)^{b}	0.36 (0.02)^{b}	0.56 (0.06)^{a}	0.70 (0.06)^{a}
	C	16.0 (1.6)	13.0 (2.1)	15.2 (1.6)	19.1 (3.0)	15.0 (3.6)	8.5 (0.4)
Forest floor	N	2.47 (0.12)	1.00 (0.20)	7.10 (1.72)	4.45 (2.05)	5.27 (2.16)	6.30 (3.22)
	P	0.30 (0.01)^{b}	0.17 (0.01)^{b}	0.54 (0.16)^{ab}	0.30 (0.05)^{ab}	0.45 (0.05)^{a}	0.59 (0.05)^{a}
	K	0.63 (0.02)^{b}	0.30 (0.04)^{b}	0.30 (0.13)^{ab}	0.26 (0.05)^{ab}	0.63 (0.07)^{a}	0.74 (0.12)^{a}
	C	35 (2)	14 (4)	140 (20)	124 (67)	122 (70)	164 (108)
Mineral	C:N	15.7 (0.5)^{a}	15.2 (0.4)^{a}	14.1 (0.5)^{ab}	15.9 (1.0)^{a}	14.6 (0.7)^{a}	12.1 (0.4)^{b}
	C:P	58.0 (4.6)^{a}	54.5 (5.7)^{a}	45.7 (4.9)^{a}	66.4 (14.5)^{a}	39.6 (9.0)^{b}	27.1 (3.8)^{b}
	C:K	74.4 (4.9)^{a}	56.5 (16.4)^{a}	40.6 (11.9)^{ab}	52.8 (8.1)^{ab}	29.9 (9.3)^{b}	15.9 (1.4)^{b}
Forest floor	C:N	14 (1)^{b}	13 (1)^{b}	21 (3)^{a}	27 (3)^{a}	19 (5)^{ab}	21 (4)^{ab}
	C:P	118 (7)	81 (19)	299 (72)	392 (162)	260 (127)	257 (163)
	C:K	117 (2)	62 (28)	229 (18)	386 (160)	205 (112)	236 (168)

Notes: Different letters indicate significant ($p<0.05$) differences in soil attributes among treatments (Tukey HSD test) following two-way ANOVA (see Appendix for F-test details). Letters absent if no significant ($p<0.05$) differences among treatments.

*Forest floor layer + mineral soil (0-50 cm) for pH.

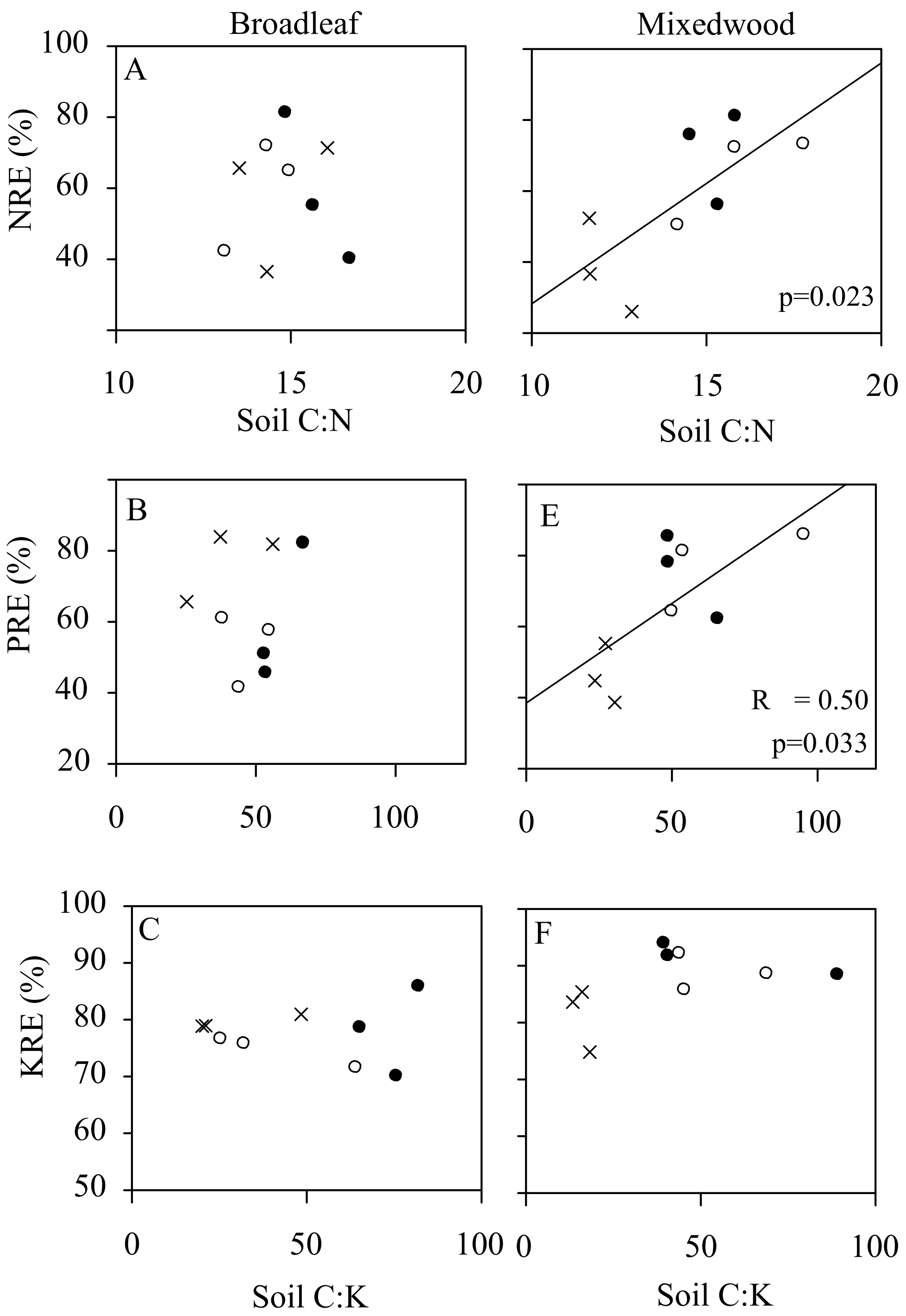

Figure 4.2 Linear regression of resorption efficiency (%) of N (NRE), P (PRE), and K (KRE) of *Populus tremuloides* (*n*=58) with respect to total nutrient concentrations in the mineral soil as carbon ratios. Filled circles = fire, open circles = full-tree logging, X = full-tree logging followed by fire.

