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Canopy Soils of Sitka Spruce and Bigleaf Maple in the Queets River Watershed, Washington

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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 and water, and accumulate allochthonous nutrients for epiphytes and their associated biota. This study characterized the chemical and physical characteristics of canopy soils developed on Sitka spruce [*Picea sitchensis* (Bong.) Carrière] and bigleaf maple (*Acer macrophyllum* Pursh) in an old-growth forest at the Queets River watershed, Washington. Bigleaf maple canopy soils were dominated by hemic horizons, had higher pH, N content, cation exchange capacity, and extractable N levels relative to Sitka spruce canopy soils, which had higher bulk density and C/N ratios. Compared with the forest floor, canopy soils had lower total C, total N, and C/N ratio. The bigleaf maple canopy soil was classified as a Typic Haplohemist, whereas the Sitka spruce canopy soil was classified as a 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.

Abbreviations: CEC, cation exchange capacity.

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). With 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 other 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); thus canopy soils might provide nutrients for within-canopy organisms as well as the entire forest ecosystem.

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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) than 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. The high concentration of fibers makes canopy soils more susceptible to rapid desiccation than their terrestrial counterparts (Bohlman et al., 1995; Enloe et al., 2006; Lindo and Winchester, 2007). Elevated fiber content also affects the bulk density of canopy soils, which can range between 0.02 and 0.3 g cm^{-3} (Perez et al., 2005; Enloe et al., 2006).

In this study, we characterized and compared the characteristics of the canopy soils on Sitka spruce and bigleaf maple trees in an old-growth temperate rainforest of the Olympic Peninsula in the state of Washington. Sitka spruce and bigleaf maple both support high epiphytic biomass (Nadkarni, 1984; Ellyson and Sillett, 2003). However, the characteristics of the canopy soils have not been described. The specific objectives of this study were to quantify and compare the chemical and physical characteristics of canopy soils developed on spruce and maple and estimate 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 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]). The mean annual air temperature is 14.7°C. Winter mean temperatures are 7.3°C, whereas summer mean temperatures are 22°C (Latterell et al., 2006; O'Keefe and Naiman, 2006; Van Pelt et al., 2006).

The dominant conifer and hardwood species are spruce and 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 series (sandy-skeletal, mixed, isomesic Vitrandic Udifluvents) and Inceptisols of the Tealwhit series (fine, isotic, acid, isomesic Vertic Endoaquepts) (Bechtold and Naiman, 2009).

Epiphytes are dominated by *Isothecium stolonipherum* (Brid.) and *Antitrichia curtipendula* [(Hedw.) Brid.]. Vascular epiphytic plants (*Polypodium glycyrrhiza* D.C. Eaton and *Selaginella oregano* D.C. Eaton) are common, with seedlings of maple and grasses (*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 particular forest, the estimated biomass of epiphytic material (epiphytic plants, leaves, and debris from the host tree and canopy soils) is >10 Mg for a single spruce and >350 kg for maple, of which 250 and 80 kg correspond to canopy soil (spruce and maple, respectively) (R. Van Pelt, unpublished data, 2012).

Additionally, these two species have contrasting architecture and phenology. Dominant spruce trees are taller and older (>60 m and ≥300 yr) than the maples (∼40 m and 200 yr); thus epiphytic mats have a longer time to develop on spruce trees than on maples (Van Pelt et al., 2006). This age distribution is typical of these forests. 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

We used single-rope tree climbing techniques (Perry, 1978) 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 as older trees that had canopy soil. Maples were sampled in June 2010 and spruces were sampled in March 2011. Samples were collected based on the presence of a canopy mat reachable from the climbing rope. Soil samples from spruce were collected at a height between 19 and 51 m, within the lower third of the canopy. Maple samples were collected at a height between 9 and 19 m, also within the lower third of the canopy. In each branch, a whole epiphytic mat cross-section of 25 cm was sampled. Samples were taken back to the laboratory and stored at 3°C until they were processed. A morphological description of each canopy soil profile was done to determine the depth and horizon sequence of each pedon (four pedons per soil type). Additionally, four forest floor samples (O horizon only) were collected under the canopy of maple in February 2013 and four forest floor samples under spruce in April 2013.

