THE IMPACT OF BLACK COTTONWOOD ON SOIL FERTILITY OF A CONIFEROUS FOREST IN THE COASTAL WESTERN HEMLOCK ZONE OF BRITISH COLUMBIA

by

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ABSTRACT

Black cottonwood (*Populus trichocarpa* Torr. and Gray) is a deciduous tree native to coastal and southern British Columbia. We examined the influence of cottonwood on soil fertility within a conifer-dominated forest. Six plots containing cottonwood were paired with six pure conifer plots, and individual pairs were compared for litterfall, early decomposition, properties of the forest floor, properties of the mineral soil, and N mineralization. Cottonwood litter relative to conifer litter had higher concentrations of almost all elements. Twice the proportion of mull humus form was found in cottonwood plots. Higher pH and total N concentrations were found in the forest floor and mineral soil under cottonwood, respectively. The concentration of NO_3^- was significantly greater under cottonwood within an incubation study. These results suggest a moderate to weak positive effect of cottonwood on soil fertility within temperate coastal forests.

Keywords: Black cottonwood; *Populus trichocarpa*; nutrient cycling; litterfall; decomposition; forest floor; mineral soil; nitrogen mineralization; forest soils

To all who have given of themselves in the fight to protect our blue planet from ourselves.

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CHAPTER 1: Introduction

1.1 Research Rationale

Forest managers traditionally view many deciduous trees as weeds that compete with conifers for resources. Black cottonwood (*Populus trichocarpa* Torr. and Gray) is specifically noted as a severe competitor due to its rapid height growth and early dominance in forest stands (Haeussler et al., 1990). However, the inclusion of deciduous species in conifer stands improves biodiversity and, depending on the species, may also impart other valuable ecosystem services. For example, deciduous species may provide forage and cover for wildlife, erosion control, or may act as nurse crops. Also, the maintenance of biodiversity within a system is of particular importance with regard to ecosystem resilience, defined as the magnitude of disturbance a system can experience before it shifts into a different state (Holling, 1973). Biodiversity increases the capacity of ecosystems to renew and reorganize after disturbance, and can therefore be seen as a kind of insurance policy against the loss of ecosystem functionality (Folke et al., 2004). The removal of broad-leaved species such as cottonwood decreases this biodiversity (Garrod and Willis, 1997).

There is also evidence that in some cases nutrient cycling and availability are higher under broad-leaved species compared to conifers (Tashe and Schmidt, 2003; Perry et al., 1987; Washburn and Arthur, 2003). However, scientific evidence is not consistent in its support of the notion that nutrient

cycling and availability are always higher under deciduous trees when compared to conifers (Binkley and Giardina 1998). It is therefore essential that the potential effect of each species be studied. Cottonwood is a native species to western North America, and is British Columbia's fastest growing tree (B. C. Ministry of Forests, 1991). There are currently no studies of the effect of cottonwood on soil fertility within conifer-dominated forest and thus the goal of my research was to address this knowledge gap.

1.2 Objective and Hypothesis

1.2.1 Research Objective

This study examined the impact of cottonwood on soil fertility in Douglas-fir/western hemlock dominated forest, in an attempt to determine if the positive effect of cottonwood on soil fertility might be enough to justify its presence within these commercially valuable stands.

1.2.2 Research Hypothesis

I hypothesized that the presence of cottonwood in conifer-dominated forest would result in enhanced soil fertility. Several sub hypotheses were employed to test this hypothesis.

The total weight and nutrient content of litterfall is greater on sites with a cottonwood component compared to pure conifer sites.

I expected the total weight of litterfall over one year would be greater on sites with cottonwood compared to conifer-dominated sites. It was also anticipated

that the concentration of nutrients (N, P, K, Ca, Mg, S, Mn, B, Zn, Fe, Cu) within cottonwood litter would be greater than that of conifer litter.

The early decay rate of cottonwood litter is faster than that of a mixture of fir/hemlock litter. Both litter types decay faster at cottonwood sites.

Cottonwood litter was expected to decay faster compared to a mixture of fir/hemlock litter. In addition, both litter types (cottonwood litter as well as the mixture of fir/hemlock litter) were expected to have a faster decay rate within cottonwood plots.

Forest floor fertility is enhanced under cottonwood compared to under Douglas-fir or western hemlock.

Thinner LF horizons and a thicker Ah horizon were expected in cottonwood plots relative to conifer plots. In addition, it was expected that the majority of humus forms persisting under cottonwood would be mulls while the majority of humus forms under pure conifer sites would be mors. I expected higher pH, higher concentrations of total N and S, available P, exchangeable K, Ca, and Mg and lower C:N ratios in the forest floor beneath cottonwood compared to conifer plots.

Mineral soil fertility is enhanced under cottonwood compared to under Douglas-fir or western hemlock.

I expected higher pH, higher concentrations of total N and S, available P, exchangeable K, Ca, and Mg and lower C:N ratios in the surface mineral soil found beneath cottonwood relative to that found under conifers.

The rate of N mineralization is enhanced in areas with cottonwood influence compared to areas without cottonwood influence.

I expected that the N mineralization rate as well as the concentration of NO_3^- and NH_4^+ would be higher within the forest floor of cottonwood plots compared to conifer plots.

1.3 Literature Review

1.3.1 Ecology and Distribution of Cottonwood

Cottonwood is regarded as the Pacific coastal race of balsam poplar (*Populus balsamifera* L.) (B. C. Ministry of Forests, 1996). It grows in climates ranging from relatively arid to humid, but achieves its best development in areas of humid climate (Haeussler et al., 1990). It is found in all biogeoclimatic zones except the spruce-willow-birch (SWB) and alpine tundra (AT). This species is highly shade intolerant and is poorly adapted to both drought and waterlogging (B. C. Ministry of Forests, 1991). Cottonwoods grow well in neutral or slightly alkaline soils (Harry and Smith, 1957). Cottonwoods may contribute to the total N input of ecosystems through N-fixing bacteria that exist in the wetwood of this species (Van Der Kamp, 1986). Wetwood is a condition in which increased moisture develops in zones within the heartwood of affected trees. Frost cracks, branch stubs or other wounds on trees are indicators that wetwood may be present.

Cottonwood grows throughout coastal and southern British Columbia (Fig. 1.1), from the coast to the Rocky Mountains (B. C. Ministry of Forests, 1996). It is absent from the western and northwestern coast of Vancouver Island, as well

as the central British Columbia Coast, and the Queen Charlotte Islands, but occurs in areas adjacent to the Alaska panhandle in northwestern British Columbia.

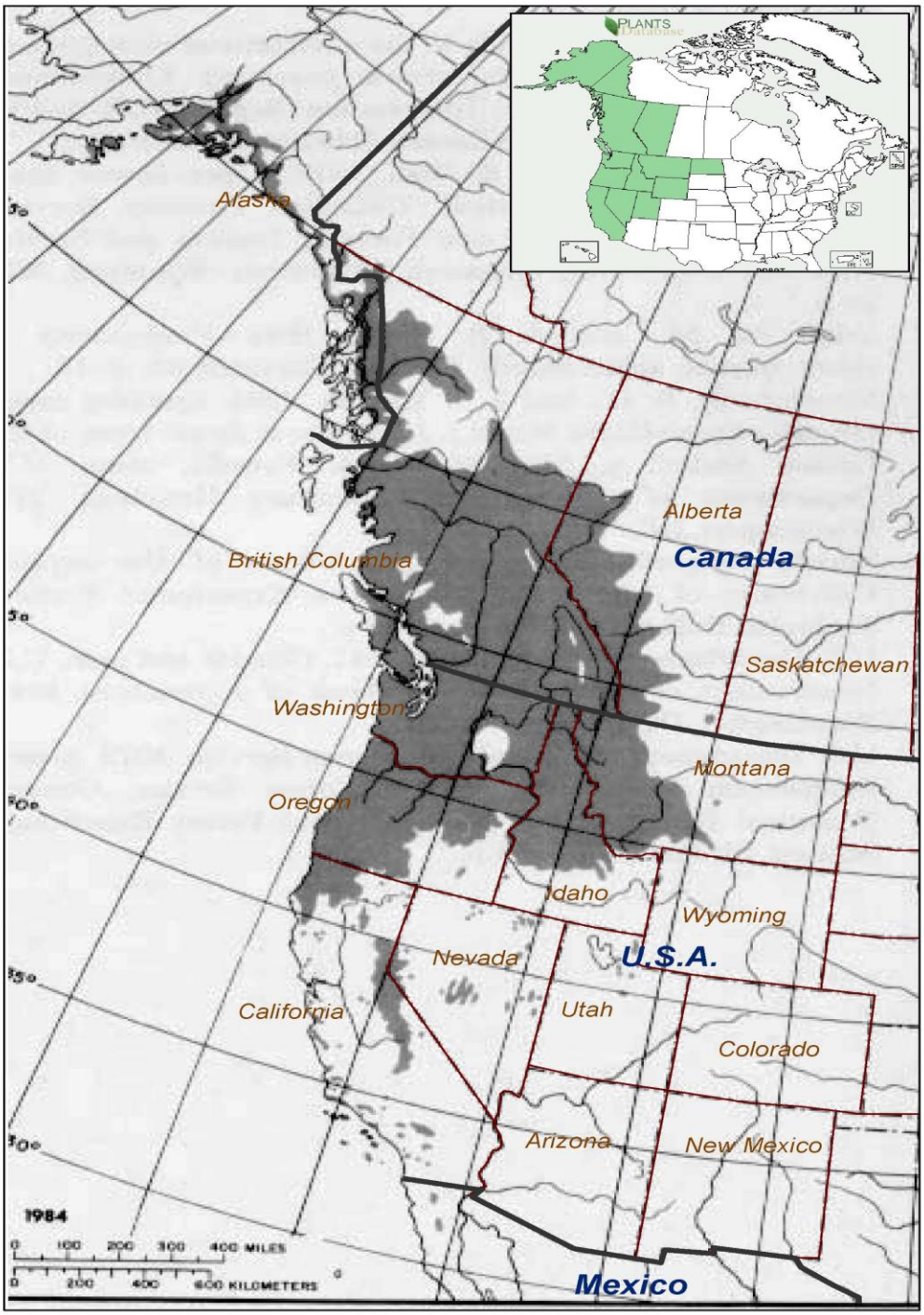


Fig. 1.1. Geographic distribution of cottonwood (modified from USDA Forest Services, 2004 & Little, 1971).

1.3.2 The Impact of Deciduous Trees on Soil Fertility in Coniferous Forests

Soils differ dramatically under different types of vegetation, and under different species of trees in forest ecosystems (Binkley 1995; Soil Classification Working Group, 1998), and many studies have shown that deciduous and coniferous species vary in their effect on forest soils (Ogden and Schmidt, 1997; Perry et al., 1987; Prescott et al., 2000; Fried et al., 1990; Washburn and Arthur, 2003). Tree species have been shown to substantially alter soil properties within decades, allowing for a relatively quick feedback on the fitness of trees (Binkley and Giardina, 1998).

1.3.2.1 Impact of Deciduous Tree Litterfall

The positive effect of deciduous trees on nutrient cycling is usually attributed to their high quality litter allowing for faster litter decomposition and faster nutrient cycling (Scott and Binkley, 1997). A literature review concerning interactions between tree species and soils reported that litterfall mass and N content differed by as much as 50% between tree species, although most studies reported approximately 20% difference between species (Binkley and Giardina, 1998).

A study by Prescott et al. (2000) concluded that litter decay is faster in deciduous and mixedwood stands compared to pure conifer stands, but that mixing of needle litter with broadleaf litter does not hasten decomposition in mixedwood forests of British Columbia. Another study comparing litter input and quality of deciduous, mixed, and coniferous stand types of a boreal mixedwood forest found that foliar litter input was significantly greater in deciduous than

coniferous stands in terms of both mass and N content (Jerabkova et al., 2006). Higher N availability was indicated in deciduous stands, and it was suggested that litter N content might be a better indicator of N availability in the forest floor than litter decomposition rates. Jerabkova et al. (2006) also concluded that, for boreal mixedwood stands, N availability was directly related to the proportion of deciduous trees in a stand, and that maintaining a deciduous component within coniferous stands may facilitate a higher proportion of N in the available form. However, Perry et al. (1987) found that average total soil N as well as mineralizable N was higher in pure conifer stands compared to mixed plots within the western hemlock zone of the Oregon Coast Range. Binkley (1995) stated that the lignin:N ratio of litterfall was the best indicator of the connection between litter production and nutrient supply.

Initial litter N concentrations are often positively correlated with initial decomposition rates (Taylor et al., 1989), and it has been suggested that the rapid decay of broadleaf litter leads to faster nutrient cycling in mixedwood forests (Perry et al., 1987). However, common garden experiments indicate that greater accumulation of undecomposed litter, as is most often the case in coniferous stands, does not necessarily indicate low fertility (Binkley, 1995). In a study of 14 species of trees in British Columbia, including cottonwood, broadleaf litter had a rapid initial but slower later decay rate compared to needle litter (Prescott et al., 2004); furthermore, broadleaf litter did not decay faster than needle litter. The lack of a relationship between first-year mass loss and long-term mass loss prompted the authors to caution against extrapolating long-term

decay rates from short-term measurements. Another study suggested that the abrupt slowing of decomposition in later stages may be an effect of the litterbag as it excludes macrofauna, and therefore may hinder the complete decomposition of litter (Prescott et al., 2000).

Individual deciduous species have been shown to have a positive effect on forest soils through the input of their litter. Ogden and Schmidt (1997) reported vine maple (*Acer circinatum* Pursh) litter to decompose significantly faster than conifer litter and to contain higher concentrations of N, P, Ca, Mg, K, Fe, and Zn. Fried et al. (1990) found that litterfall weight and nutrient content were significantly greater under bigleaf maple (*Acer macrophyllum* Pursh) compared to Douglas-fir on every site, for every macronutrient and for most micronutrients determined. The authors warn that the removal of a species like bigleaf maple from Douglas-fir forests could have negative and unintended ecological consequences. Forest litter can have a maximum decomposition limit, and this limit has a negative linear relationship with initial N concentrations (Berg et al., 1996). A good supply of N may fuel the initial decomposition rate of litter; however, this same N abundance may have the reverse effect at later stages. Berg (1991) found that nutrient rich litters had considerably lower mass-loss rates in later stages of decomposition compared with less nutrient abundant litters. It is therefore possible that deciduous litter may reach a decomposition limit faster than conifer litter. It is also possible that deciduous litter may leave behind a larger proportion of recalcitrant material compared to conifer litter, once it has reached its decomposition limit.

1.3.2.2 The Impact of Deciduous Trees on the Forest Floor

Evidence has emerged to show that tree species can greatly influence the distribution and size of nutrient pools among soil horizons (Binkley, 1995). Results are mixed; however, when considering the impact of deciduous trees versus coniferous trees on the forest floor. In some cases, the effect of tree species on forest floor mass and nutrient content is small (Perala and Alban, 1982), while in other cases the effect of species is much more pronounced (Son and Gower, 1992). In a comparative study of deciduous, coniferous, and mixed stands in a boreal region, Jerabkova et al. (2006) found that deciduous stands had higher N availability in the forest floor compared to coniferous and mixed stands. This study found N availability correlated positively with the presence of deciduous species and negatively with dense conifer stands. The same study reported less organic matter accumulation as well as higher Ca concentrations in the forest floor under deciduous stands. A study comparing forest floor differences under 40 year old pine (*Pinus coulteri* B. Don) and oak (*Quercus dumosa* Nutt.) plantations in southern California, found the forest floor under pine developed a clay-depleted A horizon and lacked earthworms while the oak plantation developed a humus and clay-enriched A horizon, 90% of which was earthworm casts (Graham and Wood, 1991).