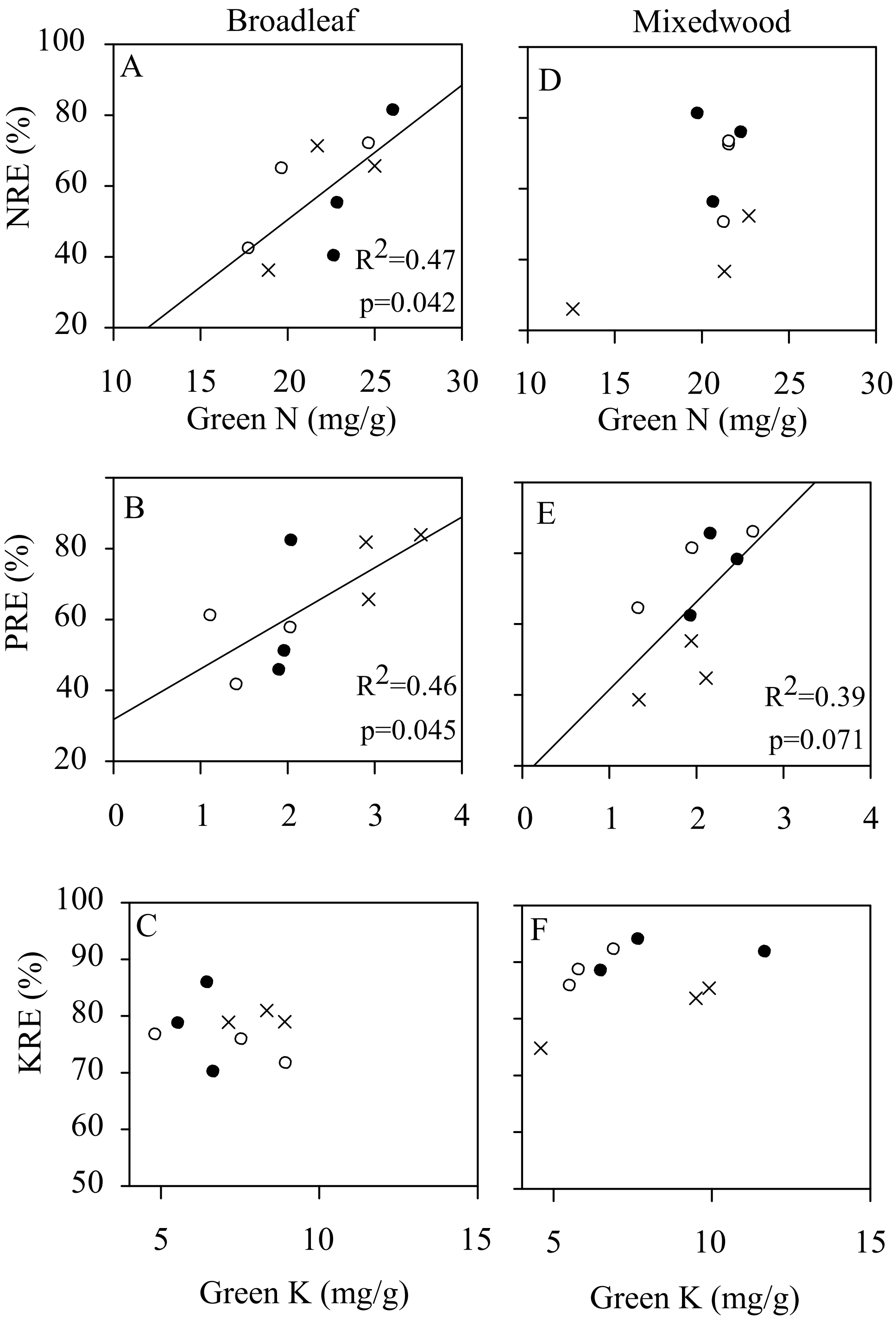

Figure 4.3 Linear regression of resorption efficiency (%) of N (NRE), P (PRE), and K (KRE) of *Populus tremuloides* (n=58) with respect to nutrient concentration in green leaves. Filled circles = fire, open circles = full-tree logging, X = full-tree logging followed by fire.

Discussion

Effects of Disturbance on Nutrient Resorption

Our predictions for the effects of disturbance origin on NuRE were partially supported; PRE was lower in all stands that followed full-tree logging plus fire, but only when found in mixes with *Pinus banksiana*. Mineral soil P was highest following this repeated disturbance, compared with fire and logging alone. Nutrient volatilization depends on the fuel load and severity of the fire; P requires a higher temperature range (770°C) than N (200-500 °C) for volatilization (Ice *et al.*, 2004). The results found here are therefore surprising, in that NRE was not altered by disturbance type as much as PRE. The lower PRE in full-tree logging plus fire stands contradicts the results reached by Huang and Boerner (2007) who found no difference in NRE or PRE across the same three disturbance origins in a perennial legume.

Prescribed fire after logging has been shown to be beneficial in the short-term for plant available P in the soil through the conversion of unavailable P to orthophosphate (Serrasolsas and Khanna, 1995; Certini, 2005; Nobles *et al.*, 2009). The higher availability of P after the repeated disturbance then may trigger the higher PRE in the *Populus tremuloides.* Stand age and conditions prior to logging is an important contributor to the variation in nutrient concentration of the soil after the disturbance has taken place (Thompson and Rothstein, 2009). Given that most logging operations target mature conifer species primarily, the conditions of the soil prior to disturbance may have had a large influence on the NuRE found in this study. The conditions of the forest prior to the fire disturbance alone are unknown, but likely follow the typical mixedwood boreal mosaic found in the area, which may explain why the most differences in soil chemistry are observed between full-tree logging plus fire and fire alone.

Role of Conifer Interaction on Nutrient Resorption

Our results suggest that PRE is affected by the origin of disturbance, but the response in the leaves of *Populus tremuloides* depends on the mix of species that are established post-disturbance. The only significant overstory effect was found for KRE, which was lower in broadleaf stands. This does not support my predictions for higher NuRE in broadleaf stands. Annual growth rate of *Populus tremuloides* is initially higher when mixed with conifers early in stand development (Cavard *et al.*, 2011). However, growth largely depends on soil fertility, which was generally unaffected by overstory composition in this study, with the exception of mineral soil N being higher for mixedwood stands following full-tree logging plus fire. Interaction with other species can affect N use efficiency and resorption efficiency in grasses, for example (Yuan *et al.*, 2007). *Populus tremuloides* in mixedwood stands in this study were co-dominant in the canopy and had access to full sunlight along with the conifers. Therefore, light availability would not be different between pure broadleaf stands and those with conifer species. Our results suggest that, while mixedwoods are beneficial for biodiversity and productivity of a stand as a whole, *Populus tremuloides* may be negatively affected by the lack of conspecifics.

As previously mentioned, *Populus tremuloides* is a unique species that can transfer nutrients to and from clonal ramets of the same organism (Lindroth and Hwang, 1996; Peltzer, 2002; Pinno and Wilson, 2014), a feature that may be hindered when this species is found in low densities under high interaction with other species. One explanation for the effects observed on NuRE following the compounded full-tree logging plus fire is that nutrient transferring among *Populus tremuloides* individuals reduces the dependence on the soil and therefore resorption of nutrients back to live tissues prior to senescence. In mixedwood stands, however, the dependence of foliar nutrition on the soil may be higher due to the fewer number of conspecifics that can share adequate nutrients in *Populus tremuloides*, which may explain the decrease in PRE with increasing mineral soil P. Another explanation for the differences with overstory is intraspecific competition within ramets of *Populus tremuloides* in pure broadleaf stands. Competition within ramets in clonal plants varies, depending on the size of the clones (Kroon, 1993) and ramet aggregation (Gough *et al.*, 2001). In this scenario, the stronger response in PRE to soil availability in mixtures may be due to the relief from competition with other *Populus tremuloides* individuals.

Conclusions

Full-tree logging followed by fire was identified as a compound disturbance, leading to a higher average mineral soil K concentration, but intermediate forest floor concentration for N, P and K, between fire (higher nutrients) alone and full-tree logging alone (lower nutrients). Full-tree logging followed by fire resulted in a lower PRE in *Populus tremuloides* when sampled in mixedwood stands. I conclude that because the soil is influenced by the effects of full-tree logging and fire, the relationships between NuRE and soil are evident, as well as the relationship with green leaf nutrient concentration, then this disturbance type does change the nutrient dynamics. The carbon storage in boreal forests is much higher than in the tropics (Pimm *et al.*, 2009). For this reason, forest management in the boreal should take into consideration the effects of compound disturbance such as fire with logging. Given that fire is a predominant source of stand establishment in the area, the two stand-replacing disturbances can have a profound effect on nutrient dynamics, which may have been previously over-looked. Overstory composition played a role in the variation of NuRE in *Populus tremuloides*. PRE was lower when sampled in mixedwood stands, with which the relationship between PRE and soil P corroborated. I proposed that the reduction in PRE in *Populus tremuloides* in mixedwood stands is due to a lower abundance of ramets of the same clone, within which either nutrient transfers or nutrient competition can take place. I proposed that because nutrient transfer between clones in broadleaf stands reduces the demand on the soil for nutrients, in mixedwood stands the reliance on the soil increases, resulting in a lower PRE with higher soil P fertility.

CHAPTER FIVE: VARIATION IN LITTERFALL PRODUCTION WITH STAND AGE, OVERSTORY COMPOSITION AND DISTURBANCE ORIGIN IN BOREAL FORESTS

Introduction

Litterfall is a fundamental process in carbon and nutrient cycling (Bray and Gorham, 1964; Meentemeyer *et al.*, 1982; Vitousek, 1984). Litterfall represent a major component of aboveground net primary productivity (ANPP) in forests (Clark *et al.*, 2001a), contributing about 27 % to ANPP (Litton *et al.*, 2007). The dynamics of litterfall production are well-studied in tropical (Vitousek, 1984; Clark *et al.*, 2001b; Kaspari *et al.*, 2008) and temperate (Persson *et al.*, 1987; Vogt, 1991; Davidson *et al.*, 2002) forests. Global litterfall estimates typically do not account for boreal forests (Meentemeyer *et al.*, 1982) and in those that have, data collected from the boreal region is under-represented (Bray and Gorham, 1964; Vogt *et al.*, 1986).

Forest productivity begins to decline after a given stand age. The causes for this phenomenon have been debated among ecologists; some claim that this decline is caused by photosynthesis-respiration imbalances, nutrient limitation, and stomatal constraints (Gower et al. 1996), increased mortality (Xu *et al.*, 2012), and increased reproductive allocation of energy (Ryan et al. 1997), competition and self-thinning (Berger *et al.*, 2004). It has been argued many times over that the combination of these factors ultimately lead to the decline of ANPP along stand development (McMurtrie *et al.*, 1995). Wildfire, as the most common natural stand-replacing disturbance in boreal forests, initiates stand development (Heinselman, 1981; Oliver, 1981; Johnson, 1996). The origin of disturbance can influence the timing and magnitude of the productivity decline with age. The metabolic scaling theory of forests is a quantitative framework that proposes that tree biomass productivity can be described mathematically with high predictability (West *et al.*, 2009), but this can be misleading when stand-replacing disturbances are not considered (Coomes *et al.*, 2012). The dynamics of litterfall production through stand development in boreal forests is unknown and can provide some insight into disturbance-productivity relationships in the boreal region.

