

The role of epiphytes in rainfall interception by forests in the Pacific Northwest. I. Laboratory measurements of water storage

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Abstract: Old-growth Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests frequently contain large populations of epiphytic lichens and bryophytes. To determine the effect these epiphytes have on canopy hydrology we measured the maximum water fraction ($f_{(x)\max}$; maximum mass of internal and external water stored by an epiphyte divided by its tissue dry mass) of common lichens, bryophytes, and dead branches in the laboratory and the water storage and interception efficiency (p_i) (the rainfall stored on a branch divided by the rainfall intercepted by the branch) of whole epiphyte-laden branches under a rainfall simulator at three intensities (11.3, 16.1, and 39.8 mm·h⁻¹). The $f_{(x)\max}$ values for epiphytic fruticose lichens, foliose lichens, and bryophytes were 2.2 ± 0.4 , 3.4 ± 0.6 , and 10.0 ± 0.5 , respectively. The water stored by an epiphyte-laden branch during and after exposure to simulated rainfall could be predicted if the biomass of epiphytic lichens and bryophytes on the branch was known ($R^2 = 0.8$, p value < 0.0001). For all three rainfall intensities, the branches required >6 mm of rainfall to saturate. Values of p_i averaged between 0.5 and 0.7 after 2 mm of rainfall and did not differ among the three intensities (all p values > 0.05). We conclude that epiphytes increase the canopy water storage of a typical old growth Douglas-fir forest by >1.3 mm.

Résumé : Les vieilles forêts de douglas (*Pseudotsuga menziesii* (Mirb.) Franco) contiennent fréquemment d'importantes populations de bryophytes et de lichens épiphytes. Dans le but de déterminer l'effet de ces épiphytes sur l'hydrologie de la canopée, les auteurs ont mesuré la proportion maximum d'eau ($f_{(x)\max}$: poids maximum d'eau interne et externe emmagasinée par un épiphyte divisé par le poids anhydre de ses tissus) des lichens communs, des bryophytes et des branches mortes en laboratoire. Ils ont aussi mesuré l'emmagasinement et l'efficacité d'interception de l'eau (p_i) (la quantité de pluie retenue sur une branche divisée par la quantité de pluie interceptée par la branche) de branches entières couvertes d'épiphytes et soumises à des pluies de différentes intensités (11,3, 16,1 et 39,8 mm·h⁻¹) dans un simulateur de pluie. Les valeurs de $f_{(x)\max}$ pour les lichens fruticuleux, les lichens foliacés et les bryophytes épiphytes étaient respectivement de $2,2 \pm 0,4$, $3,4 \pm 0,6$ et $10,0 \pm 0,5$. La quantité d'eau emmagasinée par une branche couverte d'épiphytes durant et après une exposition à une pluie simulée pouvait être prédite si la biomasse des bryophytes et des lichens épiphytes présents sur la branche était connue ($R^2 = 0,8$; $p < 0,0001$). Peu importe l'intensité de la pluie, il fallait plus de 6 mm de pluie pour saturer les branches. Les valeurs de p_i se situaient en moyenne entre 0,5 et 0,7 après 2 mm de pluie et ne différaient pas selon l'intensité de la pluie (toutes les valeurs de $p > 0,05$). Ils arrivent à la conclusion que les épiphytes augmentent de plus de 1,3 mm la capacité d'emmagasinage de l'eau dans la canopée d'une vieille forêt de douglas.

[Traduit par la Rédaction]

Introduction

Old-growth Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) – western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) forests in the Pacific Northwest have a large canopy water storage capacity (S , defined as the quantity of water per unit ground area that a canopy can hold when saturated) relative to that of younger Douglas-fir forests (Link et al. 2004; Pypker et al. 2005). Researchers have hypothesized that changes in tree species composition, increased wood surface area and deadwood, and the development of large epiphyte populations are responsible for the greater S in old-

growth Douglas-fir forests (Rothacher 1963; Keim and Skaugset 2003; Link et al. 2004; Pypker et al. 2005).

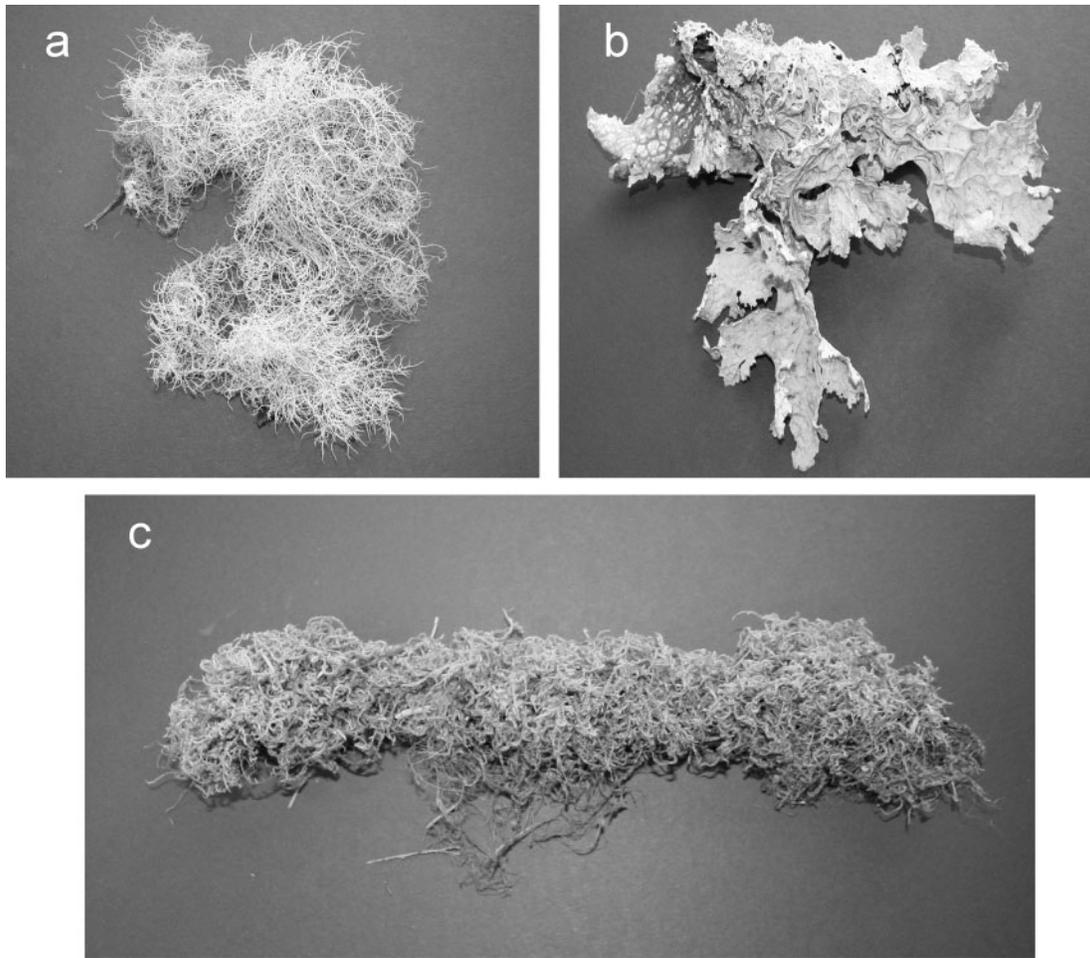
Old-growth Douglas-fir forests in the Pacific Northwest have large populations of epiphytic lichens and bryophytes. Lichens and bryophytes are poikilohydric species that have a unique ability to survive long periods of desiccation (Kappen 1973; Proctor 1982, 2000). Lichens are the result of a symbiosis between a fungus (mycobiont) and one or more algae (photobiont) (Fig. 1a, 1b). The mycobiont provides the structural support for the photobiont, and the photobiont in turn provides energy via photosynthesis. Bryophytes include all hornworts, liverworts, and mosses, but in old-growth Douglas-

