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

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Abstract: The amounts and ecological importance of epiphytic litterfall has often been overlooked in forest ecosystem studies. However, epiphytes participate in whole-ecosystem dynamics by capturing and retaining nutrients from atmospheric sources and transferring these nutrients to other ecosystem components. We quantified epiphytic litterfall under the canopy of mature bigleaf maples (*Acer macrophyllum* Pursh) and compared it with other litter components in an old-growth temperate rainforest in Washington State. Total litterfall during one year was 4760 kg·ha^{-1}, with the greatest contribution from bigleaf maple leaves. Of the total litter input, 546 kg·ha^{-1} consisted of epiphytic litter, equivalent to 12% of total fine litter input, the highest contribution of epiphyte litterfall documented for this type of forest. Compared with other studies in the Pacific Northwest, our estimations of conifer needle inputs relate to the location of the littertraps. Bigleaf maple leaves dominated carbon (C) and nitrogen (N) returns in litter; epiphytic litterfall contributed 240 kg·ha^{-1}·year^{-1} of C (~11% of total C inputs) and 5.7 kg·ha^{-1}·year^{-1} of N (~11% of total N inputs) to the forest floor. Inputs of N from epiphytes and bigleaf maple litter under the canopy of this tree could be important in augmenting N in this old-growth ecosystem.

Key words: Acer macrophyllum, carbon cycle, epiphytic litterfall, forest productivity, nitrogen cycle, old-growth forest.

Résumé : Les quantités et l'importance écologique de la chute de litière d'épiphytes a souvent été négligée dans les études sur les écosystèmes forestiers. Cependant, les épiphytes contribuent à la dynamique globale de l'écosystème en captant et retenant des nutriments provenant de sources atmosphériques et en transférant ces nutriments à d'autres composantes de l'écosystème. Nous avons quantifié la chute de litière d'épiphytes sous un couvert d'érable à grandes feuilles (*Acer macrophyllum* Pursh) matures et nous l'avons comparée à d'autres composantes de la litière dans une vieille forêt pluviale tempérée de l'État de Washington. La chute totale de litière au cours d'une année atteignait 4760 kg·ha^{-1} et la portion la plus importante provenait des feuilles d'érable à grandes feuilles. De l'apport total de litière, 546 kg·ha^{-1} était de la litière d'épiphytes, ce qui équivalait à 12 % de l'apport total de litière fine, la plus importante contribution de litière d'épiphytes rapportée pour ce type de forêt. Comparativement à d'autres études dans le Pacific Northwest, nos estimations d'apport d'aiguilles de conifères sont associées à la localisation des trappes à litière. Les feuilles d'érable à grandes feuilles retournaient le plus de C et N dans la litière; la litière d'épiphytes contribuait 240 kg·ha^{-1}·an^{-1} de C (~11 % de l'apport total de C) et 5,7 kg·ha^{-1}·an^{-1} de N (~11 % de l'apport total de N) dans la couverture morte. Les apports de N par le biais de la litière d'épiphytes et d'érable à grandes feuilles sous le couvert de cette espèce pourraient être importants pour accroître la quantité de N dans cet écosystème de forêt ancienne. [Traduit par la Rédaction]

Mots-clés : Acer macrophyllum, cycle du carbone, litière d'épiphytes, productivité forestière, cycle de l'azote, forêt ancienne.

Introduction

Epiphytes, plants that derive support but not nutrients from their host trees, are a component of many forest ecosystems (Lowman and Nadkarni 1995). Whereas terrestrially rooted vegetation (trees, shrubs, and herbs) obtain their nutrients predominantly from the soil, epiphytic plants (e.g., mosses and epiphytic ferns) and lichens garner their nutrients from wind- and rain-borne sources or arboreal soil (Enloe et al. 2006; Hietz et al. 2002; Knops et al. 1996; Nadkarni and Matelson 1991). Because epiphytic material (plants and lichens plus canopy soil; hereafter EM) captures allochthonous nutrients that settle within the canopy, the deposition of epiphytic litterfall to the forest floor can increase the total amount of nutrients (particularly nitrogen (N)) intercepted and retained within the forest. The contribution of EM to litterfall might be important in forest ecosystems where N limits productivity, a common situation in Pacific Northwest forests (Edmonds et al. 1989; Fried et al. 1990; O'Keefe and Naiman 2006).

