1.6 THE ROLE OF EPIPHYTES IN THE INTERCEPTION AND EVAPORATION OF RAINFALL IN OLD-GROWTH DOUGLAS-FIR FORESTS IN THE PACIFIC NORTHWEST

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1. INTRODUCTION

Rainfall interception loss (I_n) accounts for 10 to 40% of rainfall entering a forest canopy (Zinke, 1967). The size of I_n depends on two variables: the canopy water storage capacity (S) and evaporation during the storm (E) (Gash, 1979). Changes in either S or E will impact the quantity of water available for soil recharge, plant water uptake and the discharge of streams and rivers.

Structural changes in a forest canopy may influence the size of S. For example, S is very large in old-growth Doulglas-fir forests in the Pacific Northwest relative to a young Douglas-fir forest forests (Pypker, unpublished data; Link et al., in press). Old-growth Douglas-fir forests have a high leaf area index (LAI) and large epiphyte populations (McCune, 1993; Thomas and Winner, 2000). Could the large S associated with old-growth Douglas-fir forests result from high LAI and/or large epiphyte populations?

Researchers frequently use the LAI of a forest to estimate S (e.g. Flerchinger et al., 1996). This may be a reasonable assumption for some forests because of the high surface area associated with leaves and needles. However, LAI is not always appropriate for estimating S. For example, the use of LAI to predict S in some tropical and temperate forests has been shown to be inadequate (Herwitz, 1985; Link et al., in press). To properly assess the magnitude of S, we must incorporate other factors.

The use of LAI to estimate S is inappropriate for Douglas-fir forests in the Pacific Northwest (Link et al., in press). Young (25-y-old) and old growth (>400-y-old) forests can have similar LAI but very different S. For example, a young and an old-growth Douglas-fir forest in South Central Washington have nearly identical LAI (old-growth 9.6; young – 10.1), but S in the old-growth forest is more than double that of the young forest (old-growth 3.32 mm; young 1.26 mm) (Pypker, unpublished data; Link et al., in press). One factor that may explain the high S in temperate old-growth Douglas-fir forests is epiphytes.

Epiphytic lichens and bryophytes have high water-holding capacities and are abundant in temperate old-growth Douglas-fir forests (Kershaw, 1985; McCune, 1993; Shaw and Goffinet, 2000). Furthermore, lichens and bryophytes can store between 200 to 1500% of their dry biomass in water (Kershaw, 1985; Shaw and Goffinet, 2000). The large populations of epiphytes in conjunction with their high water-holding capacity may be sufficient to explain the elevated S in old-growth Douglas-fir forests. However, epiphytes may also indirectly influence S.

Lichens and bryophytes may further affect S by altering the time required for the canopy to dry. Old-growth Douglas-fir forests typically exceed 60 m in height (Shaw et al., in press). The tall trees may increase the time required for branches to dry lower in the canopy by diminishing the quantity of light and wind available to drive evaporation. If water storage by lichens and bryophytes primarily occurs lower in the canopy, S may be affected because the canopy will remain wet for longer periods.

The influence of lichens and bryophytes on forest hydrology may be very important for old-growth Douglas-fir forests. The purpose of this paper is to assess the influence of lichens and bryophytes on the:

- size of the canopy storage (S) in old-growth canopies
- time required for the canopy to dry

2. METHODS AND INSTRUMENTATION

2.1Study site

The study area is located in the Western Cascades within the boundaries of the H J Andrews Experimental Forest (44.2 °N, 122.2 °W). The study site is approximately 2 ha in size, is comprised of old-growth Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and has an LAI of 12.1 (Moore et al., 2004). The rainfall occurs primarily in the winter and averages 2300 mm annually.

2.2 Biomass and distribution

We estimated epiphytic lichen biomass using an established 1:100 relationship between the quantities of epiphytic lichens littered on the forest floor to the biomass of epiphytic lichens in the canopy (McCune 1994). In brief, we randomly established 27 circular plots (4 m diameter) within the study area and collected all epiphytic lichen fragments found in the plot. The lichens were sorted into two functional groups: foliose lichens (plate-like structure) and fruticose lichens (hairy structure). The lichens in each plot were oven dried at 70°C for 72 h and the mean biomass for all plots were multiplied by 100 to estimate the epiphytic lichen biomass. Epiphytic bryophyte biomass is more difficult to estimate and generally requires destructively harvesting trees (McCune, 1993). We were not permitted to harvest trees in this study area, so we used estimates of epiphytic bryophytes from nearby old-growth Douglas-fir forests within the H J Andrews Experimental forest

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(McCune, 1993; McCune, 1994; McCune et al., 1997; Pike et al., 1977).