Extractable cations were found to be highest under red maple (*Acer rubrum* L.), and lowest under pines (*Pinus echinata* Mill. or *Pinus rigida* Mill.) in an oak-pine dominated forest community of a temperate and humid climate in Eastern Kentucky (Washburn and Arthur, 2003). Fried et al. (1990)

demonstrated higher forest floor turnover rates in terms of biomass and nutrients (for every nutrient at every site) under bigleaf maple compared to Douglas-fir in an investigation at the foothills of the Oregon Coast Range. A study comparing soil characteristics in canopy gaps occupied by vine maple in a western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) forest showed a higher pH and higher concentrations of Ca, Mg, and K in the forest floor, as well as thinner forest floors in the vine maple gaps (Ogden and Schmidt, 1997). Contradictory to the above studies, Perry et al. (1987) found no differences in N mineralization or forest floor weight when comparing mixed and pure conifer stands. Mixed forest stands often have a higher forest floor pH value compared to pure conifer stands, as was demonstrated by Jerabkova et al. (2006). It is thought that the acidic litter of conifers can acidify forest floors, however acidic litter does not always acidify forest floors. In fact, acids accumulated in fresh litter are usually degraded rapidly and contribute little or not at all to the acidity of soils (Binkley, 1995). It is widely accepted that different humus types (mor, moder, or mull) can develop beneath different tree species on the same soil. Mull forest floors are generally assumed to be biologically superior to mor forest floors due to the presence of fresh litter atop a well-mixed Ah horizon (Binkley, 1995). There is evidence that deciduous trees direct humus development towards mulls by the addition of their base-rich litter to soils (van Oijen et al., 2005).

1.3.2.3 The Impact of Deciduous Trees on Mineral Soil

There is a high degree of variation found in mineral soil properties as various factors such as climate, parent material, biota, and topography affect soil formation. Available evidence suggests that species effect on mineral soil can be substantial (Binkley 1995). Tree species can influence the chemical properties of the mineral soil by several mechanisms, including leaching and through changes in the soil's biological community. Alterations to the forest floor are a first indication of species influence on soil properties (Hagen-Thorn et al., 2004). Changes to the mineral soil, which most often follow, show that the alteration process is more extensive. The chemistry of the mineral soil is more stable than that of the forest floor throughout the year, and therefore changes that occur in the mineral soil are a better indication of species' impact on that soil. Changes in mineral soil fertility are usually more pronounced in the upper layers of the mineral soil.

Species impact on mineral soils can be substantial as demonstrated by Binkley and Valentine (1991), who found that mineral soils under green ash (*Fraxnus pennsylvanica* Marsh) and white pine (*Pinus strobus* L.) had approximately double the NH4+, NO3-, extractable K, Ca and Mg than mineral soils under Norway spruce (Picea abies (L.) Karst.). Another study comparing differences in mineral soil between a conifer and mixed forest found that the pure conifer forest averaged 520 kg/ha more N in the top 12 cm of mineral soil than that of the mixed forest (Perry et al., 1987). Ogden and Schmidt (1997) found that mineral soil in vine maple gaps differed from the mineral soil of sites without

a vine maple component in a coastal western hemlock forest. Higher pH values and higher total N concentrations were found in the surface mineral soil of the vine maple gaps. Other studies; however, have found little or no influence of tree species on mineral soil. No variation among forest types in soil N availability was found between deciduous, mixed, and conifer stands in a boreal mixedwood forest, although deciduous stands had higher pH values and higher extractable-P concentrations in the mineral soil (Jerabkova et al., 2006). The bulk density of the mineral soil was significantly lower under bigleaf maple in two of five sites in a study considering the effects of bigleaf maple on mineral soils in a forest dominated by Douglas-fir (Fried et al., 1990). Three sites utilized in that study did not show significant differences for bulk density, and it was the opinion of the authors that tunnelling activity of small rodents likely contributed to variability and to low values of bulk density.

1.3.2.4 The Impact of Deciduous Trees on Nitrogen Mineralization

Nitrogen availability limits growth in more forests and in more regions than any other nutrient (Fisher et al., 2000). In general, only about 1 to 3% of total soil N will be available for tree uptake each year. Nitrogen fixation rates in forests that lack symbiotic N-fixing plants are typically very low, on the order of 1 kg N ha^{-1} yr^{-1} (Binkley, 1995). However, no method of assessing N availability in soils is perfect, as all involve a degree of disturbance or artificially created conditions. Also, the process of N mineralization is a complicated one, as microbes both release and reimmobilize N simultaneously (Fisher et al., 2000). Therefore common methods used to measure N mineralization, such as the buried bag or

resin-core methods, will only be effective in measuring the net total mineralization rate, and do not account for differences among soils in the amount of N that is mineralized but becomes remobilized (gross mineralization) during the period of incubation (Binkley, 1995).

Binkley (1995) is of the opinion that tree species have a very large effect on N mineralization rates, but that common garden experiments do not suggest that N availability is highest under the influence of deciduous species. In fact, there is mixed evidence regarding the somewhat common theory that higher rates of net N mineralization exist under deciduous compared to coniferous species. Washburn and Arthur (2003) found N mineralization rates were lowest under red maple and highest under chestnut oak (*Quercus prinus* L.), with rates for shortleaf pine (*Pinus echinata* Mill.) and pitch pine (*Pinus rigida* Mill.) falling between these deciduous tree species. Net N mineralization rates were also highest within a mixed stand when a deciduous, a coniferous, and a mixed site were compared (Jerabkova et al., 2006). Some authors point to very large differences in net N mineralization between species. Net mineralization was found to differ by at least 60% among tree species in a review of past studies by Binkley and Giardina (1998).

1.3.2.5 The Impact of Cottonwood on Soil Fertility in Coniferous Forests

Information regarding the impact of cottonwood on soils is extremely limited, especially in relation to conifer forests. No studies were found that address the impact of cottonwood on soil fertility, and very few studies address the impact of cottonwood on conifer growth. Weih (2004) states that poplars

have the ability to enrich conifer forests of boreal regions, and a publication by Forestry Canada and the B.C. Ministry of Forests (1991) indicates that a potential role of cottonwood is to help replenish nutrient depleted soils.

Some work has been undertaken to assess the effectiveness of cottonwood as a nurse trees species for conifers. MacLennan and Klinka (1990) found that the shading effect of rapidly growing cottonwood saplings suppressed the vigour of shade intolerant shrubs, thus providing better growth conditions for shade tolerant western red cedars. This study found that the height of western red cedar was greatest for saplings located between 1.5 and 2 m from the nearest cottonwood. They concluded that using cottonwood as a nurse tree was an acceptable management strategy as it required a relatively low level of effort and was ecologically preferable when compared to chemical or mechanical brush control methods.

The Cottonwood and Balsam Poplar Managers' Handbook for British Columbia (Peterson et al., 1996) states that further work is required if we are to improve our understanding of the nature and outcome of interactions between deciduous species such as cottonwood and conifers, within mixed stands. This study will help fill part of that knowledge gap as well as a more general information gap concerned with the impact of deciduous species on soil fertility.

CHAPTER 2: Methods

2.1 Study Area

This study was undertaken at the University of British Columbia's Malcolm Knapp Research Forest (MKRF). The forest is located in Haney, east of Vancouver, British Columbia (49°16'40"N, 122°34'20"W) (Fig. 2.1). Mean annual precipitation for sites included in this study is approximately 2200 mm per year (MKRF, 2008). Snow persists for about 4 months on one of the six sites used in this study, but does not generally occur on the other five sites. Mean monthly temperatures range from 1.4 to 16.8°C (Klinka and Krajina, 1986). The research forest is located within the Coastal Western Hemlock (CWH) biogeoclimatic zone (MKRF, 2008). Five of the research sites are located within the dry maritime (dm) subzone of the CWH, while one site is within the very wet subzone of the CWH. Stands used in our study are approximately 80 years old and all have regenerated naturally after a forest fire in 1931. Stands are dominated by Douglas-fir, western hemlock, and western redcedar. Deciduous trees, including bigleaf maple, cottonwood, red alder, and vine maple, also occur within the forest. Species composition varies greatly between stands.

A previous study by Tashe (1998) used two 1 m deep soil pits to determine that the soil in this area is a Gleyed Dystric Brunisol formed on morainal deposits.

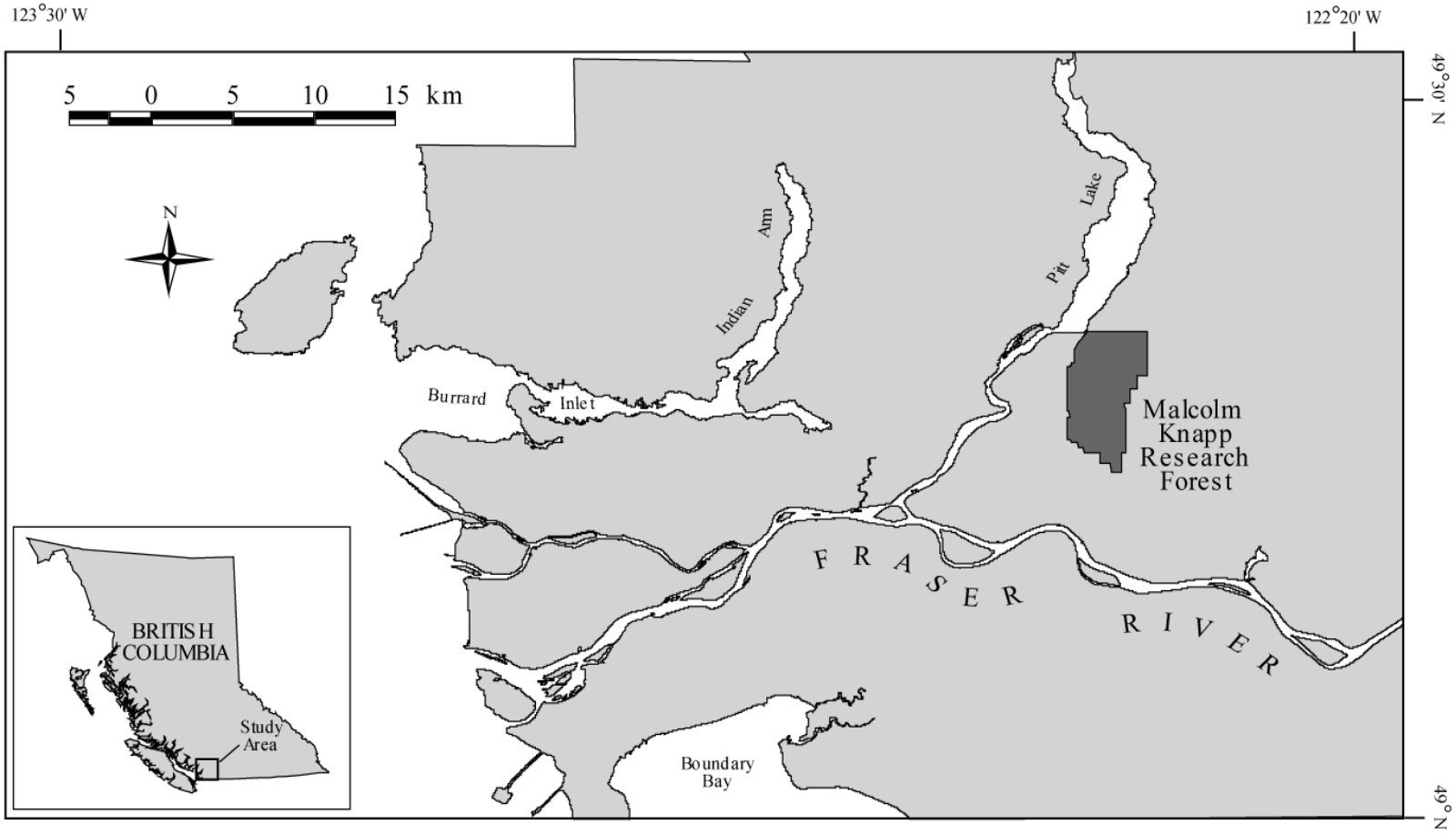


Fig. 2.1. Location of Malcolm Knapp Research Forest in southwest British Columbia.

2.2 Experimental Design

2.2.1 Plot Selection

This project employed six pairs of plots (ie. total of 12 individual plots) within conifer dominated stands of the MKRF. Each pair contained one plot with a dominant cottonwood bole at its centre and one plot centred on a dominant Douglas-fir or western hemlock tree. Plots centred on a conifer tree were free from the influence of deciduous species. Five of the pure conifer plots were centred on Douglas-fir trees, and one conifer plot was centred on a western hemlock tree. Each plot was 5 m in radius.

Comparisons were made between the two plots within each pair in order to determine the degree of cottonwood impact on soil fertility. Appropriate plots were located using forest cover maps, local knowledge of the MKRF personnel, and visual inspection.

Plots were located at least 15 m away from disturbances such as a trails or roads, and were otherwise undisturbed as far as could be determined by visual inspection Selected cottonwood trees were at least 15 m away from the boles of other deciduous trees. Conifer plots were located a minimum of 30 m and a maximum of 60 m away from their cottonwood counterpart. This placement allowed pairs to be close enough to ensure site characteristics remained similar but far away enough to remove as much effect of cottonwood on the conifer plots as possible.

We chose cottonwood plots first, because suitable cottonwood trees occur less frequently than conifers in the MKRF. Each cottonwood plot was paired with

a conifer plot displaying similar site characteristics including slope, aspect, and elevation, age of stand, moisture regime, and soil textural class. Potential pairs were eliminated if the moisture regime differed by more than one numerical unit or if the soil textural classes between pairs were not adjacent to each other on the textural triangle. The use of paired plots with similar site characteristics allowed for a comparison between plots with and without a cottonwood component.

2.2.2 Litterfall

2.2.2.1 Sample Collection

Litterfall was collected in all cottonwood and conifer plots using plastic greenhouse trays 0.125 m^2 in size. Trays were lined with nylon mesh containing 1 mm^2 sized pores. Trays were equipped with drainage holes at the bottom. Five trays were randomly placed at each plot for a total of 60 trays. Litterfall collection began on August 27, 2007 and ended on August 29, 2008. Litterfall was collected weekly throughout the autumn (14 collection periods) and monthly throughout winter, summer and spring, for a total of 22 collection periods. Weekly collections during the fall season minimized leaching of nutrients during a time of year when all litter is lost from deciduous trees. Litterfall collection followed the methods described by Tashe (1998). Upon collection, the mesh lining from the 5 trays within each plot was rolled up and placed inside the same plastic bag.