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

There is extensive information on the quantity of litterfall from terrestrially rooted plants, but very few studies have addressed the contribution of epiphytic litterfall in forests where EM is present (e.g., Kohler et al. 2008; Nadkarni and Matelson 1992; O'Keefe and Naiman 2006; Veneklaas 1991). In those forests, EM litterfall

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can be a substantial contributor to total litterfall biomass. For instance, in a Colombian montane forest, Veneklaas (1991) estimated the total litterfall as 4.3 Mg·ha^{-1}·year^{-1}, with ~5% of this litter attributed to epiphytes (vascular plants, bryophytes, and lichens). 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 is challenging because it is extremely variable spatially and temporally. In the Monteverde cloud forest, over 50% of EM litterfall was collected in less than 2% of the collection containers (Nadkarni and Matelson 1992). 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 has been estimated (Abee and Lavender 1972; Edmonds and Murray 2002; Harmon et al. 2004; Klopatek 2007; O'Keefe and Naiman 2006), but only a few studies have quantified the contribution of EM to total litter biomass (Abee and Lavender 1972; McShane et al. 1983; O'Keefe and Naiman 2006). McShane et al. (1983), in a Douglas-fir – western hemlock forest, estimated that epiphytic litterfall ranges from 46 to 115 kg·ha^{-1}·year^{-1}. 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 species. Most of these studies, however, did not specifically focus on assessing epiphyte litterfall input. Therefore, the contribution of epiphytes may have been underestimated, as EM often fall as large clumps and by "riding down" large and small branches and on whole fallen trees, which would not be captured in traditional tree litterfall collectors.

Bigleaf maple is an native tree of the Pacific Northwest, characterized by large accumulations of epiphytic biomass (Nadkarni 1984). Bigleaf maple litterfall can enhance soil fertility through the supply of nutrients to the forest floor by providing litter that is rich in N, calcium (Ca), and potassium (K) (Turk et al. 2008). Moreover, Chandler et al. (2008) reported that over 80% of bigleaf maple litter is deposited directly under the bigleaf maple canopy. The combined effects of epiphytic biomass, nutrient-rich litter, and high bigleaf maple litter inputs suggest that the presence of bigleaf maples and their epiphytes could enhance the capture of atmospheric N and its movement from the canopy to the forest floor of temperate rainforests.

The objective of this study was to determine the contributions of biomass, carbon (C), and N derived from epiphytic litterfall underneath bigleaf maples in an old-growth temperate rainforest in Washington State. In the study area, epiphytic biomass is extremely high: large trees can hold over 500 kg of dry epiphytic biomass (Naiman et al. 2010). Specifically, we (*i*) determined monthly and seasonal litter inputs under the canopy of bigleaf maple during one year, (*ii*) quantified annual C and N returns from litter components, (*iii*) related total and EM litterfall to temperature and precipitation, and (*iv*) compared EM and tree litter inputs under bigleaf maple with what has been documented for this forest and for other temperate forests.

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 warm, dry summers. The mean annual precipitation is ~3000 mm, with most precipitation falling from November to June. Mean annual air temperature is 14.7 °C, and mean winter and summers temperatures are 7.3 °C and 22 °C, respectively (Bechtold and Naiman 2009). Wind speed ranges from 6.3 km·h^{-1} to 10.5 km·h^{-1}, with the highest speeds between December to March (Quillayute station, Western Regional Climate Center (2013)).

Table 1. Mean total litterfall (kg·ha^{-1}) by litter type under the canopy of bigleaf maple between September 2010 and August 2011 at the Queets River watershed, Washington State.

Litter type	Mean total litterfall (SD)	% total litterfall
Bigleaf maple leaves	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 species	238 (174)	5
Miscellaneous material	580 (429)	12.1
Woody material	826 (481)	17.4
Total	4762 (1331)	100

