Canopy soils, litterfall and litter decomposition in a coastal old-growth temperate rainforest, Washington

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Abstract

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The canopy of trees has been an unreachable portion for scientific exploration until few decades ago, and the wonders and enigmas that the treetops enclose are increasingly unfolding. This study investigated the canopy environment and its epiphytes on the formation of canopy soil, transfers of biomass and N to the ground and decomposition processes in relation to climatic variables in a coastal temperate rainforest in the Queets River watershed, Olympic National Park, Washington. Canopy soils developed in bigleaf maple (*Acer macrophyllum* Pursh) and Sitka spruce (Picea sitchensis Bong. Carriere) canopies were studied. Canopy soils developed in bigleaf maple were classified as Typic Haplohemist, whereas Sitka spruce canopy soil was classified as Typic Haplosaprist. Bigleaf maple canopy soils are dominated by hemic horizons, have lower bulk density and C/N ratio relative to Sitka spruce canopy soils, which have lower pH, N content, CEC and extractable N. Relative to the forest floor, canopy soils have lower total C and N content, however canopy soils in this ecosystem are enhancing the pool of C and N by 20% and 25%, respectively, relative to the C and N pools of the forest floor.

Annual litter inputs under bigleaf maple were 4700 kg ha^{-1} with the biggest biomass contribution from maple leaves. Epiphytic litterfall contributed with 550 kg ha^{-1} of the total litter inputs. This is nearly 12% of total annual litter input, the highest contribution of epiphytic litterfall registered. Carbon and nitrogen returns in litter were dominated by maple; epiphytic litterfall contributed 240 kg ha^{-1} yr^{-1} of C and 5.7 kg ha^{-1} yr^{-1} of N to the forest floor. In Pacific Northwest forest productivity is often limited by N availability, and high inputs of N from leaves and epiphytes under the canopy of big leaf maple could make this tree a hotspot of N in this old-growth ecosystem.

Decomposition rates of green and senescent bigleaf maple leaves were determined in the bigleaf maple canopy and on the forest floor beneath maples. Decomposition rates of canopy and forest floor Oi horizons were also determined on the forest floor. Decomposition rates after two years ranged from 0.15 yr^{-1} (for canopy Oi) to 0.58 yr^{-1} (for green maples leaves). Soil temperatures had seasonal variation and were not significantly different between the canopy and forest floor. Moisture content was significantly lower in the canopy soils compared with soils on the ground. Despite significant differences on the moisture regime between the canopy and forest floor, there was no significant difference in decomposition rates between the canopy and forest floor. Wet/dry cycles of canopy soils and potential activity of soil organisms (that live in canopy soils) might have influenced decomposition aboveground. Decomposition rates for this study were strongly correlated to N concentration of the substrate.

The results of these studies highlighted the importance of the canopy environment in general as hotspots of C and N to the whole forest. The canopy of big leaf maple in particular could be a subsidiary of biogeochemical activity in the area.

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Chapter 1

Introduction

Forest canopies have long been a source of wonder, mystery, and inspiration, but relatively little is known about the ecology of canopy systems. Scientists have only recently begun investigating the complex systems of forest canopies and have discovered a significant biomass in the treetops and an array of species that are adapted to live in the canopy (Nadkarni 2001, Lowman and Rinker 2004, Diaz et al. 2010). Forest canopies provide habitat for an array of organisms, which increases forest diversity. Epiphytes are one of the most conspicuous components of the canopy environment and are largely composed of vascular and non-vascular plants (e.g., mosses, lichens, and ferns), which obtain water and nutrients from rainfall and dry precipitation. Epiphytic plants commonly grow and accumulate in the crowns of trees over several decades, forming carpets of material that cover the branches and main trunks of the host trees. As epiphytic carpets begin to undergo decomposition arboreal or canopy soil forms (Ingram and Nadkarni 1993, Perez et al. 2005, Enloe et al. 2006).

Canopy soils have been classified as arboreal Histosols (Enloe et al. 2006) and share some similarities with soils on the ground. As with any soil development on the ground surface, canopy soils are source of water and nutrients, such as C and N, for epiphytic plants and host trees via canopy roots, as well as providing habitat for canopy-dwelling organisms (Nadkarni 1981, Coxson and Nadkarni 1995, Lindo and Whiteley 2011). Because of their ability to capture and retain water and nutrients from precipitation, epiphytes along with associated canopy soils (hereafter referred to as epiphytic material (EM)) can be considered “nutrient capacitors” of the forest (Nadkarni 1984, Hietz et al. 2002).

Canopy research has focused on the biomass, abundance and distribution of epiphytes on the host tree (Sillett and Goslin 1999, Ellyson and Sillett 2003, Benzing 2004, Nadkarni et al. 2004, Williams and Sillett 2007, Diaz et al. 2010). However, EM interacts with the whole forest ecosystem. Accumulated nutrients aboveground move from the canopy to the ground when rainfall saturates canopy mats leaching nutrients from the canopy soils. Epiphytic material also falls to the ground and decomposes. Some information is available on fluxes of EM from the canopy to the ground in tropical ecosystems. However, questions regarding the fluxes of EM from the canopy to the ground, or decomposition of EM in the canopy have yet to be answered for temperate rainforests.

Canopy soils

Canopy soils are formed by the decomposition of epiphytic plants and tree litter that settle within the canopy. Studies that have compared canopy soils with normal terrestrial soils indicate that canopy soils have higher acidity and a higher cation exchange capacity (Nadkarni et al. 2002, Perez et al. 2005, Enloe et al. 2006). They have a low bulk density that ranges between 0.02-0.3 $g \cdot cm^{-3}$ (Perez et al. 2005, Enloe et al. 2006). Bulk density, an indicator of soil porosity, can be related to the water holding capacity of a soil (Brady and Weil 2000). Soils with low bulk density are susceptible to desiccation, which influences the activity of soil organisms. For example, in a tropical cloud forest, canopy soils experienced rapid desiccation during dry periods compared with the soils on the ground (Bohlman et al. 1995). Finally, canopy soils can be sources of N. Total N concentrations of tropical canopy soils range between 9.9-16.6 $mg \cdot g^{-1}$, with C/N ratios between 31-41 (Perez et al. 2005, Enloe et al. 2006, Lindo and Winchester 2007).

The canopy environment is important for the C and N cycles of forests because (1) epiphytes can intercept and retain nutrients (particularly N) from atmospheric deposition (Hietz et al. 2002, Clark et al. 2005, Wullaert et al. 2010), (2) N-fixing epiphytic organisms such as lichens or cyanobacteria contribute up to 15 kg ha^{-1} yr^{-1} of the mineral capital of N in temperate forests (Pike 1978, Lindo and Whiteley 2011), and (3) live and dead epiphytic plants within the tree canopy have biomasses ranging between 0.9- 44 Mg ha^{-1}, and can store over 1700 g m^{-2} of C and over 40 g m^{-2} of N (Lowman and Nadkarni 1995, Clark et al. 1998, Diaz et al. 2010).

Epiphytic litterfall

The pool of nutrients accumulated by epiphytic material (epiphytes + canopy soil, EM) can be released to terrestrially rooted plants when (1) EM falls to the forest floor, dies and decomposes, (2) epiphytic mats are leached by precipitation and (3) nutrients that are captured by EM are utilized by the host tree via canopy roots (Nadkarni 1981, Nadkarni and Matelson 1992, Campbell et al. 2010, Cardelus 2010). One of the greatest effects of epiphytes on the functioning of a forest ecosystem is this incorporation of allochthonous nutrients into the nutrient cycle.

Litterfall provides a pathway for nutrient and energy transfer from plants to soil. Litterfall is strongly related to aboveground productivity, nutrient cycling and soil organic matter accumulation in the forest floor (Edmonds and Murray 2002, Perez et al. 2003, Berg and McClaugherty 2008, Kohler et al. 2008). In forests where EM constitutes a large portion of the forest biomass, litterfall from EM can be an important constituent of the total litterfall that reaches the ground. Studies in temperate and tropical ecosystems have estimated that the contribution of EM to total litterfall ranges between 4-7% (Coxson and Nadkarni 1995, Clark et al. 1998, Nadkarni et al. 2000, O'Keefe and Naiman 2006, Kohler et al. 2008). Epiphytic material litterfall can be deposited on the ground as small fragments (e.g., small pieces of epiphytic mosses), attached to fallen branches, or when a whole tree falls onto the ground (Nadkarni and Matelson 1992, Coxson and Nadkarni 1995). Although some work has estimated EM litterfall in temperate ecosystems (O'Keefe and Naiman 2006, Chandler et al. 2008), there is no information about the total contribution of EM to litterfall.

Decomposition in the canopy

Although litterfall indicates the quantity of nutrients transferred within an ecosystem, decomposition rates estimate the return of nutrients into the soil pool. Most decomposition studies have described nutrient release of terrestrially rooted plants and have been conducted on the forest floor (Berg and McClaugherty 2008). Due to difficulties of accessing the canopy, knowledge regarding decomposition tens of meters above the ground is very limited and variable. For example, in a tropical forest in Costa Rica, Clark et al. (1998) compared decomposition rates of epiphytic bryophytes between the canopy and forest floor; and showed that cumulative mass loss after two years was 19% in the canopy and 29% on the forest floor. In the same study, the forest floor epiphytic bryophytes had a slightly higher decomposition rate than terrestrial bryophytes because some terrestrial bryophytes have high concentrations of lignin (Clark et al. 1998). However, in a temperate forest in British Columbia, Lindo and Winchester (2007) did not show significant differences in decomposition rates of cedar leaves in the canopy or on the forest floor.

Influence of bigleaf maple in coastal temperate forests

Bigleaf maple (*Acer macrophyllum* Pursh) is a broadleaf tree species native to the Pacific Northwest that occurs at low elevations from California to British Columbia (Kenkel and

Bradfield 1986, Turk et al. 2008). Several characteristics indicate that the presence of bigleaf maple could contribute to the supply of nutrients to the forest. First, bigleaf maple litter is rich in most nutrients compared with conifer litter and has high decomposition rates (Harmon et al. 1990, Chandler et al. 2008, Turk et al. 2008). This nutrient rich-litter improves soil fertility and soils developed under the canopy of bigleaf maples have higher pH and CEC because of bigleaf maple's base cation-rich litter (Chandler et al. 2008). Second, bigleaf maple has a positive influence on N availability. Soils developed under bigleaf maple have higher mineralizable N and N-NO_3^- compared with soils developed under conifers (Chandler et al. 2008, Turk et al. 2008). N availability is crucial to forest productivity in the Pacific Northwest, especially because soils in the area are deficient in N (Edmonds et al. 1989, Bechtold and Naiman 2009). Finally, bigleaf maple is distinctive for possessing extensive epiphytic mats that profusely cover the trunk and branches. The bark of bigleaf maple is rich in Ca and has a neutral pH that can influence the epiphytic diversity on the tree (Kenkel and Bradfield 1986). Epiphytic mats developing on bigleaf maple capture and retain nutrients within the canopy and contribute nearly four times that of the foliar biomass of the bigleaf maple (Nadkarni 1984). All these characteristics (nutrient rich litter, high available N and nutrients from EM) suggest that bigleaf maple can contribute significantly to nutrient availability in forests where bigleaf maples are present.

Objectives

Few studies have addressed the contribution of EM to the cycling of C and N in coastal temperate rainforests. Epiphytes and canopy soils could be greatly influenced by the biogeochemical cycles in forests where they are present, and their influence could significantly vary among host tree species.

The overall objective of this research was to determine the contributions of EM and the canopy environment to the transfers and transformations of C and N in a coastal temperate rainforest in the Queets River Watershed of Olympic National Park, Washington State. To address this objective, this dissertation is divided into three studies that are presented in the following chapters:

Chapter 2 describes and compares the canopy soils developed on Sitka spruce and bigleaf maple, species that harbor a large accumulation of EM. The main objective of this study was to quantify and compared the chemical and physical characteristics of canopy soils developed on Sitka spruce and bigleaf maple from a pedological perspective, and determine the C and N storage in these canopy soils.

Chapter 3 reports annual and seasonal inputs of epiphytic litterfall under the canopy of bigleaf maple, quantified annual C and N return from epiphytic material relative to other litter components, and compared litter inputs under bigleaf maple with what has been described for the whole forest.

Chapter 4 compares decomposition rates and moisture and temperature patterns between the canopy and forest floor environment of big leaf maple. In this chapter I specifically determined 1) decomposition rates and N release of green and senescent bigleaf maple leaves in the canopy environment, 2) decomposition rates and N release from green and senescent bigleaf maple leaves, and canopy and forest floor Oi horizon on the forest floor and 3) moisture and temperature patterns of the canopy (soil) and forest floor (below the organic layer) environment.

Finally, Chapter 5 synthesizes the information from Chapters 2 to 4 as to the influence of epiphytes and canopy soils as a valuable component of a forest ecosystem, discusses their importance to temperate rainforest functions and provides some future research questions.

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Chapter 2

Physical and chemical characteristics of canopy soils of Sitka spruce (*Picea sitchensis*) and bigleaf maple (*Acer macrophyllum*) in the Queets River Watershed, Washington State

Abstract

Canopy or arboreal soils develop from the accumulation and decomposition of epiphytes on branches and in bifurcations of trees in tropical and temperate rainforests. Canopy soils are important because they provide habitat, water, and accumulate allochthonous nutrients for epiphytes and their associated biota. This study characterizes the chemical and physical characteristics of canopy soils developed on Sitka spruce and bigleaf maple in an old-growth forest in the Queets River Watershed, WA. Bigleaf maple canopy soils are dominated by sapric horizons, have higher pH, N content, CEC and extractable N levels relative to Sitka spruce canopy soils, which have higher bulk density (BD) and C/N ratios. Compared with the forest floor, canopy soils have lower total C, total N and C/N ratio. Bigleaf maple canopy soil is classified as Typic Haplohemist, whereas Sitka spruce canopy soil is classified as Typic Haplosaprist. The main differences between these canopy soils are due to different inputs of host tree litter and decomposition states of the two species. Canopy soils in this ecosystem are enhancing the pool of C and N by 20% and 25% respectively relative to the C and N pools of the forest floor.

Introduction

Old-growth temperate rainforests harbor a diverse accumulation of epiphytic plants on the boles and branches of trees (Perez et al. 2005, Enloe et al. 2006). Epiphytic plants derive support from their host trees but acquire nutrients from precipitation, intercepted host tree foliage, and particulates that settle within the canopy (Nadkarni et al. 2002, Prescott 2002, Perez et al. 2005). Over time, epiphytes accumulate and decompose in branches and bifurcations of trees, developing a mat of canopy or arboreal soil (Nadkarni 1984, Nadkarni et al. 2002, Enloe et al. 2006). These canopy soils are formed mainly by the accumulation and decomposition of epiphytic plants, foliage and debris from the host tree (Nadkarni et al. 2002, Perez et al. 2005, Enloe et al. 2006). Canopy soils can become an "auxiliary" source of water and nutrients for epiphytic organisms by capturing and retaining water from precipitation as well as allochthonous inputs (Nadkarni 1981, Lindo and Whiteley 2011). These nutrients can be transferred to the forest floor and become available to terrestrial vegetation following decomposition when epiphytes fall from branches or "ride down with" broken branches or fallen trees. Additionally, some host trees gain access to this material directly via canopy roots (Nadkarni 1981). Because canopy soils contribute to moisture availability for epiphytic organisms and the host tree, they should be considered in light of changes predicted by many climate change scenarios (Veneklaas and Vanek 1990, Bohlman et al. 1995, Nadkarni and Solano 2002, Diaz et al. 2010). Climate predictions for the Pacific Northwest suggest higher rainfall during the winter and longer and drier summers (Nakawatase and Peterson 2006), so canopy soils may have a critical function for within-canopy ecosystem processes under this scenario.

Canopy soils have been classified as arboreal Histosols and share some similarities to the O horizon of the forest floor (Nadkarni et al. 2002, Perez et al. 2005, Enloe et al. 2006). For example, canopy soils have been documented as having higher acidity and higher cation exchange capacity (CEC) compared with soils on the ground (Nadkarni et al. 2002, Enloe et al. 2006). In tropical forests, canopy soils have similar temperature patterns to terrestrial horizons, whereas moisture levels differ between canopy soils and soils on the ground (Bohlman et al. 1995). Differences in the moisture content of canopy soils can be related to the content of fibrous material. High concentration of fiber makes canopy soils more susceptible to a rapid desiccation compared with their terrestrial counterparts (Bohlman et al. 1995, Enloe et al. 2006, Lindo and Winchester 2007). Elevated fiber content also affects bulk density (BD) of canopy soils, which can range between 0.02-0.3 $g \cdot cm^{-3}$ (Perez et al. 2005, Enloe et al. 2006).

In this study, I characterized and compared the characteristics of the canopy soils developed on Sitka spruce and bigleaf maple trees in an old-growth temperate rainforest of the Olympic Peninsula, Washington State. Both species support high epiphytic biomass (Nadkarni 1984, Ellyson and Sillett 2003). However, the characteristics of their canopy soils have not been described. The specific objectives of this study were to quantify and compare chemical and physical characteristics of canopy soils developed on spruce and maple and determine the C and N storage in these canopy soils.