Received 2 September 2005. Accepted 7 December 2005. Published on the NRC Research Press Web site at <http://cjfr.nrc.ca> on 24 March 2006.

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Fig. 1. Examples of a fruticose lichen (*a*), foliose lichen (*b*), and bryophyte (*c*).



fir forests of the Pacific Northwest the majority of the biomass comes from mosses (Fig. 1c) (McCune 1993). Both lichens and bryophytes are cryptogamic and lack a true vascular system. To compensate for their inability to remove water from the soil, lichens and bryophytes have the ability to store considerable quantities of water (Blum 1973; Proctor 2000). Fruticose and foliose lichens have the capacity to rapidly absorb between 150% and 350% of their dry mass in water (Blum 1973; Kershaw 1985). Bryophytes have an even larger range of water storage, between 500% and 1200% of their dry mass (Proctor 2000).

McCune (1993) estimated that an old-growth Douglas-fir forest in the Oregon Cascades contained 1870 and 780 kg·ha⁻¹ (dry mass) of epiphytic lichens and bryophytes, respectively. This epiphyte biomass in old-growth Douglas-fir forests consists of approximately 74 species of lichens and 32 species of bryophytes (Pike et al. 1975). Bryophytes are also common on the floor of old-growth Douglas-fir forests. While they are not usually accounted for in the calculation of S , these species, along with the litter and deadwood on the forest floor (Harmon and Sexton 1995; Helvey and Patric 1965), may considerably decrease the quantity of water that enters the mineral soil. In old-growth Douglas-fir forests located in Oregon, more than 93 species of forest-floor bryophytes cover between 25% and 50% of the forest floor (Rambo and Muir 1998; Shaw et al. 2004). The percentage of the forest floor that

is covered varies greatly between forests (Rambo and Muir 1998).

Past research has assumed that the large maximum water fraction (maximum mass of internal and external water stored by an epiphyte divided by its tissue dry mass; $f_{(x)\max}$) of epiphytic lichens and bryophytes influences rainfall interception by increasing S (Rothacher et al. 1967; Veneklaas and Van Ek 1993; Levia and Frost 2003; Link et al. 2004). For example, Rothacher (1963) assumed that the absence of stemflow in an old-growth Douglas-fir forest was the result of epiphytes storing water on the tree boles. More recently, Hölischer et al. (2004) reported that the large population of epiphytes (>1900 kg·ha⁻¹) found in a tropical montane rainforest in Costa Rica accounted for 50% of S and 6% of the total interception loss (I_n). However, there has been little other direct research on the relationship between the $f_{(x)\max}$ of epiphytes and forest-floor bryophytes and their rainfall interception efficiency (p_i) (the rainfall stored on a branch divided by the rainfall intercepted by a branch) in temperate forests of North America. The goal of this study was to (1) determine the $f_{(x)\max}$ for common lichens and bryophytes in old-growth Douglas-fir forests, (2) determine the water storage and p_i of epiphyte-laden branches under a rainfall simulator, and (3) predict the quantity of water that lichens and bryophytes will store in old-growth Douglas-fir forests of the Pacific Northwest.

Materials and methods

Lichen and bryophyte samples

Epiphytic and forest-floor lichen and bryophyte samples (epiphyte-laden branches and individual samples) were removed from an old-growth Douglas-fir forest (>400 years old) located within the H.J. Andrews Experimental Forest in the western Cascades of central Oregon, USA (44.2°N, 122.2°W). Five old-growth Douglas-fir trees were rigged for climbing, and three or four dead epiphyte-laden branches that were accessible from the mid-crown were removed per tree ($n = 18$) for analysis. Because western hemlock trees are smaller and their branches were closer to the ground, we removed dead western hemlock branches from locations that were accessible near the forest floor ($n = 10$). The dead branches were required to be less than 2 m in length and have greater than 80% epiphyte cover. Dead branches were chosen as they allow for a more direct analysis of the effect of epiphytic lichens and bryophytes on rainfall interception and storage because they are often covered by large populations of epiphytes and do not have needles. The epiphytes were classified into three functional groups: foliose lichens (plate-like structure), fruticose lichens (hairy structure), and bryophytes (Fig. 1). Individual samples of healthy foliose lichens, fruticose lichens, and bryophytes were removed from the five Douglas-fir trees or were removed from the boles and stems of trees 0–2 m above the forest floor. Forest-floor bryophytes were collected randomly along a 200 m transect. The epiphytic lichen biomass was dominated by foliose lichens (1242 kg·ha⁻¹) with a small portion in fruticose lichens (30 kg·ha⁻¹, mostly alectroid species) (Pypker 2005). Field measurements of rainfall interception by the forest canopy and individual epiphyte-laden branches are reported in Pypker et al. (2006).