Of the few studies that focus on litterfall response to disturbance, many do not account for overstory composition (Moroni and Zhu, 2012), which is highly variable (Gower *et al.*, 1996; Gower *et al.*, 2001). Competition is a common variable in most carbon models (Caspersen *et al.*, 2011); however, disturbance can compound the effects of competition, especially when fire-adapted species occupy post-fire forests. In boreal regions, ANPP is 2.7 times greater in stands with *Populus tremuloides* than stands with *Picea mariana* and *Pinus banksiana* (Gower *et al.*, 2000), and the fraction of belowground NPP to total NPP for evergreens is higher (0.36) than for deciduous tree species (0.19) in boreal forests worldwide (Gower *et al.*, 2001). Disturbance in boreal forests promotes shade-tolerant conifers in the long-term, with mortality-induced large canopy gaps providing adequate sunlight (>40 %) for some *Populus tremuloides* and *Betula papyrifera* in-growth (Chen and Popadiouk, 2002). For this reason, the boreal forests are composed mainly of conifers later in succession, justifying the need to understand how litterfall production is affected by overstory dominance through time after disturbance.

Like wildfire, clear-cut logging is a substantial source of disturbance in North American boreal forests, which has been shown to influence regeneration of tree species (Carleton and MacLellan, 1994; Ilisson and Chen, 2009), understory vegetation (Hart and Chen, 2008), forest floor carbon (Shrestha and Chen, 2010), coarse woody debris (Brassard and Chen, 2008), fine root production (Yuan and Chen, 2012b), and soil nutrient cycling (Covington, 1981; Johnson, 1996), among others. The relationship between logging and litterfall production has been studied for North American boreal forests, but many studies that have examined the effects of logging on litterfall production have not used age cohorts that describe the entire successional timeline (Reich *et al.*, 2001). Other studies have compared litterfall in thinned versus unthinned sites of the same age (Gairola *et al.*, 2009; Kunhamu *et al.*, 2009; Dyer *et al.*, 2010; Navarro *et al.*, 2013), different ages (Yang *et al.*, 2004) or litterfall production before and after logging (Santiago *et al.*, 2011), but these studies were aimed at revealing nutrient budget consequences of logging due to reduced litterfall. Variable degrees of thinning and the utilization of different age cohorts could result in incomparable stand density parameters. Therefore, litterfall production along an age chronosequence up to the canopy closure stage after logging has yet to be fully described.

The purpose of this study is to improve the understanding of the effects of stand development, overstory composition and disturbance on litterfall in boreal forests. The primary objectives of this study were i) to assess whether stand development and overstory composition following fire affect litterfall production and ii) to quantify whether origin of disturbance affects litterfall production. Firstly, we predicted that litterfall production should increase with stand development, given that carbon assimilation patterns and leaf turnover is dynamic over time. Secondly, it was predicted that, due to the higher allocation to aboveground biomass in deciduous trees, litterfall production should be highest in broadleaf-dominated stands than conifer-dominated stands, with mixedwood stands having an intermediate level of litterfall production. Finally, we predicted that litterfall production is highest after fire, given the increase in nutrient concentrations in the soil typically after fire.

Methods

Study Area

The study was conducted in the mixedwood boreal forest located west of Lake Nipigon, 150 km north of Thunder Bay, Ontario, Canada in the Upper English River (B. 11) Forest Region (Rowe, 1972), between 49°22’ N to 49°45’ N and 89°10’ W to 89°56’ W, 400 m in elevation. This region has short summers with a moderately dry, cool climate. The mean annual temperature is -0.4 °C with a mean annual precipitation of 716 mm, recorded at the closest meteorological station in Armstrong, Ontario (50º18′ N, 89º55′ W) (1970-2014, Environment Canada 2013). The primary natural disturbance in this area is fire, with an estimated average fire return interval of 100 years (Senici *et al.*, 2010). Dominant soil orders in the region are dystric brunisols, which occur under forest vegetation and often lack a developed mineral-organic surface horizon (SoilClassificationWorkingGroup, 1998). Soils in the region are acidic (pH 5.2 ± 0.03, range of 3.8 to 6.9) and are classified as sandy loam, with an average of 67 % sand, 24 % silt, and 8 % clay fractions. The average bulk density of the mineral soils is 1.07 ± 0.02 g cm^{-3} and 1.46 ± 0.06 g cm^{-3} at depths of 15 and 30 cm, respectively.

Occurring with dominance in the overstory are jack pine *(Pinus banksiana* Lamb.), white spruce (*Picea glauca* [Moench] Voss), trembling aspen (*Populus tremuloides* Michx)., paper birch (*Betula papyifera* Marsh.)., and balsam fir (*Abies balsamea* (L.) Mill.). Understory plant species common in the area are mountain maple (*Acer spicatum* Lam.), green alder (*Alnus viridis*), willow (*Salix sp.*) and beaked hazel (*Corylus cornuta* Marsh.) (Hart and Chen, 2008). Commercial logging began in the early 1970’s with successive operations occurring throughout the study area. Stands dominated by *Populus tremuloides* post-logging regenerate naturally, while *Pinus banksiana*-dominated stands are seeded along with the use of herbicide. Mixedwood stands were planted, but herbicide treatment was not used.

Sample Design

To test the effect of time since fire (TSF) on litterfall production, sampling plots were selected following a chronosequence with six development stages outlined by Chen and Popadiouk (2002): early stand initiation, late stand initiation, stem exclusion stage, early canopy transition, late canopy transition and gap dynamics stage, representing 7,15, 33, 98, 146, and 209 years since fire, respectively (Table 5.1). The chronosequence method is commonly used to describe the successional trajectories that would otherwise be time-ineffective to study (Walker *et al.*, 2010). The sampling plots in this study were selected in a way following successional pattern over a multi-decadal time scale (Walker *et al.*, 2010). To determine TSF for plots <70 years old, detailed provincial fire records were used. For stands >70 years old, tree ages were used to estimate TSF (Senici *et al.*, 2010).

The interspersion of both logged and burned stands allowed an opportunity for a completely randomized sampling design for comparison between stands originated by fire and those originated by regeneration after logging along a successional chronosequence. Harvesting records were obtained to assist with plot selection for the number of years since logging that is comparable with that of wildfire. A total of 27 logged plots were established with three stand ages (7, 15, and 33 years since logging) and three overstory compositions (broadleaf, mixedwood, and conifer).

Table 5.1 Species composition for the 78 plots sampled in the study area.

Origin	Age	Overstory*	*n*	Mean stand density** (stems ha^{-1}, ± s.e.m.) or basal area (m^2 ha^{-1} ± s.e.m.)	Stand composition (% abundance** or % basal area of total)					
					Populus tremuloides	*Betula papyrifera*	*Pinus banksiana*	*Picea glauca*	*Abies balsamea*	Others†
Fire	7	B	3	5733 (1185)	33 (11)	24 (20)	8 (4)			34 (13)
		C	3	6867 (2978)	1 (1)	1 (1)	98 (2)			
		M	3	2333 (437)	30 (11)	15 (8)	48 (24)			6 (6)
	15	B	3	9867 (874)	60 (7)	6 (1)	10 (5)			23 (4)
		C	3	4200 (416)	15 (4)	2 (2)	68 (16)	8 (8)		7 (5)
		M	3	6067 (751)	41 (12)	9 (9)	25 (1)	6 (6)		19 (6)
	33	B	3	25.6 (0.7)	93 (4)	4 (4)	1 (1)			2 (1)
		C	3	21.5 (1.1)	3 (3)	1 (1)	96 (3)			
		M	3	16.8 (3.4)	45 (14)		49 (17)	6 (6)		
	98	B	3	49.2 (7.2)	94 (1)	2 (2)		2 (2)	1 (1)	1 (1)
		C	1	52.4		4	59	30	6	
		M	3	41.3 (5.2)	42 (12)	15 (13)	10 (6)	15 (8)	18 (3)	
	146	B	3	56.7 (7.0)	86 (4)	8 (4)		4 (2)	1 (1)	2 (2)
		C	2	61.5 (1.5)		2 (2)	77 (7)	11 (3)	3 (1)	6 (6)
		M	3	35.0 (2.1)	45 (9)	21 (10)		10 (4)	23 (6)	2 (2)
	209	B	3	39.4 (3.3)	56 (23)	24 (18)		10 (6)	10 (5)	
		C	3	39.2 (7.6)	5 (5)	7 (4)		37 (19)	50 (17)	
		M	3	46.0 (3.3)	11 (4)	39 (6)	5 (3)	38 (7)	7 (3)	
Logging	7	B	3	4067 (406)	69 (7)	7 (2)		2 (2)		22 (5)
		C	3	1533 (67)			67 (27)	4 (4)	12 (12)	17 (17)
		M	3	1600 (115)	9 (4)	20 (13)	8 (4)	20 (15)	17 (6)	25 (2)
	15	B	3	8400 (529)	52 (1)	13 (4)	2 (2)	6 (1)		27 (4)
		C	3	3867 (968)	1 (1)	2 (2)	63 (14)	23 (10)	2 (2)	8 (1)
		M	3	4333 (1157)	7 (4)	17 (6)	4 (2)	30 (6)	7 (7)	34 (8)
	33	B	3	17.1 (0.7)	90 (4)	8 (5)	1 (1)	2 (1)	0	0
		C	3	24.0 (1.6)	1 (1)	0	97 (1)	2 (1)	0	1 (1)
		M	3	27.1 (1.5)	42 (9)	1 (1)	51 (5)	3 (3)	0	2 (2)