Materials and methods

Study Area

The study site is an old-growth forest located within the Queets River watershed on the western side of Olympic National Park, Washington (47.34 N, 124.09 W). The stand is dominated by Sitka spruce and has been characterized as one of the most structurally complex forests of the northwest coast (Van Pelt et al. 2006). The climate of the area is temperate, with cool-wet winters and warm-dry summers. The rainy season extends from mid-October to mid-June (mean annual precipitation of 3000 mm (O'Keefe and Naiman 2006). Mean annual air temperature is 14.7º C. Winter mean temperatures are 7.3º C, whereas summer mean temperatures are 22º C (Latterell et al. 2006, O'Keefe and Naiman 2006, Van Pelt et al. 2006).

In the oldest stands, the dominant conifer and hardwood species are Sitka spruce and bigleaf maple. Red alder (*Alnus rubra* Bong.), vine maple (*Acer circinatum* Pursh), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) are also found within the stand. Understory vegetation is dominated by sword fern (*Polystichum munitum* (Kaulf.) C. Presl) and redwood sorrel (*Oxalis oregana* Nutt.) (Van Pelt et al. 2006). Soils in this stand are Entisols of the Huel and Tealwhit series (Bechtold and Naiman 2009).

Epiphytes are dominated by *Isothecium stolonipherum* (Brid.) and *Antitrichia curtipendula*. Vascular epiphytic plants (*Polypodium glycyrrhiza* D.C. Eaton and *Selaginella oregana)* are common, with seedlings of bigleaf maple and grass (*Elymus* spp.*)* found as occasional epiphytes. Both spruce and maple trees harbor extensive mats of epiphytes and canopy organic matter (Nadkarni 1984, O'Keefe and Naiman 2006) and for this forest, the estimated biomass of epiphytic material (epiphytic plants, leaves and debris from the host tree and canopy soils, EM) is over 10 Mg for a single spruce, including 250 kg of canopy soil and over 350 kg for maples, including 80 kg of canopy soil (R.Van Pelt, unpubl. data, 2012).

Additionally, these two species have contrasting architecture and phenology. Dominant spruce trees are taller and older (>60 m and ≥300 years) than the maples (~40 m and 200 years); thus epiphytic mats have a longer time to develop on spruce trees than on maples (Van Pelt et al. 2006). Spruce retains foliage throughout the year whereas maples drop leaves during the fall, creating a contrasting light environment in each host tree which can affect the photosynthetic activity of epiphytic plants (Kenkel and Bradfield 1986, Lowman and Rinker 2004, Turk et al. 2008).

Sample collection and analysis

Single-rope tree climbing techniques (Perry 1978) were used on two spruce and four maple trees to sample canopy soils (two branches per spruce tree and one branch per maple tree). The selection of trees was based on their location within the old-growth stand (Van Pelt et al. 2006) and age, since older trees have well-developed canopy soil. Maple and spruce were sampled in June 2010 and March 2011, respectively. Soil samples from spruce were collected at a height between 19-51 m. Maple samples were collected at a height between 9-19 m. On each branch, the cross section (25 cm) of an epiphytic mat was sampled. Samples were taken back to the lab and stored at 3º C until processed. A morphological description of each canopy soil profile was done to determine the depth and horizon sequence of each profile. Additionally, four forest floor samples (O-horizon) were collected under the canopy of bigleaf maple and four forest floor samples under spruce.

To measure bulk density of canopy soils, a volume between 15 -56 cm^3 of soil of each horizon was cut and oven dried at 65º C for 48 hr. For forest floor bulk density, a volumetric sample between 17 -56 cm^3 was cut and oven dried at 65º C for 48 hr. Separate canopy samples were sieved through 12 mm and 4 mm sieves to remove coarse material (conifer cones, canopy roots). Sieved horizon samples were analyzed for rubbed fiber content and pyrophosphate color (using a saturated solution of sodium pyrophosphate) to distinguish fibric, hemic, and sapric materials and designate subordinate horizons (Burt 2004). Ash content was determined by loss on ignition (LOI) at 550º C for four hours. Soil color was determined using a Munsell color chart for moist, sieved samples. Soil pH in water was determined using a saturated paste solution.

Carbon and N concentrations of both canopy and ground O horizons were measured by dry combustion using a Perkin Elmer Model 2400 CHN analyzer (Perkin Elmer, Wellesley, MA). Total C and N mass held in the canopy soil was calculated by multiplying the mass of canopy soil (R. Van Pelt, unpublished data, 2012) by the crown area of spruce or maple with C or N concentration. Total C and N contents of the O horizons on the ground were calculated by multiplying concentration by depth and bulk density.

Extractable N (as NH_4^+ and NO_3^-) of canopy soils was determined with a 1*M* KCl extraction (Bremner and Mulvaney 1982), and analyzing solutions using an auto analyzer (Perstorps Analytical 500 Series Flow-injection, Silver Spring, MD). Cation exchange capacity (CEC already abbreviated) of canopy soils was estimated using an unbuffered 1.0 *M* NH_4Cl solution (Skinner et al. 2001). Maple and spruce canopy soils were classified according to USDA Soil Taxonomy (Soil Survey Laboratory Staff 2006).

To determine significant differences between spruce and maple canopy soils I used the Wilcoxon signed-rank test, using a significance level of $p= 0.05$. All analyses were performed using R (R Development Core Team 2012).

Results

Mean maple canopy soil thickness (23 cm) tended to be thicker than spruce canopy soil (16 cm) (Table 2.1) (Fig. 2.1), with ranges of 13-48 cm for maple and 11-18 cm for spruce. Both canopy soil types have fibric (Oi), hemic (Oe) and sapric (Oa) horizons (Fig. 2.1). Fibric horizons are composed mainly of dead epiphytes, fern roots, moss rhizomes and tree leaves. Hemic horizons (Oe and Oe2) contained abundant rhizomes, buried dead epiphytes, and *P. glycorhiza* roots. Hemic horizons were predominant on maple canopy soils. Sapric horizons (Oa) were composed of unrecognizable plant residues with moss rhizomes and canopy roots from the host tree. Sapric horizons of Sitka spruce canopy soils were thicker compared to the sapric horizons of maple canopy soils (Fig.2.1).

The dominant color for both soil types was reddish brown but with increasing depth the soil was blacker in spruce canopy soil and browner in maple canopy soil (Table 2.1, Fig. 2.1). Fiber content decreased with depth in spruce canopy soil (from 73% to 48%, Table 2.1). Maple canopy soil had over 60% fiber content, which did not decrease with depth (Table 2.1). The broad range in fiber content was related to the high abundance of rhizomes across both soil profiles. Bulk density increased with depth for both canopy soil types and was significantly higher on spruce canopy soil ($p = 0.05$, Table 2.1). No significant differences were found between bulk density of the canopy soil and the O-horizon beneath the respective host tree (Table 2.1).

The pH of canopy soils in both trees was acidic and differed significantly between spruce and (mean 4.1) maple soils (mean 4.8) ($p = 0.03$, Table 2.2). The pH for spruce canopy soil decreased with depth from 4.2 to 3.8, whereas the pH of maple canopy soils slightly increased with depth from 4.6 to 5.0. Ash content increased with depth by horizon type in maple soils whereas it decreased from hemic to sapric horizons in spruce canopy soil. There was no significant difference in ash content between soil types (Table 2.2).

Cation exchange capacity increased with depth in both canopy soil types and was significantly higher in maple canopy soils than spruce canopy soils ($p = 0.03$, Table 2.3). Base saturation did not differ between soil types but was more variable in spruce canopy soils, ranging between 18% and 58% (Table 2.3). Exchangeable cations, particularly Ca, were significantly higher in maple canopy soil ($p = 0.03$, Table 2.3).

Carbon concentration did not differ between canopy soils types, whereas N concentration was significantly higher for maple canopy soil ($p < 0.05$, Table 2.2). C/N ratios differed significantly between soil types ($p = 0.03$), with maple canopy soils having a lower C/N ratio (Table 2.2).

Total C content was >100 g cm^{-2} for maple canopy soils and >270 g cm^{-2} for spruce canopy soils (Table 2.4). For the O-horizon, total C content under spruce was > 1500 g cm^{-2} and maple and nearly 300 g cm^{-2} under maple. Total N content had the following sequence: maple canopy soil < spruce canopy soil < O-horizon under maple < O-horizon under spruce ($p = 0.03$). Carbon/Nitrogen ratios differed significantly between canopy soil types ($p = 0.03$). However, there was no difference in the O horizon C/N ratios under spruce and maple (Table 2.4).

Extractable ammonium and nitrate concentrations in maple canopy soil were significantly higher than those in spruce canopy soil ($p < 0.02$). There was little variability in either extractable ammonium or nitrate by depth in the spruce canopy soil (Fig. 2.2). Extractable N varied more with horizon depth in maple than spruce canopy soil. A much smaller fraction of N was extractable in the spruce canopy soil compared with the maple; this corresponds with the lower C/N ratio in maple soil.

Canopy soils developed on maple and spruce have distinguishable O horizons in different stages of decomposition that are a result of different pedogenic processes (essentially differences in litter inputs and decomposition) and time for these O horizons to develop. I classified maple canopy soils as Typic Haplohemist because the hemic horizons were the dominant organic materials in this soil, while spruce canopy soils were classified as Typic Haplosaprist based on the dominance of sapric materials.

Discussion

Canopy soils developed on maple and spruce trees have different physical and chemical properties that are influenced by the tree species. Tree age and consequently the time these canopy soils have had to develop play a key role in determining spruce and maple canopy soil characteristics. At the Queets River watershed, large spruce trees have a maximum age of 330 years, whereas the age of large maples is about 200 years (Van Pelt et al. 2006). Canopy soil developed only on the older trees of both species. Canopy soils developed on the spruces had a more advanced state of decomposition reflected by the dominance of sapric (Oa) horizons and higher bulk densities than maple canopy soils. Spruce are the tallest tree species present, and canopy mats on Sitka spruce have litter inputs almost exclusively from this host tree. Canopy soils of maple are at a lower height and capture some needles blown from nearby spruce in addition to accumulating maple leaves.

The thicker maple canopy soils, which are dominated by hemic (Oe) horizons, are the result of a rapid accumulation of epiphytes in canopy mats as well as inputs of nutrient-rich maple leaf litter. The thicker maple canopy soils have a lower bulk density because of the high abundance of rhizomes that increase canopy soil porosity.

Canopy soils on maples have similar bulk densities to canopy soils of *Fitzroya cupressoides* (Cupressaseae) in Chile (Perez et al. 2005), whereas spruce canopy soils have a similar bulk density to canopy soils of redwoods in California (Enloe et al. 2006). Although maple canopy soils are predominantly fibric, overall bulk density is lower than Oi horizons on the ground (D'Amore and Lynn 2002). For spruce canopy soils, the bulk density at lower depths (Oa horizons) is comparable to sapric horizons of Histosols on the ground (D'Amore and Lynn 2002). Other studies indicate that mineral soil developed under maple has a lower bulk density compared with mineral soils under Douglas-fir, with differences attributed to the large inputs of maple litter (Turk et al. 2008).

Fiber content of maple canopy soils was >60% throughout the profile, with a large contribution of rhizomes and canopy roots from the host tree. High fiber content in organic soils promotes large pore space that reduces water retention and therefore affects water availability for canopy dwelling organisms (Bohlman et al. 1995, Perez et al. 2005, Enloe et al. 2006). The more decomposed and developed horizons of the spruce canopy soil may provide more moisture to epiphytes and canopy roots during droughty periods. Furthermore, when spruce needles decompose, waxes and organic acids and phenols are released creating the dark-colored horizons of this sapric soil (Ghosal et al. 1999, Berg and McClaugherty 2008).

Ash contents were similar to those described for tropical canopy soils and are typical of Histosols (Nadkarni et al. 2002, Soil Survey Laboratory Staff 2006). Maple canopy soil ash content increased with depth but there was no clear trend with spruce canopy soil (Table 2.3). Differences in ash content are attributed to a higher litter mineral concentration (e.g., Ca) from abscised leaves that accumulate on the canopy mats of maples over time (Turk et al. 2008).

The pH of maple canopy soils was significantly higher than the pH of spruce canopy soils (Table 2.2). Higher acidity of spruce canopy soil is comparable to the O-horizon of temperate and tropical forests (Nadkarni and Solano 2002, Perez et al. 2005). Also, the lower pH of spruce canopy soils indicates an accumulation of organic acids as epiphytic mats develop over time (Ghosal et al. 1999). The lower acidity of O horizons under maple canopy compared with O horizons under spruce has been previously described for the forest floor of temperate forests in British Columbia (Chandler et al. 2008, Turk et al. 2008). This trend extends to the canopy environment as well.

Despite the acidic pH, CEC and base saturation for maple canopy soils are relatively high and could be influenced by the high Ca content of maple foliar litter (Chandler et al. 2008) that accumulates in the canopy mats. Such inputs are absent in spruce canopy soils, although calcareous material from mollusks and insects could be enhancing Ca levels of spruce soils (Lowman and Rinker 2004, Lindo and Winchester 2007). Lower CEC and base saturation of spruce canopy soil might limit nutrient availability for epiphytic plants growing on spruce trees compared with epiphytes growing on maple canopy soils. Turk et al. (2008) found similar differences in CEC and base saturation in the mineral soil beneath maple compared with conifers.

Carbon concentration of spruce canopy soil was similar to canopy soils developed on other conifers trees (Perez et al. 2005, Enloe et al. 2006). Whereas the C concentration of spruce canopy soils was higher than the C concentration of maple canopy soils, this relationship was reversed in the O-horizons on the ground (Table 2.4). Similar trends have been documented between C concentrations of the forest floor below maple and conifer species, where forest O horizons under maple had a higher C concentration than O horizons under Douglas-fir (Fried et al. 1990, Turk et al. 2008).

Extractable N differed greatly between maple and spruce canopy soils (Fig. 2.2). Ammonium was the dominant extractable form of nitrogen, which suggests higher potential mineralization rates (specifically high ammonification) in maple canopy soils compared with spruce canopy soils. Studies of forest floor soils under maple indicate that high mineralization is related to high N concentrations of maple litter (Fried et al. 1990, Turk et al. 2008). Lower C/N ratios of maple canopy soils also suggest a higher mineralization rate as well, thereby increasing

N availability for plants and microorganisms in the canopy of maple trees (Brady and Weil 2000, Berg and McClaugherty 2008).

The C/N ratio was significantly lower in maple canopy soils compared with spruce canopy soil. The C/N ratio of soils on the ground did not differ between tree types, a trend that has previously been noted for soils in British Columbia (Fried et al. 1990, Turk et al. 2008). Overall, C/N ratios were lower in the canopy environment than in the forest floor (Table 2.4), which suggests higher N mineralization rates in the canopy. Furthermore, the higher C/N ratio of the forest floor could be influenced by woody biomass accumulated on the ground (Lindo and Winchester 2007, Berg and McClaugherty 2008).

In temperate forests N concentrations of canopy soils range between 10-17 mg g^{-1}, while C/N ratios range between 31-41 (Perez et al. 2005, Enloe et al. 2006, Lindo and Winchester 2007). In this study, N concentrations and C/N ratios of spruce canopy soil are within the range typical of many temperate forests, whereas maple canopy soils have a higher total N and lower C/N ratios more similar to the soil of a Costa Rican rainforest (Nadkarni et al. 2002).

The canopy soil biomass of spruce and maple trees was over 250 kg for spruce and 80 kg for maples (R. Van Pelt, unpubl. data, 2012). This is the equivalent of 273 g m^{-2} and 114 g m^{-2} of C and 9 g m^{-2} and 5 g m^{-2} of N held in the canopy of spruce and maple trees, respectively. Although the total quantity of C and N in the forest floor is much higher that what is being held in the canopy (Table 2.4), maple canopy soils contain 50% and 30% of the total N and C mass, respectively, relative to the O-horizon under maple. Spruce canopy soils increase the total C and N mass by 18% and 20% relative to the O-horizon beneath. Lower total C and N contribution of spruce canopy soils compared with the O-horizon underneath is attributed to slower decomposition rate of spruce needles that promotes a high forest floor accumulation (Harmon et al. 1990).

Different tree species influence the properties of the soils beneath their crowns; canopy soils properties are also influenced by the properties of the host tree in which they develop, largely through its foliar litter. The canopy soils of this temperate ecosystem provide a suitable substrate for increased epiphytic growth, canopy root access, and arboreal organisms. The arboreal soils also store a substantial C and N pool that enhances that of the total forest ecosystem.

Conclusions

This study documents differences between canopy soils developed on Sitka spruce and bigleaf maple. Some of these differences are reflected in the horizon development of spruce and maple canopy soils and chemical properties of these two soils such as pH, CEC, and C/N ratio. Chemical difference between maple and spruce canopy soils are influenced by litter inputs of the host tree and the nutrient content of such litter. Nutrient rich litter from maple increases N content and mineralization, CEC, and exchangeable cations. On the other hand older canopy-dominant Sitka spruce trees have higher acidity and bulk density and lack the nutrient rich litter inputs that maple canopy soils have.