Maximum water content of lichens, bryophytes, and dead branches

Epiphyte samples were initially sorted into foliose lichens, fruticose lichens, and bryophytes. The foliose lichen lettuce lung (*Lobaria oregana*) and the fruticose lichen witch's hair (*Alectoria sarmentosa*) were chosen to represent their respective functional groups because they constitute greater than 94% and 36% of the foliose and fruticose lichen biomass in old-growth Douglas-fir forests, respectively (Pike et al. 1977; McCune 1994). The bryophyte functional group was dominated by dicranum moss (*Dicranum fuscescens*), hypnum moss (*Hypnum circinale*), and cattail moss (*Isothecium myosuroides*) (greater than 12%, 11%, and 36% of bryophyte biomass, respectively) (Pike et al. 1977; McCune 1994). These three species were selected to represent the epiphytic bryophytes. The bryophytes sampled from the forest floor were sorted into four groups: step moss (*Hylocomium splendens*), electrified cat's tail (*Rhytidiadelphus triquetrus*), Oregon beaked moss (*Kindbergia oregana*), and "other mosses".

To determine $f_{(x)\max}$ of each group, 30 samples (each approximately 1 g) of each of the different foliose lichens, fruticose lichens, canopy bryophytes, and forest-floor bryophytes were cleaned of litter and submerged in water for 30 min. After submersion, each sample was removed from the water and suspended in a sealed container at 22 °C for

Table 1. A comparison between the rainfall intensities and related mean drop size produced by the rainfall simulator and the expected mean drop size for a storm at the same rainfall intensity in the Pacific Northwest.

Rainfall intensity (mm·h ⁻¹)	Rainfall simulator mean drop size (mm)	Range of expected mean drop sizes (mm)*
11.28	1.1	1.5–1.9
16.1	1.0	1.6–2.1
39.8	1.3	2.0–2.6

*From Best (1950), Laws and Parsons (1943), and Mason and Andrews (1960).

24 h to allow excess water to drip off. To prevent evaporation from the sample, a layer of water was maintained at the bottom of each container. The saturated samples were then weighed to the nearest milligram and placed in an oven at 70 °C for 72 h to obtain dry mass.

The maximum water fraction of dead branches in the canopy ($f_{(db)\max}$) (internal storage only) was determined by placing 5 cm samples of dead branch (27 Douglas-fir and 10 western hemlock samples) in water for 30 days. The dead branches came from 19 branches collected for this study and from 18 branches (12 Douglas-fir and 6 hemlock) used in a field study on rainfall interception by epiphytic branches (Pypker et al. 2006). After being immersed in water for 30 days the branch samples were blotted dry, weighed, and then dried at 70 °C for 168 h to obtain a dry mass.

The $f_{(x)\max}$ values of the lichens, bryophytes, and dead branches were calculated as

$$[1] \quad f_{(x)\max} = \frac{WM_x - DM_x}{DM_x}$$

where WM_x (g) was the maximum wet mass of species x after immersion in the water and DM_x (g) was the sample's dry mass after 72 h at 70 °C in a drying oven.

Rainfall simulator

The water storage and rainfall interception efficiency (p_i) of the epiphyte-laden branches were determined using a rainfall simulator (A. Skaugset, Department of Forest Engineering, Oregon State University, Corvallis, Oregon, USA). For a full description of the rainfall simulator, see Keim et al. (2005b). In brief, the rainfall simulator was equipped with three nozzles (model G2.8W, G5.6W, and G25; Spray Systems Inc., Wheaton, Illinois, USA) placed 4.9 m above the ground and capable of generating multiple intensities and drop sizes (Table 1). The drop sizes were slightly smaller than the expected size distribution for rainfall at 11.3, 16.1, and 39.8 mm·h⁻¹ (Table 1). Because the drop sizes were undersized, each drop would impart a smaller force to the branch. The reduction in force would reduce the quantity of water removed by raindrop splash, thereby increasing maximum water storage during the simulation. However, the drop sizes did increase by 30%, from 16.1 to 39.8 mm·h⁻¹. The increase in drop size with higher rainfall intensity was expected to result in the dislodging of greater amounts of stored water. To estimate rainfall interception and storage, each air-dried branch was suspended on a supporting cable that was attached to a scale (Mettler-Toledo SR32001, Columbus, Ohio, USA) housed in a box located directly above

Table 2. The 2- and 50-year return intervals for the maximum length of time over which a single storm will produce a given rainfall intensity.

Rainfall intensity (mm·h ⁻¹)	2-year return interval*	50-year return interval*
11.28	0.58 h	1/3 h
16.1	0.34 h	1.3 h
39.8	<0.1 h	2 h

*From Oregon State Highway Division (1973).

the spray nozzles. The mass of the sample was recorded at 5 Hz on a desktop computer, and the specimen remained under the rainfall until its mass stabilized. The range of intensities produced by the simulator is in the upper range of what can be expected in a typical storm in the Pacific Northwest (Table 2).

Two corrections were applied to the raw data prior to estimating the water storage and p_i . First, for each rainfall intensity, the mass of water stored on the supporting cable was estimated by running the rainfall simulator with only the cable attached. The mass stored on the cable was subtracted from data acquired with samples. Second, the force imparted by the rate change of momentum as the raindrops struck the specimen was subtracted. This force varied for each specimen because the angle of impact for the droplets differed between specimens. This force was estimated by turning the rainfall off for four 10 s intervals and estimating the instantaneous change in mass when the rainfall was turned back on (Keim et al. 2005b).