2.2.2.2 Lab Analysis

Within 24 hours of collection, litter was spread out in the laboratory and left to air-dry for a minimum of 24 hours. The litter was then gently removed from the mesh and oven-dried at 70°C for 24 hours. The litter from all 5 trays belonging to one plot was composited within a single sample for oven drying. The weight of the litter after oven drying was determined and recorded. Samples were then sorted into the following four categories: cottonwood leaves, Douglas-fir/western hemlock needles, western redcedar leaves, and "other" debris (small twigs, cone scales, and any other litter). Collected branches that were larger than 2 mm in diameter were removed from the sample (Maguire, 1994). The oven dry weight for each of the four categories in each plot was recorded. An estimation of seasonal and monthly litter input relative to each plot type was determined (Tashe, 1998).

Samples from each litter type and from each season were analysed for nutrient concentrations. For this purpose, samples were combined by species on a seasonal basis. Composite litterfall samples from cottonwood, Douglas-fir/western hemlock, western red cedar, and other categories were ground in a coffee grinder separately after oven drying. A subsample weighing approximately 2 g from each litter type and from each season was sent to the B.C. Ministry of Forests and Range Analytical Laboratory for lignin and elemental analysis.

Litterfall samples were analysed for P, K, Ca, Mg, S, Mn, B, Zn, Fe, Cu, and Al by inductively coupled plasma-atomic emission spectrometer (ICP)

following the closed vessel microwave digestion method (Kalra and Maynard, 1991). For analysis of total C and N, tissue samples were ground with a Wiley mill and run through a Fisons NA-1500 Elemental Analyser. Lignin analysis followed the acid detergent method by Goering and Van Soest (1970) as modified by Ryan et al. (1990).

2.2.3 Litter Decomposition

2.2.3.1 Sample Collection

Litter was collected from all 12 plots in traps identical to those used for litterfall collection. Ten traps were placed in conifer plots and 5 traps were placed under cottonwood plots. Litter from all traps was collected weekly until the desired amount was obtained. Upon collection, litter was placed inside plastic bags and brought back to the lab. Litter was then spread out and left to air dry for a minimum of 48 hours, and separated into the following three categories: cottonwood leaves, fir/hemlock needles, and other. The other category was discarded.

Decomposition bags were made of 2-ply nylon mesh with 1 mm^2 holes. All bags were filled with the equivalent of 2 g dry weight of litter. The open end of mesh bags was closed by stapling across 3 times. Cottonwood litter was placed in 12 cm by 15 cm mesh bags while conifer needles (fir/hemlock) were placed in 6 cm by 12 cm mesh bags. Larger bags were used for the deciduous litter in order to account for the larger size of the leaves. The equivalent of 2 g dry weight of cottonwood leaves was found by the following method. Ten air-dried

samples were weighed; these samples were then oven dried at 70°C for 24 hours. The air-dried weights and the oven-dried weights were averaged in order to compute the equivalent of 2 g dry weight for cottonwood leaves. All conifer litter was oven dried before 2 g of needles were placed in the nylon decomposition bags. Decomposition bags were labelled and placed in individual envelopes for transport to the field. Any spillage into the envelopes was weighed and subtracted from the original weight of the decomposition bag.

On December 5 and 6 of 2007, nine bags of each litter type were randomly pinned to the forest floor in each of the 12 plots. In total, 18 decomposition bags were pinned to the forest floor of each plot. This allowed for three bags to be collected in each of three collection periods to have taken place at 6, 12, and 18 months after initial placement of bags on the forest floor. Due to time limitations only the 6 month collection period was included in this thesis. This collection occurred on June 13, 2008. Litterbags were handled very carefully during the collection process in order to avoid losing material. Any material found growing through the bags was gently cut away. Litterbags were then placed in labelled envelopes and brought back to the lab.

2.2.3.2 Lab Analysis

All mesh bags were carefully removed from individual paper envelopes. Any litter found to have fallen out of the mesh bags into the envelopes was recovered. All material was then removed from the mesh bags and washed over a sieve under a gentle stream of water. This was done in order to remove any accumulated debris such as roots or other plant material that had grown through

the mesh bags over the time of incubation. Litter from individual mesh bags was then placed in separate metal pie plates and left to air dry for 48 hours. All litter was then oven dried at 70°C for 24 hours. Each sample was weighed and the mass loss calculated.

2.2.4 Forest Floor

2.2.4.1 Humus Form Collection and Classification

Forest floor sampling took place during the months of July and August 2007. The forest floor is highly variable, and a single sample is therefore not sufficient to characterize the humus form of an entire plot (Green et al., 1993). Three forest floor samples were collected per plot using randomly selected bearings and distances, between 1.5 and 5 m, from the centre of each plot. The same sets of bearings and distances were used for all plots. Sampling at woody, rocky, or disturbed locations was avoided. If random sampling led to an unsuitable location, sampling was carried out at 0.5 m in each of north, south, east and west (in that order) until a suitable location was encountered.

Samples collected were approximately 20 x 20 cm and extended to the depth of the organic-mineral soil interface. Humus form samples were removed with the utmost care in order to avoid disturbance to both the sample and the excavation site. Removal of each sample was accomplished by vertically slicing through the soil with a shovel in a square pattern. Forest floor was then pulled away from one side of the sliced square in order to reveal the organic mineral soil interface. The shovel was then used to make a horizontal slice. Each intact sample was carefully removed from the ground and placed in an aluminium pan.

Roots were carefully cut away as needed during the removal process with the use of garden clippers. A second aluminum pan was placed on top of each sample and the package was then sealed inside a plastic bag. All samples were kept refrigerated until they could be described in the laboratory.

Depths of horizons affecting humus form classifications (e.g., L, F, H, Ah, and Ae) were recorded in the field in order to reduce errors of depth estimation due to disturbance of soil. Mean horizon depths were determined by measuring the depth of each horizon on each of three undisturbed sides of the excavation site, and averaging per horizon.

Where differentiation between organic and mineral soil was uncertain a sub-sample was removed and analysed for organic matter content using the loss-on-ignition (LOI) method (Kalra and Maynard, 1991). Samples were considered organic soil if they contained 30% or more organic matter by weight. Humus form was classified to the group level according to Green et al. (1993). Horizon designations for litter (L), fibric (F), humic (H), and organic-enriched mineral (Ah) horizons were determined by use of various properties including texture, composition, and organic matter content.

2.2.4.2 Forest Floor Sampling and Lab Analysis

Three additional sites within each plot were located by use of random bearings and distances. One sample from each of the three new locations was removed by use of a bulk density corer with a volume of 490.3 cm^3. The thickness of the sample was determined in the field. The sample was then placed in a labelled plastic bag. The bulk density cylinder was wiped clean

between plots in order to avoid contamination of soil samples. Where there was uncertainty about the location of the organic mineral soil interface, the LOI method was used as described above.

The moist weight of all extracted forest floor samples was determined. Samples were then oven-dried at 70°C for 24 hours, and weighed a second time (Kalra and Maynard 1991). The dry weight was used to calculate weight per unit area and bulk density of each sample. Gravimetric and volumetric water content were also determined for each sample.

A subsample of equal weight was removed from each oven dried sample. Each of these equally weighed subsamples were ground in a coffee grinder, combined on a per plot basis, and mixed thoroughly (Tashe, 1998). Composite samples from each plot were sent to the B.C. Ministry of Forests and Range Laboratory for determination of the following properties: pH, total N, C, and S, mineralizable N, exchangeable cations, available P, cation exchange capacity (CEC), NH_4^+ and NO_3^-. The pH was measured with a combination electrode and data acquisition system in a 1:1 forest floor to water solution (Kalra and Maynard, 1991). Total C, N, and S were measured on a Fisons NA-1500 Elemental Analyser. Concentrations of C and N were used to calculate the C:N ratio of the forest floor. Mineralizable N was measured using an anaerobic incubation method, where soil samples were incubated under anaerobic, water-logged conditions for 2 weeks at 30^{o}C, and N was determined colorimetrically by a Technicon Auto-analyzer II (Waring and Bremner, 1964a & 1964b; Bremner, 1996). Exchangeable cations were measured using an ARL 3560 inductively

coupled argon plasma (ICAP) spectrometer. The sum of cations included in this method was used to determine effective CEC (Carter, 1993). Available phosphate was extracted using the Bray P1 method (Kalra and Maynard, 1991, John 1970). NH_4^+ and NO_3^- were measured colorimetrically using an Alpkem Flow System IV analyzer (Carter, 1993).

2.2.5 Mineral Soil

Mineral soil sampling took place during the months of July and August, 2007. Three randomly selected mineral soil samples were collected per plot using a bulk density corer with a volume of 490.3 cm^3. Mineral soil was recognized by its lighter colour in comparison to the forest floor, and by the presence of coarse textured mineral particles. Bulk density cores were taken directly beneath forest floor sample locations. The bulk density corer was wiped clean between plots in order to avoid contamination of soil samples.

Moist weight of all soil core samples was determined. Soil core samples were then oven dried at 105°C for 48 h, and weighed again to determine the mass (Kalra and Maynard, 1991). Bulk density was calculated by dividing the mass by the volume of the cylinder. Coarse fragment content was determined by passing the samples through a 2 mm sieve, and weighing the portion of the sample greater than 2 mm. Percent coarse fragment content was calculated by taking the mass of the coarse fragment, dividing by the mass of the sample, and multiplying the result by 100. Gravimetric water content was determined by taking the water content of each sample and dividing it by the mass of the

sample. Volumetric water content was calculated by multiplying the gravimetric water content of each sample with the bulk density of the sample.

Equal portions of the remainder of the samples were thoroughly mixed on a per-plot basis and sent to the B. C. Ministry of Forests and Range Laboratory. Analysis was completed using the same methodology employed for forest floor samples and included tests for: pH, total N, C and S, mineralizable N, exchangeable cations, available P, CEC, NH_4^+ and NO_3^-.

2.2.6 Nitrogen Mineralization

2.2.6.1 Sampling

The buried bag technique (Prescott et al., 2003; Prescott, 1992) was used to quantify differences in N mineralization rates between cottonwood and conifer plots. A central point was located within 2 m of the central tree bole in each plot by use of random bearings and distances. Six samples were taken within 30 cm of this central point. Of the 6 samples, 3 were reburied in polyethylene bags, while the other 3 were removed for chemical analysis. Samples were removed in their intact form by inserting a metal cylinder into the ground, excavating the soil on one side of the cylinder and rotating the cylinder until it could be lifted gently. Excavation was carefully performed on the outer edge of the cylinder only in order to avoid disturbing the other sites around the central point. The cylinder used was 25 cm in height and 4 cm in radius. A glass plug was used to remove the sample from the cylinder. The glass plug was inserted into the top of the metal cylinder and used to push the sample out until the organic mineral soil interface could be seen. The mineral soil was carefully removed from the bottom

of the sample and the intact forest floor core was then placed in a polyethylene bag. Each polyethylene bag was sealed with a twist tie. For samples remaining on site, the bag above the twist tie was cut off before the bagged samples were carefully reburied in their parent locations. Forest floor was placed on the reburied bags in order to avoid penetration of solar radiation.

Bags were left to incubate for 40 days, from July 18 to August 27, 2007. The three samples removed from each plot were composited and delivered, within 48 hours, to Pacific Soils Analysis Laboratory in Richmond, B.C. for chemical analysis. All samples removed from the study site were kept cool at approximately 4°C in a cooler or refrigerator until delivered to the lab for analysis.

2.2.6.2 Lab Analysis

All forest floor samples were analysed for NH_4^+ and NO_3^-concentrations before and after incubation. Available NH_4^+ and NO_3^- was determined using a K_2SO_4 extract. NH_4^+ was determined colorimetrically on a Technicon Autoanalyser, and NO_3^- was determined by the CTA colour development method, and measured on a Turner colorimeter (Carter, 1993).

2.2.7 Statistical Analysis

Differences in properties between plot types (with and without cottonwood) in relation to litterfall, litter decomposition, forest floor, mineral soil, and N mineralization were quantified statistically by use of SPSS 16.0 statistical software. Each sample unit represents a mean of subsamples from each plot. All data sets were analysed for normality by use of the One-Sample Kolmogorov-

Smirnov Test. Data not appearing normal were log transformed in order to achieve normality. Data were then analysed for statistically significant differences using paired t-tests. A significance level of 0.1 was used for all analysis, however if differences were relevant at the 0.05 significance level, this was indicated. A 0.1 significance level was used due to considerable natural heterogeneity within measured properties.

Autumn litterfall data were analysed using a one-way analysis of variance (ANOVA). These tests determined if statistical differences existed in the weight or nutrient content among: cottonwood, cedar, fir/hemlock, and other litter categories within each plot type. When statistical significance was found between litter types, data sets were further analysed with the Tukey/Tamhane multiple comparison test (version16.0, SPSS Inc., Chicago, IL).

The probability of committing a Type II (ß) error was calculated when paired t-tests yielded non-statistically significant results. Power was determined by using a computer program created by Borenstein and Cohen (1988). The program determined the value of ß, and power was then determined by subtracting ß from 1. A Type II error results in a failure to reject the null hypothesis when the alternative hypothesis is true (Kleinbaum et al., 1998). A small power outcome for a t-test showing non-significant results indicates that the null hypothesis may not have been rejected had the sample size been greater.

CHAPTER 3: RESULTS

3.1 Litterfall

3.1.1 Seasonal and Annual Litterfall Weights

Seasonal litterfall weights were similar between cottonwood and conifer plots (Table 3.1; Fig. 1, App.). More than half of the annual litter fell in the autumn for both plot types, with 61% and 59% of litter falling in cottonwood and conifer plots, respectively (Fig. 2, App.), during that season. Within cottonwood plots, the next largest proportion of litterfall was in the winter (16%). Spring and summer contributed 11% and 12% of total annual litterfall, respectively in cottonwood plots. Within conifer plots, 17% of total litterfall occurred in the summer, 14% was in the winter, and 11% was in the spring.

Table 3.1. Seasonal litterfall (kg ha^{-1}) in cottonwood and conifer plots (n = 6).

Season	Cottonwood Plots	Conifer Plots	P	Power
Autumn	3071 (1282)	2666 (921)	0.15	0.15
Winter	780 (410)	635 (237)	0.47	0.17
Spring	548 (296)	527 (384)	0.80	0.06
Summer	623 (223)	786 (204)	0.22	0.34
Annual total	5025 (1212)	4614 (840)	0.22	0.16

Values in parentheses represent standard deviations.

Significantly more cottonwood litter fell in cottonwood plots compared with conifer plots, and significantly more fir/hemlock litter fell in conifer plots compared to cottonwood plots (Table 3.2; Fig. 3, App.) during the autumn. Within cottonwood plots, the amount of cottonwood litter was not significantly different from the amount of any other litter type (Table 3.2) but there was significantly more conifer litter (fir/hemlock+cedar) than cottonwood litter (P = 0.096). Within conifer plots, the amount of cottonwood litter was significantly lower (P = 0.001) than the amount of conifer litter (fir/hemlock+cedar) and the amount of all other litter types (P = 0.049).

Table 3.2 Autumn litterfall (kg ha^{-1}) in cottonwood and conifer plots (n = 6).