In the Queets River watershed the biomass held in the treetops augments the pool of nutrients and organic matter that resides on the forest floor. These accumulated nutrients could interact with the whole ecosystem when these nutrients are absorbed by epiphytic plants or the host tree (via canopy roots), leached via throughfall or stemflow, or deposited as epiphytic litterfall to the forest floor. Epiphytes and canopy soils are important in the accumulation of biomass and nutrients in the canopy compartment.

Tables

Table 2.1: Physical properties of canopy and forest floor O horizons with frequency of occurrence (n) for the four profiles sampled at the Queets River watershed, Washington. Moist color and SPEC values were visually averaged among replicates. Bulk density values are the mean with standard deviation. Mean and standard deviation of depth (of the whole profile and per horizon), bulk density of surface soil O-horizon beneath the canopy of maple and spruce is also included. Superscript letters indicates significantly different values within a column and between species ($p \leq 0.05$).

Horizon	------ Depth *(cm)* -----		Moist color	SPEC color	Rubbed fiber	Boundary	Bulk Density
(n)	Average	Maximum			*(%)*		$g \cdot cm^{-3}$
Big leaf maple							
Canopy Soil							
Oi (4)	4.8	7.5	5YR 3/4	8/3	64	ab/aw	0.04 (0.01)
Oe (4)	12	21	2.5YR 3/4	8/3	67	aw/ab	0.06 (0.01)
Oe2 (3)	3.9	7.5	5YR 3/3	8/2	66	Aw	0.06 (0.03)
Oa (1)	2.3	9	5YR 2.5/2	8/2	64		0.16
Mean	23 (6.2)				66 (7.8) ^{c}		0.06 (0.04) ^{c}
Forest Floor							
Oi (4)	1.7 (0.4)	4	ND	ND	ND	ND	0.04 (0.02) ^{c}
Sitka spruce							
Canopy soil							
Oi (3)	2.6	6	5YR 2.5/3	8/2	73	Aw	0.06 (0.04)
Oe (3)	2	3.5	2.5 YR 2.5/1	8/2	71	Ab	0.09 (0.05)
Oe2 (2)	2.5	6.5	10R 2.5/2	7/4	68	ab/aw	0.08 (0.01)
Oa (4)	5.1	6.5	10R 2.5/2	8/3	59	Ab	0.10 (0.03)
Oa2 (2)	3.1	6.5	5 YR 2.5/2	8/3	48		0.20 (0.05)
Mean	16 (2.4)				67 (11.5) ^{c}		0.11 (0.04) ^{d}
Forest Floor							
Oi (4)	6.2 (1.9)	10.5	ND	ND	ND	ND	0.07 (0.02) ^{cd}

a = abrupt; w= wavy; b=broken

ND = Not determined

Table 2.2: Mean and standard deviation of pH, percentage total carbon (C) and nitrogen (N), C/N ratio and ash content from loss on ignition for maple and spruce canopy soils from the Queets River watershed, Washington. Superscript letters indicates significantly different values within a column and between species ($p \leq 0.05$).

Horizon	pH	Ash	C total	N total	C/N
		%	------------- $mg \cdot g^{-1}$ -------------		
Big leaf maple canopy soil					
Oi	4.6 (0.5)	4.1 (0.4)	441 (18)	18 (3.2)	25 (3.2)
Oe	4.8 (0.2)	4.3 (0.7)	427 (46)	18 (1.8)	23 (2.8)
Oe2	4.9 (0.5)	5.1 (0.8)	414 (55)	19 (3.5)	21 (2.0)
Oa	5.0	6.2	378	19	20
Mean	4.8 (0.4)^{a}	4.6 (0.9)^{a}	424 (4)^{a}	19 (0.3)^{a}	22 (2.2)^{a}
Sitka spruce canopy soil					
Oi	4.2 (0.2)	4.5 (0.5)	449 (28)	14 (1)	31 (1.1)
Oe	4.1 (0.1)	6.5 (1.4)	449 (17)	16 (1.6)	29 (3.2)
Oe2	4.1 (0.2)	5.9 (0.6)	455 (1)	15 (2)	30 (4.1)
Oa	4.1 (0.1)	4.2 (0.6)	464 (30)	15 (2.6)	30 (3.6)
Oa2	3.8 (0.03)	4.2 (0.4)	442 (15)	16 (1.7)	28 (3.8)
Mean	4.1 (0.1)^{b}	5.0 (1.2)^{a}	453 (2)^{a}	15 (0.2)^{b}	30 (3.0)^{b}

Table 2.3: Cation exchange capacity (CEC), % base saturation (BS) and exchangeable cations for maple and spruce canopy soils from the Queets River watershed, Washington. Superscript letters indicate significantly different values within a column and between species ($p \leq 0.05$).

Horizon	CEC	BS	Ca	K	Mg	Na
	$cmol_c\ kg^{-1}$	*%*	——— *$mg\ g^{-1}$* ———			
Big leaf maple canopy soil						
Oi	51 (5)	70.7 (29)	4.4 (1.1)	1.0 (0.4)	1.0 (0.3)	0.2 (0.1)
Oe	55 (13)	63.9 (30)	4.1 (0.1)	0.9 (0.4)	0.9 (0.3)	0.2 (0.1)
Oe2	46 (6)	77.8 (36)	4.1	1.2 (0.7)	1.0 (0.4)	0.2 (0.0)
Oa	67	NA	TR	0.6	0.9	0.3
Mean	52 (10)^{a}	44.5 (29)^{a}	3.6 (1.8)	1.0 (0.5)	1.0 (0.3)	0.2 (0.1)
Sitka spruce canopy soil						
Oi	29 (16)	50.7 (14)	1.9 (0.6)	0.3 (0.0)	0.3 (0.1)	0.1 (0.0)
Oe	36 (12)	18.4 (3)	0.9 (0.2)	0.1 (0.1)	0.2 (0.1)	0.1 (0.0)
Oe2	32 (21)	39.5 (11)	2.0 (1.7)	0.3 (0.2)	0.3 (0.3)	0.1 (0.0)
Oa	32 (19)	30.2 (27)	2.0 (1.6)	0.1 (0.1)	0.3 (0.2)	0.1 (0.1)
Oa2	35 (1)	58.3 (7)	3.2 (0.5)	0.1 (0.0)	0.4 (0.1)	0.2 (0.0)
Mean	33 (14)^{b}	41.9 (20)^{a}	1.9 (1.2)	0.2 (0.1)	0.3 (0.2)	0.1 (0.1)

TR = trace, NA = not available

Table 2.4: Mean and standard deviation of C and N concentration and total content of canopy and surface soil O-horizon (within and beneath the canopy) and C/N ratios of maple and spruce at the Queets River Watershed, WA. Superscript letters indicates significantly different values within a column ($p \leq 0.05$).

	Carbon		**Nitrogen**		**C/N ratio**
	(mg·g^{-1})	Total (g m^{-2})	(mg·g^{-1})	Total (g m^{-2})	
Big leaf maple					
Canopy	424 (4) ^{a}	114 (8) ^{a}	19 (2) ^{a}	5 (0.5) ^{a}	22 (2) ^{a}
Forest floor	400 (27) ^{a}	298 (65) ^{a}	12 (1) ^{bc}	10 (4) ^{a}	33 (5) ^{b}
Sitka spruce					
Canopy	452 (13) ^{a}	273 (8) ^{a}	15 (1) ^{b}	9 (1) ^{a}	30 (3) ^{b}
Forest floor	366 (10) ^{a}	1550 (78) ^{a}	10 (2) ^{c}	46 (7) ^{a}	36 (5) ^{b}

Figures

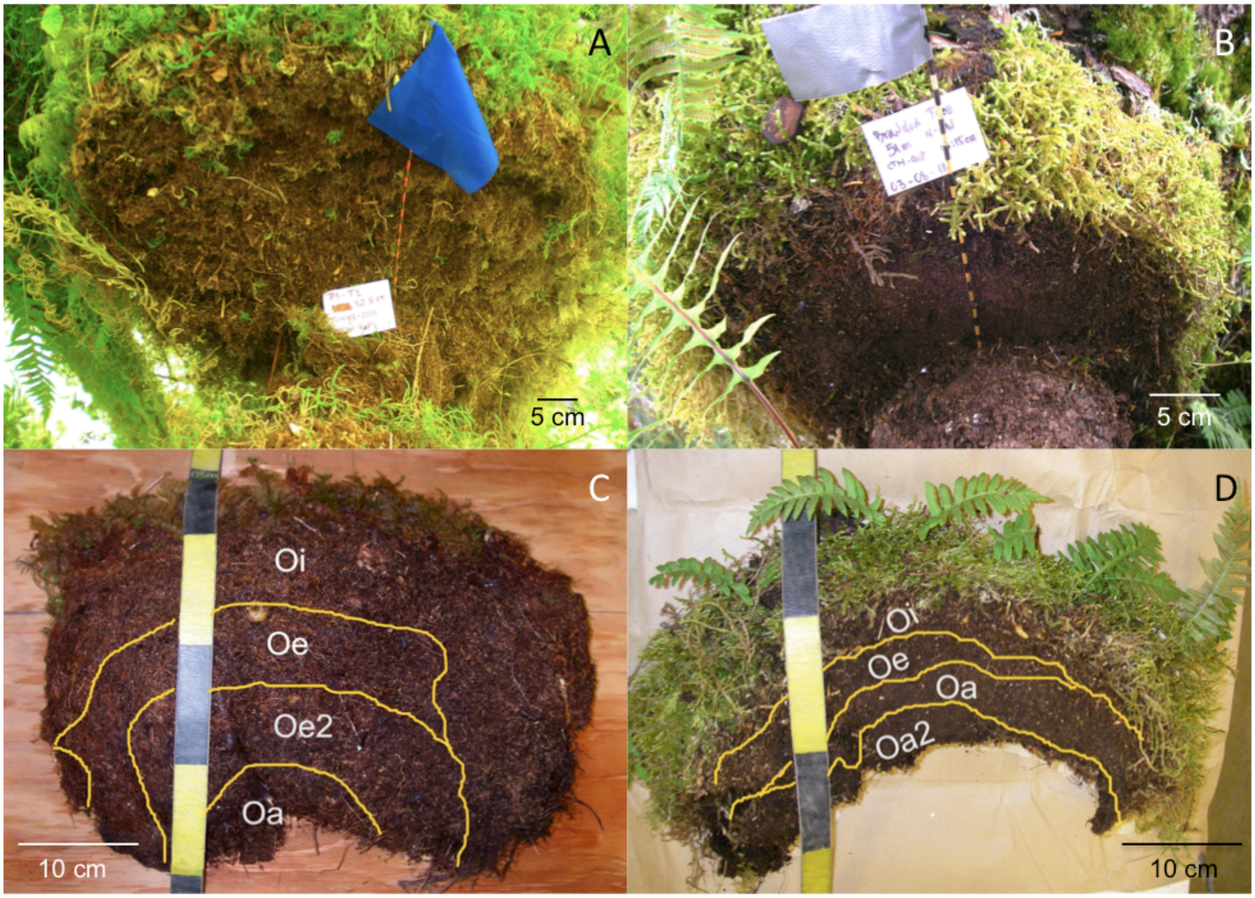

Figure 2.1: Canopy soils on maple (A, C) and spruce (B, D) trees. Photographs of in situ characteristics (A + B), laboratory measurements showing final horizons designations (C + D)

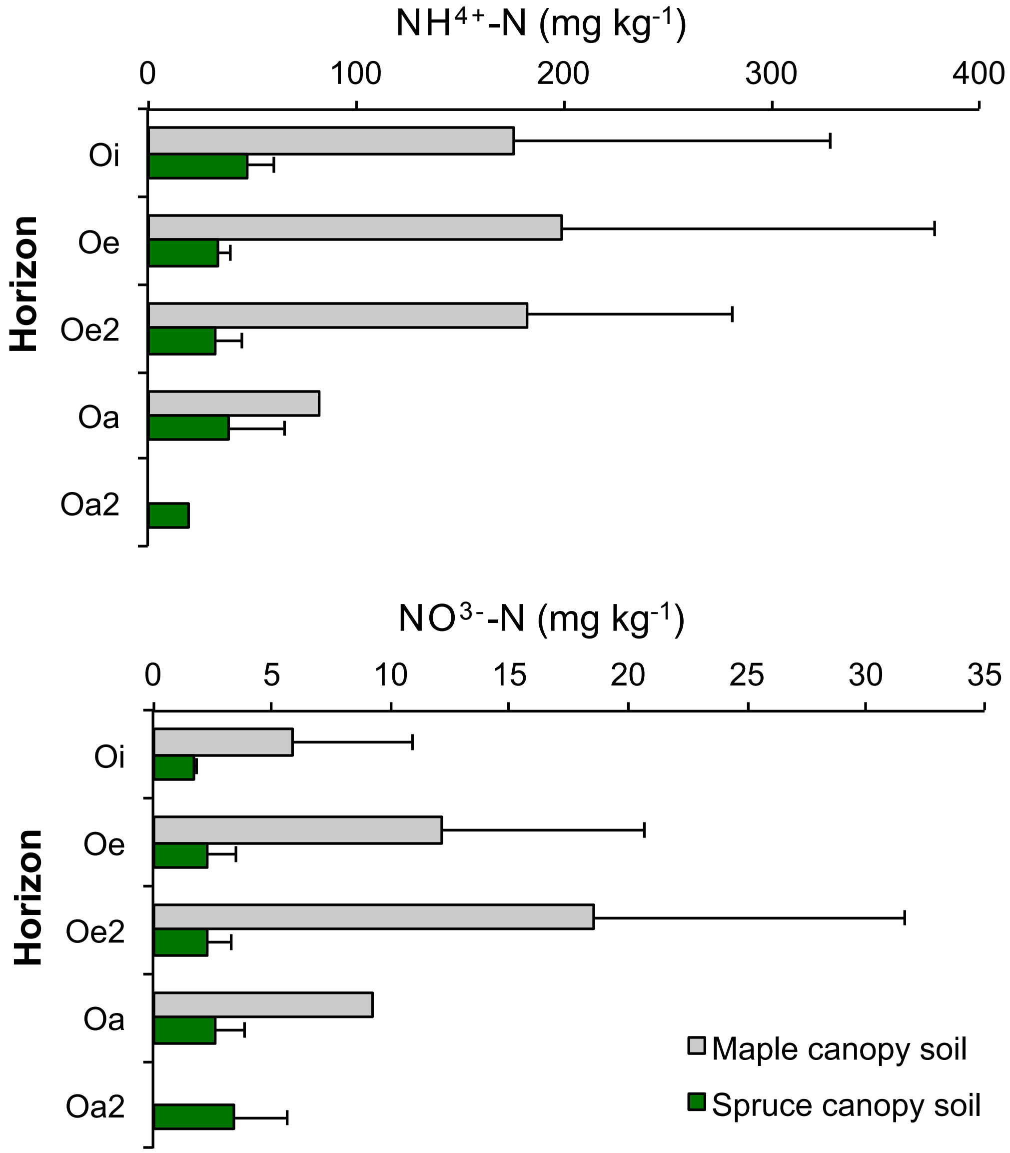

Figure 2.2: Mean extractable ammonium and nitrate N concentrations for maple and spruce canopy soils.

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Chapter 3

Epiphytic litter under the canopy of *Acer macrophyllum* in an old-growth temperate rainforest of Washington State, USA

Abstract

Inputs of epiphytic litterfall have often been underestimated in litterfall studies however they are important due to the capability of epiphytes to capture and retain nutrient from atmospheric sources and transfer these to the ground. In this study, I quantified epiphytic litter inputs under the canopy of bigleaf maple and compared them to litterfall from terrestrially rooted material in a coastal old-growth temperate rainforest in Washington State. Annual litter inputs under bigleaf maple were 4760 kg ha^{-1} with the biggest biomass contribution from maple leaves. Of the total litter input, 546 kg ha^{-1} corresponded to epiphytic litterfall. This is the equivalent to nearly 12% of total annual litter input, the highest contribution of epiphytic litterfall registered. Maple leaves also dominated annual C and N returns in litter; epiphytic litterfall contributed 240 kg ha^{-1} yr^{-1} of C and 5.7 kg ha^{-1} yr^{-1} of N to the forest floor. The productivity of Pacific Northwest forests is often limited by N availability, and high inputs of N from leaves and epiphytes under the canopy of big leaf maple could make this tree a hotspot of N in this old-growth ecosystem.

Introduction

Epiphytes, plants that live on another plant but are not parasitic, are a component of many forest ecosystems (Lowman and Nadkarni 1995). Epiphytic plants (e.g., mosses, lichens, or vascular plants) derive support from their host trees but garner their nutrients from mist, fog, rain, and particulates that settle within the canopy (Lowman and Nadkarni 1995). Epiphytes accumulate and decompose on trunks and branches of trees, developing an arboreal soil underneath epiphyte mats (Nadkarni 1984, Enloe et al. 2006). Whereas terrestrially rooted vegetation (trees, shrubs and herbs) obtain their nutrients predominantly from the soil, canopy plants use allochthonous sources of wind- and rain-borne nutrients or arboreal soil (Nadkarni and Matelson 1991, Knops et al. 1996, Enloe et al. 2006). Because epiphytic material (plants plus canopy soil, hereafter EM) captures allochthonous nutrients that settle within the canopy, the deposition of epiphytic litterfall to the forest floor can enhance the cycling of nutrients (particularly N) of the whole ecosystem. The contribution of EM to litterfall might be of great importance in forest ecosystems where N limits productivity, as often happens in Pacific Northwest forests (Edmonds et al. 1989, Fried et al. 1990, O'Keefe and Naiman 2006).