To measure the bulk density of canopy soils, a volume between 15 and 56 cm^3 of soil of each horizon was cut, oven dried at 65°C for 48 h, and then weighed. For the forest floor bulk density, a volumetric sample between 17 and 56 cm^3 was cut and oven dried at 65°C for 48 h. Separate canopy samples were sieved through 12- 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 (Soil Survey Laboratory Staff, 2004). Ash content was determined by

loss-on-ignition at 550°C for 4 h. Soil color was determined using a Munsell color book for moist, sieved samples. Soil pH 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 PerkinElmer Model 2400 CHN analyzer. Total C and N mass held in the canopy soils was calculated by multiplying the mass of the canopy soils for spruce and maple trees (R. Van Pelt, unpublished data, 2012) by the crown area of the spruce or maple with the C or N concentration. Total C and N content of the O horizons on the ground were calculated by multiplying concentration of C or N by depth and bulk density of O horizons.

Extractable N (as NH_4^+ and NO_3^-) of canopy soils was determined with a 1 mol L^{-1} KCl extraction (Bremner and Mulvaney, 1982) and analysis of the solutions using an autoanalyzer (Perstorps Analytical 500 Series flow injection). The CEC of canopy soils was estimated using an unbuffered 1.0 mol L^{-1} NH_4Cl solution (Skinner et al., 2001). Maple and spruce canopy soils were classified according to the U.S. soil taxonomy (Soil Survey Staff, 2006).

The depth-weighted average of each horizon in each pedon for each soil property was used to determine significant differences between spruce and maple canopy soils using the Wilcoxon signed-rank test at a significance level of $p \leq 0.05$. All analyses were performed using R (R Development Core Team, 2012).

RESULTS

The mean thickness of sampled maple and spruce canopy soils was 13 to 48 cm and 11 to 18 cm, respectively (Fig. 1). Both canopy soil types had fibric (Oi), hemic (Oe), and sapric (Oa) horizons. Fibric horizons were 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. glycyrrhiza* 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. The sapric horizons of spruce canopy soils were thicker than the sapric horizons of maple canopy soils (Fig. 1).

The dominant color for both soil types was reddish brown, but with increasing depth the soil was blacker in spruce canopy soils and browner in maple canopy soils. Fiber content decreased with depth in spruce canopy soils (from 73 to 48%, Table 1). Maple canopy soils had >60% fiber content, which did not decrease with depth (Table 1). Bulk density increased with depth for both canopy soil types and was significantly higher in spruce canopy soils ($p = 0.05$, Table 1). No significant differences were found between the bulk density of the canopy soils and the O horizon beneath the respective host tree (Table 1).

The pH of the canopy soils in both tree species was acidic and differed significantly between spruce and maple canopy soils ($p = 0.03$, Table 2). The pH for spruce canopy soils 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 by horizon type on maple soils, whereas it decreased from hemic to sapric horizons for spruce canopy soils. We did not find significant differences in ash content between soil types (Table 2).

Cation exchange capacity increased with depth for both canopy soil types and was significantly higher in maple canopy soils than spruce canopy soils ($p = 0.03$, Table 3). Base saturation did not differ between soil types but was more variable on spruce canopy soils, ranging between 18 and 58% (Table 3). Exchangeable cations, particularly Ca, were significantly higher for maple canopy soils ($p = 0.03$, Table 3).

Carbon concentration did not differ between canopy soil types, whereas N concentration was significantly higher for maple canopy soils ($p < 0.05$, Table 2). The C/N ratios differed significantly between soil types ($p = 0.03$), with maple canopy soils having a lower C/N ratio (Table 2).

Total C content was >100 g cm^{-2} for maple canopy soils and >270 g cm^{-2} for spruce canopy soils (Table 4). For the O horizon, the total C content under spruce canopy soils was >1500 g cm^{-2} and nearly 300 g cm^{-2} for maple canopy soils. Total N content had the following sequence: maple canopy soils < spruce canopy soils < 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 between the O horizon under spruce and the O horizon under maple (Table 4).