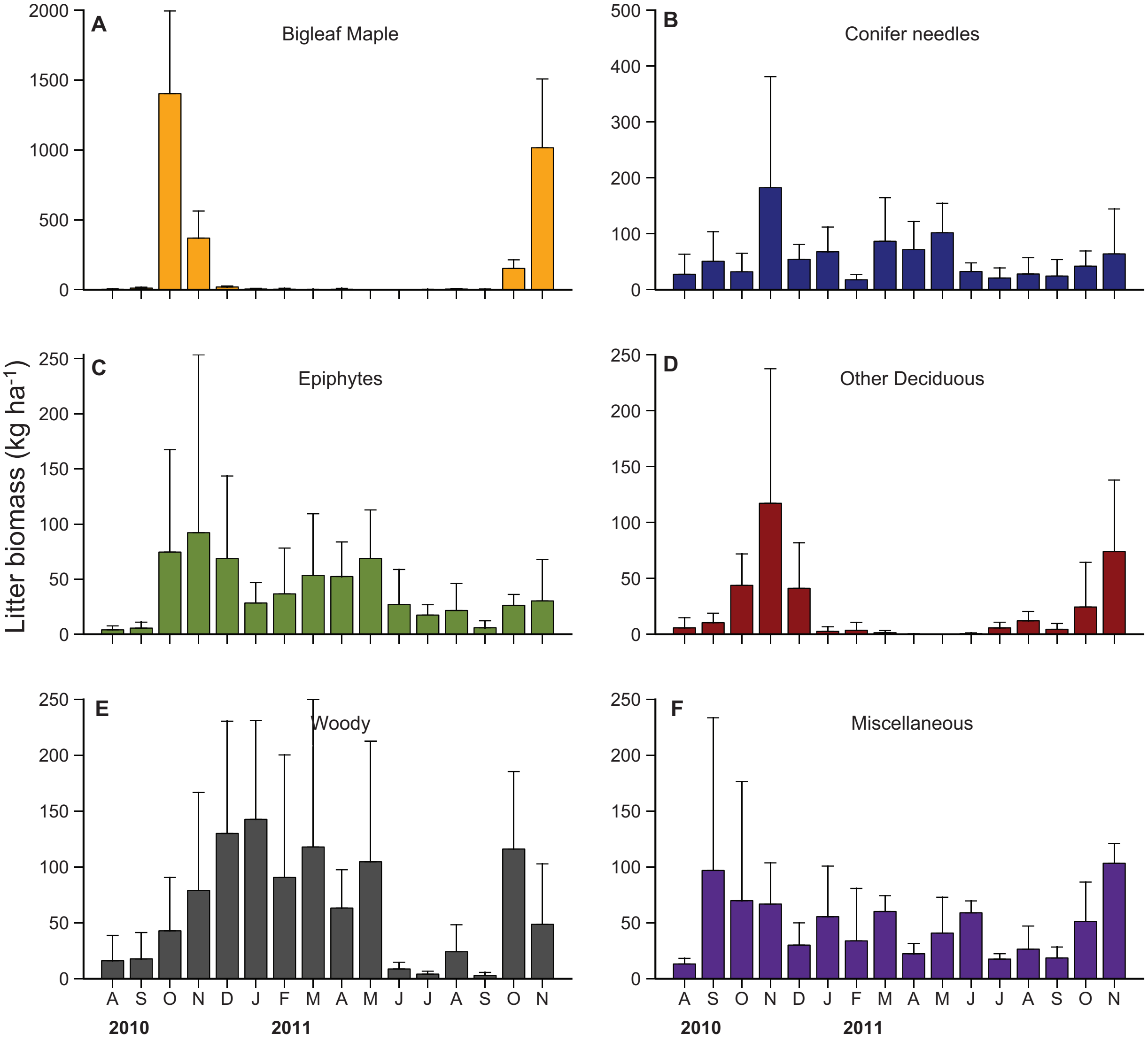
The forest is described by Van Pelt et al. (2006) and dominated by Sitka spruce. Occasional western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) also occur. Bigleaf maple is the dominant hardwood species, and its crown coverage corresponds to 34% of total forest cover, with coverage determined using the line intercept technique (Canfield 1941). Other hardwood species present are red alder (*Alnus rubra* Bong.) and vine maple (*Acer circinatum* Pursh). Understory vegetation is dominated by western swordfern (*Polystichum munitum* (Kaulf.) C. Presl) and redwood-sorrel (*Oxalis oregana* Nutt.) (Van Pelt et al. 2006). In the canopy, the predominant epiphytes are two bryophyte species: isothecium moss (*Isothecium myosuroides* Brid.) and antitrichia moss (*Antitrichia curtipendula* (Hedw.) Brid.). The epiphytic vascular plants licorice fern (*Polypodium glycyrrhiza* D.C. Eaton) and Oregon spikemoss (*Selaginella oregana* D.C. Eaton) are common in the canopy; epiphytic lichens such as lettuce lung (*Lobaria oregana* (Tuck.) Müll. Arg.) and lungwort (*Lobaria pulmonaria* (L.) Hoffm.) are also common.

Sampling and analysis

In June 2010, four 30 m × 30 m plots were installed in the study site, 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%. We used two methods to estimate tree and epiphytic litter inputs to the forest floor. For smaller materials (epiphyte fragments < 100 cm^2 and litter from trees), we installed three 50 cm × 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 reduce disturbance from elk. To collect inputs of larger EM, we 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 large traps only included clumps of epiphytes (≥100 cm^2), epiphytes attached to fallen branches, and branches and twigs (all woody material from large traps was >1 cm in diameter). Within each plot, all littertraps were randomly distributed under the canopy of bigleaf maple and were emptied monthly for 16 months (August 2010 to November 2011). The sample design did not include epiphytic litterfall from fallen trees, so the total epiphytic litterfall of the forest is still an underestimate.

Collected litterfall was taken to the laboratory, air dried for 48 h, sorted, and weighed. Air-dried masses were compared with oven-dried masses (65 °C for 48 h) and were within 1% of the

Fig. 1. Mean and standard deviation of litterfall inputs (kg·ha^{-1}) per month of (A) bigleaf maple leaves, (B) conifer needles, (C) epiphytes, (D) other deciduous species leaves, (E) woody material, and (F) miscellaneous material collected under the canopy of bigleaf maples at the Queets River watershed, Washington State between August 2010 and November 2011. Note that the scale of the *y* axis for bigleaf maple and conifer needles is 8× and 2×, respectively, the axis of other categories of litter.