Fluxes of fallen litter provide a pathway for nutrient and energy transfer from plants to soil (Coxson and Nadkarni 1995, Lindo and Winchester 2007) and this flux of litterfall has been related to forest productivity, nutrient cycling, and accumulation of soil organic matter (Edmonds and Murray 2002, O'Keefe and Naiman 2006). Litterfall is influenced by a variety of factors including climate, seasons, forest type, successional stage and site productivity (Edmonds 1980, Perez et al. 1991, Edmonds and Murray 2002, Perez et al. 2003, Berg and McClaugherty 2008).

There is extensive information regarding the quantity of litterfall from terrestrially rooted plants, but very few studies have addressed the contribution of epiphytic litterfall in forests where epiphytic material is present (Veneklaas 1991, Nadkarni and Matelson 1992, O'Keefe and Naiman 2006, Kohler et al. 2008). In forests where EM is a conspicuous component, EM litterfall can be an important contributor to total litterfall biomass. For instance, Veneklaas (1991) estimated the total litterfall of a Colombian montane forest as 4.3 $Mg \cdot ha^{-1} \cdot yr^{-1}$, with ~ 5% of this litter attributed to epiphytes (vascular plants, bryophytes and lichens). Similarly, in an upper montane forest of Costa Rica, Kohler et al. (2008) estimated the contribution of epiphytic litterfall in an old-growth tropical forest as 6% of total litterfall.

Collection of EM litterfall can be challenging, as it is extremely sporadic. Nadkarni and Matelson (1992) found that over 50% of EM litterfall was collected in less than 2% of their collection containers. A study of an old-growth forest in Costa Rica also indicated that epiphytic litterfall had high spatial and temporal variability (Kohler et al. 2008).

In the Pacific Northwest, total fine litterfall inputs have been estimated (Abee and Lavender 1972, Edmonds and Murray 2002, Harmon et al. 2004, O'Keefe and Naiman 2006, Klopatek 2007), but only a few studies have quantified the contribution of EM to total litter biomass (Abee and Lavender 1972, O'Keefe and Naiman 2006). These studies however, only accounted for the epiphytes captured in small collectors; therefore, the contribution of epiphytes was likely underestimated. O’Keefe and Naiman (2006) noted a significant relationship between epiphytic litterfall and the basal area of Sitka spruce (*Picea sitchensis* (Bong.) Carrière) and bigleaf maple (*Acer macrophyllum* Pursh), that correlated with the large biomass of epiphytes held by individual trees of these two species.

Bigleaf maple is an endemic tree of the Pacific Northwest characterized by large accumulations of epiphytic biomass (Nadkarni 1984). Compared to conifer species, bigleaf maple can increase soil fertility and thus the supply of nutrients to the forest floor through litter that is rich in N, Ca and K (Turk et al. 2008). Moreover, Chandler et al. (2008) described higher total litter inputs under bigleaf maple compared with total litter under conifer species. The combined effect of epiphytic biomass, nutrient-rich litter and higher litterfall inputs suggest that the presence of bigleaf maple could enhance the movement of N from the canopy to the forest floor of temperate rainforests.

The objective of this study was to determine the contribution of EM relative to total litterfall under the canopy of big leaf maple in a coastal old-growth temperate rainforest in Washington State. Epiphytic biomass in the area is abundant; one single Sitka spruce tree can hold over 1000 kg of dry epiphytic biomass and a single bigleaf maple tree can support over 450 kg (R. Van Pelt and others, unpublished data). Considering this abundant epiphytic biomass, I determined annual and seasonal inputs of epiphytic litterfall under the canopy of bigleaf maple, quantified annual C and N return from epiphytic material relative to other litter components, and compared litter inputs under bigleaf maple with what has been described for the whole forest.

Methods

Study Site

The study was conducted from June 2010 to November 2012 in an old-growth forest located at the Queets River watershed on the western side of Olympic National Park, Washington state (47.34 N, 124.09 W). The area has a temperate climate, with cool-wet winters and relatively warm-dry summers. The mean annual precipitation is ~3000 mm with precipitation peaking from November to June. Mean annual air temperature is 14.7 ºC ranging from 7.3ºC in the winter to 22ºC in the summer (Bechtold and Naiman 2009).

The forest is described by Van Pelt et al. (2006) and is dominated by Sitka spruce in the older stands (>300 yr.), with occasional western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*). Bigleaf maple is the dominant hardwood specie in the older stands and its crown volume corresponds to 17% of total crown volume (Van Pelt et al. 2006). Other hardwood species present in the stand are red alder (*Alnus rubra* Bong.) and vine maple (*Acer circinatum* Pursh). Understory vegetation is dominated by sword fern (*Polystichum munitum* (Kaulf.) C. Presl) and redwood sorrel (*Oxalis oregana* Nutt.) (Van Pelt et al. 2006). In the canopy, the predominant epiphytes are the bryophytes icicle moss (*Isothecium stolonipherum* Brid.) and hanging moss (*Antitrichia curtipendula* (Hedw.) Brid.). Epiphytic vascular plants such as licorice fern (*Polypodium glycyrrhiza* D.C. Eaton) and Oregon selaginella (*Selaginella oregana* D.C. Eaton) are common in the canopy; epiphytic lichens such as lettuce lung (*Lobaria oregana* (Tuck.) Müll. Arg.) and lungwort (*L. pulmonaria* (L.) Hoffm.) are also common.

Sampling and Analysis

In June 2010, four 30 m x 30 m plots were installed in the old-growth stands (> 250 yr old) based on the presence of at least two mature bigleaf maple trees. Within each plot, crown cover of bigleaf maple was estimated and ranged between 39 and 52%. I used two methods to estimate litter inputs to the forest floor. For smaller materials (epiphytes fragments <100 cm^2 and litter from trees), I installed three 50 cm x 50 cm litter traps per plot (hereafter, "small traps") lined with 1.5 mm nylon mesh across wooden frames. Each trap was 20 cm high and placed on the forest floor to avoid disturbance from elk. To collect inputs of larger EM, I installed two litter traps in each plot that consisted of 1.5 mm nylon mesh covering 2.7 m^2 and 5.4 m^2 of the ground (hereafter, "large traps"). Litter collected from larger traps were clumps of epiphytes ($\geq 100 cm^2$), or epiphytes attached to fallen branches, and branches and twigs (all woody material from large traps was >1cm in diameter). Within each plot, all littertraps were randomly distributed under the canopy of bigleaf maple. Littertraps were emptied monthly for 16 months, from August 2010 to November 2011. See Appendices 1, 2 and 3 for more details of collectors and examples of litter collected. The sample design does not include epiphytic litterfall on whole trees when they fall, therefore epiphytic litterfall estimations are underestimated.

Collected litterfall was taken to the laboratory, air-dried for 48 hr, sorted and weighed. Litter collected in the smaller traps was separated into the following categories: maple leaves, EM (bryophytes, lichens, licorice fern and canopy soil), other deciduous leaves (vine maple, red alder and black cottonwood), conifer needles (spruce, western hemlock and Douglas fir), woody (twigs, branches and bark) and miscellaneous material (reproductive material, understory litter, dead insects and unidentifiable fragments). EM collected from the larger littertraps was separated to bryophytes, lichens, licorice fern, canopy soil and woody material (twigs, branches and bark). All EM collected in small and large traps was standardized to kg ha^{-1} then averaged per plot. Determination of litterfall composition was determined monthly, seasonally, and annually as kg ha^{-1} under the maple canopy.

The relationship between autumn litter inputs and precipitation was examined using linear regression. Precipitation data for the Queets River watershed during the sampling period was modeled using the PRISM Climate Group database from Oregon State University (http://prism.oregonstate.edu, created May 14, 2013). All the data were analyzed using R software version 2.14.1 (R Development Core Team 2012).

To determined C and N inputs from EM, the sorted and weighed epiphytic litterfall was grouped by season. Total C and N were determined by dry combustion using a Perkin-Elmer Model 2400 CHN analyzer (Perkin-Elmer, Wellesley, MA) in the Analytical Lab, School of Environmental and Forest Sciences, University of Washington. For C and N analysis, a mixed litter category was created that included conifer needles, other deciduous species, and miscellaneous material. Litterfall C and N inputs for each EM category (bryophytes, lichens and licorice fern) were determined by multiplying the nutrient concentration of each category by the mass of that litter fraction for each season. The C/N ratio of epiphytic litterfall was calculated in proportion to the biomass and C and N concentration of each epiphytic component. To determined annual C and N inputs in litter for each category, total C and N from September 2010 through August 2011 were summed.

Results

Litterfall biomass and seasonality

The mean total annual overstory litterfall under the canopy of big leaf maple was 4760 kg ha^{-1} (Table 3.1). Maple leaves were the dominant litter fraction and accounted for over one third of total annual litterfall. Woody material, conifer needles and miscellaneous material were the next largest fraction of litter biomass. Other deciduous species contributed only 5% of total litterfall. Inputs from epiphytes were nearly 12% of total annual litter inputs. Within the epiphytic category, bryophytes contributed 475 kg ha^{-1} yr^{-1}, whereas lichens and licorice fern contributed 23 and 28 kg ha^{-1} yr^{-1}, respectively. Although canopy soil is part of EM, there was no canopy soil litterfall collected during the sampling period.

Litterfall inputs showed a distinct seasonality with highest monthly inputs in October and November. Leaves from bigleaf maple and other deciduous species were present mainly during the autumn (September - November) and almost completely absent between March and June (Fig. 3.1). Needle litter had a maximum in November 2010 (183 kg ha^{-1}), while for the rest of the year, needle litter biomass averaged 48 kg ha^{-1} mo^{-1}. Woody litterfall showed high spatial and temporal variability, particularly during the fall and winter months, when it reached 142 kg ha^{-1} mo^{-1} (Fig. 3.1). Inputs of total litterfall during the autumn were positively correlated with precipitation pattern during that time period ($r^2 = 0.97$, $p < 0.01$) (Fig 3.2). I did not find a correlation between total litter inputs and temperature during the sampling period.

Epiphytic litterfall

The inputs from epiphytic litterfall were highly variable over time, with biomass ranging from 4 to 90 kg ha^{-1} mo^{-1} during the sampling period (Figs. 3.1 and 3.3). The lowest and highest inputs of epiphyte biomass were in August and November 2010, respectively. In July 2011 the contribution of EM litterfall corresponded to 26% of the total litter inputs for that month. Such high contribution of EM litterfall was mainly driven by litter inputs from licorice fern.

The biomass of epiphytic litter (bryophytes, lichens and licorice fern) was dominated by bryophytes during the sampling period (Table 3.1, Fig. 3.3). Bryophyte litterfall showed a strong seasonal pattern, and particularly between October and December 2010, bryophyte litterfall was derived mainly from larger clumps in the large littertraps. Small clumps and small fragments of bryophytes were continuously collected during the entire collection period (Fig. 3.3). Lichen inputs were collected every month during the sampling period but were greatest between January and June 2011 (ca. 2 - 3.5 kg ha^{-1} mo^{-1}). Licorice fern litterfall contributed the least of all three epiphyte categories and was the only one that was not collected in some months (Fig. 3.3). Highest inputs of licorice fern were between July and October 2011 (12 and 8 kg ha^{-1} mo^{-1}, respectively) with some small amounts scattered throughout the other months.

Carbon and Nitrogen in litterfall

Carbon concentration across litter categories ranged between 37 to 49%, whereas N concentration ranged between 1% and 2% (Table 3.2). Nitrogen concentration of litter components followed the sequence: lichens > maple leaves > bryophytes and mixed litter > licorice fern and woody material.

The largest C and N inputs to the forest floor were from maple leaf litter, followed by mixed litter, woody material and bryophytes (Table 3.2). Lichens and licorice fern had the lowest annual C and N contribution respectively. Maple leaves and mixed litter (conifer needles, other deciduous and miscellaneous category) contributed nearly 80% of total annual N litter. Overall, epiphytic litterfall (bryophytes, lichens and licorice fern) and woody material each contributed ~10% of total annual N in litter (Table 3.3).

Total C and N inputs varied among seasons (Fig. 3.4). Maple leaves were present only during the autumn, with C and N inputs from maple leaf litter higher in November 2010 than in November 2011. Woody material had higher C and N transfer during the winter and spring, which coincides with high precipitation in December 2010 and January and March 2011 (Fig. 3.2). The mixed litter category had higher C and N inputs during the autumn, which correspond to a higher deposition of litter from non-bigleaf maple deciduous species. On average, C/N ratios ranged from 29 in lichens to 71 in woody material (Table 3.2).

Total C and N inputs from epiphytes were mainly due to litter inputs from bryophytes. However, total N inputs from epiphytic litterfall during the spring correspond to lichen litterfall, which has a higher N concentration. The epiphytic litterfall C/N ratio was 42 and was strongly related to the biomass of bryophytes, the dominant epiphytic litterfall component. Throughout the seasons, I found changes in the C/N ratio of EM. The lowest C/N ratio for epiphytic litterfall (36) occurred during the autumn 2010, coinciding with the lowest C/N ratio of bryophytes. However, during the summer 2010 C/N ratios of the epiphytic litterfall were influenced by contribution of licorice fern with a high C/N ratio (71).

Discussion

Annual litterfall inputs under the canopy of big leaf maple in this forest are consistent with litter production of forest in the local area (O'Keefe and Naiman 2006) and with other old-growth forests in the region (Abee and Lavender 1972, Edmonds and Murray 2002). Highest litter inputs under bigleaf maple were maple leaves. Similar findings were described by Chandler et al. (2008) who indicate that bigleaf maple leaves are predominantly deposited directly under maple's canopy. In previous litterfall studies of the region, the dominant component of total annual litterfall was conifer needles (Edmonds and Murray 2002, O'Keefe and Naiman 2006). Annual conifer needle inputs under the canopy of bigleaf maple were much lower than that reported by O'Keefe and Naiman (2006) for the entire forest in the same area. Low estimations of conifer needles could be related to the location of my littertraps and leaf dispersal pattern of tree leaves. For example, Hirabuki (1991) in his study of spatial dispersal patterns of litterfall, determined that litter distribution corresponded with a tree's canopy distribution. In this area, the dominant conifers reach heights above 60 m and their needles can be carried to the area covered by bigleaf maple, while bigleaf maple (which is ≤ 40m tall) deposits its leaves mainly beneath its crown.

The difference in the total litter inputs between autumn 2010 and autumn 2011 may be attributed to a later start of the rainfall season in 2011 compared with 2010. While in 2010 the beginning of the rainy season began in August, in 2011 the rain began to peak in September (Fig. 3.2). Furthermore, while in the dry period in 2010 lasted from July to August, in 2011 the dry period extended from June through August, which could also have affected the peak in litterfall.

Although the presence of EM has been increasingly acknowledged as an important component of forest ecosystems, collections of epiphytic litterfall have often been included with miscellaneous litter or mixed with other litter categories (Abee and Lavender 1972, Edmonds and Murray 2002). Studies that have specifically measured inputs of EM relative to total litterfall, have estimated EM litterfall contribution between 4-7% to total litterfall (Table 3.3). At the Queets River watershed, O'Keefe and Naiman (2006) documented epiphytic litter between 4-6% of total litter inputs. My estimation of epiphytic litterfall biomass under the canopy of bigleaf maple is nearly 12% of the total litter biomass, the highest contribution of epiphytic litterfall recorded.

Following this litterfall biomass trend, total N inputs under the canopy of bigleaf maple were much higher than reported by other studies in temperate ecosystems (Edmonds and Murray 2002) (Table 3.3). In my study high N inputs are related to the biomass of maple litter, which is known to have a high N (and other nutrients) concentration (Chandler et al. 2008, Turk et al. 2008). However, in contrast to a tropical ecosystem, total N inputs under maple canopy were much lower (Nadkarni and Matelson 1992). Total annual N inputs from epiphytic litterfall were also the highest recorded for temperate ecosystems, corresponding to 11% of total N inputs. The highest N inputs from EM litterfall in a tropical ecosystem was reported by Nadkarni and Matelson (1992) who estimated the contribution of epiphytic litterfall as 7% of total N in litterfall.

Annual total N input from epiphytic litterfall (5.7 kg ha^{-1}) to the forest floor was almost double the annual atmospheric N deposition from bulk precipitation in the region (3.1 kg ha^{-1}) (Edmonds et al. 1998). Because of their location in the canopy, epiphytes capture and retain allochthonous nutrients that become available to the whole forest via litter deposition, throughfall or stemflow. Furthermore lichens such as *L. oregana* fix N, increasing the N pool of

EM. Considering the N inputs of epiphytic litterfall, my results highlight the contribution of epiphytic N to the total N pool of the forest floor.