Litter Type	Cottonwood plots		Conifer plots		P	Power
Cottonwood	767a	(748)	147a	(199)	0.07	
Conifer (fir/hemlock+cedar)	1606	(651)	1727	(576)	0.19	0.09
Fir/hemlock litterfall	506a	(277)	748b	(327)	0.09	
Western red cedar	1100a	(758)	979ab	(872)	0.40	0.08
'Other' litterfall	589a	(213)	809b	(319)	0.10	0.37
Total autumn litterfall	2963	(1077)	2684	(829)	0.27	0.12

Values in parentheses represent standard deviations.
Underlined values indicate significant differences at P < 0.1 between plots.
Different letters in the same column indicate significant differences between litterfall types (excluding total conifer litter) within site types at P < 0.05 using a Dunnett multiple comparison test.

3.1.2 Elemental Analysis

All elemental concentrations in litterfall were significantly different among the three litter types (cottonwood, fir/hemlock and cedar) with the exception of Fe and Al (Table 3.3). Cottonwood litter had higher concentrations of N, P, K, Ca, Mg, S, B, Zn, Cu, and lower concentrations of C and Mn than fir/hemlock litter. Cottonwood litter had higher Zn content than mixed conifer litter. Cottonwood plots had higher contents of K, Mg, S, B, and Cu in autumn litterfall (composite of all litter types) than conifer plots (Table 3.4). The only significant differences found for elemental concentrations of fir/hemlock litter, cedar litter, and 'other' litter compared between plot types was lower S within cedar litter, and higher Cu within 'other' litter in cottonwood plots (Table 3.5, Table 3.6 and Table 3.7). No differences were found in lignin concentration or lignin: N ratio between cottonwood and fir/hemlock litter (Table 3.8).

.

Table 3.3. Concentrations and contents of elements in autumn litter from cottonwood plots (n = 6).

Element	Cottonwood litter		Fir/hemlock litter		Red cedar Litter		Anova P
			Mean Concentration (µg g^{-1})				
C	507530a	(3746)	542373b	(6351)	543258b	(10963)	0.00
N	14563a	(2093)	9772b	(1076)	5693c	(768)	0.00
P	643a	(61)	492b	(80)	362c	(85)	0.00
K	4885a	(1384)	1532b	(552)	1115b	(243)	0.00
Ca	19215a	(1732)	9995b	(1832)	16523a	(2545)	0.00
Mg	1993a	(351)	785b	(85)	603b	(124)	0.00
S	1385a	(229)	837b	(66)	543c	(38)	0.00
Mn	122a	(57)	300b	(207)	109a	(34)	0.01*
B	38a	(6)	15b	(4)	12b	(2)	0.00
Zn	339a	(112)	42b	(16)	19c	(7)	0.00
Fe	141	(25)	169	(68)	119	(21)	0.17
Cu	10a	(1)	8a	(3)	4b	(1)	0.00
Al	125	(22)	125	(22)	264	(349)	0.41
			Mean Content (kg ha^{-1})				
C	389	(380)	274	(150)	603	(416)	0.26
N	10.2	(8.9)	5.1	(3.0)	6.3	(4.2)	0.32
P	0.50	(0.52)	0.25	(0.16)	0.42	(0.29)	0.48
K	3.53	(3.08)	0.78	(0.52)	1.14	(0.81)	0.17*
Ca	14.92	(15.22)	5.06	(2.54)	19.63	(14.47)	0.14
Mg	1.44	(1.22)	0.40	(0.21)	0.71	(0.50)	0.35*
S	0.94	(0.76)	0.43	(0.23)	0.60	(0.42)	0.25
Mn	0.08	(0.07)	0.15	(0.11)	0.13	(0.11)	0.45
B	0.03	(0.02)	0.01	(0.003)	0.01	(0.008)	0.24*
Zn	0.30a	(0.36)	0.02b	(0.01)	0.02b	(0.01)	0.01*
Fe	0.10	(0.08)	0.08	(0.04)	0.14	(0.11)	0.44
Cu	0.007	(0.007)	0.003	(0.002)	0.004	(0.003)	0.27
Al	0.088	(0.074)	0.125	(0.050)	0.250	(0.272)	0.24

*Data were log transformed to meet underlying statistical assumptions.
Single and double underlined values indicate significant differences at P < 0.1 and P < 0.05.
Values in parentheses represent standard deviations.
Different letters in the same rows indicate significant differences at P<0.05.

Table 3.4. Element contents (kg ha^{-1}) of autumn litter in cottonwood and conifer plots (n = 6).

Element	Cottonwood plots		Conifer plots		P	Power
C	1578	(569)	1437	(432)	0.28	0.12
N	28.02	(9.97)	23.34	(6.47)	0.10	0.23
P	1.57	(0.70)	1.30	(0.54)	0.25	0.17
K	6.74	(3.93)	4.77	(2.83)	<u>0.08</u>	
Ca	44.14	(22.54)	33.59	(14.77)	0.13	0.23
Mg	3.12	(1.59)	2.29	(1.04)	<u>0.07</u>	
S	2.49	(0.91)	2.02	(0.49)	0.11	0.27
Mn	0.45	(0.21)	0.56	(0.13)	0.24	0.27
B	0.05	(0.03)	0.04	(0.01)	<u>0.04</u>	
Zn	0.38	(0.37)	0.14	(0.06)	0.13	0.43
Fe	0.70	(0.31)	0.97	(0.84)	0.30	0.17
Cu	0.022	(0.007)	0.018	(0.005)	<u>0.03</u>	
Al	0.79	(0.35)	1.15	(1.02)	0.31	0.19

Values in parentheses represent standard deviations.
Single and double underlined values indicate significant differences at $P < 0.1$ and $P < 0.05$.

Table 3.5. Element concentrations and contents of autumn Douglas-fir/western hemlock needle litter in cottonwood and conifer plots (n = 6).

Element	Cottonwood plots		Conifer plots		P	Power
			Concentration (µg g^{-1})			
C	542373	(6350)	543391	(4594)	0.76	0.09
N	9771	(1076)	10370	(1067)	0.16	0.23
P	491	(80)	488	(127)	0.94	0.06
K	1531	(552)	1701	(622)	0.61	0.12
Ca	9995	(1831)	10711	(1389)	0.34	0.18
Mg	785	(85)	838	(140)	0.44	0.18
S	836	(65)	856	(77)	0.63	0.12
Mn	299	(207)	346	(147)	0.59	0.11
B	15.20	(4.36)	14.84	(4.19)	0.74	0.07
Zn	41	(16)	36	(4)	0.33	0.18
Fe	168	(67)	166	(38)	0.96	0.06
Cu	7.52	(3.23)	7.23	(2.59)	0.86	0.07
Al	278	(108)	319	(87)	0.30	0.16
			Content (kg ha^{-1})			
C	274	(149)	406	(178)	<u>0.09</u>	
N	5.07	(3.04)	7.78	(3.49)	<u>0.08</u>	
P	0.25	(0.16)	0.36	(0.21)	<u>0.09</u>	
K	0.78	(0.52)	1.24	(0.76)	0.15	0.31
Ca	5.06	(2.54)	7.87	(3.26)	<u>0.06</u>	
Mg	0.40	(0.21)	0.62	(0.30)	0.09	0.39
S	0.43	(0.23)	0.64	(0.29)	<u>0.06</u>	
Mn	0.15	(0.11)	0.26	(0.15)	<u>0.04</u>	
B	0.007	(0.003)	0.010	(0.003)	<u>0.08</u>	
Zn	0.02	(0.01)	0.03	(0.01)	<u>0.08</u>	
Fe	0.08	(0.04)	0.12	(0.05)	0.12	0.41
Cu	0.003	(0.002)	0.005	(0.003)	0.22	0.35
Al	0.13	(0.05)	0.23	(0.10)	<u>0.04</u>	

Values in parentheses represent standard deviations.
Single and double underlined values indicate significant differences at $P < 0.1$ and $P < 0.05$.

Table 3.6. Element concentrations and contents of autumn cedar litter in cottonwood and conifer plots (n = 6).

Element	Cottonwood plots		Conifer plots		P	Power
			Concentration (µg g^{-1})			
C	543258	(10963)	542695	(14387)	0.77	0.06
N	5693	(767)	6015	(1011)	0.59	0.14
P	361	(84)	413	(105)	0.36	0.22
K	1115	(243)	1260	(541)	0.37	0.14
Ca	16523	(2544)	16813	(1902)	0.68	0.08
Mg	603	(124)	630	(102)	0.49	0.10
S	543	(38)	591	(60)	<u>0.08</u>	
Mn	108	(34)	103	(31)	0.50	0.08
B	11.87	(1.82)	12.82	(3.38)	0.37	0.14
Zn	18.68	(6.84)	17.82	(4.89)	0.56	0.46
Fe	119	(21)	128	(27)	0.18	0.02
Cu	3.74	(1.19)	3.24	(0.55)	0.25	0.22
Al	263	(349)	146	(30)	0.46	0.19
			Content (kg ha^{-1})			
C	602	(416)	537	(478)	0.40	0.08
N	6.34	(4.16)	5.45	(4.94)	0.35	0.09
P	0.42	(0.29)	0.38	(0.37)	0.58	0.07
K	1.14	(0.81)	1.20	(1.31)	0.81	0.06
Ca	19.63	(14.47)	17.28	(15.40)	0.41	0.08
Mg	0.71	(0.50)	0.63	(0.58)	0.45	0.07
S	0.60	(0.42)	0.56	(0.51)	0.73	0.06
Mn	0.13	(0.11)	0.11	(0.13)	0.53	0.07
B	0.01	(0.01)	0.01	(0.01)	0.35	0.07
Zn	0.02	(0.01)	0.02	(0.01)	0.23	0.14
Fe	0.14	(0.11)	0.14	(0.13)	0.81	0.06
Cu	0.004	(0.003)	0.003	(0.003)	0.29	0.13
Al	0.25	(0.27)	0.15	(0.14)	0.48	0.18

Values in parentheses represent standard deviations.
Single underlined values indicate significant differences at P < 0.1.

Table 3.7. Element concentrations and contents of autumn 'other' litter in cottonwood and conifer plots (n = 6).

Element	Cottonwood plots		Conifer plots		P	Power
			Concentration (µg g^{-1})			
C	529505	(6792)	519580	(12605)	0.14	0.48
N	11040	(2765)	9845	(3544)	0.30	0.15
P	668	(158)	555	(171)	0.19	0.3
K	2215	(807)	2003	(966)	0.43	0.1
Ca	7893	(2341)	7085	(2699)	0.47	0.13
Mg	946	(238)	923	(395)	0.89	0.06
S	893	(167)	793	(271)	0.32	0.18
Mn	155	(62)	221	(118)	0.29	0.3
B	16	(3)	13	(4)	0.25	0.31
Zn	87	(43)	66	(25)	0.13	0.24
Fe	618	(263)	735	(507)	0.48	0.12
Cu	12.49	(2.52)	9.59	(2.54)	<u>0.02</u>	
Al	522	(157)	753	(618)	0.32	0.21
			Content (kg ha^{-1})			
C	311	(112)	417	(154)	0.11	0.35
N	6.37	(2.83)	8.06	(4.47)	0.31	0.18
P	0.40	(0.21)	0.46	(0.25)	0.48	0.11
K	1.29	(0.68)	1.61	(1.05)	0.41	0.14
Ca	4.54	(2.03)	5.78	(3.16)	0.35	0.19
Mg	0.57	(0.31)	0.76	(0.46)	0.31	0.19
S	0.52	(0.22)	0.63	(0.28)	0.37	0.17
Mn	0.09	(0.04)	0.16	(0.08)	0.13	0.56
B	0.0096	(0.0045)	0.0106	(0.0041)	0.64	0.07
Zn	0.046	(0.014)	0.052	(0.023)	0.55	0.05
Fe	0.38	(0.24)	0.69	(0.77)	0.25	0.22
Cu	0.007	(0.003)	0.008	(0.004)	0.71	0.12
Al	0.32	(0.19)	0.75	(0.95)	0.25	0.26

Values in parentheses represent standard deviations.
Double underlined values indicate significant differences at $P < 0.05$.

Table 3.8. Properties of cottonwood and Douglas-fir/hemlock litter (n = 4).

Property	Cottonwood litter		Douglas-fir/hemlock litter		P	Power
	Concentrations (µg g^{-1})					
Fibre (total)	664912	(102715)	574955	(47523)	0.13	0.41
Cellulose	320432	(17317)	307089	(21107)	0.43	0.22
Lignin	338274	(91506)	260898	(50242)	0.11	0.37
Lignin:N	24	(6.30)	25	(4.73)	0.87	0.07

Values in parentheses represent standard deviations.

3.2 Litter Decomposition

The mass loss after 6 months in-field incubation did not differ between cottonwood and fir/hemlock litter at either cottonwood or conifer sites (Table 3.9). The decomposition of cottonwood litter or fir/hemlock litter did not differ between site types.

Table 3.9. Percentage of original litter remaining after 6 month decomposition period (n = 6).

	Cottonwood plots		Conifer plots		P	Power
Cottonwood litter	78.9	(3.9)	78.3	(2.7)	0.53	0.09
Fir/hemlock litter	79.0	(1.9)	78.4	(5.0)	0.84	0.08
	Cottonwood litter		Fir/hemlock litter			
Cottonwood site	78.9	(3.9)	79.0	(1.9)	0.95	0.06
Conifer site	78.3	(2.7)	78.4	(5.0)	0.93	0.05

Values in parentheses represent standard deviations.

3.3 Forest Floor

3.3.1 Forest Floor and Ah Horizon Depths

None of the forest floor or upper mineral horizon depths were significantly different between plot types (Table 3.10; Fig. 4, App.).

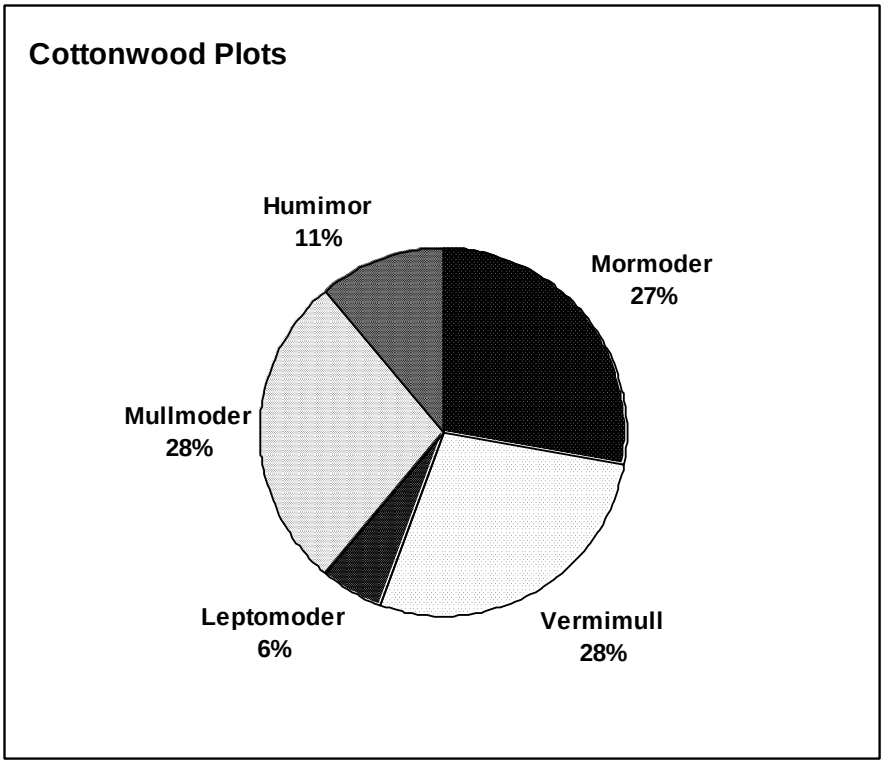
Table 3.10. Depth (cm) of the forest floor and upper mineral horizons for cottonwood and conifer plots (n = 6).