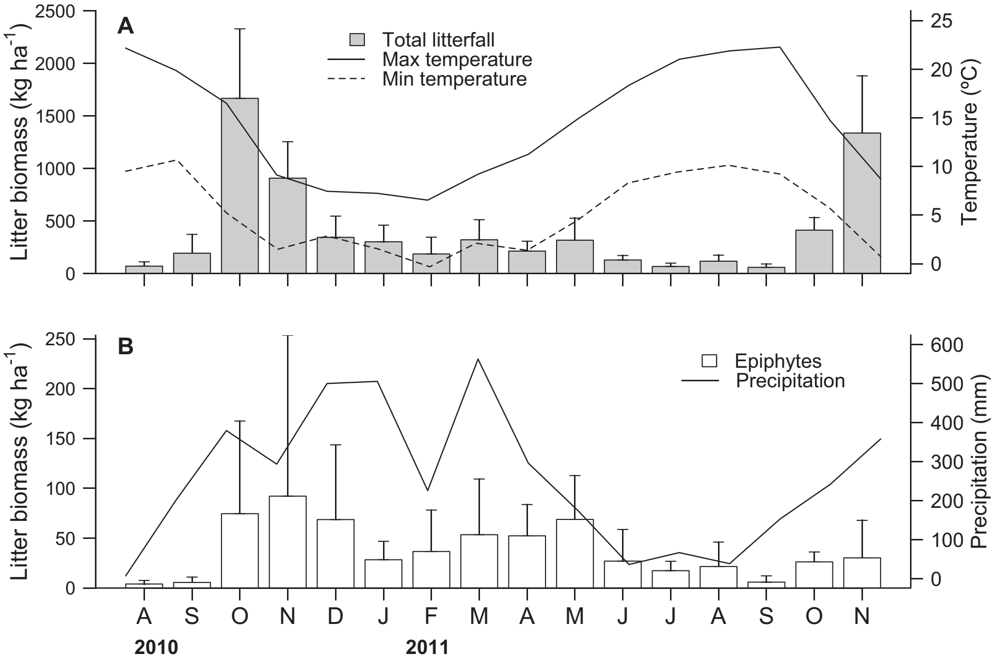


oven-dried mass. Litter collected in the smaller traps was separated into the following categories: bigleaf maple leaves, other deciduous leaves (vine maple, red alder, and black cottonwood (*Populus nigra* L.)), conifer needles (spruce, western hemlock, and Douglas-fir), woody materials (twigs, branches, and bark), EM (bryophytes, lichens, licorice ferns, and canopy soil), and miscellaneous material (reproductive material, understory litter, dead insects, and unidentifiable fragments). The EM collected from the larger littertraps was separated to bryophytes, lichens, licorice fern, canopy soil, and the woody material (twigs, branches, and bark) was separated from the EM. Monthly litter inputs of each trap for each litter category were standardized to kilograms per hectare and then averaged per plot. Monthly litter collected in small and large traps (EM and woody material) was standardized to kilograms per hectare, summed, and then averaged per plot.

The relationship between litter inputs and climatic variables (precipitation and temperature) was examined using Pearson's correlation coefficients (*r*). Precipitation and temperature data for the Queets River watershed during the sampling period was obtained from the PRISM Climate Group database from Oregon State University (available from http://prism.oregonstate.edu [accessed 23 November 2014]).

Total C and N were determined by dry combustion using a PerkinElmer 2400 CHN/O analyzer (PerkinElmer, Wellesley, Massachusetts) in the analytical lab, School of Environmental and Forest Sciences, University of Washington. The sorted and weighed litterfall of each plot was grouped by season. A mixed litter category was created that included conifer needles, other deciduous species, and miscellaneous material. Litterfall C and N inputs for each litter category (epiphytes, bigleaf maple, woody material, and mixed litter) were determined by multiplying the nutrient concentration of each category by the mass of that litter fraction for each season. The C to N ratio of epiphytic litterfall was calculated in proportion to the biomass and C and N concentration of each epiphytic component. To determine annual C and N inputs in litter for each category, total C and N from September 2010 through August 2011 were summed. All the data were analyzed using R software version 2.14.1 (R Development Core Team 2012).

Fig. 2. Mean and standard deviation of total and epiphytic litterfall inputs (kg·ha⁻¹) per month plotted against modeled (A) maximum and minimum temperatures and (B) precipitation data for the area from August 2010 to November 2011.



Results

Litterfall biomass and seasonality

The mean total overstory litterfall under the canopy of bigleaf maple was 4760 kg·ha⁻¹ during one year (Table 1). Bigleaf maple leaves were the dominant litter fraction and accounted for over one-third of total litterfall. In decreasing order, woody material, conifer needles, and miscellaneous material were the next largest fractions of litter biomass. Other deciduous species contributed only 5% of total litterfall. Inputs from epiphytes were 12% of total litter inputs during one year (546 kg·ha⁻¹·year⁻¹). Surprisingly, no canopy soil litterfall was collected during the sampling period even though it is a large component of the arboreal canopy ecosystem. No larger branches were collected in either the small or large litter plots, and the only canopy soil that was noted on the forest floor was attached to larger branches. Determining the amount of canopy soil litter may require a longer sampling period, more litter collectors, or larger plots, as it appears to be a rare component of litterfall.