The contribution of bigleaf maple trees to total annual litter inputs to the forest floor as a whole might have a disproportionate effect compared with annual litter inputs of conifer trees in the stand. In this area, bigleaf maple form clusters underneath the conifer-dominant canopy (Van Pelt et al. 2006). Still, the inputs of litterfall under the canopy of big leaf maple are almost equivalent to average litter inputs of the whole forest (Table 3.3), making bigleaf maple a hotspot of nutrient deposition. However, since bigleaf maple drops its leaves directly under its canopy, and considering the biomass and litterfall of EM associated with bigleaf maple, the influence that bigleaf maple has on the surrounding vegetation may be directly limited to the area where bigleaf maples are present until decomposers and other organisms transfer it to other areas of the forest or the surrounding vegetation takes up this pool of nutrients through their root system.

Conclusions

Litterfall estimations are of interest in understanding nutrient returns to the forest floor, especially in areas where nutrients such as N are a limiting factor to forest productivity. Under the canopy of bigleaf maple, maple leaves that are deposited directly beneath their crowns dominate total litter inputs. Epiphytic litterfall under bigleaf maple trees was higher than epiphytic litter relative to the whole forest, corresponding to over 10% of total annual litter inputs. Nitrogen inputs from EM litterfall could have a positive influence on N availability to the surrounding vegetation, especially when litter inputs from bigleaf maple are nonexistent. Furthermore, as EM captures and retains allochthonous nutrients in the canopy mats, litter deposition from EM is enhancing the inputs from atmospheric sources to the forest floor. Annual differences in litter deposition might be influenced by rainfall inputs from late summer and early autumn. The combined effect of nutrient-rich litter and large accumulations of EM within bigleaf maple canopies suggests the importance of bigleaf maple as a source of nutrients for the whole ecosystem.

Table 3.1: Mean total annual litterfall (SD) by litter type under the canopy of bigleaf maple between September 2010 and August 2011 at the Queets River watershed, Washington State.

Material	Annual litterfall ($kg \cdot ha^{-1}$)	% Total litterfall
Bigleaf Maple	1820 (690)	38
Epiphytic material	546 (333)	11.5
Bryophytes	495 (317)	10.4
Lichens	23 (25)	0.5
Licorice fern	28 (27)	0.6
Conifer Needles	748 (412)	16
Other Deciduous	238 (174)	5
Miscellaneous	580 (429)	12.1
Wood	826 (481)	17.4
Total	4762 (1331)	100

Table 3.2: Carbon and nitrogen concentrations (%), annual returns (kg ha^{-1}) and C/N ratios by litter category under the canopy of big leaf maple at the Queets River watershed, Washington State. Values were calculated by multiplying the nutrient concentration of each litter fraction by the total accumulated biomass for that fraction in each plot. Values are means with standard deviation in parenthesis.

	Carbon		**Nitrogen**		**C/N**
Litter component	(%)	(kg ha^{-1})	(%)	(kg ha^{-1})	
Bigleaf maple	47 (0)	875 (324)	1.6 (0)	23 (9)	36 (5)
Epiphytic material		240 (144)		5.7 (3)	
Bryophytes	43 (1)	215 (137)	1.1 (0)	5 (3)	42 (3)
Lichens	41 (6)	10 (11)	1.7 (1)	0.5 (1)	29 (7)
Licorice fern	37 (11)	13 (12)	0.7 (0)	0.2 (0)	48 (10)
Mixed Litter†	48 (1)	775 (437)	1.1 (0)	17 (9)	47 (7)
Woody	49 (1)	405 (234)	0.7 (0)	5.4 (3)	71 (9)
Total		2290 (634)		51 (18)	

†This category includes conifer needles, other deciduous species and miscellaneous material.

Table 3.3: Mean annual biomass and N inputs (kg ha^{-1}) in total and epiphytic litterfall under the canopy of bigleaf maple at the Queets River watershed (this study) in comparison with other studies that reported epiphytic litterfall.

	Total Litterfall		Epiphytic material			
Ecosystem/Source	Biomass	N inputs	Biomass		N inputs	
	(kg ha^{-1})		(kg ha^{-1})	% total	(kg ha^{-1})	% total
Temperate forest						
This study	4760	51	546	11.5	5.7	11
O'Keefe and Naiman 2006	5613		238	4.2		
Abee and Lavender 1972	6325	27			1.4	5.2
Tropical Forest						
Nadkarni and Matelson 1992	7500	100	500	7	7.5	7
Kohler et al 2008	17200		790	6		
Veneklaas 1991	4300		230	5		

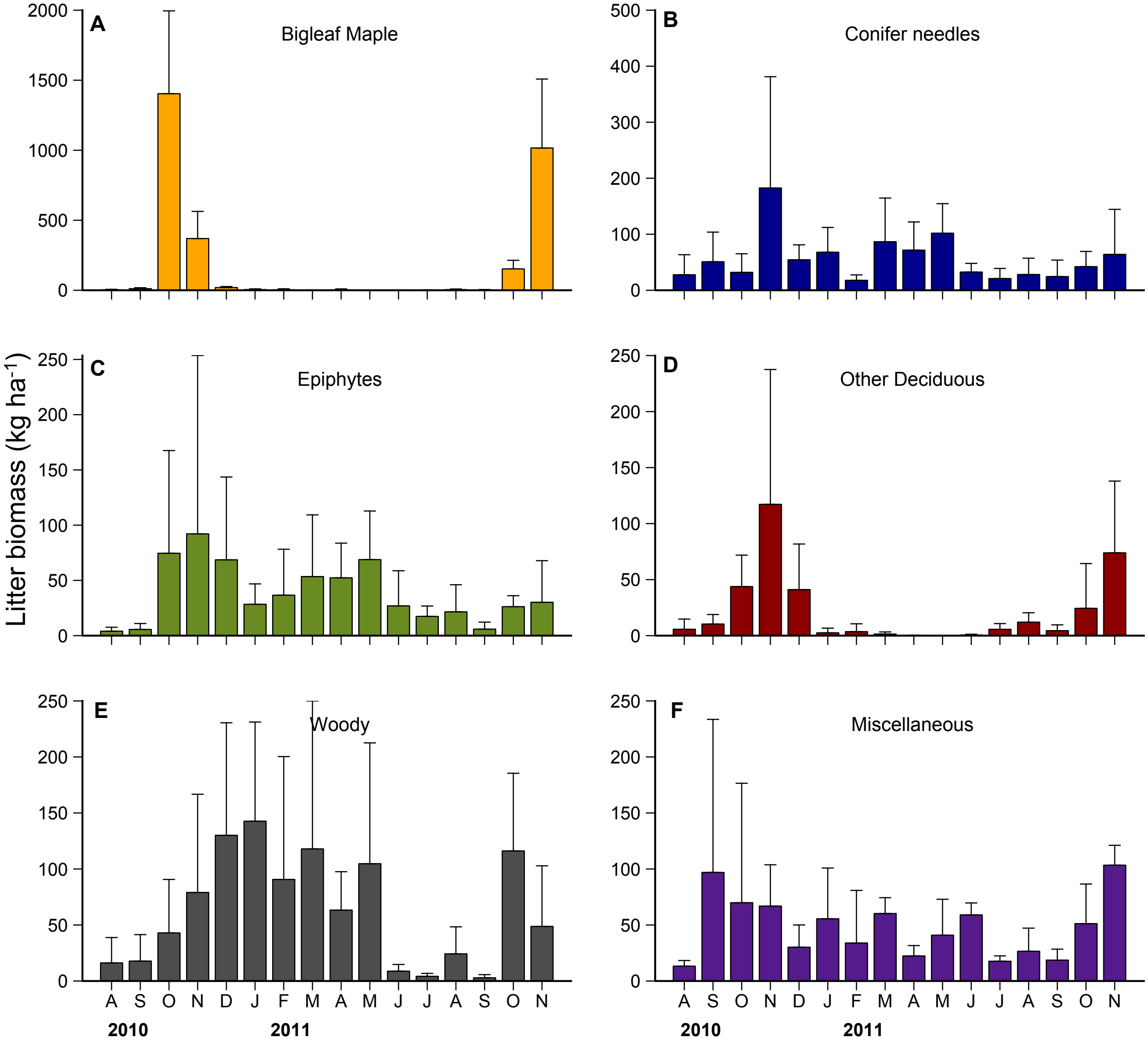

Figure 3.1: Mean and SD of monthly litterfall inputs (kg·ha^{-1}) of bigleaf maple leaves (A), conifer needles (B), epiphytes (C), other deciduous species leaves (D), woody material (E) and miscellaneous material (F) collected under the canopy of big leaf maples at the Queets River watershed, Washington State between August 2010 to November 2011. Note that the scale of the y-axis for bigleaf maple and conifer needles is 8x and 2x that of all other categories of litter.

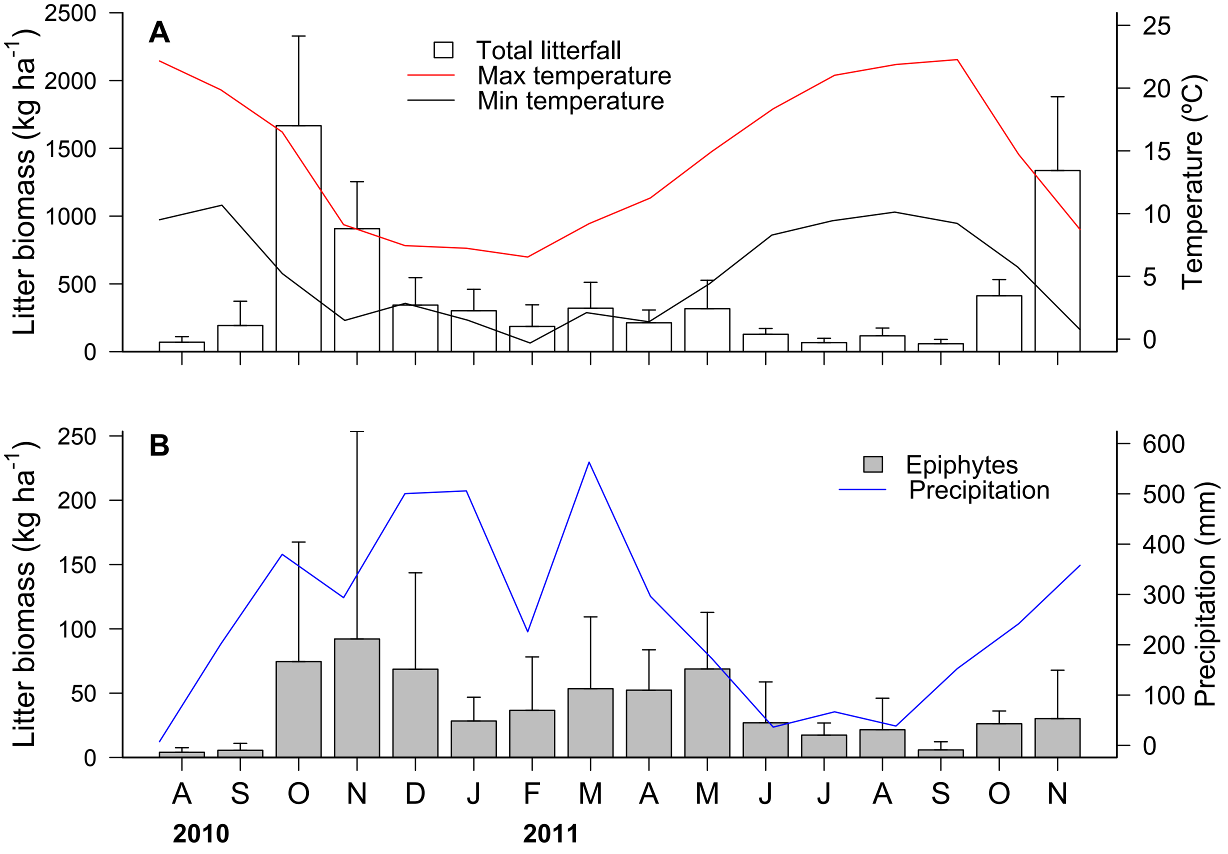

Figure 3.2: Mean and SD of total and epiphytic monthly litterfall inputs (kg·ha^{-1}) plotted against modeled maximum and minimum temperatures (A) and precipitation (B) data for the area from August 2010 to November 2011.

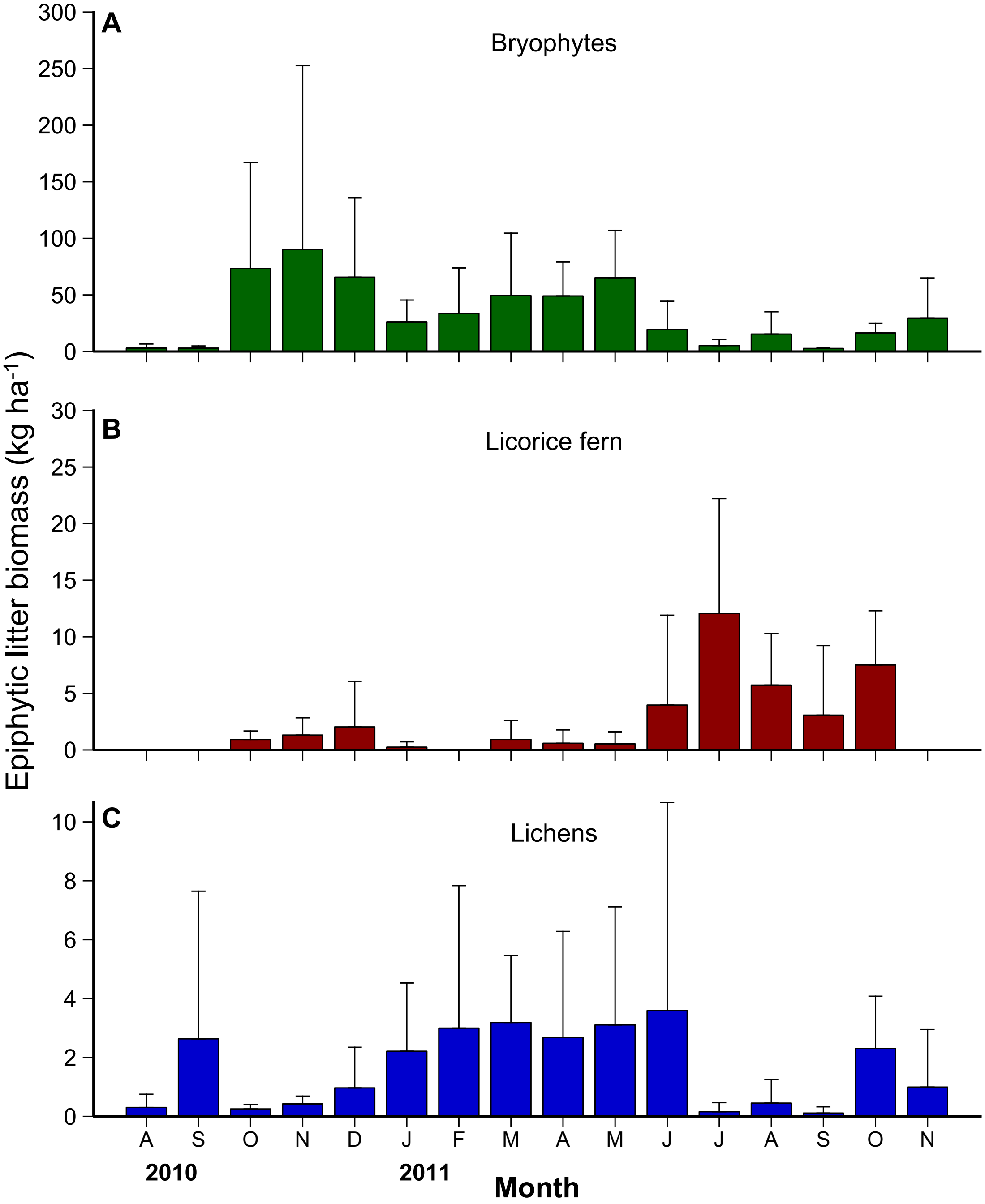

Figure 3.3: Mean and SD of monthly epiphytic litter biomass (kg ha^{-1}) by component, bryophytes (A), licorice fern (B), and lichens (C), collected under the canopy of bigleaf maple between August 2010 to November 2011 at the Queets River watershed, Washington state. Note that the scale of the y-axis for bryophytes and licorice fern are 30x and 3x that of lichen category.