Forest floor bryophyte biomass was estimated by randomly selecting 20 plots along a 200 m transect through the study area. At each plot a 0.12 m quadrat was placed on the forest floor and all the bryophytes were removed. The forest floor bryophytes were sorted into 4 categories: step moss (*Hylocomium splendens*), electrified cat's tail (*Rhytidiadelphus triquetrus*), Oregon beaked (*Kindbergia oregona*) and other mosses. The bryophytes were cleaned of forest floor litter and dried at 70°C for 72 h prior to weighing

Canopy biomass distribution was estimated along two vertical transects through the canopy. Along each transect visual estimates of epiphyte cover were recorded at 5 m intervals at 2 or 3 randomly selected cardinal directions. The observations were made by a single observer who climbed a fixed rope and visually estimated the percent cover of foliose lichens, fruticose lichens and bryophytes. The observer held a 0.2 m by 0.5 m quadrat horizontally at eye level, and arm's length, and estimated the percent cover of the different functional groups in the two-dimensional view (McCune et al., 1997). This method has been demonstrated to satisfactory predict relative abundance of different epiphytes (McCune et al., 1997).

2.3 Water-holding capacities

We estimated the water-holding capacities of the dominant epiphytic and forest floor lichens and bryophytes by immersing 2 to 4 gram biomass samples of each species into water for 30 minutes (n = 30 for each species). The biomass sample was removed from the water and sealed container to allow excess water to drip off. To prevent evaporation from the epiphyte, a layer of water was maintained at the bottom of each container. After 24 hours the saturated sample was weighed to the nearest milligram. The samples were placed in an oven at 70°C for 72 h to attain the dry weight.

2.4 Rainfall measurement

We measured gross precipitation (P_G) and net throughfall (P_n) beneath the canopy using an array of 24 randomly placed tipping bucket rain gauges (Texas Electronics Inc.) from 1 September to 30 November 2003. To decrease sampling error the tipping buckets were cleaned and randomly relocated every 4 weeks (Wilm, 1943). S was estimated using a regression-based method for individual storms (see Link, 2002; Link et al., in press). In short, this method creates two regression lines relating P_G to P_n for the period prior and subsequent to canopy saturation. The difference between the intersection point of the two regression lines and P_G provides an estimate of S. We only calculated S for events where rainfall began 12 h after the previous storm ended, P_G exceeded 10 mm of rain and > 75% of the tipping bucket array was functioning. I_n was calculated as the difference between P_G and P_n.

2.5 Rainfall interception by Branches

In the laboratory we monitored rainfall interception of seven 0.4 to 1 m long epiphyte laden branches under a 5 m tall rainfall simulator. The branches were subjected to a rainfall intensity of 11.7 mm h^{-1} until the weight stabilized.

To measure epiphyte rainfall interception in situ, we rigged two Douglas-fir trees for climbing and installed meteorological stations at 3.1, 24.8 and 46.5 m above the ground. Each station consisted of a cup anemometer (Thornwaite), a quantum sensor (LiCor), a relative humidity/temperature probe (Vaisala), and a strain gauge (Futek). The strain gauge was calibrated and an epiphytic laden branch was hung on it and continuously monitored. All data was monitored on 15 s intervals and averaged over 15 minutes using dataloggers and multiplexers (Campbell Scientific). The stations were established in the summer of 2003 and the branches were replaced periodically. While changing the branches the strain gauges were recalibrated using steel weights.

The surface temperature of the lichen or bryophyte was monitored using a thermistor placed on the underside of the lichen thallus or bryophyte leaf. The surface temperature for every branch was recorded at 5-minute intervals and stored on a mini datalogger (Onset).

Epiphytes and branches were destructively sampled subsequent to their use in the rainfall simulator or in the field. The epiphytes on the branches were cleaned and then sorted into three functional groups: foliose lichens, fruticose lichens and bryophytes. We measured the branch dimensions (volume, surface area and length) and the litter (needles/dirt) present on the branch. The dry weight of the branch, litter and epiphytes was measured after drying at 70°C for 72 h.