Fourteen dead Douglas-fir branches were exposed once to each of three rainfall intensities (11.28, 16.1, 39.8 mm·h⁻¹). Six hemlock branches were exposed only to the lowest rainfall intensity to determine whether there was a difference in water storage on dead epiphyte-laden hemlock and Douglas-fir branches. Each branch was saturated at the given intensity and stored at room temperature for at least 1 week to allow it to return to its original mass. After being exposed to the final rainfall intensity, each branch was photographed from above and the vertical projected area was determined using image processing software (Vegmeasure 1.6, D. Johnson, Department of Rangeland Resources, Oregon State University). The branch volume and surface area were estimated by measuring the branch diameter at 5 cm intervals and treating each section as a cylinder. The epiphytes were removed from the branches and sorted into foliose lichens, fruticose lichens, bryophytes, and litter. Dry masses of epiphytes, branches, and litter were determined by placing them in an oven at 70 °C for 72 h.

Branch biomass description

The branches placed under the rainfall simulator contained between 7.2 and 70.2 g of epiphytes (Table 3). The epiphytes were predominately foliose lichens and bryophytes, with the fruticose lichens representing very little of the biomass (Table 3).

Calculation of epiphyte-laden branch water storage

The maximum water storage (m_m) for each branch during a rainfall simulation was determined by fitting a hyperbolic curve to the change of mass, $m(t)$, with time.

$$[2] \quad m(t) = \frac{m_m t}{b + t}$$

where b is a fitting parameter and t is time (decimal time, day). It was necessary to fit this equation because some of the epiphyte-laden branches did not reach an equilibrium mass even after 2 h of sustained rainfall.

To determine how much water would remain on a branch after the rainfall simulator was turned off (field water storage capacity, m_f) a second regression was fitted to the portion of the data immediately after the rainfall ceased. We could not determine m_f by waiting for the water to stop dripping from the branch because immediately after turning off the rainfall simulator evaporation began. Therefore, we took the first 3 min of the drying curve where water drip dominated the water loss from the branch and fit the following empirical equation:

$$[3] \quad m(t) = y_0 + \frac{ct}{d + t}$$

where y_0 , c , and d are fitting parameters. Equation 3 was selected because it fit the data very well (all $R^2 > 0.99$). The derivative of this equation was used to determine time when the sample was losing 0.01 g·s⁻¹. To determine m_f , the variables t and y_0 were replaced by the time when the sample was losing 0.01 g·s⁻¹ and m_m , respectively. The mass of water on the branch when the specimen was losing water at 0.01 g·s⁻¹ was considered a good estimate of m_f because it defines the point where dripping has nearly ceased but evaporation has not substantially altered the branch mass.

To provide an estimate of the potential epiphyte-laden branch water storage (m_{be}), the $f_{(x)\max}$ of the epiphytes on the branch were combined with the water storage on the branch surface. The branch surface storage capacity (m_{bs}) was estimated by weighing each branch before and after immersing the whole branch in water. The m_{be} was estimated by multiplying the biomass of epiphytic fruticose lichens (w_{fr}), foliose lichens (w_{fo}), and bryophytes (w_{br}) with their respective $f_{(x)\max}$ (Table 4):

$$[4] \quad m_{be} = 2.23w_{fr} + 3.42w_{fo} + 9.99w_{br} + m_{bs}$$

Calculation of rainfall interception efficiency (p_i)

The proportion of rainfall striking a branch that does not drip to the ground provides an estimate of the p_i for the branch. For the three rainfall intensities, p_i was calculated for each branch using the following equation:

$$[5] \quad p_i = \frac{w_b}{a_b I_t t_h}$$

where w_b is the branch dry mass (kg) at time t_h (h), a_b is the branch projected surface area (m²), and I_t is the rainfall intensity (kg·h⁻¹·m⁻²).

Results

Maximum water fraction ($f_{(x)\max}$) of lichens, bryophytes, and dead branches

Table 4 summarizes the $f_{(x)\max}$ of the lichens and bryophytes after immersion in water. The $f_{(x)\max}$ (intercellular and surface water storage) of the dominant epiphytic bryophyte species (dicranum moss, hypnum moss, and cattail moss) were not significantly different ($n = 30$ for each species, p value > 0.05) and were therefore pooled. The $f_{(x)\max}$ values of the epiphytic bryophytes were significantly greater than those of the foliose and fruticose lichens (p values < 0.001). In contrast,

Table 3. Descriptions of the epiphyte biomass, litter biomass, branch biomass, branch surface water storage (S_b), maximum water content expressed as a percentage of dry mass ($f_{(db)max}$; eq. 1), and maximum dead branch surface storage capacity (m_{bs}) for 20 branches (14 Douglas-fir (DF) and 6 western Hemlock (HEM)) exposed to the rainfall simulator.

Branch	Species	Biomass (g)			Litter	Branch	m_{bs} (g)	$f_{(db)max}$ (%)	Projected surface area (cm ²)
		Fruticose	Foliose	Bryophyte					
1	DF	0	12.1	0.6	0.1	84.3	19.6	178	246
2	DF	0.2	55.5	14.7	27.3	281.5	36.8	186	956
3	DF	0	12.6	2.5	1.9	40.8	14.3	188	367
4	DF	0	13.8	0.8	3.9	226.5	16.4	193	406
5	DF	0.6	19.3	14.7	22.4	369.7	55.8	166	737
6	DF	2.5	35.5	19	13.9	287.5	25	185	905
7	DF	0	15.7	1.9	1.2	313.4	14.5	178	299
8	DF	0.3	30.9	4	2.5	79.1	15.7	212	458
9	DF	1.3	8.4	37.2	32.3	351.3	65.5	224	877
10	DF	0.3	4.1	17.8	22.5	712	96.6	164	546
11	DF	0	0.2	21.4	10.2	222.7	38.5	171	570
12	DF	0.7	9.6	11	4.3	85.5	31.5	214	426
13	DF	0	12.3	22	13.6	106.9	21.9	202	429
14	DF	0.1	13.3	38.8	46.9	593.2	73.8	175	1000
15	HEM	0	0	19.7	9.5	52.5	16.8	224	913
16	HEM	0	0	38.4	14.5	736.9	11.6	156	739
17	HEM	0	0	20.1	4.3	49.8	15.2	164	972
18	HEM	0	0	7.2	2	74.1	20.9	146	606
19	HEM	0	0.3	23.9	3.5	40.6	11.1	242	1229
20	HEM	0	0	36.6	8.2	96.6	20.1	281	1201
	Average	0.29	12.2	17.6	12.3	240	31.1	192	694

Table 4. The biomass and maximum water content fraction ($f_{(x)max}$) (including the 95% confidence interval) of the bryophytes and lichens for an old-growth forest in the Pacific Northwest.