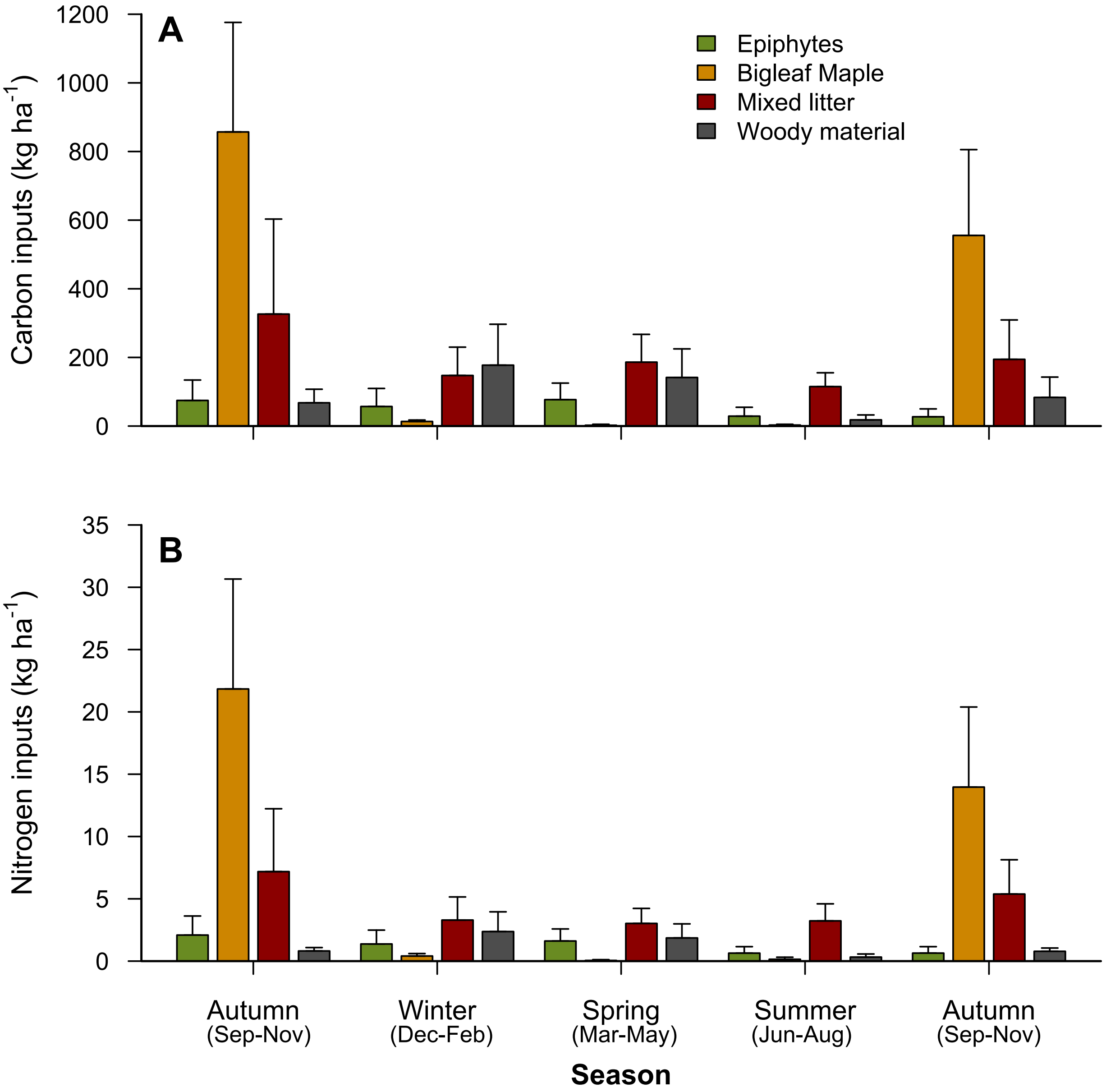

Figure 3.4: Mean and SD of seasonal carbon (A) and nitrogen (B) inputs from September 2010 to November 2011 by litter type under the canopy of big leaf maple at the Queets River watershed, WA. Mixed litter category includes conifer needles, other deciduous species and miscellaneous material.

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Chapter 4

Litter decomposition within and beneath the canopy of *Acer macrophyllum* at the Queets River watershed, Olympic National Park.

Abstract

Decomposition is a fundamental process in forest ecosystems that releases nutrients bound in organic matter. Decomposition rates can vary by environment, substrate quality and abundance and type of decomposers. This study compared decomposition rates of green and senescent bigleaf maple leaves the canopy and on the forest floor beneath bigleaf maple trees at the Queets River Watershed, Olympic National Park. Decomposition rates of canopy and forest floor Oi horizons were also determined on the forest floor. Decomposition data were related to N concentration, and moisture and temperature patterns in the canopy and in the forest floor to assess factors affecting decomposition rates. To gain access to the canopy, I used single-rope tree climbing techniques. Decomposition rates after two years ranged from 0.15 yr^{-1} (for canopy Oi) to 0.58 yr^{-1} (for green maples leaves), and these values were strongly correlated to N concentration of the substrate. Moisture content was significantly lower in the canopy soils compared with soils on the ground. Soil temperatures on the other hand, had seasonal variation and were not significantly different between the canopy and forest floor. Despite significant differences in the moisture regime between the canopy and forest floor, there was no significant difference in decomposition rate between the canopy and forest floor. Wet/dry cycles of canopy soils and potential activity of soil organisms (that live in canopy soils) might have influenced decomposition aboveground.

Introduction

Decomposition is a fundamental process of nutrient cycling in forests that mineralizes nutrients bound in organic matter (Lindo and Winchester 2007, Berg and McClaugherty 2008). The decomposition of organic matter is often controlled by three main factors: the chemical composition of the substrate, the community of soil organisms and the physical environment (Berg and McClaugherty 2008, Perry et al. 2008). For instance, litter with a high nutrient content (e.g. high N concentration) is often more rapidly decomposed by soil organisms. However, the abundance and composition of soil organisms is affected by the litter quality of the substrate and moisture and temperature patterns. Climate can affect decomposition by regulating the activity of microbial communities (Edmonds 1980, Paul and Clark 1996, Chapin et al. 2002, Prescott 2002).

Decomposition has typically been examined on the ground, although decomposition in a forest also occurs in the canopy. In many forests considerable amounts of epiphytic biomass exist (up to 44 Mg ha^{-1}) on the branches and boles of trees (Lowman and Nadkarni 1995, Diaz et al. 2010). This epiphytic biomass is composed of epiphytic plants (vascular and non-vascular plants), tree foliage that gets intercepted within the canopy, and canopy soils (Lowman and Rinker 2004, Enloe et al. 2006, Diaz et al. 2010). Arboreal or canopy soils are the result of the accumulation and decomposition of epiphytic plants, tree litter and other epiphytic organisms. This epiphytic material (canopy soils + epiphytic plants, hereafter EM) captures and retains water and nutrients that can be used by epiphytic organisms, the host tree (via canopy roots) or reach the forest floor as litterfall or throughfall (Nadkarni 1981, Bohlman et al. 1995, Clark et al. 1998, Cardelus and Mack 2010).

While decomposition of material has been well described for the forest floor (Ewel 1976, Edmonds 1980, Kaspari et al. 2008, Harmon et al. 2009, Wieder et al. 2009, Campbell et al. 2010), decomposition in the canopy has been determined in very few studies (Pike 1978, Clark et al. 1998, Lindo and Winchester 2007, Cardelus 2010).

In a tropical lowland forest in Costa Rica, Cardelus (2010) estimated that decomposition rates in the canopy were slower than that of the forest floor, whereas Lindo and Winchester (2007) did not find differences in decomposition rates between the canopy and the forest floor associated with western red cedar in British Columbia. In these studies, common substrates (cellulose filter and conifer needles, respectively) were used to compare decomposition rates between canopy and forest floor environments, and in both cases, moisture limitation was the primary reason given for differences in decomposition rates (Lindo and Winchester 2007, Cardelus 2010). Microclimatic conditions, specifically moisture and temperature, affects decomposition by influencing the activity of the microbial communities (Chapin et al. 2002, Berg and McClaugherty 2008). Compared with the forest floor, the canopy environment has more extreme moisture patterns and epiphytic material is susceptible to desiccation due to the high fibrous content of canopy soils (Bohlman et al. 1995, chapter two). I hypothesized that decomposition rates in the canopy would be slower due to lower moisture availability in the canopy soil compared with the forest floor (Bohlman et al. 1995, Enloe et al. 2006).

Many forests of the Pacific Northwest harbor a large accumulation of epiphytes and canopy soils, particularly those found in the temperate rainforest (Nadkarni 1984, O'Keefe and Naiman 2006, Lindo and Winchester 2007). Bigleaf maple (*Acer macrophyllum* Pursh), is a common deciduous species found throughout the Pacific Northwest and is particularly abundant in the coastal temperate rainforest. Bigleaf maple is known for its nutrient-rich litter that rapidly decomposes and its prominent accumulation of epiphytes and canopy soils (Nadkarni 1984, Harmon et al. 1990, Chandler et al. 2008). A single maple tree can hold more than 35 kg of epiphytic material (Nadkarni 1984). Based on these special features of maples, how do decomposition rates differ between the canopy and forest floor of big leaf maple trees? Is there any difference between the moisture and temperature patters between the canopy and the forest floor? How do decomposition rates relate to moisture and temperature? To answer these questions I determined decomposition rates and moisture and temperature regimes within and beneath the canopy of bigleaf maple.

Specific objectives of this study were to determine: 1) decomposition rates and N release of green and senescent maple leaves in the canopy; 2) decomposition rates and N release of green and senescent maple leaves and canopy and forest floor Oi horizon on the forest floor, and 3) moisture and temperature patterns of the canopy (soil) and forest floor (below the organic layer) environment.

Methods

Study Site

The study site is an old-growth forest located within the Queets River watershed on the western side of Olympic National Park, Washington (47.34 N, 124.09 W). The stand is dominated by Sitka spruce (*Picea sitchensis* (Bong.) Carrière) and has been characterized as one of the most structurally complex forests of the northwest coast (Van Pelt et al. 2006). The climate in the area is temperate, with cool-wet winters and warm-dry summers. The rainy season extends from mid-October to mid-June with a mean annual precipitation of 3000 mm. Mean annual air temperature is 14.7 ºC. Winter and summer mean temperatures are 7.3 ºC and 22ºC respectively. The conifers western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and occasional Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) are also present in the stand. In the older stands bigleaf maple is the dominant hardwood specie, followed by red alder (*Alnus rubra* Bong.) and vine maple (*Acer circinatum* Pursh). Understory vegetation is dominated by sword fern (*Polystichum munitum* (Kaulf.) C. Presl) and redwood sorrel (*Oxalis oregana* Nutt.) (Van Pelt et al. 2006). Soils in this stand are Entisols of the Huel and Tealwhit series (Bechtold and Naiman 2009).

Plot establishment and experimental design

In June 2010, four 30 m x 30 m plots were installed in the old-growth stands (>250 yrs) based on the presence of at least two mature bigleaf maple trees. To compare decomposition rates between the canopy and forest floor environment I used green and senescent leaves of big leaf maple. Samples on the ground were also compared to canopy and forest floor Oi horizon.

Using single rope tree-climbing techniques, green maple leaves and Oi canopy soil samples were obtained by climbing two maple trees per plot. Within each tree, one branch was selected for its accessibility and a 25 cm cross section of the epiphytic mat (between 12-15 m high) was sampled to obtain Oi canopy soil. Green maple leaves were collected between 10-15m aboveground from branches adjacent to the climbing rope transect. The canopy Oi horizon was the recognizable dead organic matter underneath the green tissues of epiphytes.

Forest floor Oi horizon samples were collected from randomly selected areas under the canopy of bigleaf maple within each plot. Samples of green maple leaves and Oi horizons (canopy and forest floor) were collected in June 2010, whereas samples of senescent maple leaves were collected from the ground in November 2010. All samples were collected one month prior to placement in the field.

Samples were homogenized by plot and air-dried for at least 48 hours before filling litterbags. Litterbags of 10 cm x 10 cm nylon mesh (1.5 mm mesh size top and 0.5 mm mesh size bottom) were used to determined decomposition rates. Each litterbag was filled with 3-5 g of air-dry material. In each plot, litterbags were placed on top of the canopy mats (also between 12-15 m high on horizontal branches). Forest floor litterbags were randomly placed on top the of the forest floor under the canopy of big leaf maple (Appendix 1). Three replicate bags of each substrate were retrieved from the canopy and forest floor of each plot after 6, 12 and 24 months of incubation in the field (6 canopy litterbags + 12 forest floor litterbags) x 4 plots = 72 litterbags per collection time or 216 litterbags total).

At each collection time, litterbags were taken from both the canopy and forest floor, transported to the laboratory, air dried and weighed. Decomposition rates of materials in the canopy and forest floor were determined as loss of mass over time (calculated as a percent weight loss of initial sample mass).

Following each collection, air dried samples of each material were pooled by plot to determine total C and N and C/N ratios (after oven-dry correction) using a Perkin Elmer Model 2400 CHN analyzer (Perkin Elmer, Wellesley, MA) located in the Analytical Lab, School of Environmental and Forest Sciences, University of Washington, Seattle, WA). The decomposition constant (k) was calculated by dividing the natural logarithm of the fraction of litter remaining by the time incubated (yr) from the equation $M_t = M_0 \cdot e^{-kt}$ (Berg and McClaugherty 2008).

To determined moisture and temperature patterns of forest floor and canopy soils I used EM50R (canopy) and EM5 (forest floor) data loggers (Decagon Devices, Pullman, WA). Volumetric water content (%) under the canopy of bigleaf maple and beneath the O-horizon was measured with Decagon soil moisture sensors (5TM soil moisture sensor for the canopy and EC-5 for the forest floor). Moisture data in the canopy and forest floor were converted using the potting soil equation from Decagon Inc. The potting soil equation (organic-rich) from Decagon Inc. was chosen after comparing the potting soil equation with a calibration equation developed in the lab using canopy soils to verify the best equation for volumetric moisture content of canopy and forest floor soils.

Soil temperature (ºC) was determined using Decagon temperature sensors (5TM temperature sensor for the canopy and ECT for the forest floor). Moisture and temperature data were recorded every 12 hr from July 2010 through November 2012. Canopy sensors were installed at least 5cm beneath the EM surface while forest floor sensors were installed at the bottom of the O-horizon.

Statistical analysis

I used a three way ANOVA and Tukey's HSD to compare mass loss and C/N ratios between substrates (green maple leaves versus senescent maple leaves) for both the canopy and forest floor environment over time. The effect of time and material on decomposition rates and C/N ratios on the forest floor was analyzed using repeated measurements ANOVA. Significant differences were considered at a p-value ≤ 0.05. Stepwise regressions were used to determined correlations between decomposition rates, N concentrations and environmental data. All statistical analysis were done using R (R Development Core Team 2012).

Results

Mass loss and decomposition rates

Mass loss in the canopy varied from 39 to 78% after one year and from 33 to 73% after two years (Table 4.1, Fig. 4.1). On the forest floor, mass loss varied from 42 to 80% after one year and from 34 to 75% after two years. There were no significant differences in mass loss over time between the canopy and forest floor for either green or senescent leaves of big leaf maple. However, there was a significant difference between mass loss of green and senescent maple leaves ($p \leq 0.05$, Table 4.1).

Decomposition rates after two years ranged from 0.15 yr^{-1} for canopy Oi to 0.58 yr^{-1} for green maples leaves. Values of k determined after one year for all material in the forest floor were smaller than k values determined after two years. Mean residence time ($1/k$) was 1.8 and 1.7 yr for green maple leaves (canopy and forest floor respectively), 6.2 and 5.3 yr for senescent maple leaves (canopy and forest floor respectively), 4 yr for forest floor Oi and 6.7yr for Oi canopy.

In the canopy and forest floor, a significant mass loss for all materials occurred in the first six months ($p \leq 0.05$) with 44, 84, 84 and 71% mass remaining for green maple leaves, senescent maple leaves, canopy Oi and forest floor Oi, respectively. Although senescent maple leaves were placed six month after the other materials, decomposition still proceeded similarly, and after two years mass remaining was similar to that of the forest floor Oi (Table 4.1, Fig. 4.1).

Carbon, N and C/N ratios

Initial C and N concentrations and C/N ratio for material in the canopy and forest floor are summarized in Table 4.2. As with the data for decomposition rates, C/N ratios did not show significant differences between the canopy and forest floor environment for green and senescent maple leaves. In each environment, green maples leaves had the lowest C/N ratio over time compared with the other materials (Fig. 4.2). For the materials on the ground, I did not find significant changes in the C/N ratio after two years.

Moisture and temperature

Mean temperature during the sampling period was lower in the forest floor (6ºC, Table 4.3) compared with the canopy (air and soil temperatures). Canopy soil temperatures were closely related to air temperatures (Fig. 4.3), and I did not found significant differences between canopy and forest floor temperatures. Highest temperatures were reached in the canopy and in contrast to the forest floor, and the canopy soil did not reach temperatures below freezing. Overall air temperature was slightly lower than average for the area over the study period. Air temperature had the greatest fluctuations (-2.6 to 28.1 ºC). Temperatures of both canopy and forest floor environments showed seasonal fluctuations (Fig. 4.3).

Average soil moisture in the canopy (as percent volumetric water content) during the sampling period was significantly lower in the canopy compared to the forest floor (Table 4.3). Moisture levels in the canopy and forest floor had similar seasonal fluctuations (Fig. 4.4), with the lowest moisture content during the summer months (June through August), especially for the canopy soils. Moisture content during winter and spring months (Dec through May) in 2011 was lower compared to the mean of the winter and spring months in 2012. Canopy and forest floor soils had a strong response to precipitation events, especially after summer drought (Fig. 4.4).