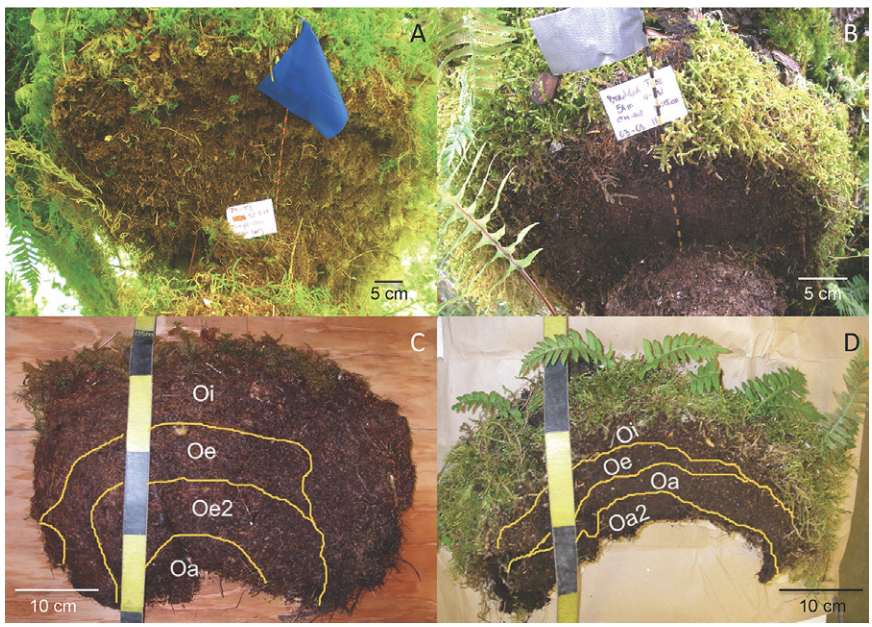

Fig. 1. In situ characteristics of (A) maple and (B) spruce canopy soils and laboratory measurements showing final horizons designations (C) maple and (D) spruce canopy soils.

Table 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 sodium pyrophosphate extract color (SPEC) values were visually averaged among replicates.

Horizon	*n*	Depth		Moist color	SPEC color	Rubbed fiber	Boundary†	Bulk density
		Avg.	Max.					
		cm				%		g cm^{-3}
				Bigleaf maple				
Canopy soils								
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		7.8 (5.3)					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 soils								
Oi	3	2.6	6	5YR 2.5/3	8/2	73	aw	0.06 (0.04)
Oe	3	2	3.5	2.5YR 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		4.4 (1.8)					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.

‡ Mean with standard deviation in parentheses.

§ Means followed by different letters within a column and between species are significantly different.

¶ ND, not determined.

Extractable NH_4^+ and NO_3^- concentrations of maple canopy soils were significantly higher than for spruce canopy soils ($p < 0.02$). There was little variability in either extractable NH_4^+ or NO_3^- by depth in the spruce canopy soils (Fig. 2). Extractable N varied more with horizon depth in the maple canopy soil. A much smaller fraction of N was extractable in the spruce canopy soils than the maple; this corresponds with the lower C/N ratio of the maple soils.

We classified the maple canopy soils as Typic Haplohemists, while spruce canopy soils were classified as Typic Haplosaprists.

Table 2. The pH, total C and N, C/N ratio, and ash content from loss-on-ignition for maple and spruce canopy soils from the Queets River watershed, Washington. Values were weighted by horizon depth.

Horizon	pH	Ash	Total C	Total N	C/N ratio
		%	g kg^{-1}		
		Bigleaf maple canopy soils			
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 (30) a	19 (0.3) a	22 (2.2) a
		Sitka spruce canopy soils			
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	452 (13) a	15 (0.2) b	30 (3.0) b

† Mean with standard deviation in parentheses.

‡ Means followed by different letters within a column and between species are significantly different.