Group	Biomass* (kg·ha ⁻¹)	Maximum water content (relative to dry mass)	Potential storage (mm)
Epiphytes			
Foliose lichens	1242±452	3.42±0.35	0.42
Fruticose lichens	31.0±22.0	2.23±0.64	0.072
Bryophytes	780 [†]	9.99±0.48	0.80
Forest floor			
Oregon beaked	345±177	14.0±0.78	0.485
Electrified cat's tail	68.0±68.8	11.5±0.90	0.030
Step moss	26.2±27.9	8.38±0.43	0.057
Other moss	25.6±53.5	11.30 [‡]	0.029
Total	2518±494	—	1.89

Note: The $f_{(x)max}$ of the lichens and bryophytes were estimated by immersing the lichen or bryophyte in water and representing the increase relative to dry mass (eq. 1). The potential storage is an estimate of the water storage by lichens and bryophytes for the whole old-growth Douglas-fir forest.

*From Pypker (2005).

[†]From McCune (1993).

[‡]Estimated using the mean maximum water contents of the three dominant bryophytes on the forest floor.

the $f_{(x)max}$ of all the forest-floor bryophytes were statistically different from each other (Bonferonni multiple-comparison test, all p values > 0.05) (Table 4). The average $f_{(db)max}$ for the Western hemlock and Douglas-fir branches were not statistically different (p value > 0.73) (Table 3).

Epiphyte-laden branch water storage under varying intensities

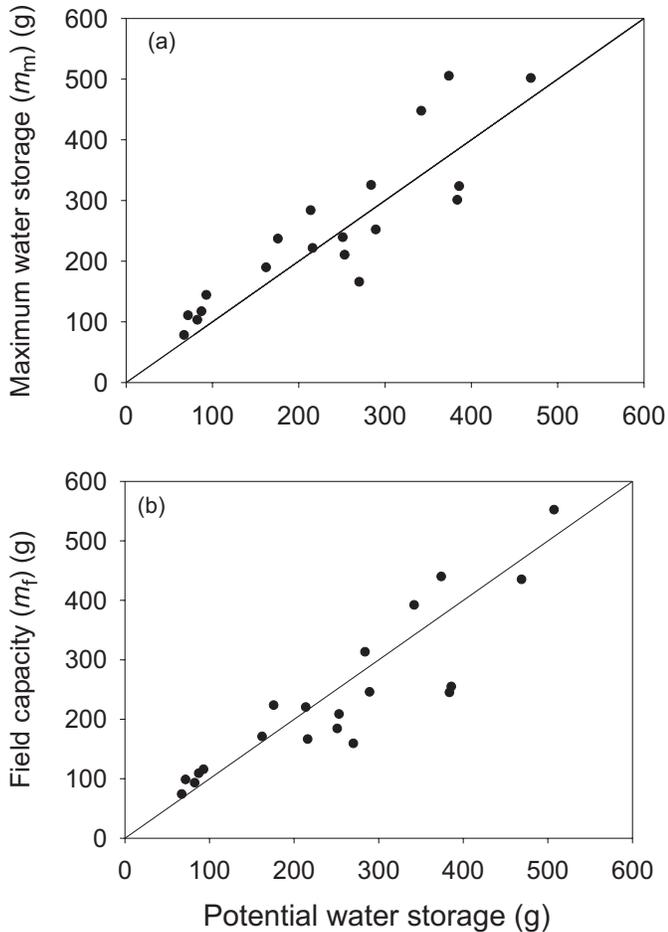
After allowing for water storage on the branch surface (Table 3), the m_m and m_f of the epiphyte-laden branches could be predicted using the biomass of fruticose lichens, foliose lichens, and bryophytes in conjunction with the measured $f_{(x)max}$ of each epiphyte type (eq. 4; Fig. 2). The $f_{(x)max}$ of the dead branch was not included in the measurements because the simulations ran for a maximum of 2 h and did not provide enough time for substantial amounts of water to penetrate the dead branch. The m_{bc} as estimated by eq. 4 and the measured epiphyte-laden branch water storage did not differ significantly for the estimates of m_m or m_f (p values > 0.05) (Fig. 2).

For all of the rainfall intensities the m_m or m_f of the branches were not statistically different (Bonferonni multiple comparisons, all p values > 0.05) (Table 5). However, while not statistically significant, the m_f for 12 of the 14 branches after exposure to 39.8 mm·h⁻¹ was smaller than after exposure to 11.3 mm·h⁻¹ (Table 5). Finally, after accounting for the effect of the epiphytic foliose lichens, fruticose lichens, and bryophytes, the m_m and m_f of epiphyte-laden hemlock branches did not differ statistically from values for the Douglas-fir branches (m_m , p value > 0.68; m_f , p value > 0.43).

Rainfall interception efficiency (p_i) under varying intensities

At rainfall intensities of 11.3, 16.1, and 39.8 mm·h⁻¹, the p_i of the branches did not statistically differ (Bonferonni multiple comparisons, all p values > 0.05) (Fig. 3). After 2 mm of rainfall the branches had an average p_i between

Fig. 2. The relationships between (a) the measured maximum water storage (m_m) and (b) the measured field water storage capacity (m_f) and the potential water storage predicted from the use of eq. 4 with the biomass and maximum water fraction ($f_{(x)\max}$) of the three classes of epiphytes. Each point represents one branch. The 1:1 line is shown.