Notes: *B=broadleaf, C=conifer, M=mixedwood. **Stand density/% abundance for 7-15 years since fire. †Includes *Salix sp.*, *Acer spicatum*, *Populus balsamifera*, *Alnus viridis*, *Sorbus decora*, *Corylus cornuta*, *Amelanchier*, *Pinus resinosa*, and *Larix laricina*

Three overstory compositions were identified to represent the species composition of mesic sites in the south end of the North American boreal forest (Bonan and Shugart, 1989): 1) conifer plots including *Pinus banksiana* in the early-successional plots and *Picea glauca* mixed with *Pinus banksiana*, and *Abies balsamea* in the later-successional plots, 2) broadleaf plots including *Populus tremuloides* and *Betula papyrifera*, and 3) mixedwood, which can include any of the former species (Table 5.1). Due to a higher merchantability for coniferous species after the stand age of 90 years, only one representative plot for the 98-year-old fire conifer dominance and two for the 146-year-old fire conifer dominance were established and used in this study, while the remaining of disturbance and stand age combinations all have three replicate plots, with a total of 51 fire plots for stand age and overstory composition.

In order to minimize the confounding effects of soil characteristics on litterfall production, sampling plots were located on mesic sites positioned on flat midslope positions (<5 % slope) on well-drained moraine soils >50 cm in thickness. Plots were selected within stands that were visually homogenous for at least 1 ha in size. Plots with different overstory compositions were selected within one given stand for a stand age and disturbance origin, and efforts were made to minimize spatial auto-relationship (Legendre and Legendre, 2012) by allowing for at least 100 m between each selected plot within a given stand. Plots were also selected at least 50 m from a roadway to avoid edge effects.

Field Methods

Circular 0.04 ha plots were established within selected stands. A large-tree inventory for trees ≥9 cm diameter-at-breast-height (DBH) was performed to determine the density and relative basal area of overstory and understory tree species in the plot in order to confirm relative dominance by broadleaf or coniferous tree species in the field. The DBH in cm of each tree meeting these requirements within the plot was measured with a calibrated tape and recorded. Basal area was calculated in m^2 and expressed on a per-hectare scale.

In each of the 78 plots, four litterfall traps, manufactured by Jiffy Products of America Inc. with dimensions 35 × 92 cm (0.322 m^2), were randomly allocated to collect litterfall. Tulle fabric with a mesh size of 1.5 mm was used to line the bottom of the traps to prevent litterfall from escaping through the holes at the bottom of the traps, while allowing for rainwater infiltration to the forest floor beneath. The four trays within each plot represented a total area of 1.288 m^2, which is greater than the recommended size for sampling litterfall in forest ecosystems (McShane *et al.*, 1983; Finotti *et al.*, 2003). To reduce litter decomposition between collection dates, wooden rectangular blocks were placed beneath the four bottom corners of the traps to elevate at a height of 10 cm.

All traps were placed in late August 2012 and collected every four weeks until late October 2013. Monthly collections increase sampling accuracy by preventing loss of litter materials due to decomposition or wind (Dellenbaugh *et al.*, 2007). Samples collected from each trap were placed in paper bags and then sorted into the following constituents: leaves with petioles attached, needles, other materials, and arboreal epiphytic lichens (hereafter referred to as epiphytes). The other category consisted of: cone scales and seeds, catkins, twigs and branches <1.0 cm in diameter, following the recommendations by Clark *et al.* (2001a). Epiphytes were only measured when detached from other litter; the epiphytes attached to twigs and small branches were included in the other materials category, as they would have been shed as woody debris, not as dispersal or shedding. Insects and fecal matter from small mammals and birds were commonly found in the traps but were discarded. The samples were dried at 65°C for 48 hours until constant mass was achieved and recorded to the nearest 0.0001 g.

Calculations

Litterfall samples were first processed and analyzed at trap level. Litterfall production at plot level was estimated by taking the mean of production in the traps for a given month and then expressed as Mg ha^{-1} year^{-1} for annual production. Monthly litterfall samples were used to determine average daily production rates over the given collection period for seasonal variation. Although inter-annual variation of litterfall in the study area between the two years was very low, as confirmed with a student's t-test for autumn 2012 and 2013 ($t = 0.6231$, $p = 0.53$), using multi-year data for litter production always improves accuracy (Yanai *et al.*, 2012). For this reason, the values from the production periods from September to October 2012 and from September to October 2013 were averaged to express an overall mean for the autumn litterfall season and used in the annual litterfall production calculation.

Statistical Analyses

Since the number of levels for the independent variable of stand age is unbalanced for stands originated by wildfire (6 levels) and those originated by logging (3 levels), two separate analyses of variance (ANOVA) were conducted. Data normality was examined with Q-Q plots, histograms and the Shapiro-Wilk test. Data homogeneity was considered using Bartlett's test. Log transformation or square root transformation was applied when original data did not confirm the assumptions. After transformation, all dependent variables confirmed the assumption.

To determine the effects of overstory composition and stand age on annual litterfall production, the following model was used:

1) $Y_{ijk} = \mu + A_i + C_j + AC_{ij} + \varepsilon_{(ij)k}$

where: Y_{ijk} is annual litterfall production (Mg ha^{-1} year^{-1}) of a given constituent, μ = overall mean, A_i = fixed effect of *i*th stand age class (*i*= 1, 2,3…6), C_j = fixed effect of the *j*th overstory composition (*j*=1, 2, 3), $\varepsilon_{(ij)k}$ = random error from random replication with *k*=3 replicates.

To test the effects of disturbance origin (logged *vs*. wildfire), overstory composition, and stand age on annual litterfall production, the following general linear model was used:

2) $$Y_{ijkl} = \mu + A_i + C_j + AC_{ij} + D_k + AD_{ik} + CD_{jk} + ACDi_{jk} + \varepsilon_{(ijk)l}$$

where: Y_{ijkl}, μ, C_j, = eq. 1; Ai is fixed effect of the *i*th age class (*i*=7, 15, 33) D_k is fixed effect of the *k*th disturbance origin type (*k*=1, 2), $\varepsilon_{(ijk)l}$ = random error from random replication with *k*=3 replicates.

An ANOVA was performed to express the effect of month on litterfall production, as a supplement to the paper. All stand age classes were combined for seasonal effects. The following model was used:

3) $$Y_{ijk} = \mu + C_i + M_j + CM_{ij} + \varepsilon_{(ij)k}$$

where: μ, C_i = eq. 1; Y_{ijk} = mean daily litterfall production over a given month (28-day-period), M*j* = collection date (month) where *j*=June, July, August, September, October, $\varepsilon_{(ij)k}$ = random error from random replication with *k*=18 replicates.

Statistical significance for ANOVA was based on α=0.05 and all statistical analyses were conducted using R version 2.15.2. Tukey-HSD multiple comparisons were performed using the *glht* function in the *multicomp* package when significant main effects or interaction effects on annual litterfall production were found.

Results

Annual Litterfall Production in Stands of Fire Origin

The average annual total litterfall production was estimated at 2.1 ± 0.2 Mg ha^{-1} $year^{-1}$ (*n*=18). Total annual litterfall consisted of: 78.6 ± 1.6 % foliage, ie. leaves and needles combined, 20.6 ± 1.6 % other materials, ie. woody debris and reproductive parts, and 0.7 ± 0.2 % shed epiphytes.

Stand age significantly affected total annual litterfall production, annual foliage production, and the annual production of other materials (Table 5.2), where total, foliar and other production were significantly higher for stand ages of ≥33 years than stand ages of 7 and 15 years, but 146-year-old stands had significant more total litterfall production than 33-year-old

Table 5.2 Effects of time since fire (A = 7, 15, 33, 98, 146, 209 years) and overstory composition (O=broadleaf, conifer, mixedwood) on annual litterfall production and its constituents. Values in bold are significant at 0.05.