Litterfall inputs showed a distinct seasonality, with highest monthly inputs in October and November (Fig. 1). Leaves from bigleaf maple and other deciduous species were present mainly during the autumn (September–November) and were almost completely absent between March and June. Conifer needle litter had a maximum in November 2010 (183 kg·ha⁻¹·month⁻¹), whereas for the rest of the year, needle litter biomass averaged 48 kg·ha⁻¹·month⁻¹. Woody litterfall showed high spatial and temporal variability, particularly during the fall and winter months, when it reached 142 kg·ha⁻¹·month⁻¹ (Fig. 1). When relating inputs of total litterfall with climatic variables, we found a positive correlation between total litterfall and precipitation during the autumn months (September–November; $r = 0.98$, $p = 0.0001$) (Fig. 2), whereas total litter inputs and temperature were positive correlated only during the winter months (December–February; $r = 0.99$, $p \leq 0.05$).

Epiphytic litterfall

The inputs from epiphytic litterfall were highly variable over time, with biomass ranging from 4 to 90 kg·ha⁻¹·month⁻¹ during the sampling period (Figs. 1 and 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. This contribution of EM to total litterfall was mainly litter from licorice fern.

Overall, bryophytes contributed 90% of total EM litterfall, whereas lichens and licorice fern were 5% and 6% of total EM litterfall, respectively (Table 2; Fig. 3). Bryophyte litterfall showed a strong seasonal pattern, and particularly between October and December 2010, bryophyte litterfall was derived mainly from larger clumps of mosses in the large littertraps. Nevertheless, small clumps and small fragments of bryophytes were continuously present in littertraps during the entire collection period (Fig. 3). Lichen litter was also collected every month during the sampling period but was greatest between January and June 2011 (ca. 2–3.5 kg·ha⁻¹·month⁻¹). Licorice fern litterfall contributed the least of all three epiphyte categories, and there was no licorice fern litterfall during some months (Fig. 3). Highest inputs of licorice fern were between July and October 2011 (12 and 8 kg·ha⁻¹·month⁻¹, respectively), with small amounts scattered throughout the other months. Epiphytic litterfall was positive correlated with precipitation during the sampling period ($r = 0.53$, $p = 0.02$).