	Cottonwood Plots		Conifer Plots		P	Power
Litter Horizon (L)	1.5	(0.5)	1.6	(0.4)	0.72	0.10
Fibric Horizon (F)	2.3	(1.2)	2.6	(1.4)	0.60	0.11
Humic Horizon (H)	3.2	(1.8)	3.8	(2.0)	0.64	0.20
Ah	12.2	(7.7)	7.0	(2.6)	0.18	0.46
Total Forest Floor	6.9	(2.7)	8.5	(4.4)	0.46	0.18
F plus H	5.4	(2.7)	7.2	(4.5)	0.42	0.19
Ah plus H	15.6	(6.6)	11.6	(3.2)	0.22	0.35
Forest Floor and Ah	19.4	(6.9)	15.5	(3.5)	0.25	0.31

Values in parentheses represent standard deviations.

3.3.2 Humus Form Classification

The same humus forms; humimor, mormoder, vermimull, leptomoder, and mullmoder were present in both cottonwood and conifer plot types (Fig. 3.1). There was; however, almost double the amount of vermimull humus form (28%) in the cottonwood plots compared to conifer plots (14%). Both plot types had a low percentage of mors and all of these were in the form of humimor. Forty nine percent of all conifer plot humus forms were mormoders compared to only 27% mormoders in the cottonwood plots.



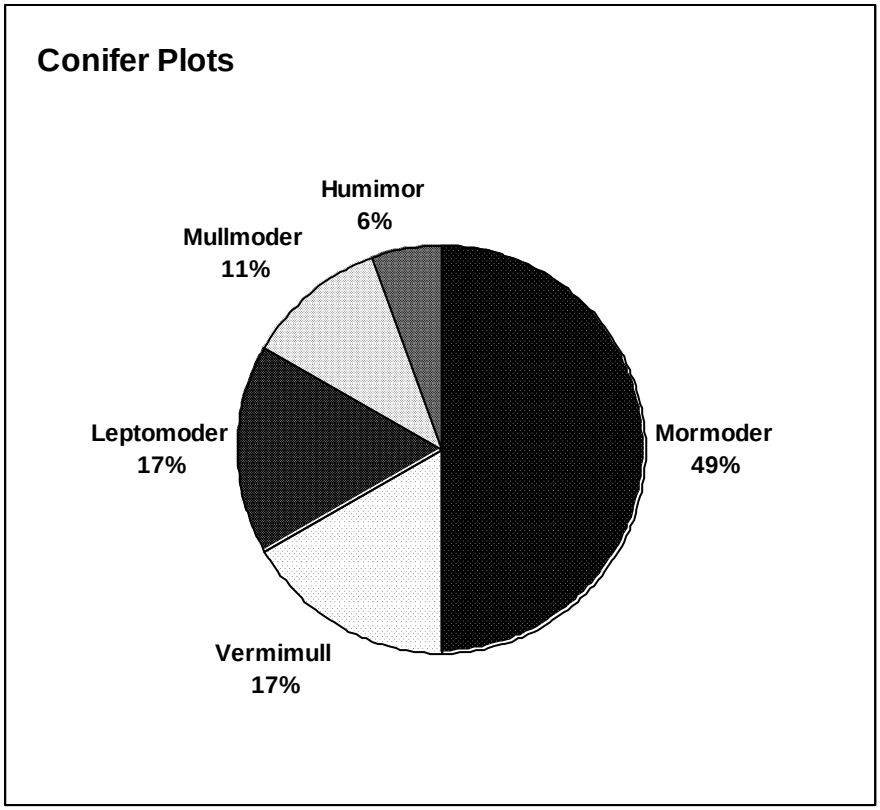


Fig. 3.1. Frequency of humus forms within cottonwood and conifer plots (n = 6).

3.3.3 Forest Floor Chemical Properties

The pH was higher and the concentrations of total C and exchangeable K and Fe were lower within the forest floor of cottonwood plots compared to conifer plots (Table 3.11). See Fig. 5 (App.) for a visual representation of total C content in the forest floor of all plots.

Table 3.11. Properties of the forest floor in cottonwood and conifer plots (n = 6).

Property	Cottonwood plots		Conifer plots		P	Power
Forest Floor (kg ha^{-1})	144922	(37113)	133190	(114625)	0.77	0.08
Bulk Density (g cm^{-3})	0.23	(0.04)	0.20	(0.05)	0.21	0.28
pH (1:1 $CaCl_2$)	4.37	(0.45)	3.87	(0.52)	0.04	0.51
Total C (g kg^{-1})	308	(94)	372	(89)	0.09	0.30
Total C (kg ha^{-1})	43891	(13678)	46193	(36339)	0.86	0.10
Total N (g kg^{-1})	10.2	(1.5)	12.1	(2.9)	0.12	0.38
Total N (kg ha^{-1})	1477	(428)	1827	(2042)	0.64	
C:N ratio	30.2	(7.6)	30.8	(2.9)	0.77	
Mineral N (mg kg^{-1})	242	(51)	254	(44)	0.76	
Mineral N (kg ha^{-1})	34.4	(8.6)	38.0	(42.6)	0.85	0.07
NO_3-N (mg kg^{-1})	0.83	(0.92)	0.91	(1.16)	0.90	0.06
NO_3-N (kg ha^{-1})	0.11	(0.12)	0.07	(0.08)	0.49	0.16
NH_4-N (mg kg^{-1})	27.4	(9.3)	32.8	(15.9)	0.51	0.16
NH_4-N (kg ha^{-1})	3.96	(1.52)	5.76	(8.32)	0.60	0.12
Available P (mg kg^{-1})	59.7	(22.0)	54.4	(11.6)	0.39	
Available P (kg ha^{-1})	8.09	(2.24)	6.54	(4.09)	0.55	0.19
Total S (g kg^{-1})	1.25	(0.19)	1.44	(0.32)	0.16	0.32
Total S (kg ha^{-1})	180	(49)	214	(233)	0.70	0.09
Exch K (cmol kg^{-1})	0.81	(0.21)	1.02	(0.14)	0.07	
Exch Ca (cmol kg^{-1})	25.3	(6.9)	23.0	(7.1)	0.64	0.13
Exch Mg (cmol kg^{-1})	2.56	(0.80)	2.74	(0.34)	0.55	0.12
Exch Mn (cmol kg^{-1})	0.50	(0.19)	0.48	0.18)	0.89	0.07
Exch Fe (cmol kg^{-1})	0.06	(0.04)	0.21	(0.15)	0.03	
Exch Al (cmol kg^{-1})	1.71	(0.84)	3.07	(1.81)	0.15	0.47
Exch Na (cmol kg^{-1})	0.34	(0.02)	0.33	(0.03)	0.29	0.16
CEC (cmol kg^{-1})	31.3	(7.0)	30.7	(5.5)	0.93	0.06
Total Exchangeable Bases (cmol kg^{-1})	29.0	(7.7)	27.1	(7.4)	0.71	0.11
Base Saturation (%)	91.7	(5.7)	86.6	(8.9)	0.32	0.30

Values in parentheses represent standard deviations.
Single and double underlined values indicate significant differences at $P < 0.1$ and $P < 0.05$.

3.4 Mineral Soil

3.4.1 Mineral Soil Properties

The coarse fragment content was significantly higher in cottonwood plots compared to conifer plots (Table 3.12). Total N concentration and base saturation were higher in cottonwood plots, while exchangeable Fe and Al concentrations were significantly higher in conifer plots (Table 3.12).

Total C within both the mineral soil and the forest floor was not significantly different between plot types (P = 0.92 and P = 0.86, respectively). See Fig. 6 (App.) for a visual representation of total C in the mineral soil of individual plots, and Fig. 7 (App.) for a visual representation of total C in the mineral soil and the forest floor on a combined plot basis.

Table 3.12. Properties of mineral soil in cottonwood and conifer plots (n = 6).

Property	Cottonwood plots		Conifer plots		P	Power
Wt/unit area (kg ha^{-1})	470504	(101087)	466748	(183801)	0.95	0.05
Bulk Density (g cm^{-3})	0.74	(0.15)	0.72	(0.26)	0.95	0.07
Coarse Frag. Content (%)	42.0	(9.9)	31.8	(13.8)	0.05	
W_G (g H_2O g^{-1} soil)	0.58	(0.24)	0.54	(0.25)	0.79	0.08
W_V (g H_2O cm^{-3})	0.35	(0.10)	0.32	(0.06)	0.53	0.15
pH ($CaCl_2$)	4.50	(0.20)	4.15	(0.33)	0.12	0.67
Total C (g kg^{-1})	73.9	(16.2)	71.8	(15.2)	0.62	0.08
Total C (kg ha^{-1})	34980	(12098)	35604	(22820)	0.92	0.01
Total N (g kg^{-1})	3.33	(0.78)	2.98	(0.53)	0.07	
Total N (kg ha^{-1})	1557	(477)	1432	(733)	0.54	0.09
C:N ratio	22.5	(3.4)	24.2	(3.0)	0.18	0.20
Mineral N (mg kg^{-1})	79.2	(24.1)	71.0	(12.4)	0.30	0.17
Mineral N (kg ha^{-1})	37.9	(15.3)	34.0	(16.2)	0.48	0.11
NO_3-N (mg kg^{-1})	3.30	(1.41)	2.33	(2.30)	0.44	0.21
NO_3-N (kg ha^{-1})	1.63	(0.91)	1.04	(0.92)	0.33	0.27
NH_4-N (mg kg^{-1})	8.26	(2.79)	7.75	(1.11)	0.62	0.10
NH_4-N (kg ha^{-1})	3.87	(1.49)	3.72	(1.90)	0.84	0.07
Available P (mg kg^{-1})	6.29	(2.75)	4.16	(2.66)	0.16	0.36
Available P (kg ha^{-1})	3.00	(1.55)	2.33	(2.56)	0.49	0.13
Total S (g kg^{-1})	0.46	(0.13)	0.38	(0.06)	0.13	0.36
Total S (kg ha^{-1})	215	(72)	181	(89)	0.35	0.17
Exch K (cmol kg^{-1})	0.08	(0.03)	0.09	(0.06)	0.51	0.10
Exch Ca (cmol kg^{-1})	3.55	(2.24)	2.48	(1.11)	0.31	0.25
Exch Mg (cmol kg^{-1})	0.28	(0.13)	0.23	(0.12)	0.21	0.16
Exch Mn (cmol kg^{-1})	0.06	(0.05)	0.02	(0.01)	0.15	0.56
Exch Fe (cmol kg^{-1})	0.01	(0.00)	0.05	(0.04)	0.04	
Exch Al (cmol kg^{-1})	1.50	(0.73)	2.85	(1.23)	0.07	
Exch Na (cmol kg^{-1})	0.04	(0.01)	0.04	(0.01)	0.70	0.05
CEC (cmol kg^{-1})	5.52	(2.20)	5.77	(1.71)	0.75	0.07
Total exchangeable bases (cmol kg^{-1})	3.96	(2.35)	2.84	(1.27)	0.31	0.25
Base Saturation (%)	68.0	(16.0)	49.5	(14.8)	0.10	

Values in parentheses represent standard deviations.
Single and double underlined values indicate significant differences at $P < 0.1$ and $P < 0.05$ respectively.

3.5 Nitrogen Mineralization

The initial measurements of NH_4-N and NO_3-N revealed no significant differences between the two plot types (Table 3.13). After incubation, the conifer plots were found to have significantly higher levels of NH_4-N compared to cottonwood plots, and cottonwood plots were found to have significantly higher NO_3-N concentrations compared to conifer plots. The net ammonification between day 0 and day 40 was significantly higher in conifer plots. The net mineralization was also significantly higher in conifer plots.

Table 3.13. Nitrogen mineralization (mg kg^{-1}) results for buried bag experiment within cottonwood and conifer plots (n = 6).

Day		Cottonwood plots		Conifer plots		P	Power
Day 0	NH_4-N	49.2	(24.2)	82.5	(52.8)	0.21	0.37
	NO_3-N	20.0	(15.6)	10.5	(3.9)	0.18	0.38
Day 40	NH_4-N	71.5	(33.9)	236.5	(159.6)	0.03	
	NO_3-N	31.8	(11.3)	14.3	(6.6)	0.01	
Net Ammonification	NH_4-N	22.3	(41.1)	154.0	(115.9)	0.03	
	NO_3-N	11.8	(12.2)	3.8	(4.4)	0.17	0.41
Net Mineralization	NH4-N + N03-N	34.17	(52.02)	157.83	(112.49)	0.041	

Values in parentheses represent standard deviations.
Double underlined values indicate significant differences at $P < 0.05$.

CHAPTER 4: Discussion

4.1 Litterfall Inputs and Composition

4.1.1 Seasonal and Annual Inputs

A comparison of litterfall weights between plot types revealed no significant difference in total annual litterfall. Turk (2006), who undertook a study within the same forest as our own, reported similar results, since no differences were found in total annual litterfall weights between bigleaf maple and conifer plots. Ogden and Schmidt (1997) also found no significant differences in total annual litterfall when vine maple plots were compared to pure conifer plots in 80 year old stands within an area transitional between the moist maritime (CWHmm) and dry maritime (CWHdm) subzones of the Coastal Western Hemlock biogeoclimatic zone. It should be noted that vine maple is an understory species often described as a shrub, while mature cottonwood trees are dominant in the canopy and therefore are expected to contribute a greater amount of litter to the forest floor.

In contrast, other studies have reported significantly greater amounts of annual litterfall in mixed versus pure conifer stands. Wang et al. (2008) concluded that the introduction of broadleaved tree species into a monoculture of conifers (20 to 25 year old stands within a subtropical region) increased litter production. Specifically, they found the mean annual litter production to be significantly higher (24%) in a mixed compared to a pure conifer stand. Fried et

al. (1990) found substantially greater litterfall weights under bigleaf maple compared to Douglas-fir in all five studied sites of Douglas-fir dominated stands located within the foothills of the Oregon Coast Range.

Litterfall amount did not differ between cottonwood and conifer plots in any of the four time periods (autumn, winter, spring or summer) used in our study. It was expected that total autumn litterfall would be significantly higher in cottonwood plots since these plots would produce both cottonwood litter as well as conifer litter during that season, but this was not observed. A similar study by Turk (2006) found significantly more litter in bigleaf maple sites compared to conifer sites during the autumn. A study by Wang et al. (2008) comparing litterfall between a monoculture of conifers and a mixed deciduous conifer stand similarly found no significant differences in seasonal litterfall between the two site types.