Annual production (kg ha^{-1} $year^{-1}$)	Source	df	*SS*	MS	F	P
Total	**A**	**5**	**46.78**	**9.355**	**69.3**	**<0.001**
	O	**2**	**1.18**	**0.589**	**4.4**	**0.021**
	A × O	10	1.72	0.172	1.3	0.284
	Error	33	4.46	0.135		
Foliage	**A**	**5**	**26.424**	**5.285**	**66.4**	**<0.001**
	O	**2**	**1.947**	**0.973**	**12.2**	**<0.001**
	A × O	10	1.093	0.109	1.4	0.235
	Error	33	2.625	0.080		
Other	**A**	**5**	**2.521**	**0.504**	**12.7**	**<0.001**
	O	2	0.062	0.031	0.8	0.462
	A × O	10	0.377	0.038	0.9	0.500
	Error	33	1.306	0.040		
Epiphytes	**A**	**5**	**0.345**	**0.069**	**38.7**	**<0.001**
	O	**2**	**0.051**	**0.025**	**14.3**	**<0.001**
	A × O	**10**	**0.056**	**0.006**	**3.2**	**0.006**
	Error	33	0.059	0.002		

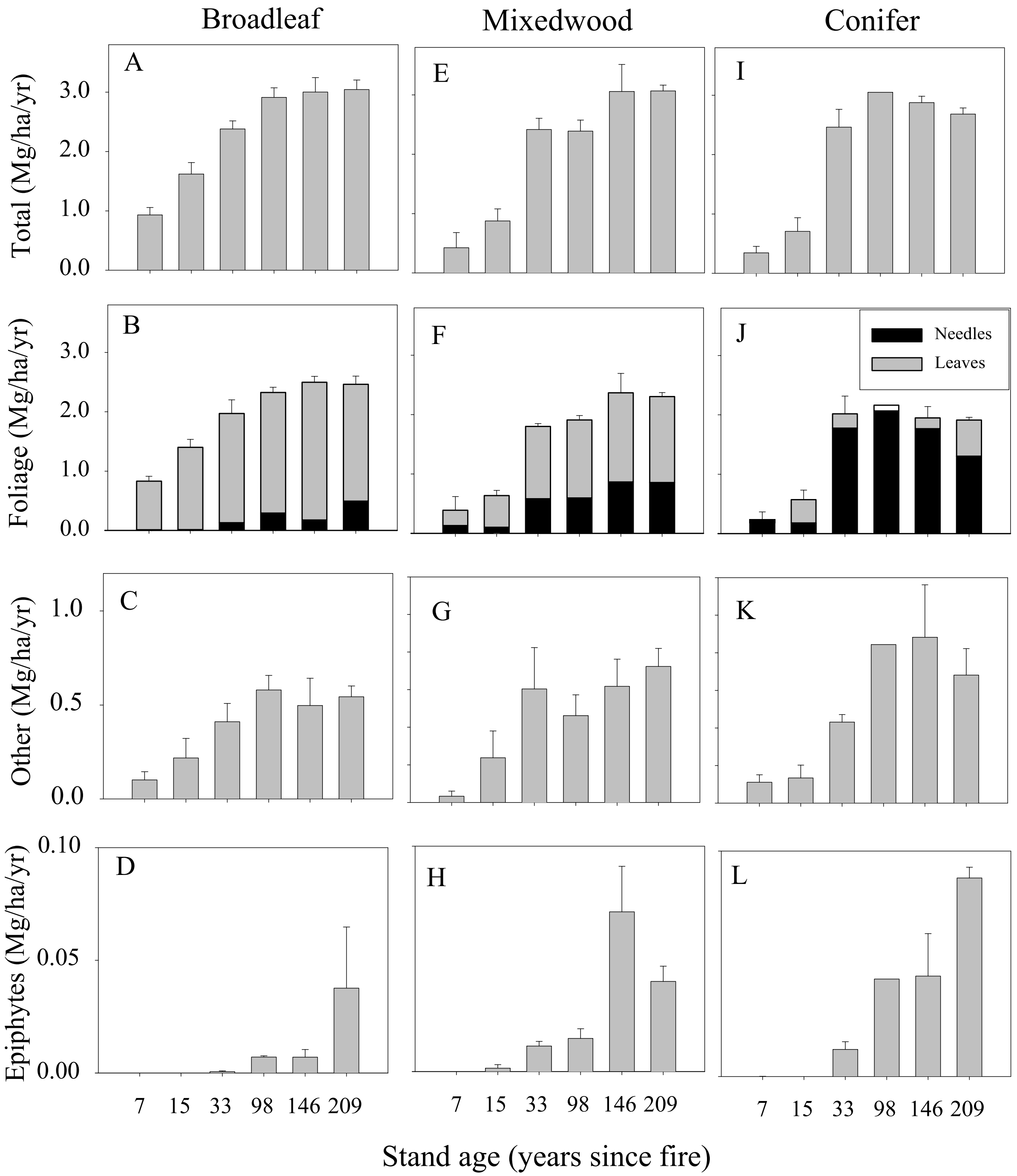

Figure 5.1 Annual production (Mg ha^{-1} year^{-1}) of litter in fire origin stands in relation to stand age and overstory.

stands (Figure 5.1A-C, E-G, I-K). Overstory significantly affected total and foliar annual production (Table 5.2), with broadleaf stands producing more total (Figure 5.1A,E,I) and foliar (Table 5.2B,F,J) litterfall production than conifer and mixedwood stands. There was a significant interaction between stand age and overstory effects on the annual epiphyte fall (Table 5.2). Epiphyte fall was only significantly higher for conifer stands when compared to broadleaf stands at 209 years old, with no difference between mixedwood and conifer stands for any age class (Figure 5.1D-L). Epiphyte fall increased with stand age, highest in the 209-year-old stands for stands with conifer and broadleaf overstory compared with ≤33-year-old stands (Figure 5.1D,L). In mixedwood stands, 146-year-old stands had higher epiphyte fall than all younger stands (Figure 5.1H).

Monthly Litterfall Production

There was a significant interaction between overstory composition and month of collection on the total litterfall production, foliage production, and the production of other materials (Table 5.3). Total and foliar litterfall production was significantly higher in September and October for all overstory compositions (Figure 5.2A-B). Total production was higher for broadleaf stands in October when compared with mixedwood and conifer stands, and foliar production was higher in broadleaf stands in September and October compared with conifer stands only (Figure 5.2A-B). The production of other materials was highest in October in broadleaf stands, compared to July to September (Figure 5.2C). In mixedwood stands, the production of other materials was significantly higher in June than August (Figure 5.2C). There were no significant differences across months for production of other materials in the conifer stands and in September and October, production of other materials was higher in broadleaf stands than conifer stands (Figure 5.2C). Overstory composition had a significant effect on epiphyte fall (Table 5.3), with significantly production in conifer stands than broadleaf and mixedwood stands (Figure 5.2D). Month of collection also had a significant main effect on epiphytes (Table 5.3); production was higher in June than in August to October (Figure 5.2D).

Table 5.3 Effects of overstory composition (O=broadleaf, conifer, mixedwood) and month (M) on litterfall production and its constituents. Values in bold are significant at 0.05.

Mean daily production (kg ha^{-1} day^{-1})	Source	df	*SS*	MS	F	P
Total	**O**	**2**	**12.1**	**6.06**	**4.6**	**<0.001**
	M	**4**	**675**	**168.80**	**129.1**	**<0.001**
	O × M	**8**	**57.5**	**7.19**	**5.5**	**<0.001**
	Error	237	309.7	1.31		
Foliage	O	2	0.8	0.43	1.4	0.259
	M	**4**	**256.4**	**64.1**	**204.3**	**<0.001**
	O × M	**8**	**15.1**	**1.89**	**6.0**	**<0.001**
	Error	237	74.4	0.31		
Other	O	2	0.3	0.99	0.4	0.373
	M	**4**	**11.9**	**2.99**	**9.2**	**<0.001**
	O × M	**8**	**6.1**	**0.76**	**2.4**	**0.019**
	Error	237	76.8	0.32		
Epiphytes	**O**	**2**	**0.3**	**0.19**	**7.3**	**<0.001**
	M	**4**	**0.4**	**0.10**	**3.9**	**0.004**
	O × M	8	0.1	0.01	0.5	0.855
	Error	237	6.1	0.03		

Annual Litterfall Production with Disturbance Origin

Annual litterfall production did not vary significantly with disturbance type for total litterfall, foliage, production of other materials, or epiphytes (Table 5.4; Figure 5.3).