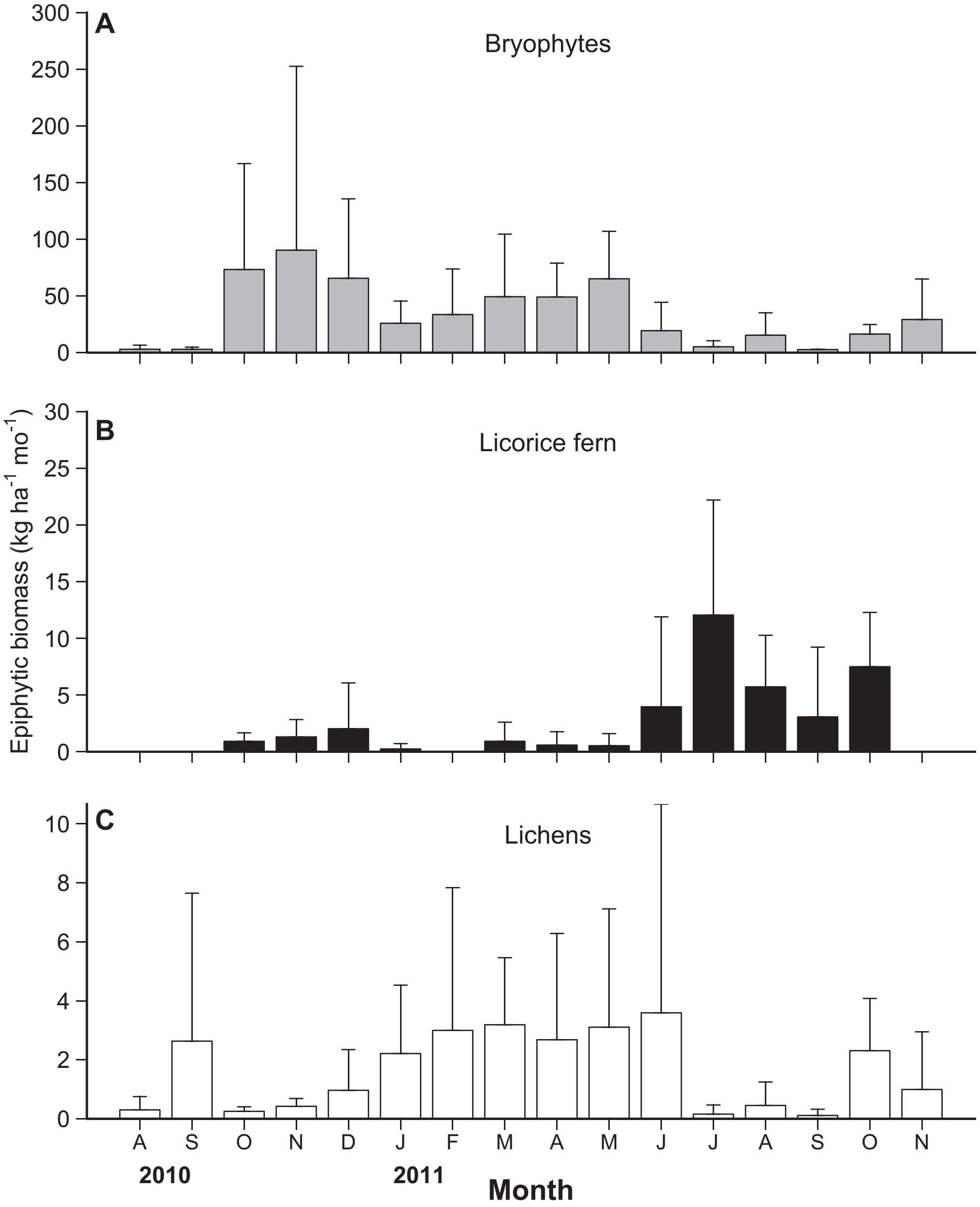
C and N in litterfall

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

The largest quantity of C and N inputs to the forest floor was bigleaf maple leaf litter, followed by mixed litter, woody material, and bryophytes (Table 2). Lichens and licorice fern had the lowest C and N deposition during one year, respectively. Bigleaf maple leaves and mixed litter (conifer needles, other deciduous, and miscellaneous category) contributed nearly 80% of total litter N during one year. Overall, epiphytic litterfall (bryophytes, lichens, and licorice fern) and woody material each contributed ~10% of total N in litter (Table 2).

Total C and N inputs varied among seasons (Fig. 4). Bigleaf maple leaves were present only during the autumn, with C and N inputs from bigleaf maple leaf litter higher in November 2010

Fig. 3. Mean and standard deviation of epiphytic litter biomass (kg·ha^{-1}) per month by component, (A) bryophytes, (B) licorice fern, and (C) lichens, collected under the canopy of bigleaf maple between August 2010 and November 2011 at the Queets River watershed, Washington State. Note that the scale of the *y* axis for bryophytes and licorice fern is 30× and 3×, respectively, the axis of the lichens.



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 of 2011 (Fig. 2). The mixed litter category had higher C and N inputs during the autumn, which corresponds to a higher deposition of litter from non bigleaf maple deciduous species. On average, C to N ratios ranged from 29 for lichens to 71 for woody material (Table 2).

Total C and N inputs from epiphyte litter were mainly derived from bryophytes. However, total N inputs from epiphytic litterfall during the spring correspond to lichen litterfall, which had the highest N concentration (Table 2). The C to N ratio for epiphytic litterfall was 42 due to the large biomass of bryophytes, the dominant epiphytic litterfall component. Throughout the seasons, changes in the C to N ratio of EM occurred. The lowest C to N ratio for epiphytic litterfall (36) occurred during autumn 2010 when bryophytes were the major epiphytic litter component. However, during the summer of 2010, C to N ratio of the epiphytic litterfall had a high C to N ratio (71) and was dominated by licorice fern.

Discussion

Although the presence of EM has been increasingly acknowledged as an important component of forest ecosystems (Cardelus 2010; Lindo and Whiteley 2011; Nadkarni et al. 2011), collections of epiphytic litterfall have often been included with miscellaneous litter or mixed in 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 to be between 4% and 7% of total litterfall (Table 3). At the Queets River watershed, O'Keefe and Naiman (2006) documented epiphytic litter between 4% and 6% of total litter inputs. Although we did not collect epiphytic litter from whole trees or large fallen branches, our estimation of epiphytic litterfall biomass under the canopy of bigleaf maple was 12% of the total litter biomass, which was the highest contribution of epiphytic litterfall reported for this forest type. Using larger litter-traps may have allowed us to collect a more accurate measure of

Table 2. Carbon (C) and nitrogen (N) concentrations (%), annual returns (kg·ha^{-1}) between October 2010 and September 2011 and C to N ratios (C:N) of litter collected under the canopy of bigleaf maple at the Queets River watershed, Washington State.

	Carbon		Nitrogen		
Litter type	Concentration	Annual return	Concentration	Annual return	C:N
Bigleaf maple leaves	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 material	49 (1)	405 (234)	0.7 (0)	5.4 (3)	71 (9)
Total		2290 (634)		51 (18)	

Note: Values were calculated by multiplying the nutrient concentration of each litter fraction by the total accumulated biomass of that fraction in each plot. Values are means with standard deviation in parenthesis (n = 18). Mixed litter includes conifer needles, other deciduous species, and miscellaneous material.