3.0 RESULTS AND DISCUSSION

3.1 Biomass distribution of lichens/mosses

The lichens and bryophytes occupy specific niches within the forest canopy. The bryophytes are dominant below 30 m, with the surface area of foliose and fruticose lichens increasing above 30 m (Figure 1). The stratification of the lichens and bryophytes in the canopy may, in part, result from microclimatic changes in the canopy. Greater light and wind speeds higher in the canopy increase evaporative demand; creating an environment that favors lichens and precludes the hydrophilic bryophytes (McCune, 1993; McCune et al., 1997). For example, the diurnal surface temperatures of the epiphytes are more extreme higher in the canopy because of increased solar radiation (Figure 2). Therefore, the distribution

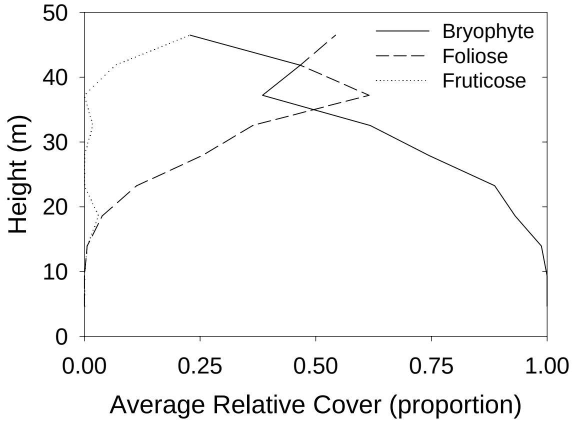

Figure 1 – The vertical distribution of foliose lichens, fruticose lichen and bryophytes from 0 to 50 m.

of the lichens and bryophytes in the canopy may be influenced by the vertical gradient in microclimate.

The forest contains 1273 and 1245 kg ha^{-1} of lichens and bryophytes, respectively (Table 1). The lichens in this forest are primarily epiphytic with the foliose lichens comprising >97% of the biomass (Table 1). The biomass estimates are similar to another old-growth stand in the HJ Andrews Experimental Forest. McCune (1993) estimated that a nearby 400 y-old forest to contained 1870 kg ha^{-1} of lichen biomass with the foliose lichens being the dominant group (1140 kg ha^{-1}). We assumed the epiphytic bryophyte biomass for the old-growth forest in this study to be same as the nearby old-growth forest described by McCune (1993) (780 kg ha^{-1}). The forest floor contained an additional 465 kg ha^{-1}; >95% of the biomass was comprised of step moss, electrified cat's tail and Oregon beaked moss (Table 1). The combined total for the forest floor and epiphyte bryophyte biomass nearly equals the estimates for the epiphytic lichen biomass (Table 1).

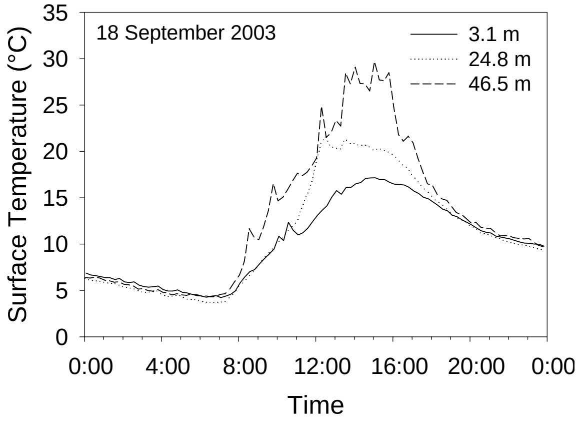

Figure 2 – The diurnal changes in surface temperature of a lichen thallus/bryophyte leaf at 3.1, 24.8 and 46.5 m.

3.2 Water-holding capacities

The water-holding capacities of the dominant bryophyte species (*Dicranum fuscescens, Hypnum circinale, Isothesium myosuroides*) were not significantly different (n=30 for each species, no p-value<0.05) and were therefore, pooled together. In contrast, the water-holding capacity of the epiphytic bryophytes was significantly greater than the foliose for fruticose lichens (p-value<0.001) (Table 1). Furthermore, the forest floor bryophytes were statistically different from each other, with the step moss, electrified cat's tail and Oregon beaked moss holding, 838 ±43, 1149 ±90 and 1404 ±77% of their dry weight in water, respectively (Table 1). Combining the biomass values of the lichens and bryophytes with their corresponding water-holding capacity produces an estimate of 1.88 mm of water storage for the canopy and forest floor.

3.3 Canopy storage

There were 23 storms between 9 September and 29 November 2003. S was calculated to range between 1.98 to 5.30 mm for the storms where P_G exceeded 10 mm of rainfall (Table 2). The storm on 7 September 2003 was the first significant storm in 67 days and the canopy was extremely dry. Hence, S was greatest in September after the summer drought and then rapidly decreased as the wet season progressed (Figure 3).