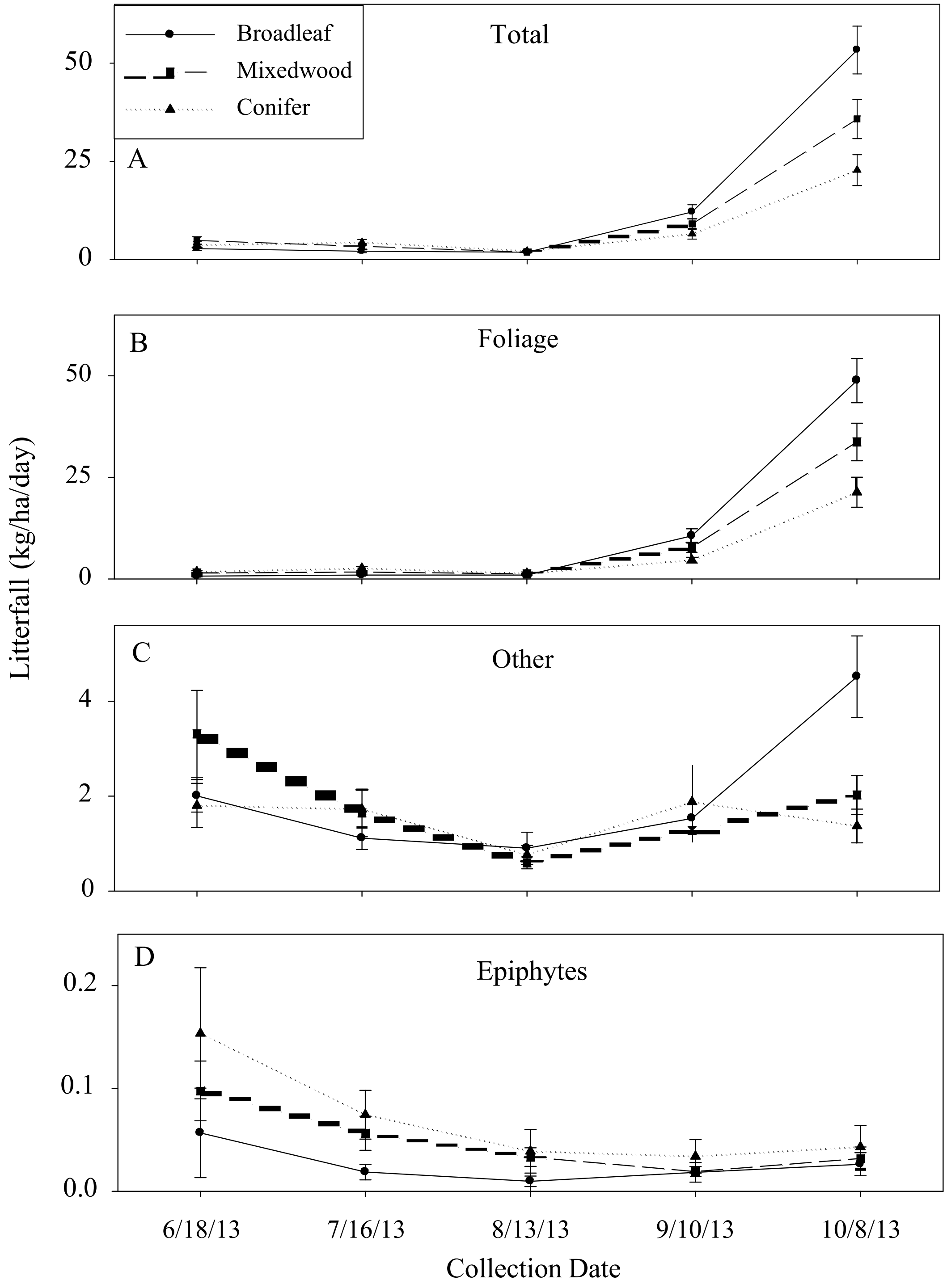

Figure 5.2 Monthly litterfall production (kg ha^{-1} day^{-1}) in 2013 for each litter constituent across overstory compositions with fire origin (ages 7-209). Months of September and October averaged for 2012-2013. *n*=18 for broadleaf stands (all months), *n*=18 for mixedwood stands (all months), *n*=15 for conifer stands for Jun-Jul, *n*=14 for Aug-Oct.

Table 5.4 Effects of time since disturbance (A=7, 15, 33 years), overstory composition (O=broadleaf, conifer, mixedwood) and disturbance type (D=fire and logging) on total annual litterfall production. Values in bold are significant at 0.05.

Annual production (kg ha^{-1} year^{-1})	Source	df	SS	MS	F	P
Total	**A**	**2**	**39.910**	**19.953**	**139.9**	**<0.0001**
	O	**2**	**3.770**	**1.886**	**13.2**	**<0.0001**
	D	1	0.010	0.015	0.1	0.748
	A × O	**4**	**2.650**	**0.661**	**4.6**	**0.004**
	A × D	2	0.570	0.283	2.0	0.153
	O × D	2	0.410	0.207	1.4	0.248
	A × O × D	4	0.800	0.199	1.4	0.254
	Error	36	5.140	0.143		
Foliage	**A**	**2**	**23.865**	**11.932**	**177.1**	**<0.0001**
	O	**2**	**2.980**	**1.490**	**22.1**	**<0.0001**
	D	1	0.024	0.024	0.4	0.553
	A × O	**4**	**1.342**	**0.336**	**5.0**	**0.003**
	A × D	2	0.217	0.109	1.6	0.213
	O × D	2	0.122	0.061	0.9	0.413
	A × O × D	4	0.239	0.060	0.9	0.481
	Error	36	2.426	0.067		
Other	**A**	**2**	**1.982**	**0.991**	**35.0**	**<0.0001**
	O	2	0.167	0.084	3.0	0.065
	D	1	0.006	0.006	0.2	0.640
	A × O	4	0.284	0.071	2.5	0.059
	A × D	2	0.060	0.030	1.1	0.356
	O × D	2	0.126	0.063	2.2	0.123
	A × O × D	4	0.099	0.025	0.9	0.486
	Error	36	1.0186	0.029		
Epiphytes	**A**	**2**	**0.069**	**0.03443**	**81.8**	**<0.0001**
	O	**2**	**0.011**	**0.00543**	**12.9**	**<0.0001**
	D	1	5 x 10^{-04}	5 x 10^{-04}	1.3	0.268
	A × O	**4**	**0.016**	**0.004**	**9.4**	**<0.0001**
	A × D	2	1 x 10^{-04}	7 x 10^{-05}	0.2	0.854
	O × D	2	1 x 10^{-04}	6 x 10^{-05}	0.1	0.863
	A × O × D	4	0.002	5 x 10^{-04}	1.1	0.347
	Error	36	0.015	4 x 10^{-04}		

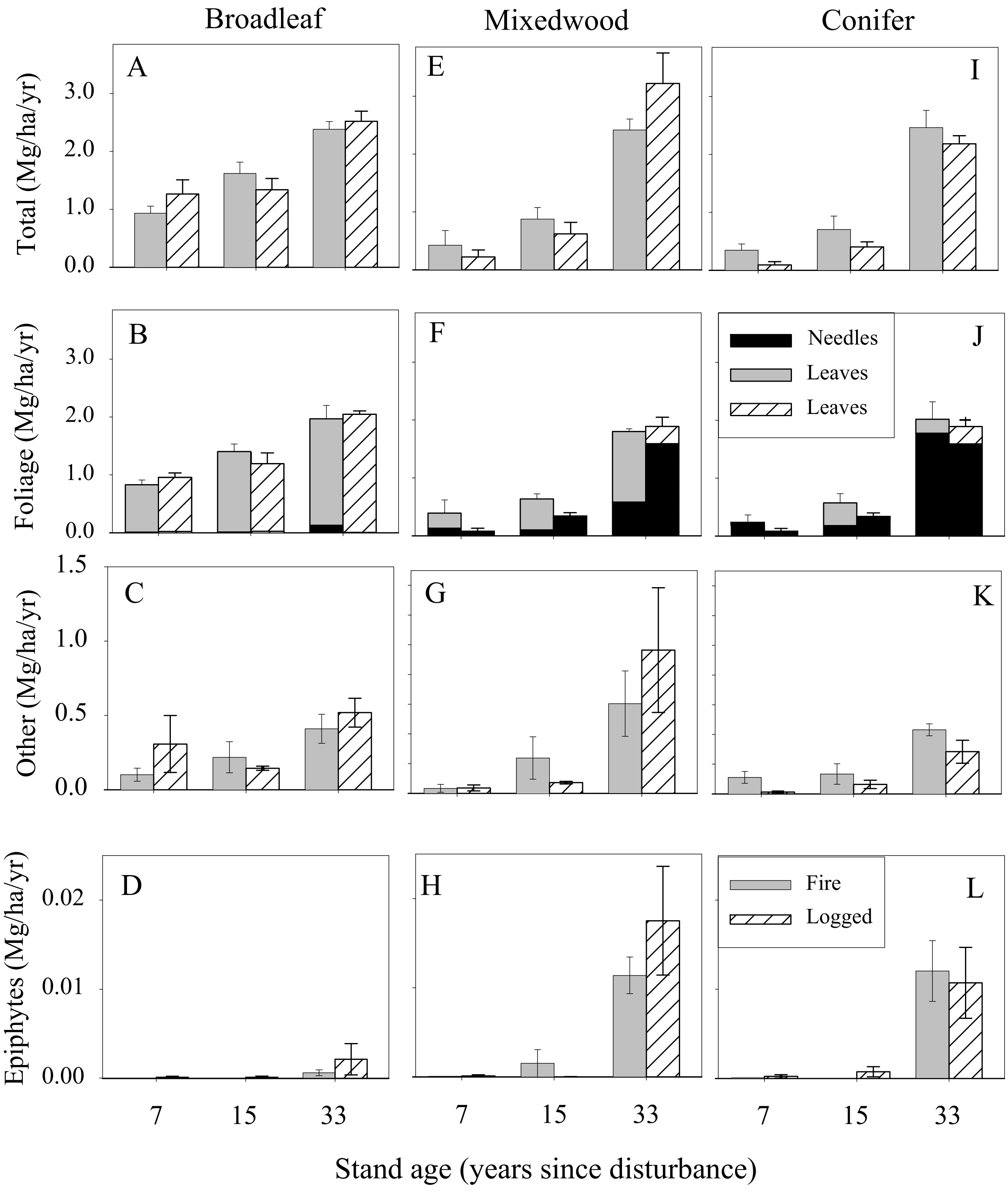

Figure 5.3 Annual production (kg ha^{-1} year^{-1}) of total litterfall for the 3 overstory compositions across stand age with the two disturbance types: fire and logging. *n*=3 for each treatment.