0.50 and 0.70. The p_i for all branches gradually decreased to approximately 0.2 after 16 mm of rain. The relationship between the cumulative “rainfall” during the “storm event” (P_{cG}) and p_i can be described by the hyperbolic equation

$$[6] \quad p_i = \frac{xy}{y + P_{cG}}$$

where $x = 0.9$ and $y = 5.03$ (Fig. 3). This empirical equation was selected because it fit the data well ($R^2 = 0.98$), and being hyperbolic, would approach zero as P_{cG} approached infinity.

Discussion

Lichen and bryophyte maximum water fraction ($f_{(x)\max}$)

When considering the influence of lichens and bryophytes on canopy water storage capacity, it is important to calculate both the water absorbed into the thallus or leaf and the water stored on the surface. The ability of lichens and bryophytes to store water is important for these species because they collect the majority of their water from rainfall and dew (Blum 1973; Proctor 2000). Past studies have demonstrated that lichens and bryophytes store between 100% and 1200%

Table 5. The maximum branch water storage (m_m) and field capacity branch water storage (m_f) for 20 branches exposed to three rainfall intensities.

Branch	Rainfall intensity					
	11.3 mm·h ⁻¹		16.1 mm·h ⁻¹		39.8 mm·h ⁻¹	
	m_m (g)	m_f (g)	m_m (g)	m_f (g)	m_m (g)	m_f (g)
1	78.4	74.3	—	—	74.3	62.3
2	103.5	93.3	110.8	91.2	90.4	78.4
3	110.9	98.9	122.7	110.7	125.7	113.7
4	116.0	159.5	156.2	144.2	161.2	149.2
5	447.8	392.3	385.5	335.1	367.8	352.0
6	117.6	109.3	112.5	96.5	107.6	87.2
7	189.8	171.1	193.7	177.2	196.9	157.9
8	501.8	435.3	461.8	396.4	486.5	384.8
9	382.6	357.7	383.6	325.7	383.5	294.4
10	352.2	246.1	243.8	237.5	203.1	183.9
11	210.6	208.9	249.6	246.5	223.3	206.8
12	273.1	223.7	234.9	215.0	214.7	184.8
13	325.6	313.4	322.0	322.0	322.6	280.2
14	602.9	552.4	581.2	529.3	426.7	362.4
15	284.0	220.5	—	—	—	—
16	301.2	245.2	—	—	—	—
17	221.7	166.7	—	—	—	—
18	144.5	116.0	—	—	—	—
19	239.5	184.5	—	—	—	—
20	323.8	255.2	—	—	—	—

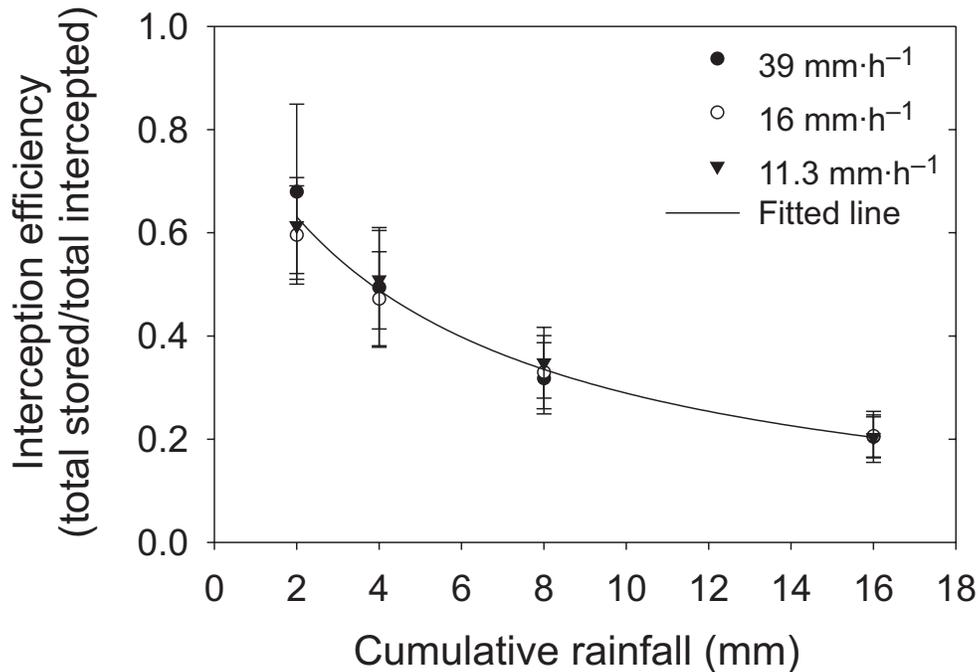
of their dry mass in water (Blum 1973; Proctor 2000). However, these studies excluded surface water storage because the specimens were blotted dry. This study measured both the water absorbed within and the water stored on the surface of the thallus or leaf. Hence, the $f_{(x)\max}$ values of the lichens and bryophytes reported here are higher than the average water-holding capacities reported in the literature. For example, Blum (1973) found that *Lobaria pulmonaria* stored 190% of its dry mass in water. In contrast, the results from this study indicate that lettuce lung, a close relative of *L. pulmonaria*, can store 342% of its dry mass in water. Thus, the potential water storage of the epiphytes increases when both the internal and surface water storage are considered.

Water storage on epiphyte-laden branches

The maximum water storage (m_m) and field capacity (m_f) of branches can be predicted if the biomass of foliose lichens, fruticose lichens, and bryophytes on the branch is known (Fig. 2). The water storage by epiphytic lichens and bryophytes on Douglas-fir and western hemlock branches did not differ statistically between the tree species. Hence, if the quantities of lichens and bryophytes in the canopy are known, their potential contribution to S in old-growth Douglas-fir forests can be calculated. However, this estimate is useful only for predicting the total potential water storage of the epiphytes. If the epiphytes are not dry at the start of the storm, they will store less of the intercepted rainfall because a portion of their $f_{(x)\max}$ is already filled (Hölscher et al. 2004; Pypker et al. 2006).