Relationship between decomposition rates, N concentration and environmental variables

Decomposition rates after two years were not significantly correlated ($p > 0.05$) with mean, maximum or minimum temperature, soil moisture or any combination of these variables as evaluated by stepwise linear regressions. Decomposition rates were positively related to N concentrations ($r^2 = 0.89$ for materials on the canopy and forest floor, and $r^2 = 0.81$ for materials on forest floor only). Decomposition rates were slightly better explained using N concentration and minimum soil temperature as independent variables ($r^2 = 0.91$ for materials on the canopy and forest floor, and $r^2 = 0.83$ for materials on forest floor only).

Discussion

Result for the first year decomposition constant of green maple leaves is similar to *k* of green needles of western hemlock and pacific silver fir (0.44 and 0.45) in sites at the West Twin Creek and Cedar River watershed in Washington (Edmonds 1980, Edmonds and Thomas 1995). Faster decomposition rates were described for western hemlock in the Twin Creeks Research Area (Harmon et al. 1990). For the canopy and forest floor environment, decomposition rates were slower during the second year compared with the first year (Table 4.1). For green leaves of bigleaf maple *k* values after two years are similar to that described by Harmon et al. (1990), whereas senescent leaves of big leaf maple and Oi horizons have *k* values after two years similar to that described by Edmonds and Thomas (1995).

Rates of decomposition between the canopy and forest floor of big leaf maple trees were not significantly different, a pattern previously described between the canopy and forest floor of Sitka spruce trees (Lindo and Winchester 2007). However, in tropical ecosystems decomposition rates between the canopy and forest floor had significant differences (Clark et al. 1998, Cardelus 2010) with differences likely caused by lower humidity and faster drying of the canopy soils (Bohlman et al. 1995, Cardelus 2010). Canopy soils have lower bulk densities than their ground counterpart (Perez et al. 2005, Enloe et al. 2006) (chapter 2), making canopy soils susceptible to desiccation (Bohlman et al. 1995). Lower moisture in soils limits microbial activity slowing down decomposition (Chapin et al. 2002, Lindo and Winchester 2007, Berg and McClaugherty 2008). On the ground, Oi horizons are in direct contact with the mineral portion of the soil, which explains the maintenance of moisture levels on the ground, even during dry periods (Fig 4.4). In the canopy the combination of low bulk densities, a high fiber content and the absence of a mineral soils contribute to the rapid drying of canopy soils in periods without rainfall.

Forest floor Oi had higher mass loss than canopy Oi after two years. Slower decomposition rates of canopy Oi can be related with properties of the canopy soils. Canopy Oi are composed mainly of epiphytic bryophytes and abscised leaves of bigleaf maple (chapter 2) and have a higher C/N ratio compared to Oi from the forest floor under maple (Table 4.3). Furthermore, mean residence time of canopy Oi is the highest of all material, therefore to further undergo decomposition, canopy Oi might need to increase N content first.

Decomposition studies in the Pacific Northwest have related *k*-values with minimum air temperature (Edmonds 1980) or the chemical characteristics of the substrate, particularly the lignin: N ratio (Harmon et al. 1990, Edmonds and Thomas 1995). At the Queets river watershed, decomposition rates within and beneath the canopy of big leaf maple trees were correlated with N concentrations of the substrate. Significant differences between green and senescent maple leaves for both environments relate to lower N concentration of senescent maple leaves (Table 4.2), suggesting a high N retranslocation before leaf abscission (Parker 1995, Chapin et al. 2002, Berg and McClaugherty 2008). Even though lignin:N ratio has been described as a strong indicator or litter decomposition for the Pacific northwest (Harmon et al. 1990, Edmonds and Thomas 1995), N concentration could be used as indicator to compare decomposition rates between the canopy and forest floor, however information about lignin:N ratios is needed to relate to decomposition rates in the canopy.

Litter decomposition is also influenced by microclimate (such as moisture and temperature) (Edmonds and Thomas 1995, Berg and McClaugherty 2008). Edmonds (1980) and Edmonds and Thomas (1995) found a strong relation of temperature and decomposition rates during the first year, whereas Harmon et al. (1990) did not found a clear relationship between climatic variables and decomposition rates. While I found significant differences in the moisture content between the canopy and forest floor environment, at the Queets River watershed I did not find a significant influence of soil moisture on decomposition rates. Bohlman et al. (1995) found similar results between the canopy and forest floor environment in a tropical forest in Costa Rica. Moisture and temperature also affect decomposition by controlling the composition and activity of soil organisms. Nadkarni and Longino (1990) and Lindo and Winchester (2007) reported lower densities of invertebrates in the canopy relative to the forest floor as a response to lower moisture conditions in the canopy. Although there is no information about soil microbes or invertebrates in the canopy of bigleaf maple, my environmental data would suggest that densities of invertebrates in the canopy might be lower compared to the ground.

Despite lower moisture levels of canopy soils and a potentially lower density of invertebrates, decomposition rates in the canopy of big leaf maples did not differ from those of the ground. The nutrient properties of canopy soils could compensate for decreased microbial activity during dry periods and therefore decomposition rates in the canopy would remain similar to that of the ground Oi. Specifically, canopy soils on maple trees had much lower C/N ratio than soils underneath maple (22 and 33 respectively, chapter 2).

Finally, dry-wet cycles in soils can increase rates of decomposition by increasing litter fragmentation and surface area for microbial mineralization (Sørensen 1974), and could also explain the similar decomposition rates I found between the canopy and the forest floor of maple trees.

Conclusions

At the Queets river watershed decomposition rates between the canopy and forest floor of maple trees are strongly related to the N concentration of the substrate, independent of the environment (canopy or forest floor). Green maple leaves had the fastest *k*-values and lowest C/N ratio of all materials. The slowest decomposition rates after two years were for canopy Oi and correspond to the material with the highest C/N ratio at that period. Temperature patterns between the canopy and forest floor did not shown significant differences, although I did not register freezing temperatures in the canopy soils. Moisture regime for canopy and forest floor soils relates to precipitation patterns especially after the summer months (June thought August). Decomposition in the canopy did not differ with that of the forest floor despite the drastic differences in moisture; this could be due to a compensatory activity of soil organisms in a more nitrogen rich environment of the canopy soil. In temperate ecosystems where productivity is limited by N inputs, decomposition in the canopy promotes the development of canopy soils, and therefore also the accumulation of N in canopy soils. Available N in the canopy can support the activity of canopy-dwelling organisms, could be utilized as a food source for the host tree (via canopy roots) and ultimately interact with terrestrially rooted vegetation via litterfall and throughfall.

Tables

Table 4.1: Mean and standard deviation of mass remaining and decomposition constants determined after 1 and 2 years for different materials in the canopy and forest floor of bigleaf maple trees at the Queets River watershed, Washington. Within a column, uppercase superscripts letters show differences between materials and environments, while lowercase superscripts letters indicate significant differences among materials on the forest floor ($p \leq 0.05$).

Environment	Mass remaining (%)		Decomposition constant *k* (years $^{-1}$)	
Material	Year 1	Year 2	Year 1	Year 2
Canopy				
Green maple leaves	39 (7.9)^{A}	33 (7.9)^{A}	0.49 (0.1)^{A}	0.57 (0.1)^{A}
Senescent maple leaves	78 (4.9)^{B}	73 (5.7)^{B}	0.12 (0.03)^{B}	0.16 (0.04)^{B}
Forest Floor				
Green maple leaves	42 (10.5)^{Aa}	34 (13)^{Aa}	0.44 (0.1)^{Aa}	0.58 (0.2)^{Aa}
Senescent maple leaves	76 (3.9)^{Bbc}	69 (6.7)^{Bb}	0.14 (0.03)^{Bb}	0.19 (0.05)^{Bb}
Oi canopy	80 (4.5)^{b}	75 (15)^{b}	0.11 (0.03)^{b}	0.15 (0.1)^{b}
Oi forest floor	68 (12.3)^{e}	62 (9.8)^{b}	0.20 (0.1)^{b}	0.25 (0.1)^{b}

Table 4.2: Initial C and N concentrations and C/N ratios for the different substrates in the canopy and forest floor of bigleaf maple trees at the Queets River watershed, Washington. Values are the mean with standard deviation in parenthesis. Within a column, uppercase superscripts letters show differences between materials and environments, while lowercase superscripts letters indicate significant differences among materials in the forest floor ($p \leq 0.05$).

Substrate	Carbon %	Nitrogen %	C/N ratio
Canopy			
Green maple leaves	47 (0.3)^{A}	2.9 (0.3)^{A}	16 (1.8)^{A}
Senescent maple leaves	49 (0.4)^{A}	1.4 (0.3)^{B}	36 (8.4)^{B}
Forest Floor			
Green maple leaves	47 (0.3)^{Aa}	2.9 (0.3)^{Aa}	16 (1.8)^{Aa}
Senescent maple leaves	49 (0.4)^{Ab}	1.4 (0.3)^{Bb}	36 (8.4)^{Bbc}
Oi canopy	45 (1.8)^{a}	1.1 (0.0)^{b}	42 (1.1)^{b}
Oi forest floor	40 (2.7)^{c}	1.2 (0.1)^{b}	33 (5.2)^{c}

Table 4.3: Mean and standard deviation of air, canopy soil and forest floor temperatures, and mean and standard deviation of canopy soil and forest floor volumetric water content on big leaf maple trees at the Queets River watershed, Washington during a two-year period. For each variable (moisture or temperature), superscript letters indicate significantly different values between canopy and forest floor ($p \leq 0.05$).

Environment	Average	Maximum	Minimum
Moisture (volumetric water content, %)			
Canopy soil	15.5 (5.8)^a	26.8	5.7
Forest floor	39 (5.5)^b	52.5	27.3
Temperature (ºC)			
Air (canopy)	9.4 (5.4)^a	28.1	-2.6
Canopy soil	9.4 (4.7)^a	22.6	0.5
Forest floor	6.0 (3.8)^a	15.5	-2.6

Figures

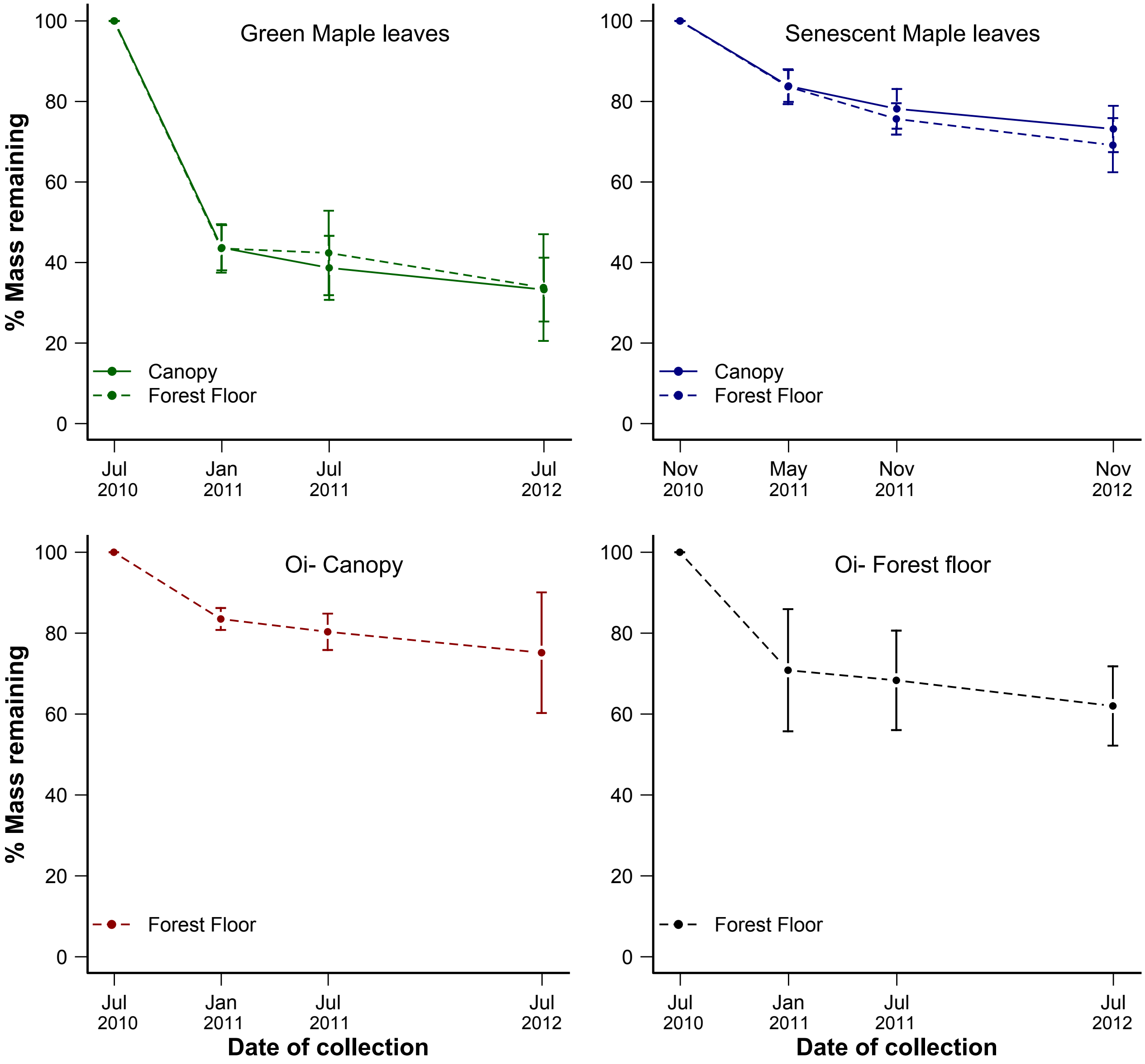

Figure 4.1: Mass loss over time of green and senescent maple leaves, canopy Oi and forest floor Oi in the canopy (solid line) and beneath maple trees (dashed lines) at the Queets River watershed, Washington. Results are the mean and SD. Note that the scale of the y-axis for senescent maple leaves started in November 2010.

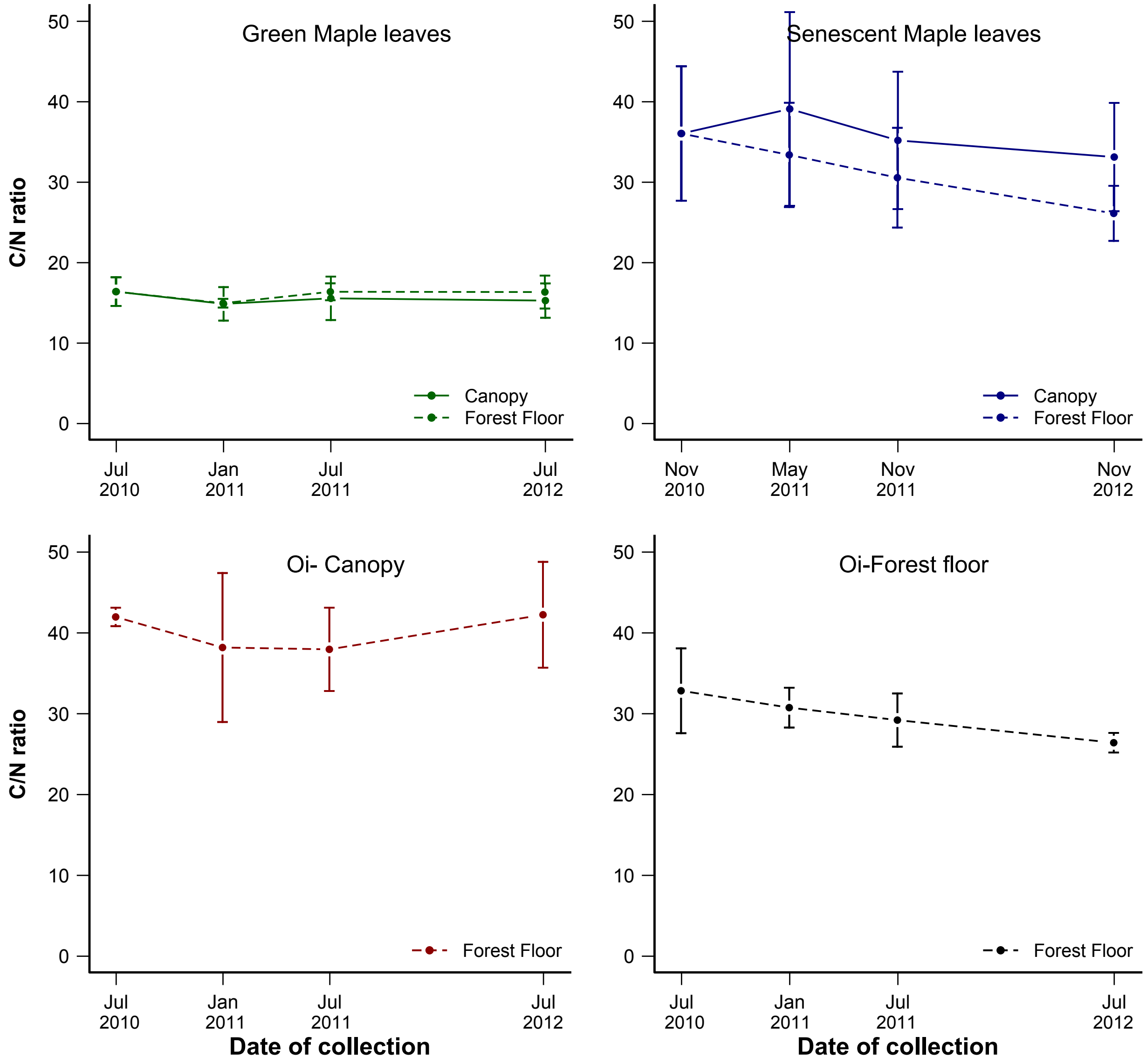

Figure 4.2: C/N ratio over time of green and senescent maple leaves, canopy Oi and forest floor Oi in the canopy (solid line) and beneath maple trees (dashed lines) at the Queets River watershed, Washington. Results are the mean and standard deviation. Note that the scale of the y-axis for senescent maple leaves started in November 2010 relative to the other categories.