Discussion

Effects of Time Since Fire

Our findings support the first prediction that stand age affects litterfall production. For all overstory types, litterfall production was highest for stands ≥33 years old. The long duration of litterfall production over time since disturbance may then be attributed mostly as a compensation for lower overall nutrient availability in the boreal region. Forests with higher soil fertility will result in an earlier decline in productivity (Ryan *et al.*, 1997) because these forests tend to use nutrients more efficiently to produce aboveground biomass than forests with lower nutrient availability (Vicca *et al.*, 2012). In *Eucalyptus* plantations, litterfall production declines after canopy closure 1 to 2 years after planting (Ryan *et al.*, 2004) and in *Alnus nepalensis* plantations in the Indian monsoon region, litterfall increases to age 17 years, then stabilizes to 56 years old (Sharma and Ambasht, 1987). Given that boreal forests are known to have lower measures of nutrient availability as a result of colder soil temperatures and thus slower rates of litter decomposition (Bonan and Shugart, 1989), one of the primary causes for the continued litterfall production in our study may be the well-recognized nutrient limitation and temperature-induced slower production of the boreal region. Although NPP in temperate forests is double (740 g C m^{-1} $year^{-1}$) that of boreal forests (340 g C m^{-2} $year^{-1}$), it declines earlier; at approximately 70 years for temperate and 100 years for boreal (Tang *et al.*, 2014).

There was a decline in the relative importance of *Populus tremuloides* in the broadleaf stands with increasing stand age along with an increase of *Betula papyrifera*. Typically, *Populus tremuloides* contributes a significant portion of the stand basal area for the first 167 years of succession, but its importance then carries over to later-successional species (Bergeron, 2000).

Thus, litterfall inputs are higher in the broadleaf stands due to this change in species dominance from the removal of pioneer species from the stands. Throughout development, the age of the stand will eventually exceed the age of the oldest trees found within it, due to increasing rates of mortality caused by competition, disease, pests, ageing and other non-stand-replacing disturbances (Luo and Chen, 2011). This point in time has been identified in boreal mixedwood forests as the early canopy transition phase, where pioneer tree mortality increases while the canopy is being replaced with shade-tolerant species (Chen and Popadiouk, 2002). The age-related decline in productivity has been linked to competition and mortality by means of self-thinning (Ryan *et al.*, 1997; Berger *et al.*, 2004), so the stabilization of litterfall production with stand age may also be explained with shifts in species assemblages throughout the successional chronosequence.

The same species shift can be described for conifer stands. In loblolly pine (*Pinus taeda* L.) needlefall increases as stand basal area increases (Hennessey *et al.*, 1992) to a threshold of 26 m^2 ha^{-1}, after which it remains constant at about 4,000 kg ha^{-1} yr^{-1} (Gresham, 1982). The basal area of *Pinus banksiana* in the present study increased to 47.6 ± 5.4 m^2 ha^{-1} in the 146-year-old stand age class, while *Picea glauca* basal area was highly variable throughout the chronosequence, increasing to 17.4 ± 9.7 m^2 ha^{-1} in the 209-year-old conifer stand. The basal area for which needlefall began to stabilize in conifer stands, at year 33, was 21.0 ± 1.7 m^2 ha^{-1} for *Pinus banksiana*, with *Picea glauca* absent at this stand age. Another factor sometimes overlooked in aboveground productivity studies is the leaf turnover rates. The average needle lifespan of *Picea glauca* is 5 years, much longer than *Pinus banksiana*'s 2.25-year needle lifespan (Reich *et al.*, 1999). Despite this, the foliar and needlefall production in the older (≥33 year-old) conifer and mixedwood stands remains statistically constant to 209 years after *Picea* *glauca* has succeeded *Pinus banksiana*. The longer turnover time in *Picea glauca* may be reconciled with the higher aboveground foliar organic matter (11.7 t ha^{-1}) than *Pinus banksiana* (4.9 t ha^{-1}) on sandy soils for similar stand ages (Perala and Alban, 1982) and more needlefall (2.8 Mg ha^{-1} year^{-1}) than other members of the *Picea* genus (1.8 Mg ha^{-1} year^{-1}for *P. rubens* and 1.6 for *P. mariana*) (Gordon *et al.*, 2000). This may be one reason why our study found a consistent needlefall over time despite the succession from *Pinus banksiana* to *Picea glauca*.

Stands in the 209-year-old age class produced higher amounts of annual epiphyte fall. This result is consistent with the higher diversity and abundance of epiphytic lichen communities found in old growth forests (Lesica *et al.*, 1991; Lie *et al.*, 2009). The annual production of other materials such as twigs, small branches, and reproductive parts were only influenced by stand age, not overstory composition. Although asexual reproduction dominates the spread of *Populus tremuloides*, seeds are still produced in catkins (Mitton and Grant, 1996) and the number of seeds increases with age (Schopmeyer, 1974).

Effects of Overstory

Litterfall production was higher in broadleaf stands than conifer and mixedwood stands. Broadleaved trees shed all of their leaves annually, whereas conifers are more variable in their needlefall and are therefore more complex with respect to litterfall production. The lower litterfall production in the mixedwood stands is most likely a consequence of having found both broadleaf and coniferous species in these stands, both operating on different strategies for growth and competitive success. Conifer-dominated forests host a higher number of macrolichen species than broadleaf forests (Cleavitt *et al.*, 2009), which may explain why a higher mass of epiphyte fall was found in the older (209 years since fire) conifer stands. Our results support the notion that lichen fall will correlate to lichen abundance, but it has not yet been established whether the measurement of lichen via litterfall sampling is a reliable way to accurately estimate shedding and dispersal patterns in this taxonomic group. Our results support the prediction that broadleaf stands have higher amounts of litterfall production, with the exception of epiphytic litter in the conifer stands.

Seasonal Patterns

Epiphyte fall peaked in the late spring (late May to early June). This finding suggests that, although tree foliage follows the typical pattern for autumn seasonal senescence cued by temperature and shading, the shedding of epiphytic lichen is governed by other factors. For epiphytic lichen, seasonal growth depends on precipitation (Muir *et al.*, 1997). Lichen fall from *Quercus* trees occurs mainly in the early spring (April) in the Himalayas, also coinciding with periods of high precipitation (Kumar *et al.*, 2009) and epiphyte fall from *Picea abies* in Sweden occurred in the highest volumes from autumn to the beginning of summer (Esseen, 1985). For the weeks sampled in the present study (May 21 to June 18), there was a heavy influx of water in the area, with snowmelt playing a factor in the increased discharge of water. The shedding of epiphytic lichen from the trunks and branches of the tree may have peaked in spring due to: the onset of spring thawing, wind, or a combination of these factors.

The shedding of woody materials is heavily influenced by wind patterns (Cragg *et al.*, 1977; Weber, 1987), rainfall (Fyles *et al.*, 1986) and possibly grazing by wildlife mainly occurring during early spring months when food availability is low. Squirrel activity can also trigger the release of other materials to the ground in both spring and fall (Steele *et al.*, 2005). In the present study, other litterfall production peaked in June for mixedwood stands and in October for broadleaf stands. The other materials category consisted of both woody debris and reproductive parts, so we discuss these separately. Male and female catkins in *Populus* *tremuloides* on average contribute 14 % of non-foliar litter material (Cragg *et al.*, 1977), produced in early spring (Mitton and Grant, 1996) and typically falling in May (Ovington, 1963). Male cones from *Pinus banksiana* average about 20 % of production of non-foliar litter (Fyles *et al.*, 1986). Both male and female cones fall throughout the year (Ovington, 1963; Moore and Nozzolillo, 1991), but non-serotinous cones open with higher temperatures late in the growing season (Despland and Houle, 1997). The peak of shedding of other materials in the spring and autumn could then be attributed to catkin and cone litterfall in the spring due to snowmelt and rainfall, and woody litter in the fall months due to wildlife activity.