No significant weight differences were found in conifer (fir/hemlock, and cedar) litter in the autumn between plot types. This indicates that the presence of cottonwood did not decrease the amount of conifer litterfall. Furthermore, the input of conifer (fir/hemlock + cedar) litter was greater than that of cottonwood litter in cottonwood plots indicating that conifer litter dominated both cottonwood and conifer plots. Ogden and Schmidt (1997) also found that conifer litter contributed more to autumn litter inputs than did vine maple litter within vine maple plots. Overall, our seasonal and annual litter input results did not indicate a positive or negative influence of dominant cottonwood trees on the amount of litter reaching the forest floor.

Some cottonwood litter was found within conifer plots (Table 3.2) and this was unexpected. The placement of plot pairs a minimum of 30 m away from each other, but no more than 60 m apart, was intended to ensure that the influence of the cottonwood trees would not reach the conifer pair of the plot while still allowing site characteristics to remain similar. Strong winds and at least one storm during the 2007 winter season caused some cottonwood litterfall to be blown into adjacent conifer plots. Considering this contamination, it is possible that the influence of cottonwood within conifer forests may be even more pronounced than this study suggests.

4.1.2 Composition of Litterfall

Cottonwood litter had significantly greater concentrations of almost all elements tested for. Only two elemental concentrations were found to be significantly higher within conifer litter, that of C and Mn. The first had a significantly greater concentration in both cedar and fir/hemlock litter, the latter had a significantly higher concentration in cedar litter only. Similarly, Ogden and Schmidt (1997) found the concentration of N, P, Ca, Mg, K, Fe, and Zn to be higher in vine maple litter compared to a mixture of conifer litter, and this lead those researchers to suggest that vine maple may improve the nutritional status of soils.

We found a greater contribution of K, Mg, S, B, and Cu from autumn litterfall within cottonwood as compared to conifer plots. Other studies have shown greater nutrient quantities within deciduous litters. Kavvadias et al. (2001) tested litter types for the contents of six nutrients and found four of them (N, Ca,

Mg, and Na) were highest in the litter of beech trees compared to two species of pine and one species of fir (in sub-Mediterranean to temperate study sites). A study comparing a pure beech forest to a pure pine forest in a Mediterranean climate (mean tree age of 50 years) concluded that beech forest litter returned greater amounts of all nutrients tested for except N (Regina and Tarazona, 2000). Tashe and Schmidt (2001) reported significantly higher contents of all measured nutrients (N, P, K, Ca, Mg, Mn, B, Zn) within autumn litterfall from vine maple plots compared to conifer plots. Fried et al. (1990) concluded that litterfall nutrient contents were significantly greater under bigleaf maple compared to Douglas-fir for every studied site, for every macronutrient and for most micronutrients.

There were no differences in nutrient concentrations of fir/hemlock litter between plot types indicating that the presence of cottonwood did not influence the uptake of nutrients by surrounding conifers. This was somewhat unexpected as a similar study on vine maple trees found significantly higher concentrations of N on both measured sites and higher concentrations of P, and Mn on one of two measured sites within Douglas-fir/hemlock needles from vine maple plots compared to needles from pure conifer plots (Tashe and Schmidt, 2001).

The content of all elements of fir/hemlock litter type was higher within conifer plots when compared to cottonwood plots, and all except K, S, Fe, and Cu were significantly so. This content result was expected as there is a greater amount of fir/hemlock litter present in the pure conifer plots, compared to the

mixed plots where the dominance of tree species was shared between conifers and cottonwood trees.

Analysis of both western red cedar and 'other' litter revealed almost no differences in concentration and content of various elements between plot types. Sulphur concentration was significantly higher in cedar litter within conifer plots. For 'other' litter, only the concentration of Cu differed significantly between plot types, and it was found to be higher within cottonwood plots. It is unclear why S was significantly higher within cedar litter of conifer plots, but the higher concentration of Cu within 'other' litter type in cottonwood plots may have been caused by the presence of cottonwood reproductive parts within this litter type; these parts would not have existed in the 'other' litter type found within conifer plots.

We found no significant differences in lignin concentrations or the lignin:N ratio between cottonwood and fir/hemlock litter ($P = 0.11$). Available literature implies that lignin concentrations tend to be lower in deciduous trees compared to conifers and lower lignin concentrations have been linked to faster decomposition rates (Pandey and Singh,1982; Prescott and Blevins, 2000; Fisher et al., 2000). The lignin:N ratio has been found to be inversely related to decay (Prescott et al., 2000; Harmon et al., 1990; Xu and Hirata, 2005). Therefore we expected cottonwood litter, being a deciduous litter, would have a significantly lower lignin and lignin:N ratio; this, however, was not the case.

Overall, litterfall results indicate that cottonwood litter tends to be higher in nutrient concentrations compared to fir/hemlock and 'other' litter types. This

implies that cottonwood litter is of higher quality. The presence of cottonwood does not seem to improve the quality of the other litter types (fir/hemlock litter, cedar litter, and 'other' litter).

4.2 Litter Decomposition and Nutrient Release

No statistically significant differences were found between the mass loss of cottonwood litter when compared to the mass loss of conifer litter after 6 months of decomposition. This was the case within both plot types. Initially, it was hypothesized that cottonwood litter would decay faster than conifer litter within this initial stage of decomposition.

Other studies have reported that deciduous litters tend to have faster initial decay compared to conifer litters (Ogden and Schmidt, 1997; Prescott et al., 2004; Prescott et al., 2000). Specifically, Prescott et al. (2004) found that broadleaf litter decayed faster than needle litter during the first year of decomposition but thereafter decay slowed down. The decomposition aspect of that study was carried out within a mixed conifer stand located within the same research forest (MKRF) as this study. Prescott et al. (2000) conducted a study in the moist–warm subzone of the Boreal White and Black Spruce biogeoclimatic zone (BWBSmw1), with a seasonal start date similar to our own (November), and found that aspen leaf litter lost significantly more (65.5%) of its mass during the first year of decomposition while spruce needle litter lost 29.2% mass during that same time. Prescott et al. (2000) also demonstrated that alder litter decomposed faster than Douglas-fir litter during the first 6 months, although that decomposition study was started during the month of July unlike our study which

was started in December. Prescott et al. 2000 also found that birch decomposed faster than both Douglas-fir and pine during the first 2 years of decomposition. Overall, Prescott (2000) suggests that broadleaf litter tends to reach the humus stage sooner than conifer litter, even though decomposition beyond the humus stage tends to be abruptly slowed.

Both our litter types showed minimal weight loss after the first 6 months of in-field incubation. One possibility for this minimal loss may be the timing of the start of the incubation cycle. Our litterbags were first placed in the plots in the month of December, and although December is a fairly wet month it is also cold. Pandey and Singh (1982) recorded their greatest decomposition during the warmest and wettest periods of the year within a temperate environment. It is possible that significant differences between litter types may emerge with increased incubation time. It is also possible that the similar loss in mass between the two litter types is the result, at least partially, of similar initial composition of the litters as suggested by Prescott et al. (2004). Most notably within our own results, the lignin concentration showed a lack of significant difference between cottonwood and fir/hemlock litter.

Our results failed to show faster decomposition of litter under its own canopy type. There does not appear to be a consensus among studies regarding the rate of decomposition of litter within its own habitat type. Vivanco and Austin (2008) suggest that plant species can create conditions within their own habitat that enhance decomposition of their own litter. However, Zhang et al. (2008) found that deciduous litter decomposed faster within a conifer habitat,

while coniferous litter decomposed faster within its native conifer habitat (study conducted within two forests in close proximity to each other with an annual mean temperature of 15.5°C and annual precipitation of 1670 mm; the decomposition study was initiated in the winter (December) and lasted for 310 days). Neither of the above cases proved true for our study within the first 6 months of decomposition. Our initial decomposition results do not indicate that the presence of cottonwood trees within a conifer dominated forest increases the rate of nutrient turnover in those systems. However, this does not necessarily mean that the deciduous litter is not of a higher quality. Within our study, many of the elemental concentrations of cottonwood litter were significantly higher compared to fir/hemlock litter. This may allow cottonwood litter to decompose faster at a later stage of decomposition due to its higher quality, and this warrants further investigation.

4.3 Forest Floor and Mineral Soil

4.3.1 Forest Floor and Ah Horizon Depths

Deciduous tree species are generally associated with higher quality litter and higher rates of decomposition, therefore we expected thinner forest floors beneath cottonwood compared to pure conifer stands. However, there was no difference in the thickness of any of the horizons or of the forest floor as a whole below cottonwood compared to conifer plots. Other studies have shown significantly thinner forest floors below mixed stands compared to pure conifer stands, including within mixed stands of big leaf maple and conifers (Turk et al., 2008), vine maple within conifer forests (Ogden and Schmidt, 1997), and within

an oak-pine forest (Washburn and Arthur, 2003). These studies therefore suggest that there is a faster nutrient turnover rate within mixed forests when compared to pure conifer forests. Our own results do not seem to indicate this, nor do the results of Tashe and Schmidt (2003) who found no statistical difference between vine maple and conifer plots for the L, F, or H horizon depths or of total forest floor depth in two age classes of forests.

Our two plot types were shown to receive a similar total annual weight of litterfall, and this particular result indicates that the long term decomposition rates of the two litter types and the two plot types may be similar. This is in contradiction with our own elemental concentration results showing cottonwood litter to be of higher quality, and in contradiction with the widely held belief that deciduous tree litter is higher in quality, as litter of higher elemental quality tends to decompose faster than conifer litter (Schulp et al., 2008, Kavvadias et al., 2001, Fried et al., 1990, Pandey and Singh, 1982).

There was no difference in Ah thickness between cottonwood and conifer plots indicating the degree of mixing of organic material into the mineral soil from the forest floor by soil organisms may be similar between the two plot types. Schulp et al. (2008) implies that there is more biological activity, more fragmentation, and more humification of forest floor material in broadleaf stands compared to conifer stands. In addition, studies have shown that earthworm density tends to be higher under deciduous trees (Binkley, 1995, Noirfalisse and Vanesse, 1975 as cited in Augusto et al., 2001), and Tashe and Schmidt (2003) found thicker Ah horizons under vine maple compared to Douglas-fir or western

hemlock. That study attributes the thicker Ah horizons to more active biotic communities being supported under vine maple. The thickness of the Ah horizon within our study does not suggest more active biotic communities under cottonwood, however we did find more favorable humus form conditions within the forest floor of our cottonwood plots (see section 4.3.2), and those results do suggest increased biological activity in the presence of cottonwood. There was substantial variation in Ah thickness depths throughout our study, and this in combination with a weak trend towards thicker Ah horizons within cottonwood plots suggests that our sample size may have been too small to capture significant differences. It is therefore possible that cottonwood plots do support more biologically active forest floors but that our study was not able to capture the evidence for this.

There may also be a legacy effect from the stand that persisted on these sites previous to logging approximately 80 years ago. The historical stand on these sites was an old growth forest and likely contained few if any deciduous species. Therefore the effect of the present second growth stand on horizon depths and mixing may increase with time if deciduous trees such as cottonwood persist within the stand.

4.3.2 Humus Form Classification

Both plot types were dominated by moders, 61% moders in conifer plots and 77% moders in cottonwood plots. The moders within both plot types were in the form of mormoder, leptomoder, and mullmoder. These results suggest an intermediate level of biological activity and rate of decomposition within a large

proportion of the forest floors of both plot types as moders are considered to be an intermediate humus form between mulls and mors. Results showed 28% of sampled forest floor within cottonwood plots to be of the mull humus form, and this was in the form of vermimull. Conifer plots contained just over half this percentage of mulls (17%).

When added together the vermimulls plus mullmoders represent 56% of humus forms in cottonwood plots but only 28% of humus forms in conifer plots. Additionally, when the humimors and the mormoders are added together they represent 38% of humus forms in cottonwood plots compared to 55% in conifer plots. This indicates that humus forms are more mull like under cottonwood, and that therefore the biological activity there may be increased compared to conifer plots. Mull humus forms are considered to be the most biologically dynamic (Green et al., 1993).

Tashe and Schmidt (2003) found that mull humus forms dominated under vine maple when compared to pure conifer plots. That study found three and a half times more mulls under vine maple compared with the forest floors under Douglas-fir or western hemlock. In a similar study, also undertaken within the MKRF, more than half of the humus forms examined under bigleaf maple were mulls compared to only 12% mulls in conifer plots (Turk et al., 2008). Both of these studies support the idea the mull forest floors are generally formed under hardwoods and mors are more often found under conifers (Fisher et al., 2000). Our study does not show strong evidence for this theory as evidenced by the dominant presence of moders. Still, cottonwood plots had almost twice the

proportion of mull humus forms compared to conifer plots, indicating potentially greater site productivity. Therefore, it is possible to expect that cottonwood has a positive influence on forest floor quality on sites where it is present among conifers.

4.3.3 Forest Floor and Mineral Soil Properties

4.3.3.1 Forest Floor Mass and Mineral Soil Bulk Density

The forest floor mass showed no significant difference between plot types. I had expected that cottonwood plots would have lower forest floor mass due to an expected faster decomposition rate of cottonwood litter compared to conifer litter. As previously indicated, we did not find a faster decomposition rate for cottonwood and this could explain the lack of difference in forest floor mass.

Other studies have shown similar results. Fried et al. (1990) compared mixed plots of bigleaf maple/conifers to pure conifer plots and found no overall significant differences in the forest floor weight between the two plot types. Forest floors beneath vine maple also showed no significant differences in weight when compared to conifer forest floors (Ogden and Schmidt, 1997). In contrast, Washburn and Arthur (2003) reported a greater mass of organic horizons under a conifer (shortleaf pine) compared to organic horizons under two deciduous tree species (chestnut oak and red maple). This study was carried out in an oak-dominated forest with a temperate, humid and continental climate. Turk et al. (2008) showed greater mass per unit area of forest floor beneath bigleaf maple compared to pure conifer plots. That study suggested that the cause may be

deciduous litter becoming recalcitrant and stable in the forest floor once its decomposition reaches the humus stage.

The bulk density of the surface mineral soil was not significantly different between cottonwood and conifer plots. We expected mineral soil within cottonwood plots to have lower bulk density compared to conifer plots as deciduous species are generally thought to have higher rates of organic matter incorporation into the mineral soil, especially surface mineral soil. Results from our study suggest that soils within a conifer forest influenced by cottonwood do not experience greater mixing by fauna. Other studies have shown mineral soil below deciduous species to have a significantly lower bulk density compared to mineral soil of conifers. Turk et al. (2008) found lower bulk densities below bigleaf maple compared to Douglas-fir and western hemlock. Schulp et al. (2008) also showed lower bulk density of surface mineral soil below European beech and English oak compared to Douglas-fir, Scots pine, and Japanese larch. However, similar to the results of this study, Tashe and Schmidt (2003) and Ogden and Schmidt (1997) observed no significant difference in bulk density of surface mineral soil in vine maple compared to conifer plots.

4.3.3.2 Carbon, Nitrogen, and Phosphorous

The concentration of C was significantly lower in the forest floor of cottonwood plots as compared to conifer plots. Litterfall results indicated significantly lower C in cottonwood litter compared to fir/hemlock and cedar litter, and this may explain the lower C in the forest floor beneath cottonwood.