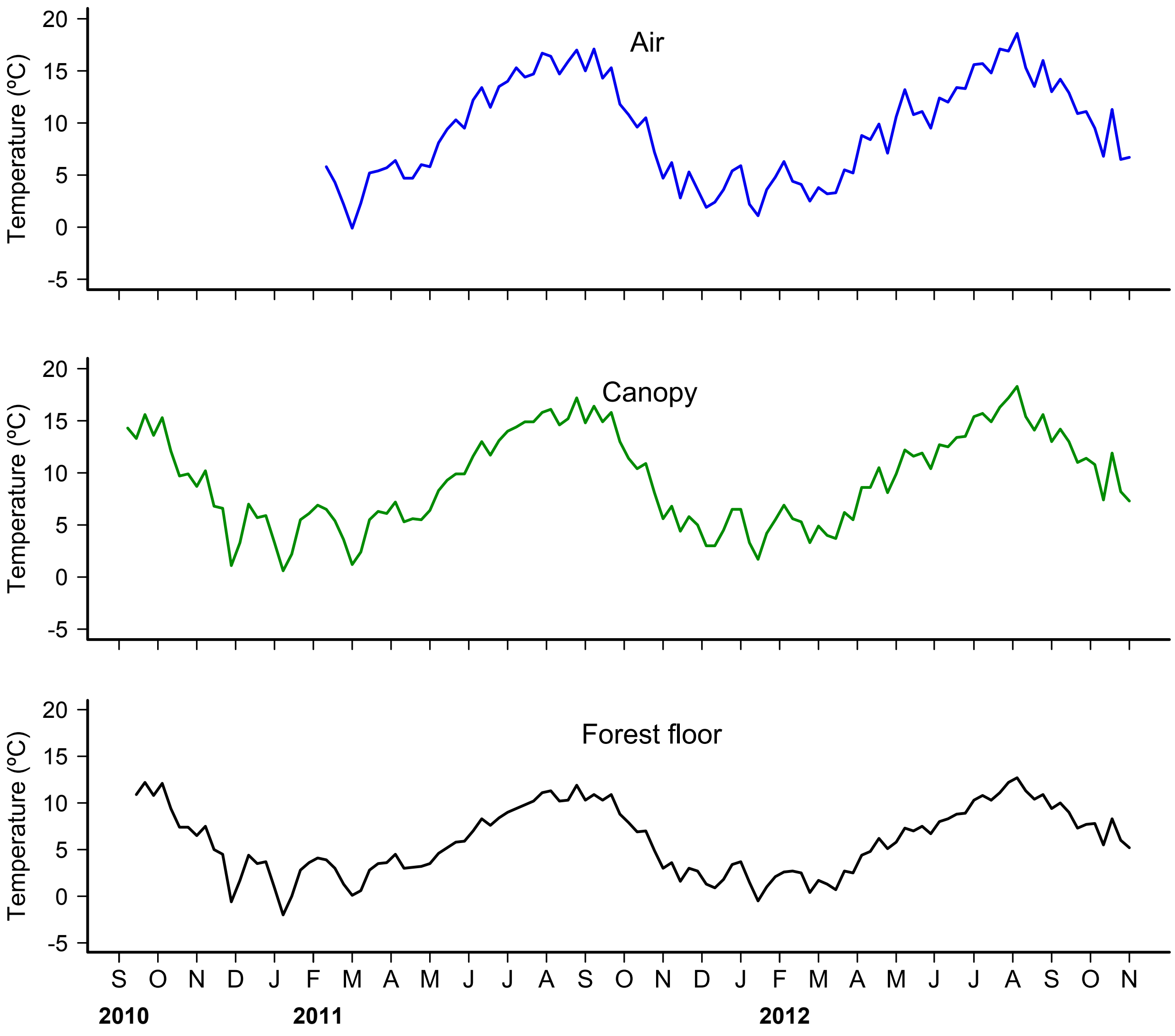

Figure 4.3: Weekly average temperature of canopy soils (green), forest floor (black) and air above canopy mats (blue) from September 2010 to November 2012 at the Queets River watershed, Washington.

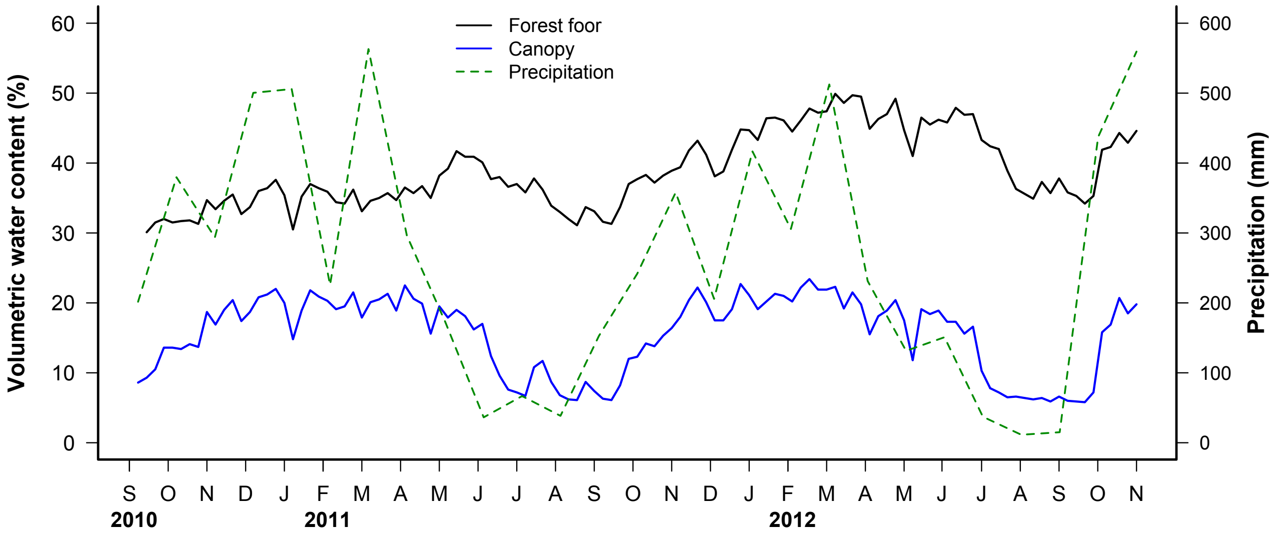

Figure 4.4: Weekly average volumetric water content of canopy soils (solid blue line) and forest floor (solid black line) and monthly-modeled precipitation (dashed green line) data for the Queets River watershed from September 2010 to November 2012 at the Queets River watershed, Washington. Climatic data were obtained from the PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu, accessed on May 14, 2013.

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Chapter 5

Conclusions

This research focused on understanding the relevance of epiphytic material and the canopy environment to the transfers of C and N in a coastal temperate rainforest. Canopy soils are formed by the accumulation and decomposition of epiphytic material and host tree litter, provide moisture and nutrients for epiphytic plants and the host tree (via canopy roots) and can influence the activity of soil organisms (Nadkarni et al. 2002, Enloe et al. 2006).

Chapter 2 described the properties of canopy soils developed on Sitka spruce and bigleaf maple trees and compares total C and N held by canopy soils relative to the forest floor. There are significant differences between the canopy soils developed on spruce and maples. Maple canopy soils have higher pH, CEC, total and extractable N and lower bulk density than spruce canopy soils. However, because spruce trees have a larger canopy soil biomass, total C and N held by these trees is 273 g m^{-2} and 9 g m^{-2} respectively (compared to the 114 g m^{-2} of C and 5 g m^{-2} of N help by maple canopy soils). Although the mass of C and N held by the canopy soils is lower compared to the pool in the ground, the canopy environment is increasing the pools of C and N for the ecosystem, and this pool contributes to nutrient accumulation the whole forest.

Canopy soils are the source of nutrients and water for insects and microorganisms that form part of the canopy biota. Processes such as litter decomposition, N mineralization and moisture retention are actively occurring in this habitat.

The nutrients of canopy soils are interacting with the whole forest in three ways: 1) nutrients can be leached out of the canopy mat via throughfall, 2) nutrients are adsorbed via canopy roots or 3) epiphytic material (EM) gets deposited in the forest floor via litterfall roots (Nadkarni and Matelson 1992, Campbell et al. 2010).

Chapter 3 described the fluxes of this EM under the canopy of bigleaf maple and the annual returns of C and N from EM to the forest floor. Total annual litter inputs under the canopy of bigleaf maple were 4760 kg ha^{-1}, a value slightly lower than what has been measured for the whole forest in the area (O'Keefe and Naiman 2006). Epiphytic material litter inputs were 546 kg ha^{-1} yr^{-1}, equivalent to nearly 12% of total annual litter inputs. This is the highest contribution of epiphytic litterfall registered.. However, that epiphytic litterfall calculations are underestimated since inputs from EM attached to fallen trees were not measured.

Maple leaves contributed the highest to annual C and N returns (875 kg ha^{-1} yr^{-1} of C and 23 kg ha^{-1} yr^{-1} of N respectively), while epiphytic litterfall contributed 240 kg ha^{-1} yr^{-1} of C and 5.7 kg ha^{-1} yr^{-1} of N. In the region, annual atmospheric deposition from precipitation is 3.1 kg ha^{-1} (Edmonds et al. 1998), thus the N inputs underneath maple canopy to the O horizon on the ground is almost ten times that of N atmospheric inputs. Considering that productivity is limited by N availability, these high inputs of N under the canopy of big leaf maple make this tree and its epiphytes a hotspot of N for the whole ecosystem.

The decomposition of litter is the key step necessary to release the nutrients that are bound in organic compounds (Berg and McClaugherty 2008). Decomposition in the canopy might differ from that of the forest floor because the canopy environment is exposed to more extreme climatic conditions than the forest floor (Bohlman et al. 1995) and because canopy soils can harbor a reduce abundance and diversity of canopy invertebrates (Nadkarni and Longino 1990, Lindo and Winchester 2007). However, as described in Chapter 4,decomposition did not differ between the canopy and forest floor environment, and I found a strong correlation of *k* and the N concentration of the substrate. This result indicates that the canopy of bigleaf maple is a supplementing of decomposition in the area, an important function for the formation of canopy soils and the maintenance of the canopy soil biota.

During my field work, I observed on discrete occasions canopy soil inputs, specifically under the canopy of Sitka spruce. Since the considerable biomass of canopy soils held aboveground and the lack of litter inputs form canopy soils, it might be that the largest influence of the canopy soils to the C and N transfers to the forest relies of the movement of nutrients via stemflow or throughfall, but further studies are be needed to test this idea..

Overall, my studies from chapter 2, 3 and 4 highlighted the importance of the canopy environment and bigleaf maple as hotspots of C and N to the whole forest.

Implications for management and future research

This study highlights the importance of epiphytes in the pools and transfers of materials within and beneath the crown of bigleaf maples. In the Pacific Northwest, deciduous species have been considered as competitors of conifers or ignored from silvicultural practices, (Edmonds et al. 1989, Franklin et al. 2002, Chandler et al. 2008). Since the contribution of N under maple can be almost 10 kg ha^{-1} yr^{-1}, the incorporation of hardwood species as bigleaf maple could improve silvicultural applications by increasing soil fertility through its rich litter and the deposition of EM litterfall. From a conservation point of view, one of the main contributions of maples and its epiphytes resides in the development of canopy soils. Maple canopy soils are rich in N that is available for epiphytic plants, the host tree and soil organisms. Complex ecosystems such as old-growth temperate rainforests that support the development of epiphytic mats are enhancing the pathways of C and N, providing and maintaining habitat for canopy dwelling organisms and increasing trophic interactions in the forest (e.g., birds used canopy mats as habitat for nesting or foraging). The conservation of tree species that hold epiphytic loads could be critical for the maintenance of biodiversity considering climate change scenarios.

Further research is always needed to understand patterns and processes of natural systems, and to enhance the understanding of the "black box" of the canopy world. As I already stated above, understanding the full extend of the importance of canopy soils in the N transfers in this forest it might be a first step. A second follow up of this research could include a comparison between decomposition rates of EM between the canopy and forest floor environments and finally estimating the whole contribution of epiphytic litterfall "riding down" whole trees would provide an insightful understanding of the ecological role of canopy soil and epiphytes in forest processes and function.

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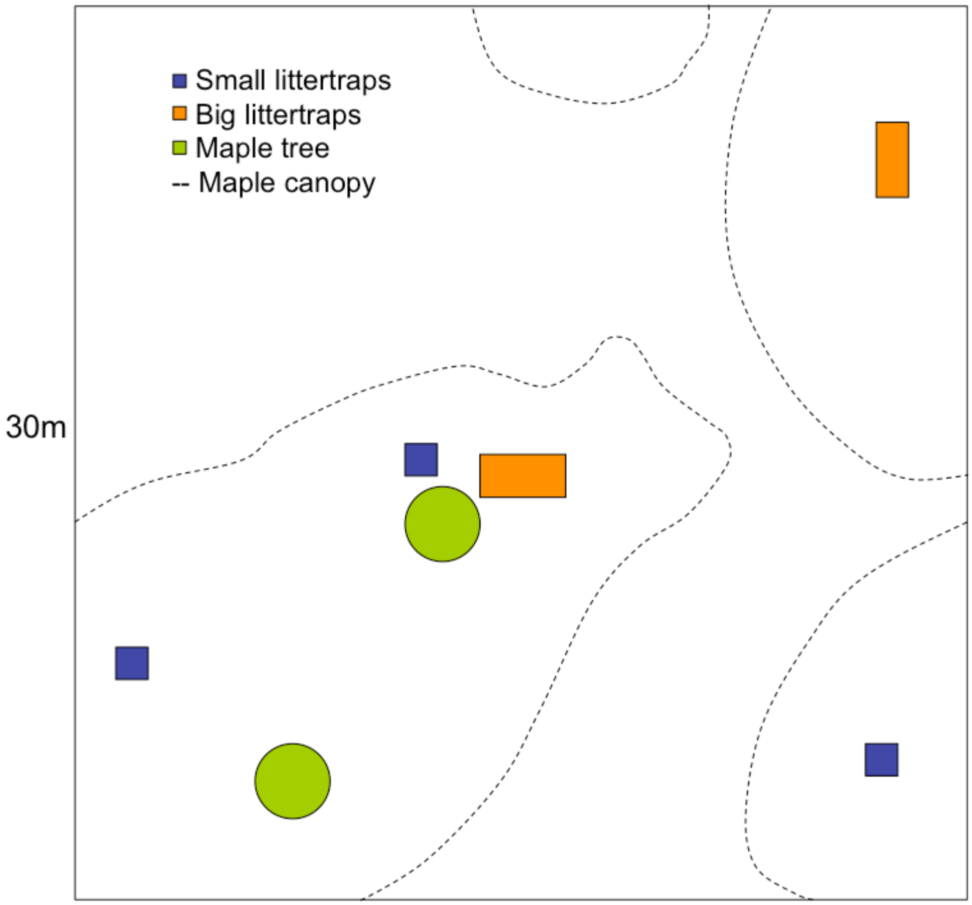
Appendices



Appendix 1: Diagrammatic representation of the plot layout and sampling design used to collect epiphytic litterfall under the canopy of big leaf maple at the Queets River Watershed, WA. Each plot had at least two bigleaf maple trees (green circles) and the area covered by bigleaf maple was estimated (dashed line). In each plot tree small littertraps (blue) and two large littertraps were installed under the area covered by bigleaf maple.

Appendix 2: Detail of small littertraps. Littertraps were installed in July 2010 and emptied monthly trough November 2011. The sequence of images represents the installed trap July 2010 (A) through October 2010 (D).

Appendix 3: Detail of large littertraps. Large littertraps were installed in July 2010 (left). Epiphytic material collected by the large littertraps included epiphytes attached to fallen branches and trunks, and clumps of epiphytes unattached to branches larger than *ca* 100cm^2. Although large traps had inputs of all types of litter (right), only epiphytic and woody material were sampled with this large traps.

VITA

Camila Francisca Tejo Haristoy was born and raised in Santiago, Chile. She pursued a degree in biology at the Pontificia Universidad Católica de Chile, where she discovered the wonders of forest canopies. After graduate in 2006, Camila worked for two years as a ecology research assistant and botany professor until she decided to go to graduate school. In 2008, Camila was awarded with a Fulbright-Conicyt scholarship to pursue a PhD. She was accepted at the Forest soils program at the then College of Forest Resources at University of Washington, where she begun her Doctoral career under the guidance of Dr. Darlene Zabowski and Dr. Nalini Nadkarni.