In a typical old-growth Douglas-fir forest in the Pacific Northwest there is two or three times more lichen biomass than bryophyte biomass in the canopy (McCune 1993; Pypker

Fig. 3. The mean interception efficiencies (p_i) of epiphyte-laden branches placed under a rainfall simulator at three different rainfall intensities. The fitted line represents a hyperbolic equation (eq. 6) that relates cumulative rainfall to p_i for all three rainfall intensities ($R^2 = 0.98$).



2005). In terms of water storage the greater biomass of epiphytic lichens is offset by the larger $f_{(x)\max}$ of the bryophytes. For example, the forest that provided the branches for this study was estimated to contain 1240, 30, and 780 kg·ha⁻¹ of foliose lichens, fruticose lichens, and bryophytes, respectively (Pypker 2005). This is comparable to the quantity of epiphytic foliose lichens (1690 kg·ha⁻¹), fruticose lichens (180 kg·ha⁻¹), and bryophytes (780 kg·ha⁻¹) found in another old-growth Douglas-fir forest in the Pacific Northwest (McCune 1993). By multiplying the biomass of epiphytic lichens and bryophytes by their respective $f_{(x)\max}$, it is apparent that an old-growth Douglas-fir forest could store between 1.2 and 1.4 mm of water in epiphytes alone. Hölischer et al. (2004) found a similar result when investigating the effect of epiphytic lichens and bryophytes on interception in a tropical montane forest. They reported that the forest contained greater than 1900 kg·ha⁻¹ of nonvascular epiphytes, which accounted for 0.81 mm of storage. Thus, the water stored by epiphytic lichens and bryophytes in forests is comparable to the canopy storage capacities reported for many young, closed-canopy coniferous forests without significant epiphyte populations (Zinke 1967; Rutter et al. 1975; Tiktak and Bouten 1994; Klaassen et al. 1998; Pypker et al. 2005).

The quantity of water storage by bryophytes increases when the water storage by forest-floor bryophytes is accounted for. Forest-floor bryophytes in a typical old-growth Douglas-fir forest cover 25%–50% of the ground area (Rambo and Muir 1998; Shaw et al. 2004), provide 485 kg·ha⁻¹ of biomass (Pypker 2005), and absorb between 8 and 14 times their dry mass in water (Table 4). If the biomass of the forest-floor bryophytes is multiplied by their respective $f_{(x)\max}$, it can be shown that forest-floor bryophytes will provide an additional 0.60 mm of potential water storage (Table 4).

Water storage in dead branches

Water storage in dead branches also contributes to the large S observed in old-growth Douglas-fir forest canopies. Based on the allometric equations provided by Grier and Logan (1977) for a nearby old-growth Douglas-fir forest, the forest canopy in this study contains about 550 kg·ha⁻¹ of dead branches. Assuming that these dead branches have an $f_{(db)\max} = 1.92$ (Table 3), they will store an additional 1.06 mm of water. However, dead branches do not represent the majority of wood biomass in an old-growth Douglas-fir canopy. The same allometric equations estimate that the canopy has about 1070 kg·ha⁻¹ of bark. The storage in this bark may be considerable; for example, Herwitz (1985) estimated that water storage by bark accounted for 30%–50% of S for a tropical rainforest in northeast Queensland, Australia. Storage in dead plant material is not limited to the forest canopy; water stored in dead plant material on the forest floor may also contribute to water storage.

The forest floor in old-growth Douglas-fir forests generally contains 4–8 mm of litter (Pypker et al. 2005; Shaw et al. 2004) and has 25% of its ground surface area covered by deadwood (Harmon and Sexton 1995). Forest-floor litter is estimated to store between 100% and 150% of its dry mass in water (Helvey and Patric 1965), and the deadwood on the forest floor is estimated to intercept and store 2%–5% of gross precipitation (Harmon and Sexton 1995). Thus, the storage of water by deadwood and litter may be important in old-growth Douglas-fir forests and requires further study.

Rainfall storage and preferential flow

When exposed in the rainfall simulator, epiphyte-laden branches took up to 9 h to saturate. Generally, lichens and bryophytes immersed in water become saturated within

5 min (Blum 1973). However, for 19 of the 20 branches, only 50%–79% of the initial 2 mm of water intercepted was stored (Fig. 3). Based on eq. 2, the branches required between 0.5 and 9 h at $11.3 \text{ mm}\cdot\text{h}^{-1}$ to reach 95% of m_m . In contrast, foliage samples placed under a rainfall simulator at $20 \text{ mm}\cdot\text{h}^{-1}$ typically saturate in less than 8 min (Keim et al. 2005b). A closed-canopy coniferous forest that does not contain significant populations of epiphytes and has a leaf area index between 8 and 12 will saturate after 1.4–4 mm of rainfall (Klaassen et al. 1998; Pypker et al. 2005). Thus, a single epiphyte-laden branch requires a greater quantity of rainfall to saturate than the canopy of a young coniferous forest with a small epiphyte population. The low p_i of the epiphyte-laden branches indicates that intercepted rainfall is not absorbed by the lichens and bryophytes (Fig. 3); rather it may be following preferential flow routes off the branch.

We suggest that water that is intercepted by an epiphyte-laden branch may establish preferential flow routes through the epiphyte mats, just as water commonly follows preferential flow routes in soils (Hill and Parlange 1972; McDonnell 1990; Weiler and Naef 2003). In soil, once water has established a route, there is less resistance to further flow along that pathway. Furthermore, preferential flow routes are not limited to an individual storm, but persist from storm to storm (McDonnell 1990; Weiler and Naef 2003). Just as with soil, epiphyte-laden branches form a three-dimensional structure. It is highly probable that as the rainfall infiltrates the epiphyte mats it will be routed along preferential flow routes. If preferential flow routes are present in epiphyte-laden branches, the saturation of a branch would be delayed, as water would have difficulty reaching all the epiphyte and branch surfaces.