EM litterfall, particularly inputs from canopy soils, as larger clumps were more likely to be collected in the larger traps. Collection of canopy soils is challenging as canopy soils developed underneath epiphytes are attached to branches and crotches of the host tree (Haristoy et al. 2014). When found on the ground, canopy soils are part of the EM conglomerate or remain attached to the fallen branch or tree. On the other hand, some lichen litter could have been lost from littertraps due to animal predation of alectorioid lichens (Esseen and Renhorn 1998; McCune and Daly 1994).

Litterfall under the canopy of bigleaf maple during one year was similar to litter biomass sampled from the entire forest around the bigleaf maple plots including coniferous and other hardwood trees (O'Keefe and Naiman 2006), as well as to other old-growth forests of the region (Abee and Lavender 1972; Edmonds and Murray 2002). Maple leaves were the dominant litter component under bigleaf maple trees, which indicates that bigleaf maple leaves are predominantly deposited directly under bigleaf maple canopy similar to the finding of Chandler et al. (2008). Hirabuki (1991) also determined that litter distribution corresponded with a tree's canopy distribution.

In previous studies, the dominant component of litterfall in this region was conifer needles (Edmonds and Murray 2002; O'Keefe and Naiman 2006). At the Queets River watershed, the dominant conifers reach heights above 80 m, and their needles are carried by the wind to the area covered by bigleaf maple. Although O'Keefe and Naiman (2006) reported 2980 kg·ha^{-1}·year^{-1} of annual conifer needle inputs, in our study, we only collected 25% of that value under the canopy of bigleaf maple. This lower biomass of conifer needles is undoubtedly related to the location of the littertraps under bigleaf maple, but it shows that needles are still a major contributor to litter biomass under bigleaf maple.

Litterfall seasonality in the Pacific Northwest has been linked with temperature and precipitation patterns (Abee and Lavender 1972; Edmonds and Murray 2002). The difference in the total litter inputs between autumn 2010 and autumn 2011 may be attributed to a later start of autumn rains in 2011 compared with 2010. In 2010, the beginning of the rainy season occurred in August, but in 2011, the rain began to increase in September (Fig. 2). Furthermore, although the dry period in 2010 lasted from July to August, in 2011, the dry period extended from June through to August, which could also have affected the peak in litterfall.

N inputs from total litterfall under the canopy of bigleaf maple were much higher than reported by other studies in the Pacific Northwest (Abee and Lavender 1972; Edmonds and Murray 2002) (Table 3). High N inputs are related to the high proportion of bigleaf maple biomass in the litter, which has a high N concentration (Chandler et al. 2008; Turk et al. 2008). Total N inputs from EM litterfall under bigleaf maple during one year are the highest recorded for temperate ecosystems, corresponding to 11% of total N inputs. A previous study in tropical ecosystems estimated the N contribution of epiphytic litterfall as 7% of total N in litterfall (Nadkarni and Matelson 1992).

Table 3. Mean annual biomass and N inputs (kg·ha^{-1}) in total and epiphytic litterfall under the canopy of bigleaf maple between October 2010 and September 2011 at the Queets River watershed (this study) in comparison with other studies from Washington State and tropical forests that reported epiphytic litterfall.

	Total litterfall		Epiphytic material	
Source	Annual biomass	N inputs	Annual biomass	N inputs
Temperate forest ecosystem				
This study	4760	51	546 (11.5%)	5.7 (11%)
O'Keefe and Naiman 2006	5613		238 (4.2%)	
Lebret et al. 2001	4710		171 (3.6%)	
Callaway and Nadkarni 1991	3495	42	166 (4.7%)	2.2 (5.2%)
McShane et al. 1983	2941		62 (2.1%)	
Abee and Lavender 1972	6325	27		1.4 (5.2%)
Tropical forest ecosystem				
Kohler et al. 2008	17 200		790 (6%)	
Nadkarni and Matelson 1992	7500	100	500 (7%)	7.5 (7%)
Veneklaas 1991	4300		230 (5%)	

Note: Data presented for epiphytic material are mean values, with the % total in parentheses. The Callaway and Nadkarni 1991 source includes only data from June 1986 to May 1987. For McShane et al. 1983, values are the mean of their data.