The concentration of C in mineral soils was not significantly different beneath cottonwood and conifers. I had expected higher C concentrations in the mineral soil beneath cottonwood as there is thought to be a greater degree of mixing from soil organisms beneath some deciduous species. I did not find higher C concentrations beneath cottonwood. This suggests a similar degree of biological activity between cottonwood and conifer plots. It is also possible that cottonwood litter is not decomposing fully, thus leaving recalcitrant material within the forest floor (Prescott et al., 2000; Prescott et al., 2004). Ogden and Schmidt (1997) and Turk et al. (2008) found no difference in C concentrations in mineral soil beneath vine maple and bigleaf maple respectively when compared to conifer plots. However, Fried et al. (1990) and Tashe and Schmidt (2003) found a significantly higher C concentration within the mineral soil under bigleaf maple compared to conifer plots.

Total N concentration in the mineral soil was greater beneath cottonwood than beneath conifers. The greater total N concentration in the mineral soil beneath cottonwood is likely related to greater concentration of N in the litter of cottonwood. Mineralizable N in forest floor and mineral soil as well as total N in forest floor were not significantly different between the site types. It is surprising that cottonwood did not have a greater influence on measures of N since cottonwood litter had significantly higher concentration of N compared to all other litter types.

Fried et al. (1990) found significantly greater total N, but no difference in mineralizable N in mineral soils beneath bigleaf maple compared to conifers.

Turk et al. (2008) found greater total N and mineralizable N concentrations in surface mineral soil beneath bigleaf maple. Tashe and Schmidt (2003) found greater mineralizable N beneath vine maple as compared to conifers. Similarly, pine microsites had significantly lower total N within organic soil when compared to two species of oak and one species of maple in a study by Washburn and Arthur (2003).

C:N ratios in both forest floor and mineral soil did not differ between site types. Both site types had forest floor C:N ratios above 25:1 indicating that soil organisms will likely need to scavenge the soil solution in order to obtain enough N (Brady and Weil, 2002) in both plot types. The mineral soil C:N ratios for both site types were below 25:1. Fried et al. (1990) found significantly lower C:N ratios in the mineral soil below bigleaf maple in two of five sites studied. Tashe and Schmidt (2003) did not find significant C:N ratio differences within the forest floor of understory vine maple, but did find a significantly lower C:N ratio in the mineral soil for one of two studied sites. In a study with a similar climate and 30 year old trees, Perry and Choquette (1987) reported C:N ratios that were significantly lower in pure conifer plots dominated by Douglas-fir, compared to mixed plots containing a variety of deciduous species; however, all ratios were below 25:1.

No significant differences in available P were observed between plot types in either the forest floor or the mineral soil. Soil P comparisons between deciduous and coniferous species in other studies have revealed no consistent differences (Fried et al., 1990), no effect (Turk et al., 2008; Ogden and Schmidt,

1997), or a possible negative effect (Tashe and Schmidt, 2003) of deciduous species on soil P levels.

4.3.3.3 Soil pH, Base Saturation, and Exchangeable Cations

The pH of the forest floor and the base saturation of the mineral soil were higher within cottonwood plots compared to conifer plots. However, no significant differences were found between plot types for the pH of the mineral soil, the base saturation of the forest floor or the CEC of the forest floor. The pH and base saturation results indicate a positive effect of cottonwood on the acidity of soil. This positive effect on pH is evident in the forest floor, but does not appear to extend to the mineral soil. With time, the pH of the mineral soil underneath the mixed plots may also increase, as changes often take longer to occur within the mineral soil compared to the forest floor.

A similar study on bigleaf maple reported significantly higher pH in the forest floor soil under maples growing within a conifer forest compared to pure conifer plots (Turk et al., 2008). Fried et al. (1990) found significantly higher pH in the mineral soil for two of five paired big leaf maple plots. In the presence of vine maple, Tashe and Schmidt (2003) found a significantly higher pH in both the forest floor and the mineral soil in one of two studied stands, although the reported significance was in different stands for the forest floor and the mineral soil. Also under vine maple, Ogden and Schmidt (1997) found a significantly higher pH in the forest floor when compared to soil under pure conifer plots, but this significance was not present in the mineral soil. It appears that cottonwood

has a similar influence on pH as other deciduous species of the Coastal Western Hemlock forest in that it tends to increase the pH of soil.

None of the exchangeable cations, except exchangeable K in the forest floor, were significantly higher in cottonwood plots in either forest floor or mineral soil. Since cottonwood litter had higher concentrations of bases compared to conifer litter, exchangeable bases were expected to be higher in cottonwood plots than in conifer plots, but we did not find this.

Turk et al. (2008) also failed to show evidence of significantly higher exchangeable bases within the forest floor of bigleaf maple plots. In contrast, Ogden and Schmidt (1997) reported higher Ca, Mg, and K concentrations within the forest floor of vine maple gaps compared to the forest floor under conifers, while Tashe and Schmidt (2003) reported higher Ca and Mg under vine maple compared to conifer plots in only one of two sites. For mineral soil, Turk et al. (2008) and Fried et al. (1990) both found evidence of significantly higher Ca, K, and Mg for plots containing bigleaf maple compared to pure conifer plots. Tashe and Schmidt (2003) also found evidence of significantly higher Ca, K, and Mg within the mineral soil under vine maple.

4.4 Nitrogen Mineralization

Our results indicate a significantly higher rate of ammonification and overall significantly higher net mineralization within the forest floor of conifer plots compared to that of cottonwood plots. Post incubation NH_4^+ concentrations were

also significantly higher within conifer plots. However, post incubation NO_3^- concentrations were significantly higher under cottonwood plots.

The majority of soil N (95 to 99%) is in the form of organic compounds and this N is largely unavailable for plant use (Brady and Weil, 2002). Only 1.5 to 3.5% of organic N within soil mineralizes annually. There is mixed evidence (Binkley and Giardina, 1998) concerning the effect of deciduous versus coniferous trees on rates of N mineralization. A greater proportion of studies seem to support the notion that deciduous trees have a positive effect on the rate of N mineralization (Chandler et al., 2008; Côté et al., 2000, Paré and Bergeron, 1996; Ollinger et al., 2002; Perez et al., 1998; Devito et al., 1999) than not (Binkley, 1995; Washburn and Arthur, 2003). Surprisingly, the results of this study indicate greater overall N mineralization within conifer plots compared to cottonwood plots.

No other studies have looked at N mineralization under wild types of the cottonwood species, however a few have considered this process under trembling aspen (*Populus tremuloides* Michx.), a species within the same genus as cottonwood. It should be noted that the studies discussed below were conducted in various climates and ecosystems, all of which differ from the climate and conditions of our own study area. Overall, the results of our study are dissimilar to those reported for trembling aspen. Côté et al. (2000) found a higher rate of N mineralization per gram of organic C in both the forest floor and mineral soil under trembling aspen compared to soil under a mixture of conifer

trees. Similarly, Flannagan and Van Cleve (1983) reported higher rates of N mineralization in the forest floor of trembling aspen relative to conifers.

The rate of N mineralization has been correlated with several other soil and litterfall traits, including the lignin:N ratio, the concentration of N in litter, and the C:N ratio of soil. Specifically, N mineralization has been reported to have an inverse relationship with the lignin:N ratio of litter (Washburn and Arthur, 2003; Pastor et al., 1987), a direct relationship with litterfall N (Reich et al., 1997), and an inverse relationship with C:N ratio (Devito et al., 1999). Our results showed no significant difference between the lignin:N ratio of cottonwood compared to fir/hemlock litter, and no significant differences within the C:N ratios of the forest floor or the mineral soil, but we did find a significantly greater concentration of N in cottonwood litter. These results led us to believe that the rate of N mineralization would be higher overall under cottonwood trees, but this was not the case. The reasons for the lack of greater N mineralization beneath cottonwood are unclear; it is possible that the determinants of N mineralization are so specific to particular ecosystems or even to forest stands that comparisons cannot be made between them.

Overall, the results of this study indicate that the presence of cottonwood within mixed conifer stands of Coastal Western Hemlock forests does not have a positive influence on the availability of NH_4^+ or the rate of N mineralization within the forest floor, although this species does seem to improve the availability of NO_3^- within the forest floor.

CHAPTER 5: Conclusion

5.1 Summary of Findings

The function deciduous trees play within an ecosystem, including their effect on soil fertility is expected to differ from that of conifers. Preceding this study, very little was known about the influence of cottonwood on soil fertility. Therefore, this study set out to determine the influence of cottonwood on soil fertility within a CWH subzone forest dominated by Douglas-fir and western hemlock. We sought to quantify the impact of cottonwood by comparison of litterfall, decomposition, properties of the forest floor and mineral soil, and N mineralization rates between plots with and without a cottonwood component.

Cottonwood litter was found to be of higher quality in terms of nutrient concentrations compared to conifer litter. A comparison of early decomposition rates revealed no significant differences between litter types or plot types, although it is possible this will change with increased incubation time. Decomposition results, in combination with no difference in forest floor thickness, or forest floor weight below cottonwood compared to conifers, suggests a lack of influence of cottonwood on litter decomposition within conifer forest.

The proportion of mull humus form under cottonwood was almost double that under conifers. Also, higher total N concentrations in the mineral soil and higher pH in the forest floor were found under cottonwood. These results suggest a positive influence on soil fertility related to the presence of cottonwood.

The net mineralization and net ammonification were lower under cottonwood than under conifers. These results fail to indicate an overall positive influence of cottonwood on N availability within conifer dominated forests.

This study found less significant differences than expected between plot types. We expected to find more evidence of a positive effect of cottonwood on soil fertility of conifer-dominated stands. The low power encountered in a large number of our statistical tests indicates that the presence of cottonwood may actually have a greater influence than this study was able to capture. Increased statistical differences would likely emerge with an increased sample size.

Results from all components of the project combined suggest a moderate to weak positive effect of cottonwood on soil fertility within conifer dominated forests of coastal British Columbia.

5.2 Significance of Research

There is little doubt that removing any component of an ecosystem has consequences, often unpredictable in scope and scale. Therefore, it is not surprising that forest mangers and those that regulate forestry are currently moving away from the use of monocultures within managed stands. The idea of incorporating deciduous species into areas where they historically persisted is receiving increased attention, as soil fertility can often decline in response to long term use of monocultures. Although no species uniformly pushes all soil variables in favourable or unfavourable conditions (Binkley, 1995), deciduous trees have been shown to enrich soil fertility and diversify soil microbial

communities. Nevertheless, all deciduous species do not act as one; Binkley and Giardina (1998) state that differences among tree species are not consistent among studies and that it is therefore difficult to generalize about species effect. Difficulty in predicting the effect of any one species demonstrates the need to conduct the kind of research undertaken by this study; results can then be used to make increasingly more informed forest management decisions.

This was the first ecological study of the effect of cottonwood on soil fertility in the CWH subzone forest. Our results suggest only a moderate to weakly positive effect of cottonwood on the components of soil fertility considered. Many questions regarding the interaction of this species with the biotic and abiotic components of its ecosystem remain unanswered and therefore future study is required. In addition, there are reasons beyond soil fertility that may warrant the inclusion of cottonwood within CWH forests. Firstly, its inclusion will contribute to biodiversity. It will do so directly through its presence in what might otherwise be a monoculture of conifers, but also by providing appropriate conditions for insects, microbial life, and other organisms that may only be able to persist in the presence of deciduous tree species. It is generally accepted that increased biodiversity within an ecosystem is directly related to ecosystem health and resilience. Also, Binkley and Valentine (1991) have stated that substantial changes in ecosystem biogeochemistry can be developed through selection of species. Lastly, cottonwood is a native species to British Columbia and therefore its presence within its native habitat should be maintained for ecological as well as intrinsic reasons.

5.3 Future Research

This project is an important step in developing a deeper understanding of the ecology of cottonwood. Many questions regarding the interaction of cottonwood with conifers through the soil medium remain. Further research should consider the following suggestions.

One of the most important aspects of soil that this study was not able to consider is the soil biotic community. Time and financial restraints did not allow us to incorporate this important component into our own research design. However, there is little doubt about the importance of soil microorganisms. Hagen-Thorn et al. (2004) listed microbial activity as one of the most important reasons for differences in soil chemistry among species; and earthworms are known to incorporate material from the forest floor into deeper soil horizons (Devliegher and Verstraete, 1997 as cited in Vesterdal et al., 2008). In a similar study to our own Tashe and Schmidt (2003) have suggested a link between soil biotic communities and soil properties.

Some of the statistical analyses employed by our study encountered low power. Low power is an indication that the sample size chosen may be too small to detect significant differences even when they exist. A number of different computer programs can be used to determine the appropriate number of samples required to detect significance. The intention for this study was to use a larger sample size; however, finding enough appropriate sites proved very difficult within the time frame allotted. The difficulty was in finding cottonwood plots that had a similar moisture regime to nearby conifer plots. Very often

cottonwood was found in wetter microenvironments within a forest otherwise dominated by conifers. Many of the sites that were originally identified could not be sampled due to very dissimilar moisture regimes between paired plots. It is our suggestion that future studies with a larger scope and with less financial restraint consider spending more resources on locating a greater number of appropriate sites. It would also be useful and interesting to study the characteristics of forest sites that cottonwood tends to persist in.

Our initial litter decomposition results revealed no significant differences between plot or litter types. Had our decomposition study continued beyond the 6-month mark, significant differences might have emerged. It was not possible within the restraints of a MSc project to continue this aspect of the project further in time; however, it is our suggestion that any future study employ a longer time period for litter decomposition work. There are also inherent problems with the mesh litterbag technique used to detect decomposition rates of litter types. Prescott and Blevins (2000) discuss several sources of error associated with litterbags. Specifically, the moisture levels may be different inside the bags than in the surrounding litter layer, and the movement of litter through soil is likely restricted by enclosure in the litterbag. Most importantly, litter bags exclude the presence of an unknown proportion of soil fauna whose activity likely contributes to decomposition. Prescott and Blevins (2000) suggest that this problem may be offset somewhat by using the smallest and the largest mesh bags possible that will retain the litter. This concept could be considered for future studies. Future studies could also consider mixing litter types within one decomposition bag.

Litter within a mixed forest does not decompose separately from other litter types, and therefore mixing litter within one decomposition bag may provide information not attainable from un-mixed decomposition designs. Litter rarely decompose in mixtures in a way that can be foreseen from their behaviour as pure litter (Binkley and Giardina, 1998; Polyakova and Billor, 2007).

It would also be interesting and beneficial to study the interaction of cottonwood with soil over a longer period. A study that tracked changes over a period of several years, perhaps 5 or 10 years, would likely provide insight into trends not distinguishable from a short snapshot study. Also, one way of directly determining the effect of cottonwood on conifers would be to measure the DBH of nearby conifers and compare that with the DBH from conifers free from the influence of cottonwood. It would also be interesting to study how cottonwood compared to conifers, affects stemflow and throughfall. This knowledge may help explain variations in forest floor properties (such as humus form), on a spatial scale (Turk, 2006).

Much work remains to be done concerning the impact of cottonwood on soil fertility within conifer-dominated forests. The results of this study provide a good starting point for asking further questions. Scientists designing future research projects should always keep in mind the following: “distinguishing cause from effect is an inherent problem in studies of plant-soil interactions” (Ollinger et al., 2002).