Disturbance: Fire and Logging

Our findings suggest that sites originated from logging are no different in terms of litterfall production than those originated from wildfire. In logged stands, litterfall production followed the same pattern as stands originated from wildfire: a marginal increase from year 7 to year 15, followed by a statistically significant increase to year 33. This study filled in the missing gap of information from a similar study conducted by Reich *et al.* (2001) which did not include stands younger than 25 years old. In our study, litterfall production was marginally higher in stands originated from fire in the conifer and mixedwood stands for age 7 and 15 years. This observation, although statistically insignificant, coincides with a higher basal area for years 7 and 15 in all overstory compositions for fire stands. The lower basal area in the logged stands could be explained by the use of herbicide. While logging removes substantial amounts of C from the site (Johnson and Curtis, 2001), severe fires can release much more C from all layers of the forest stand as well as soil organic carbon (Chen and Shrestha, 2012). We know that understory vegetation dynamics and succession are different between the two disturbance types (Hart and Chen, 2008; Ilisson and Chen, 2009) and that logging promotes *Populus tremuloides* dominance over long periods of time in the absence of post-disturbance silviculture (Carleton and MacLellan, 1994). The evidence provided in our study does not support our prediction that logging affects litterfall production at the same degree that it affects plant regeneration and nutrient cycling.

Conclusion

The use of a forest stand age chronosequence showed that time since fire only influenced litterfall production at the initial stages of development, from 7 to 33 years post-fire. After canopy closure at year 33, litterfall production stabilized at approximately 2.5 Mg ha^{-1} $year^{-1}$. The lack of an evident decline in litter productivity with age was attributed to the relatively later decline in productivity for boreal forests with low nutrient availability and temperatures, as compared with more temperate or tropical regions. Our finding that epiphyte litter increases significantly when the stand reaches 209 years since fire is consistent with high diversity and abundance of epiphytic lichen in boreal forests, but this was the first study to our knowledge to account for epiphytic shedding, which plays an important component of soil nutrient capital upon integration. Litterfall production was also consistent across overstory composition past the stand age of 33 years since fire. Inputs of leaves in the total foliage production were few until after canopy closure at year 33, but on a larger scale, this mixedwood forest produced the same amount of litter annually. Productivity is only one measure of ecosystem function, and while needles decompose slower than broadleaves, our findings imply that litterfall production within mixedwood forests in northern latitudes is consistent across successional change and species dominance. Disturbance origin (fire and logging) had no effect on litterfall production for the study area. Our findings provide a baseline framework for future study in ecosystem productivity, but for the purpose of gaining better understanding of how forests regenerate after disturbance, more research is needed on other measures of productivity including soil, root, understory biomass, and nutrient dynamics.

CHAPTER SIX: GENERAL CONCLUSIONS

The findings of this thesis imply that time since fire, overstory composition and disturbance origin can influence the way that trees conserve nutrients at the end of a growth period but litterfall production is generally sustained. A summary of my main results and their implications are as follows:

1. Nitrogen resorption efficiency (NRE) was conserved throughout stand development in trembling aspen (*Populus tremuloides*) from 7 to 209 year since fire and from 98 to 209 years since fire in white birch (*Betula papyrifera*). Nitrogen limitation for the region may justify this result. The resorption efficiency of phosphorus (PRE) and potassium (KRE) decreased with increasing stand age in *Populus tremuloides* and in *Betula papyrifera*, consistent with an increase in soil P and K over time since fire. PRE and KRE were positively related to soil P and K, except for the relationship for P in *Populus tremuloides*. This implies a response to the soil fertility in both species for KRE and for PRE in *Betula papyrifera*. I suggest that PRE in *Populus tremuloides* depends more on age-related factors than soil fertility and more research is needed on the effects of stand development and NuR with a higher variety of tree species to understand more about these findings.
2. The decrease in PRE and KRE in *Populus tremuloides* with stand age was only present in mixedwood stands, while in *Betula papyrifera* the decrease was present regardless of overstory composition. Variation in the response of PRE and KRE to the soil environment for *Populus tremuloides* may derive from either life history traits or competition within ramets of the same clone. Future study on this species could

concentrate on direct effects on NuR from nutrient sharing among clonal ramets and intraspecific competition in this species.

3. Full-tree logging followed by fire, when compared with fire and full-tree logging alone, resulted in a lower PRE in 7-year-old *Populus tremuloides* in mixedwood stands. This finding was attributed once again to clonal reproduction in this species where lack of neighbouring ramets could result a shift from the acquisition of nutrients from neighbours to direct acquisition from the soil environment. The carbon to P ratio was lowest in stands with this disturbance origin. I suggested the soil and overstory as main drivers in the lower PRE, given the positive relationship between soil C:P and PRE in mixedwood stands. My findings can be used as a starting point for more research on disturbance-nutrient relationships in this species.
4. Total, foliar and other litter production increased to 33 years since fire regardless of overstory composition then was sustained to the end of the stand age chronosequence of 209 years since fire. Inevitable declines in forest productivity have been suggested in other studies. For the boreal region, the lack of an identifiable decline in litterfall production as far as 209 years since fire may imply a delay in the onset of the suggested decline in productivity. This finding can assist with further study on productivity decline in forests or with the role of litterfall production in total aboveground primary production, for which there has been a long-believed direct relationship. Epiphyte litter was higher in the oldest stands with broadleaf and conifer overstory composition, compared with stands 33 years old and younger, while epiphyte litter in mixedwood stands peaked at 146 years since fire, compared with stands 98 years old and younger. This finding is consistent with many supporting observations that old-growth forests support more epiphyte

communities, but this to my knowledge is the first study to corroborate this with epiphyte litter.

5. Total and foliar litter production varied among broadleaf, mixedwood, and conifer overstory tree species composition, but the post-hoc analysis did not reveal any significant comparisons among overstory compositions. The oldest conifer stands had more epiphyte litter than the oldest broadleaf stands, mixedwood stands had comparable epiphyte litter. This finding further supports the well-documented observation that epiphyte abundance is high in conifer-dominated stands, but my findings also imply that stands with broadleaf species admixed with conifer species can produce a comparable amount of epiphytic litter to the soil environment as a pure conifer stand.
6. Production of all litter constituents was seasonal; not surprisingly foliar production peaked in October. The production of other materials peaked in June for broadleaf and mixedwood stands and October for broadleaf stands only, with no apparent seasonality in the conifer stands. For all overstory compositions, epiphyte litter peaked in June The spring and summer peaks for non-foliar litter could be attributed to wildlife, rainfall events or reproductive strategies in these trees. Further research into seasonality of non-foliar litter may provide some insight into the turnover of organic matter in these forests.
7. Disturbance origin (fire and logging) did not affect annual litterfall production. Both fire and logging are stand-replacing disturbances and, although they result in different patterns of vegetative regeneration during stand establishment, my findings suggest that the total annual mass of litter introduced back to the soil is comparable between fire and logging. This provides some insight on the study of disturbance-productivity relationships in boreal forests.

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APPENDIX

Table S1 P-values and model R^2 from ANOVA for effects of stand age and overstory composition on soil attributes. Values in bold are significant at 0.05.

Variable	Age	Overstory	Age × Overstory	
	P-value	P-value	P-value	Model R^2
pH	0.355	0.624	0.069	0.432
Mineral soil total N	0.092	0.444	0.538	0.396
Mineral soil total P	**<0.001**	0.653	0.555	0.666
Mineral soil total K	**<0.001**	0.618	0.877	0.733
Mineral soil total C	0.167	0.829	0.628	0.331
Forest floor total N	**<0.001**	0.247	0.101	0.743
Forest floor total P	**<0.001**	0.206	**<0.050**	0.753
Forest floor total K	**<0.001**	0.854	**0.003**	0.856
Forest floor total C	**0.001**	0.680	0.601	0.644
Mineral soil C:N	**0.048**	0.068	0.697	0.468
Mineral soil C:P	0.139	0.751	0.752	0.330
Mineral soil C:K	**<0.001**	0.722	0.605	0.602
Forest floor C:N	**0.011**	0.326	0.117	0.604
Forest floor C:P	**0.001**	0.547	0.506	0.538
Forest floor C:K	**0.005**	0.953	0.719	0.566

Table S2 P-values and model R^2 from ANOVA for effects of overstory and disturbance on soil attributes. Values in bold are significant at 0.05.

Variable	Overstory	Disturbance	Overstory × Disturbance	
	P-value	P-value	P-value	Model R^2
pH	0.212	0.175	0.878	0.335
Mineral soil total N	0.259	0.176	0.269	0.411
Mineral soil total P	0.085	**0.011**	0.829	0.589
Mineral soil total K	0.961	**<0.001**	0.631	0.830
Mineral soil total C	0.321	0.135	0.088	0.497
Forest floor total N	0.578	0.085	0.643	0.409
Forest floor total P	0.322	**0.009**	0.080	0.670
Forest floor total K	0.337	**0.002**	0.084	0.735
Forest floor total C	0.958	0.126	0.839	0.329
Mineral soil C:N	0.439	**0.015**	**0.018**	0.668
Mineral soil C:P	0.809	**0.019**	0.134	0.572
Mineral soil C:K	0.434	**0.004**	0.292	0.646
Forest floor C:N	0.442	**0.047**	0.640	0.463
Forest floor C:P	0.887	0.115	0.828	0.341
Forest floor C:K	0.658	0.159	0.595	0.336