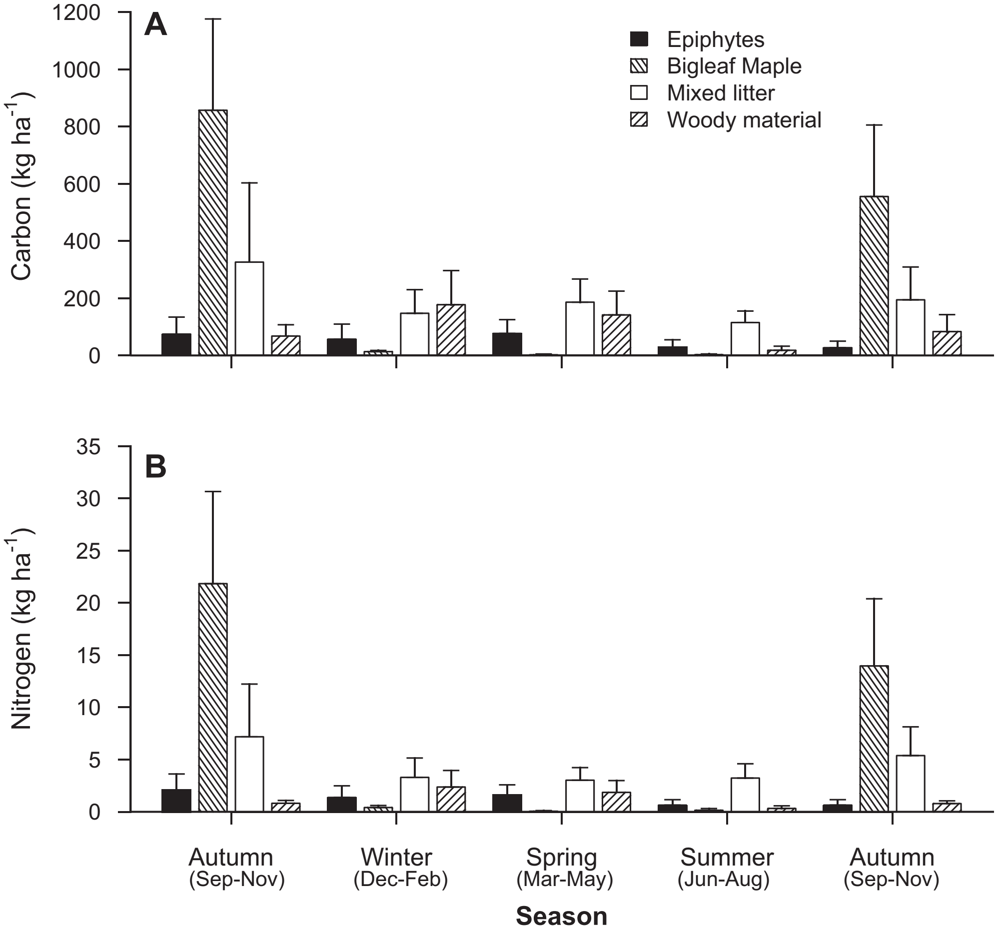
Total N input from epiphytic litterfall (5.7 kg·ha^{-1}·year^{-1}) to the forest floor was almost double the annual atmospheric N deposition with precipitation in the region (3.1 kg·ha^{-1}·year^{-1}; Edmonds et al. 1998). Because of their location in the canopy, epiphytes capture and retain allochthonous nutrients that become potentially available to the whole forest via litter deposition, throughfall, or stemflow. Furthermore, N-fixing lichens such as *L. oregana* can contribute up to 16 kg·ha^{-1} of N in Pacific Northwest forests, increasing the N pool of EM (Antoine 2004). The contribution of epiphytic N inputs to the forest floor should be considered in future studies to understand nutrient cycling in these ecosystems.

The contribution of bigleaf maple trees at the ecosystem level might have a disproportionate effect on N cycling compared with litter inputs of conifer trees in the stand. In this area, bigleaf maples form clusters surrounded by the conifer-dominant canopy (Van Pelt et al. 2006). The inputs of litterfall under the canopy of bigleaf maple are nearly equivalent to mean litter inputs of the whole forest, as estimated by O'Keefe and Naiman (2006) (Table 3), making bigleaf maple a rich focal point of nutrient deposition. Furthermore, because 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 in which bigleaf maples are present until whole trees and their associated EM biomass falls into the ground, 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 critical for 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 dominated total litter inputs, and

Fig. 4. Mean and standard deviation of (A) total litter carbon and (B) nitrogen per season from September 2010 to November 2011 by litter type under the canopy of bigleaf maple at the Queets River watershed, Washington State. Mixed litter category includes conifer needles, other deciduous species, and miscellaneous material.



epiphytic litterfall under these trees was higher than the mean epiphytic litterfall for the whole area at the same location. Annual variation in litter deposition correlates with precipitation from late summer and early autumn. N inputs to the forest floor from EM litterfall could have a positive influence on N availability to the surrounding vegetation, as this N is released during decomposition. Furthermore, as EM captures and retains nutrients in the canopy mats, litter deposition from EM is enhancing the sources of these nutrients to the forest floor. The combined effect of nutrient-rich litter and large accumulations of EM within bigleaf maple canopies suggests that bigleaf maple is a focal point for N movement to the forest floor, and its conservation could be critical for long-term contributions to forest productivity.

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