APPENDIX

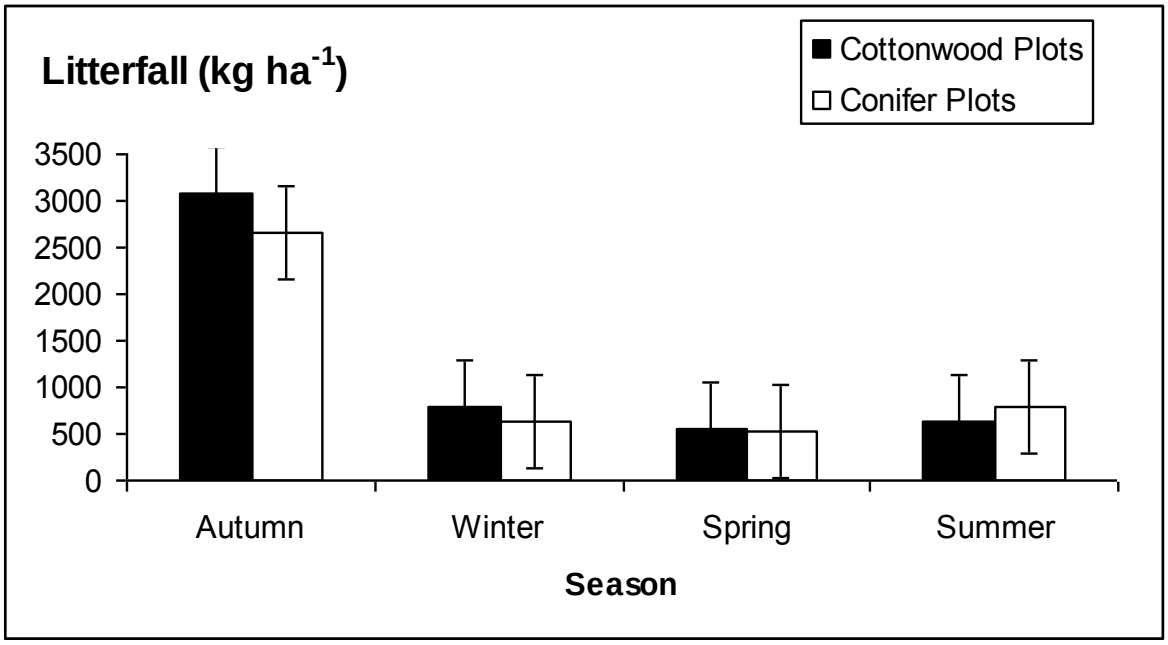
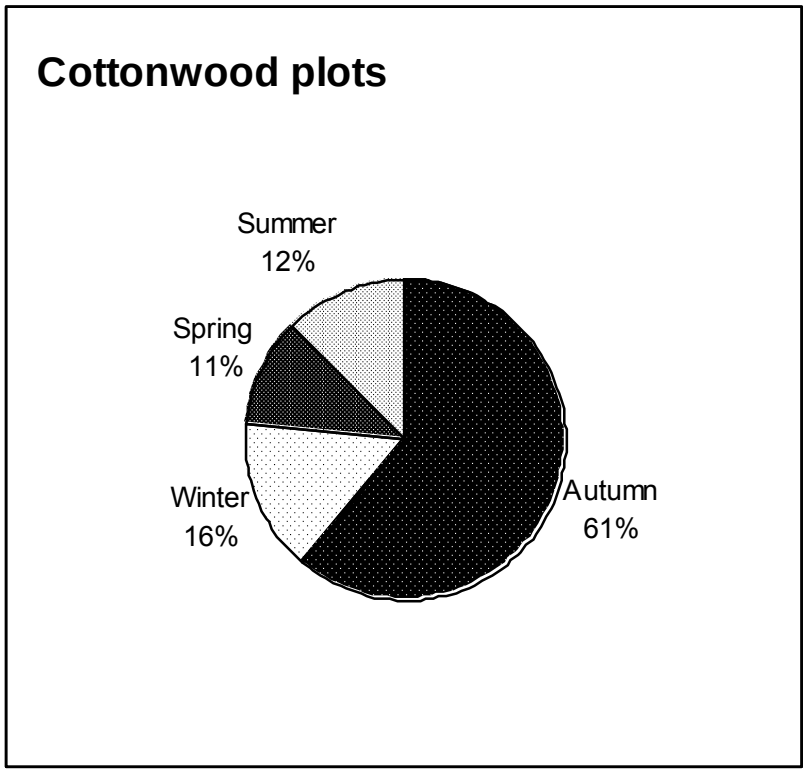


Fig. 1. Mean seasonal litterfall amounts for cottonwood plots and conifer plots (n = 6). Error bars represent standard errors.



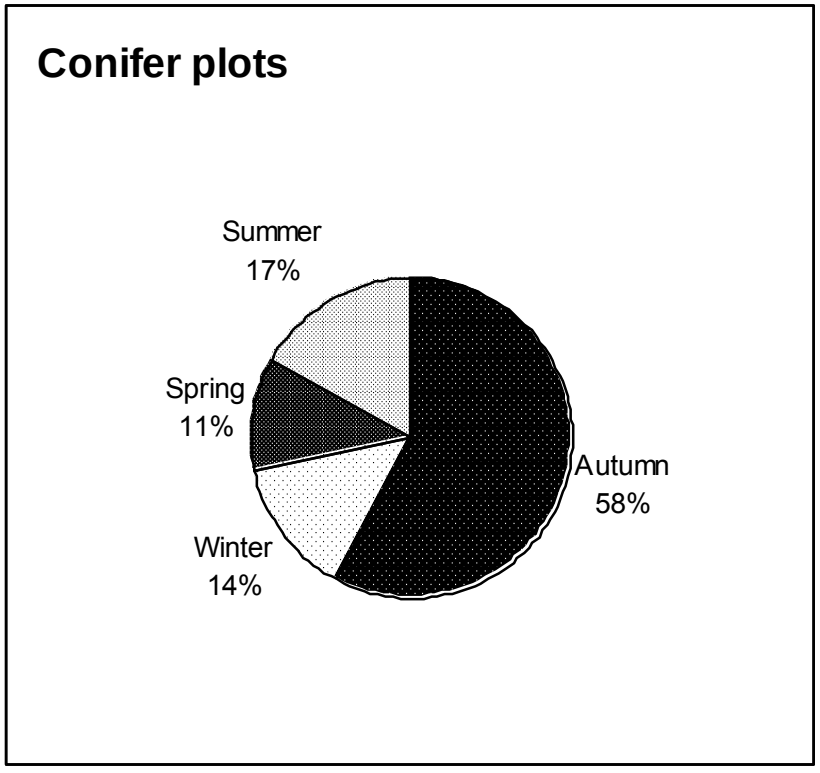


Fig. 2. Total annual litterfall showing proportions of seasonal contributions by weight (n = 6).

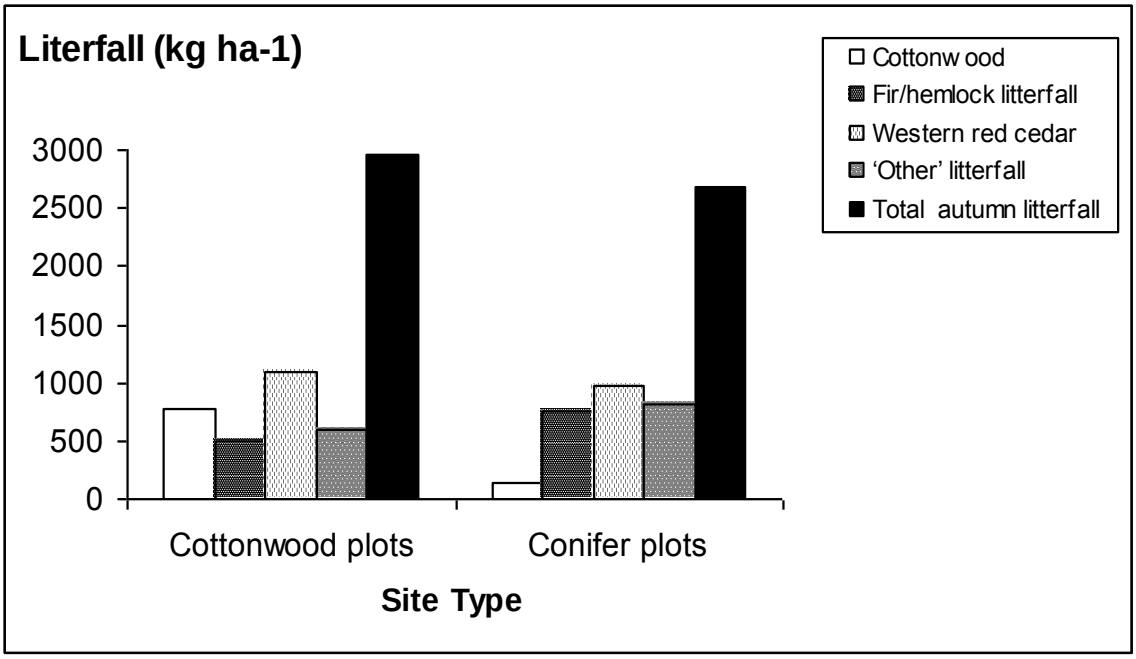


Fig. 3. Autumn litterfall amounts showing proportions of litterfall types (n = 6).

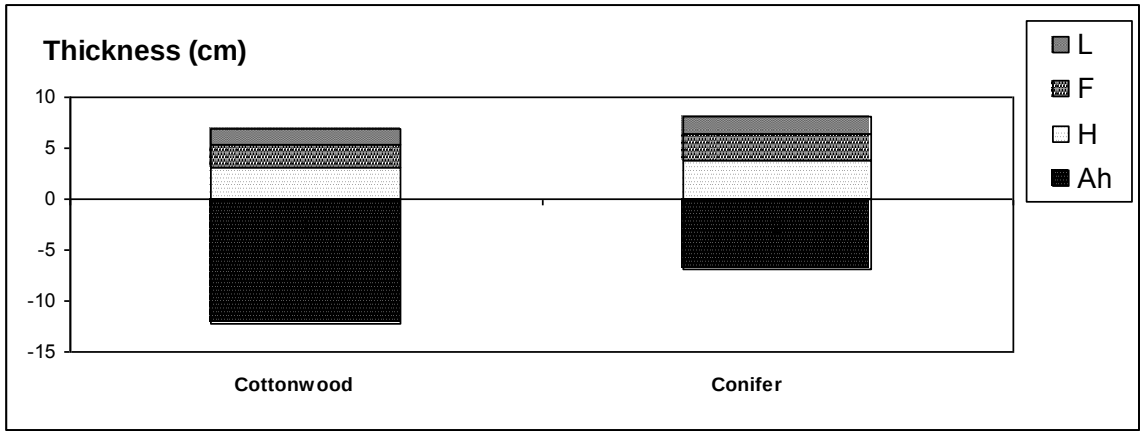


Fig. 4. Mean thickness of forest floor horizons and Ah horizons for cottonwood and conifer plots (n = 6).

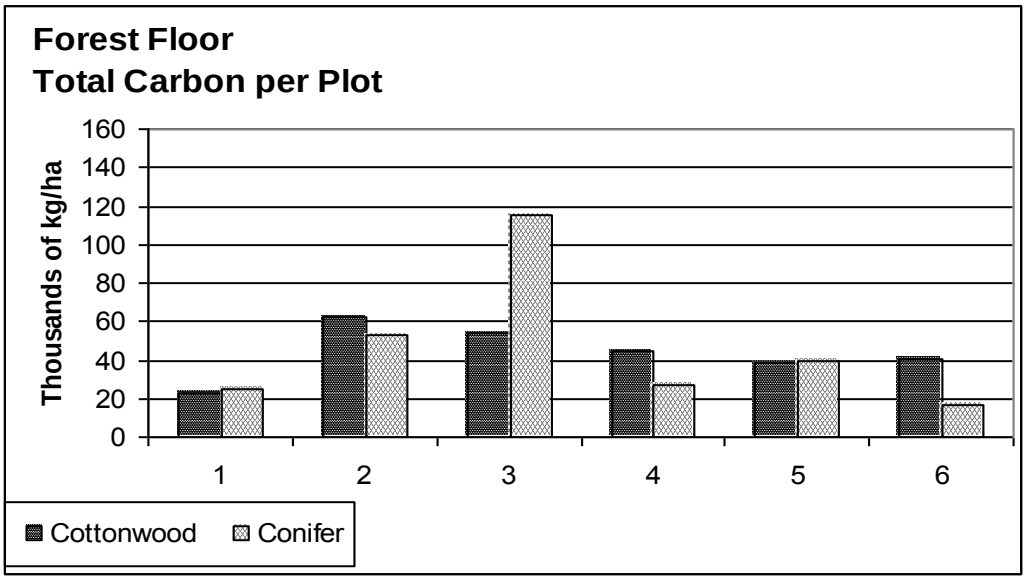


Fig. 5. Total carbon in the forest floor of cottonwood and conifer plots.

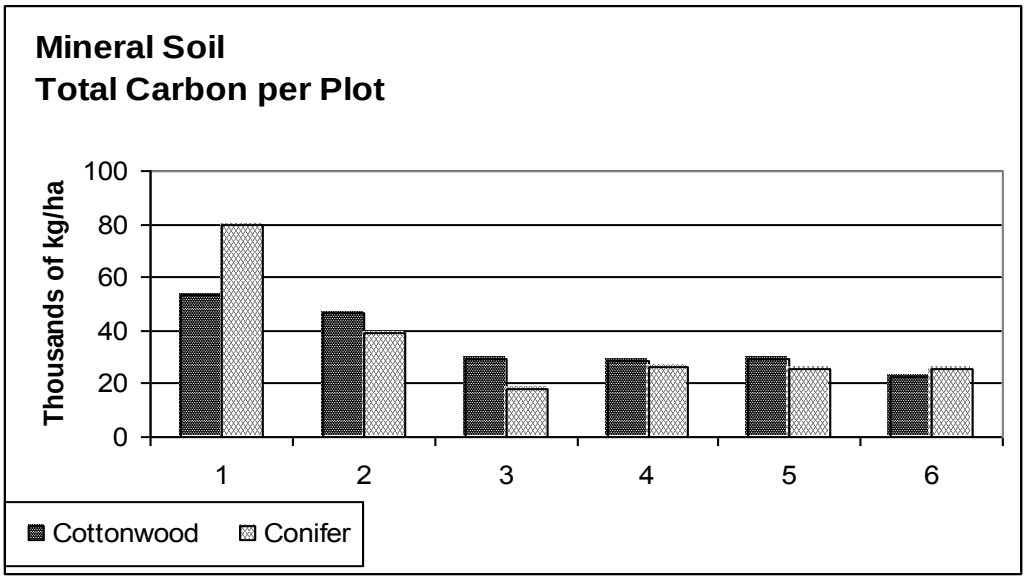


Fig. 6. Total carbon in the mineral soil of all plots.

Fig. 7. Total carbon in the mineral soil and forest floor of both plot types.

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