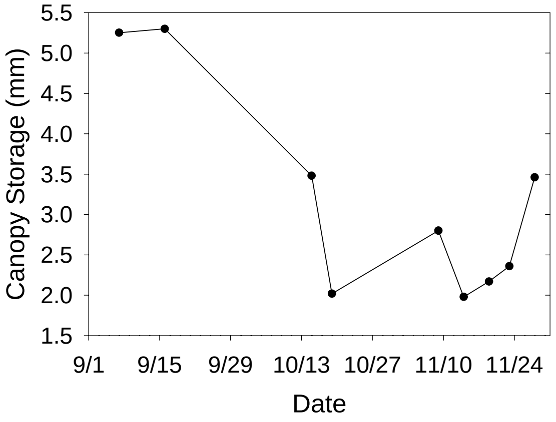

Figure 3 – The change in canopy storage (S) for an old-growth forest from 1 September to 29 November

3.4 Branch interception of Rainfall

Epiphytes significantly increased the water storage of a branch (Table 1). The calculated water-holding capacity of the foliose lichens, fruticose lichens and bryophytes (Table 1) accurately predict the water retention of a branch laden with epiphytes under a rainfall simulator (Figure 4). Hence, it is possible to predict the influence epiphytes have on S if their biomass is known. Young Douglas-fir forests that have the same LAI as old-growth forests hold between 1.2 to 2.4 mm of rainfall (Pypker, unpublished data; Klaassen et al., 1998). S in this old-growth forest exceeds 5 mm during the first two storms in September. Hence, water storage by epiphytes can account for 1.3 mm of the 2.9 mm difference between the upper limits of a young Douglas-fir forest and this old-growth forest. The rest of difference may result from species differences, increased bark surface area and/or litter in the canopy (Keim, 2003).

3.5 Drying time subsequent to rainfall

The time required for the canopy to dry was protracted at all heights within the canopy. The high S in this old-growth Douglas-fir forest results in drying times exceeding 60 hours. For example, after a storm from the 9-12 November 2003, there was no rainfall for 3 days and the branch at 46.5 m returned to its pre-storm weight after approximately 60 h (Figure 5). However, the branches at 3.1 and 24.8 m absorbed a greater quantity of water and were unable to dry to their original weight prior the next storm. Therefore, during the wet season the canopy will remain partially saturated unless there is sufficient time between storms.

Bryophytes are likely to increase the time required for branches to dry lower in the canopy. Bryophytes have large water-holding capacities and are primarily located lower in the canopy (Figure 1). These two characteristics will result in a large reservoir of water located lower in the canopy were the energy for evaporation is reduced. Hence, the time required to dry the canopy will increase because of the distribution of the epiphytes.

The extended canopy drying time has some important implications for I_n and the calculation of S. First, for many of storms in the rainy season the canopy will be partially wet when the storm begins. Hence, I_n will be reduced because less rainfall is required to saturate the canopy. Second, S is frequently calculated by generating a regression between P_G and P_n for multiple storms that saturate the canopy and have low evaporative losses during the storm (see Leyton et al., 1967; Llorens and Gallart, 2000). The x-intercept of the regression provides the estimate of S. However, in this forest S varies significantly throughout the season because the canopy is unable to dry between storms. Unless there is a long period between storms, a regression-based approach that requires data from multiple storms will likely underestimate the maximum value of S.

Table 1 – The biomass and water-holding capacities of the bryophytes and lichens. The water-holding capacities of the canopy bryophytes were pooled together because they were not statistically different. Numbers behind the ± represent the 95% confidence interval.

Group	Biomass kg ha^{-1}	Water-holding Capacity (% dry weight)	Potential Storage (mm)
Epiphytes			
Foliose	1242 ±452	342 ±34.8	0.425
Fruticose	31.0 ±22.0	223 ±63.7	0.072
Bryophytes	780[1]	999 ±47.7	0.779
Forest Floor			
Oregon beaked	345 ±177	1404 ±77.5	0.485
Elect. Cat's Tail	68.0 ±68.8	1149 ±90.0	0.030
Step Moss	26.2 ±27.9	838 ±43.2	0.057
Other moss	25.6 ±53.5	1130[2]	0.029
Total	2518±494	-	1.88

[1] From (McCune, 1993)

[2] Estimated using the mean water-holding capacities of the three dominant bryophytes on the forest floor.