If these preferential flow routes persist from storm to storm, the drip points below a canopy will also persist and will be predictable. Recent work by Keim et al. (2005a) investigated the spatial pattern of throughfall beneath an old-growth Douglas-fir forest for multiple storms. Once Keim et al. (2005a) determined the spatial pattern of throughfall from one storm, they could predict the spatial pattern of throughfall for subsequent storms. However, they could not determine the spatial pattern a priori using variables such as distance from tree boles. If the preferential low paths in epiphytic lichens and bryophyte mats persist from storm to storm, they may be important in determining the spatial pattern throughfall. Thus, the occurrence of preferential flow through epiphyte communities will alter the rainfall intensity and spatial distribution at the forest floor, and this may decrease erosion and hillslope failure (Keim and Skaugset 2003).

The slow rate of saturation of branches may not be entirely due to preferential flow. Equation 6 indicates that as P_G approaches zero, the p_i for an epiphyte-laden branch is 0.9. This suggests that when P_G is small, 10% of the rainfall striking a branch is not absorbed. It is possible that this fraction is rain which strikes a branch but splashes off the surface on impact. Raindrop splash has previously been implicated in changing the water stored on a branch (Calder et al. 1996; Calder and Wright 1986).

Rainfall intensity and interception efficiency (p_i)

Past research has affirmed that S is negatively associated with increasing windspeeds and rainfall intensities (Calder et al. 1996; Calder and Wright 1986; Hörmann et al. 1996;

Rutter et al. 1971). Greater windspeeds shake the branches and dislodge the stored water. Higher rainfall intensities have larger drop sizes (Laws and Parsons 1943; Best 1950; Mason and Andrews 1960) that should impart a greater force to the surface of a leaf. Therefore, it has been hypothesized that at higher rainfall intensities the water stored on a branch will decrease because the bigger raindrops will splash greater quantities of water off of the surface (Rutter et al. 1971; Calder et al. 1996). There is some debate over whether this mechanism is correct (Keim et al. 2005b), but it is generally accepted that changes in rainfall intensity alter S (Calder et al. 1996; Keim et al. 2005b; Price and Carlyle-Moses 2003).

In this study branches did not have a greater p_i or water storage at lower rainfall intensities. The lack of association between water storage and rainfall intensity may be the result, in part, of the raindrop sizes generated by the simulator not mimicking natural rainfall (Table 1). However, the drop size did increase by 30% as rainfall intensity increased from 16.1 to $39.8 \text{ mm}\cdot\text{h}^{-1}$, and this increase was expected to result in less water storage. It may be that the morphology of epiphytes dampens the effect that changes in rainfall intensity have on branch water storage. When compared with the surfaces of leaves and branches, the surfaces of the lichens and bryophytes on the branch are very rough and flexible. Hence, the momentum of falling drops might be absorbed more easily, decreasing the probability of the drop splashing off the surface.

Past research on rainfall interception by tree branches placed under a rainfall simulator conflicts with the hypothesis that canopy water storage decreases with increasing rainfall intensity (Aston 1979; Keim et al. 2005b). In these studies branch water storage increased with greater rainfall intensity because the rate that water was dripped and splashed off the branch was exceeded by the greater quantities of rainfall impinging upon the branch. The water storage by the epiphyte-laden branches did not follow this pattern. The difference may result from the morphology of epiphytes changing the effect that changes in rainfall intensity have on branch water storage. Epiphyte-laden branch water storage is a combination of surface water storage and internal water storage both within the leaves of the lichens and within the mats of epiphytes. Therefore, differences in momentum changes at the interception surface combined with how water is stored on the branch may alter epiphyte-laden branch water storage at high rainfall intensities relative to branches with little epiphyte biomass.

Conclusions

Lichens and bryophytes substantially increase the interception and storage of rainfall in old-growth Douglas-fir – western hemlock forests. The maximum water fractions ($f_{(x)\text{max}}$) of lichens and bryophytes are significantly different, with the epiphytic bryophytes storing three times more water per unit dry mass than the lichens. Because of their high $f_{(x)\text{max}}$, epiphytic fruticose lichens, foliose lichens, and bryophytes have the potential to increase the canopy water storage capacity (S) in the old-growth Douglas-fir forests by about 1.3 mm. However, this study showed that the epiphyte-branches require >6 mm of rainfall to saturate. This relatively large amount of rainfall is required to saturate a branch

because the rainfall interception efficiency (p_i) of a branch is typically less than 0.7 after only 2 mm of rain. The low p_i likely occurs because water is following preferential flow routes through the epiphyte mats on the branch. In summary, the large $f_{(x)\max}$ of epiphytic lichens and bryophytes increases the canopy water storage capacity of old-growth Douglas-fir canopies, and their low p_i may influence slope stability by delaying the saturation of the canopy and altering rainfall intensity at the forest floor.

Acknowledgements

We wish to thank Dr. R. Keim and Dr. A. Skaugset for providing a rainfall simulator and high-precision scale. We thank C. Tarasoff, Dr. J. McDonnell, Dr. T. Link, and Dr. M. Meigs for their helpful comments on the manuscript. We also thank our two reviewers for their helpful comments. Funding for this project was provided by Sigma Xi and the Department of Forest Science, Oregon State University.

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- br Bryophyte
fo Foliose lichen
fr Fruticose lichen
- $f_{(x)\max}$ Maximum internal and external epiphyte (br, fo, fr) or dead branch (ds) water storage (g water)·(g epiphyte dry mass)⁻¹)
- I_t Rainfall intensity (kg·h⁻¹·m⁻²)
- m Mass of rainfall impinging on a surface (kg·s⁻¹)
- m_{be} Potential epiphyte-laden branch water storage capacity (g)
- m_{bs} Potential water storage capacity on the surface of a dead branch (g)
- m_f Quantity of water stored on a branch after the rainfall ceased and the water stopped dripping from the branch (field capacity) (g)
- m_m Maximum water stored on a branch during a rainfall simulation (g)
- P_G Gross rainfall (mm)
- P_{cG} Cumulative gross rainfall during a single storm (mm)
- p_i Interception efficiency (dimensionless)
- S Canopy water storage capacity (mm)
- w_b Branch dry mass (kg)
- w_{br} Dry mass of bryophytes
- w_{fo} Dry mass of foliose lichens
- w_{fr} Dry mass of fruticose lichens

List of symbols

a_b Projected surface area of an epiphyte-laden branch