DISCUSSION

Canopy soils developed on maple and spruce soils have different physical and chemical properties that are linked with the host tree on which these soils form. The age of the tree and consequently the time these canopy soils have had to develop might play a key role in spruce and maple canopy soils characteristics. At the Queets River watershed, large spruce trees have a maximum age of 330 yr, whereas the age of large maples is about 200 yr (Van Pelt et al., 2006). 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. When spruce needles decompose, waxes, organic acids, and phenols are released, creating the dark-colored horizons of this sapric soil (Ghosal et al., 1999; Berg and McClaugherty, 2008). Additionally, spruce trees are the tallest tree species present, and canopy mats on spruce have litter inputs almost exclusively from this host tree. Canopy soils on 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, may be the result of a rapid accumulation of epiphytes in the canopy mats and inputs of the nutrient-rich litter from maple leaves. Thicker canopy soils of maple trees have a lower bulk density because of the high abundance of rhizomes that increase the porosity of these canopy soils.

Other studies on the ground have indicated that mineral soil developed under maple has a lower bulk density than mineral soils under Douglas-fir; this difference was attributed to the large inputs of maple litter (Turk et al., 2008). Compared with other canopy soils, canopy soils on maples have similar bulk densities to canopy soils of *Fitzroya cupressoides* (Cupressaseae) (Perez et al., 2005), whereas spruce canopy soils have a similar bulk density to canopy soils of redwoods (Enloe et al., 2006).

The fiber content of maple canopy soils was >60% throughout the profile, with a large contribution of rhizomes

and canopy roots from the host tree. A high fiber content in organic soils promotes a large pore space that reduces water retention and therefore affects water availability to 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 soils may provide more moisture to epiphytes and canopy roots during droughty periods.

Ash contents were similar to those described for tropical canopy soils and are typical of Histosols (Nadkarni et al., 2002; Soil Survey Staff, 2006). Maple canopy soil ash content increased with depth, but there was no clear trend with spruce canopy soils (Table 3). Differences in ash content are attributed to a higher litter mineral-derived nutrient concentration (such as Ca) from abscised leaves that accumulates on the canopy mats of maples with time (Turk et al., 2008).

Table 3. Cation exchange capacity (CEC), base saturation (BS), and exchangeable cations for maple and spruce canopy soils from the Queets River watershed, Washington.

Horizon	CEC	BS	Ca	K	Mg	Na
	$cmol_c\ kg^{-1}$	%	$g\ kg^{-1}$			
			Bigleaf 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)

† Mean with standard deviation in parentheses.

‡ NA, not available.

§ TR, trace.

¶ Means followed by different letters within a column and between species are significantly different.

The pH of maple canopy soils was significantly higher than the pH of spruce canopy soils (Table 2). The higher acidity of spruce canopy soils 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 with time (Ghosal et al., 1999). The higher pH 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. Base saturation particularly 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 the Ca levels of spruce soils (Lowman and Rinker, 2004; Lindo and Winchester, 2007). The lower CEC and base saturation of the spruce canopy soils 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 for the mineral soil underneath maple compared with conifer plots.

The C concentration of spruce canopy soils was similar to other canopy soils developed on other conifer trees (Perez et al., 2005; Enloe et al., 2006). Whereas the total C of spruce canopy soils was higher than the total C concentration of maple canopy soils, this relationship was reversed for the O horizons on the ground (Table 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). Ammonium was the dominant extractable form of N, which suggests higher potential mineralization rates (specifically high ammonification) for maple canopy soils than spruce canopy soils. Studies of forest floor soils under maple have indicated that high mineralization is related to the high N concentrations of maple litter (Fried et al., 1990; Turk et al., 2008). The 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 for maple canopy soils than spruce canopy soils. The C/N ratio of soils on the ground did not differ between the 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 envi-

Table 4. Carbon and N concentrations and total contents of canopy and surface soil O horizons (within and beneath the canopy) of maple and spruce at the Queets River watershed, Washington.