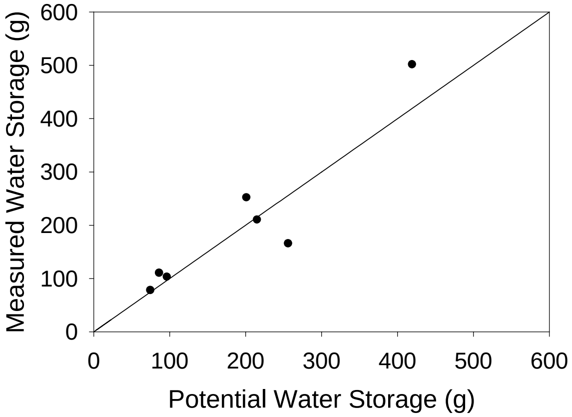

Figure 4 - The relationship between the potential water storage of a branch using the estimated water storage for foliose lichens, fruticose lichens and bryophytes verse the measured storage under a rainfall simulator

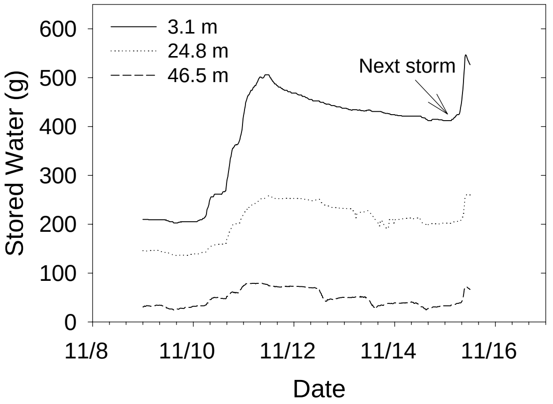

Figure 5 – The time required for a branch at 3.1, 24.8 and 46.5 m to dry subsequent to a storm.

Table 2 – The gross precipitation (P_G), net throughfall (P_n), interception loss (I_n) and canopy storage (S) for storms from 1 September to 29 November 2003.

Start Date	End Date	Duration (h)	P_G (mm)	P_n (mm)	I_n (%)	S (mm)
7-Sept-03	9-Sept-03	65.3	58.2	44.8	23	5.25
11-Sept-03	11-Sept-03	4.37	0.89	0.16	81	
16-Sept-03	17-Sept-03	35.1	19.6	12.4	37	5.30
6-Oct-03	13-Oct-03	93.1	61.1	37.7	38	N/A[1]
14-Oct-03	14-Oct-03	0.87	2.03	0.68	66	
15-Oct-03	15-Oct-03	6.9	21.1	15.0	28	3.48
16-Oct-03	16-Oct-03	1.73	1.14	0.60	47	
19-Oct-03	19-Oct-03	11.8	10.4	6.39	39	2.02
22-Oct-03	23-Oct-03	10.2	2.67	2.31	13	
28-Oct-03	29-Oct-03	10.1	7.62	3.05	60	
2-Nov-03	2-Nov-03	4.95	6.60	3.54	49	
3-Nov-03	3-Nov-03	5.17	2.03	0.58	71	
5-Nov-03	5-Nov-03	4.88	3.56	1.65	54	
7-Nov-03	8-Nov-03	19.0	1.78	0.73	59	
9-Nov-03	11-Nov-03	48.1	24.8	16.0	35	2.80
14-Nov-03	18-Nov-03	78.8	80.3	59.6	26	1.98
19-Nov-03	20-Nov-03	36.0	29.7	14.2	52	2.17
21-Nov-03	21-Nov-03	9.20	6.10	4.10	33	
22-Nov-03	22-Nov-03	1	0.25	0.06	78	
23-Nov-03	24-Nov-03	22.2	22.4	11.4	49	2.30
25-Nov-03	26-Nov-03	36.6	43.4	33.9	22	N/A[1]
27-Nov-03	27-Nov-03	5.52	1.27	1.00	21	
28-Nov-03	29-Nov-03	10.57	76.6	66.7	14	3.46
TOTAL			484	386	30	
AVERAGE		22.6				3.20

[1] >25% of the tipping buckets failed during this storm

4. CONCLUSIONS

Lichens and bryophytes in old-growth Douglas-fir forests are not evenly distributed throughout the canopy. Lichens are most dominant above 30 m and bryophytes become increasingly abundant towards the forests floor. Lichens have a greater portion of the biomass in the canopy, but the epiphytic bryophytes in this canopy store nearly two times more water because of their greater water-holding capacity. Furthermore, when the forest floor bryophytes are included, the biomass of lichens and bryophytes are nearly identical. Hence, the biomass and water-holding capacities of epiphytic lichens and bryophytes account for a significant portion of the difference in S between young and old-growth Douglas-fir forests. The affinity of bryophytes for the lower portions of the forest canopy increases storage of water lower in the canopy. The combination of increased water storage and decreased energy for evaporation lower in the canopy results in the canopy remaining wet for protracted periods. The increased drying time may decrease I_n and cause regression-based methods for calculating S to under estimate the maximum capacity of the canopy to store water.

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