

The role of epiphytes in rainfall interception by forests in the Pacific Northwest. II. Field measurements at the branch and canopy scale

Thomas G. Pypker, Michael H. Unsworth, and Barbara J. Bond

Abstract: To determine how epiphytes affect the canopy hydrology of old-growth Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests, we measured rainfall interception by individual branches and an entire stand from March 2003 to May 2004. Epiphyte-laden branches at heights of 3.1, 24.8 and 46.5 m remained partially saturated for most of the wet season and required more than 30 mm of rainfall to become saturated. We used the mean, minimum, and individual storm methods to estimate canopy water storage capacity. Canopy water storage capacity averaged 3.1–5.0 mm, but these are probably underestimates of the maximum canopy water storage capacity, because the canopy was partially saturated prior to most storm events and the saturation of the canopy was delayed by preferential flow through the epiphyte-laden branches. Contrary to expectation, the water stored on epiphyte-laden branches after exposure to natural rainfall increased with rainfall intensity because the rough three-dimensional structure of the lichen and bryophyte mats limits water loss from raindrop splash and impedes the drainage of water from the branch. We conclude that epiphytic lichens and bryophytes increase canopy water storage capacity, prolong the time required for the canopy to saturate and dry, and alter the transfer of water through the canopy.

Résumé : Dans le but de déterminer comment les épiphytes affectent l'hydrologie de la canopée des vieilles forêts de douglas (*Pseudotsuga menziesii* (Mirb.) Franco), les auteurs ont mesuré l'interception de la pluie par des branches individuelles et par le peuplement, du mois de mars 2003 au mois de mai 2004. Les branches couvertes d'épiphytes à 3,1, 24,8 et 46,5 m de haut sont demeurées partiellement saturées pendant presque toute la saison humide et nécessitaient plus de 30 mm de pluie pour être saturées. Ils ont utilisé les méthodes de la moyenne, du maximum et de l'orage individuel pour estimer la capacité d'emmagasinage de l'eau de la canopée. La capacité d'emmagasinage de l'eau de la canopée atteignait en moyenne 3,1 à 5,0 mm mais ces quantités sont probablement sous-estimées parce que la canopée était partiellement saturée avant la plupart des orages et que la saturation de la canopée était retardée à cause de l'écoulement préférentiel à travers les branches couvertes d'épiphytes. Contrairement aux attentes, l'eau emmagasinée sur les branches couvertes d'épiphytes après une exposition à une pluie naturelle augmentait avec l'intensité de la pluie parce que la structure tridimensionnelle grossière des thalles de lichen et de bryophyte limite la perte d'eau due à l'éclaboussure des gouttes de pluie et entrave l'écoulement de l'eau sur la branche. Ils arrivent à la conclusion que les bryophytes et les lichens épiphytes augmentent la capacité d'emmagasinage de l'eau de la canopée, prolongent le temps nécessaire pour que la canopée se sature et sèche et modifient le mouvement de l'eau à travers la canopée.

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Introduction

The quantity of rainwater stored in an old-growth Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forest and available for evaporation during a storm (canopy water storage capacity (S)) is at least twice that stored in a young Douglas-fir forest canopy of similar leaf area index (LAI) but with few epiphytes (Link et al. 2004; Pypker et al. 2005). Epiphytic lichens and bryophytes can store large quantities of water (Blum 1973; Proctor 2000; Pypker et al. 2006) and are abundant in the old-growth Douglas-fir forests of the Pacific Northwest (McCune 1993; Pike et al. 1975; Sillett and Rambo 2000). Hence, epiphytic lichens and bryophytes

may alter the water budget of a watershed by intercepting considerable quantities of rainfall. However, despite their potential impact on rainfall interception, the significance of epiphytic lichens and bryophytes to the hydrology of these forests is not well understood.

Lichens and bryophytes can rapidly absorb large quantities of liquid water (Blum 1973; Proctor 2000). The maximum water storage (internal and external water storage; $f_{(x)\max}$) of epiphytic foliose lichens, fruticose lichens, and bryophytes that are typical of an old-growth Douglas-fir forest is approximately 2.2, 3.4, and 10.0 times their dry mass, respectively (Pypker et al. 2006). The potential water storage capacity of an epiphyte-laden branch (m_{be}) can be estimated

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by multiplying the biomass of the three epiphytic groups by their respective $f_{(x)\max}$. The m_{be} successfully predicted the water storage of epiphyte-laden branches exposed to different rainfall intensities under a rainfall simulator (Pypker et al. 2006). If epiphytic lichens and bryophytes saturate in a similar manner in situ, a typical old-growth Douglas-fir forest will store 1.4 mm of rainfall ($14\,000\text{ kg}\cdot\text{ha}^{-1}$) in epiphytic lichens and bryophytes (assuming 180, 1650, and $780\text{ kg}\cdot\text{ha}^{-1}$ of fruticose lichens, foliose lichens, and bryophytes, respectively (McCune 1993)). This storage is large compared with that of many mature, closed-canopy coniferous forests without large populations of epiphytic lichens and bryophytes, which store between 1 and 2.5 mm of rainfall (Gash et al. 1980; Pypker et al. 2005; Rutter et al. 1975; Zinke 1967).

The large $f_{(x)\max}$ and physical structure of epiphytic lichens and bryophytes may also influence the interception efficiency (p_i) of a branch (total rainfall stored on a branch divided by the total rainfall impinging upon the branch). To saturate an epiphyte-laden branch, the rainfall must infiltrate the mats of lichens and bryophytes. As the water infiltrates, preferential flow routes likely form, and water may fall from the branch before it can be absorbed (Pypker et al. 2006). This branch infiltration process will delay saturation of the forest canopy, alter the rainfall intensity at the forest floor, and may influence the accuracy of traditional regression-based techniques used for estimating S .