Soil	Carbon		Nitrogen		C/N ratio
	Concentration	Total	Concentration	Total	
	$g\ kg^{-1}$	$g\ m^{-2}$	$g\ kg^{-1}$	$g\ m^{-2}$	
		Big leaf maple			
Canopy	424 (30) 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

† Mean with standard deviation in parentheses. Means followed by different letters are significantly different.

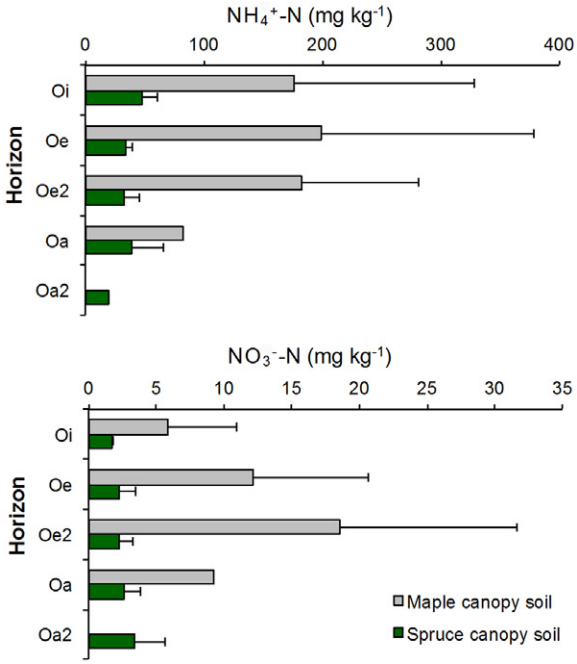

Fig. 2. Mean extractable NH_4–N and NO_3–N concentrations for maple and spruce canopy soils.

ronment than in the forest floor (Table 4), which suggests higher N mineralization rates in the canopy. Furthermore, the higher C/N ratio of the forest floor could be influenced by the woody biomass accumulated on the ground. Woody debris has a higher C/N ratio than foliage litter, and this woody material is less likely to accumulate in the canopy than in the forest floor (Lindo and Winchester, 2007; Berg and McClaugherty, 2008).

In temperate forests, the N concentration of canopy soils ranges between 10 and 17 g kg^{-1}, with C/N ratios ranging between 31 and 41 (Perez et al., 2005; Enloe et al., 2006; Lindo and Winchester, 2007). In this study, the N concentration and C/N ratio of spruce canopy soils were within the range typical of many temperate forests, whereas the maple canopy soils had a higher total N and lower C/N ratio more similar to the soil of a Costa Rican forest (Nadkarni et al., 2002).

The canopy soil biomass of spruce and maple trees is, on average, 250 kg for spruce and 80 kg for maple (R. Van Pelt, unpublished data, 2012). This is the equivalent of 273 g m^{-2} of C and 9 g m^{-2} of N held in the canopy of spruce, and 114 g m^{-2} of C and 5 g m^{-2} of N held in the canopy of maple. Although the total quantity of C and N in the forest floor is much higher that what is being held in the canopy (Table 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. The lower total C and N contribution of spruce canopy soils compared with the O horizon underneath has been attributed to the slower decomposition rate of spruce needles that promotes a high accumulation of the forest floor (Harmon et al., 1990).

As different tree species influence the properties of the soil beneath their crowns, canopy soil properties are also related to the properties of the host tree on 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 documented the differences between canopy soils developed on Sitka spruce and bigleaf maple. Canopy soils developed on maple and spruce have distinguishable O horizons at different stages of decomposition that are a result of different pedogenic processes and the time that these O horizons have to develop. These differences are also reflected in the chemical properties of spruce and maple canopy soils such as pH, CEC, and C/N ratio. Chemical differences 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 the N content and mineralization, CEC, and exchangeable cations, while older canopy-dominant spruce trees have higher acidity and bulk density and lack the nutrient-rich litter inputs that maple canopy soils have.

This study highlights the importance of epiphytes and canopy soils and the accumulation of biomass and nutrients in the canopy compartment. At 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 they are absorbed by epiphytic plants or the host tree (via canopy roots), leached via throughfall or stem flow, or deposited as epiphytic litterfall on the forest floor.

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