Three indirect, regression-based techniques are commonly used for estimating S , the proportion of direct throughfall (p), and the ratio of evaporation to rainfall intensity after canopy saturation (\bar{E}/\bar{R}). These are the minimum (S only), mean, and the individual storm (IS) methods (Klaassen et al. 1998; Leyton et al. 1967; Link et al. 2004). All these methods require measurement of the gross precipitation above the canopy (P_G) and the net precipitation below the canopy (P_n). The mean and minimum methods estimate S , p , and \bar{E}/\bar{R} using multiple storms and the IS method estimates them on a "per-storm" basis (see Calculation of canopy variables section for a complete description of each technique). All three methods assume that the entire canopy is dry prior to a storm and that the whole canopy saturates simultaneously during the storm. Rainfall interception by old-growth Douglas-fir canopies may not satisfy these assumptions because the canopy may (1) not dry between storm events because of its large canopy water storage (C) and (2) not saturate simultaneously because it is very heterogeneous (Franklin et al. 2002; Franklin and Van Pelt 2004). If these assumptions are violated, these methods will underestimate S and overestimate \bar{E}/\bar{R} , because the canopy water storage is partially filled prior to the storm and the mean and IS methods will be unable to accurately determine S .

In addition to delaying saturation and increasing S , the physical structure of epiphytes may also affect the relationship between branch water storage and rainfall intensity. Branch water storage has often been reported to decrease with increasing rainfall intensity (Calder et al. 1996; Calder and Wright 1986; Price and Carlyle-Moses 2003). As rainfall intensity increases, the size of the raindrops increases (Best 1950; Laws and Parsons 1943; Mason and Andrews 1960). With larger terminal velocities and greater masses

than that of small raindrops, these larger raindrops will impart a greater force (rate of change of momentum) when impacting on a surface. It has been hypothesized that the increased momentum of larger raindrops will splash a greater quantity of water off a leaf or branch, thereby reducing the leaf or branch water storage (Calder et al. 1996; Calder and Wright 1986). Although epiphytic lichens and bryophytes can resemble leaves (e.g., foliose lichens), they often have a different structure than that of leaves and branches. For example, the thalli of lichens can be hairy and pendulous (e.g., fruticose lichen), and the leaves of bryophytes frequently form mats that have a very rough surface compared to that of a tree leaf. Hence, epiphyte-laden branches may dissipate the momentum of large raindrops more effectively than tree leaves and branches and consequently can be efficient at retaining water in heavy rain.

Despite the large maximum water content of lichens and bryophytes there has been little direct research on how they influence S . Generally, past research has assumed that lichens and bryophytes increase the S of a canopy (Levia and Frost 2003; Link et al. 2004; Rothacher et al. 1967; Veneklaas and Van Ek 1993). Recently, Hölscher et al. (2004) have confirmed this assumption. They reported that epiphytic mosses in a tropical forest in Costa Rica increased the S of the forest by 0.8 mm and accounted for 6% of the interception loss (I_n). We hypothesized that epiphytic lichens and bryophytes considerably alter the hydrology of Pacific Northwest forests. To test this hypothesis and better understand the impacts of epiphytes on canopy hydrology of old-growth Douglas-fir forests, we used a combination of stand- and branch-scale measurements of rainfall interception in an old-growth Douglas-fir forest to determine (1) whether laboratory-based estimates of m_{be} (Pypker et al. 2006) can be used to predict water storage by epiphyte-laden branches in the field; (2) the effect that epiphyte distribution has on canopy wetness following storms; (3) whether water storage and routing through epiphytic lichens and bryophytes influence estimates of S produced by the minimum, mean, and IS methods; and (4) the relationship between rainfall intensity and epiphyte-laden branch water storage.

Materials and methods

Study site

The study area was in the H.J. Andrews Experimental Forest located within the western Cascades of central Oregon, USA (44.2°N , 122.2°W). The study area was in an old-growth Douglas-fir and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) forest that is greater than 450 years old. The canopy is greater than 60 m tall, has an LAI of approximately 12 (Moore et al. 2004), and has large canopy gaps that are typical for old-growth Douglas-fir forests in the Pacific Northwest (Franklin et al. 2002; Gray and Spies 1996). There are approximately $1240\text{ kg}\cdot\text{ha}^{-1}$ of epiphytic foliose lichens, $30\text{ kg}\cdot\text{ha}^{-1}$ of epiphytic fruticose lichens, $780\text{ kg}\cdot\text{ha}^{-1}$ of epiphytic bryophytes, and $465\text{ kg}\cdot\text{ha}^{-1}$ of forest-floor bryophytes (Pypker 2005). The site has wet, mild winters and warm, dry summers, with a mean annual precipitation of 2300 mm. The soil is described as gravelly clay loam (Swanson and James 1975).

Measurement of gross precipitation and net precipitation

Gross precipitation (P_G) and net precipitation (P_n) were measured from 30 March to 1 December 2003 and from 22 March to 14 May 2004 using tipping bucket rain gauges (TE-525I, Texas Electronics Inc., Dallas, Texas, USA). The tipping buckets were placed approximately 1 m above the ground and monitored using individual dataloggers (HOBO event, Onset Computer Corp., Bourne, Massachusetts, USA). Each tipping bucket rain gauge has a diameter of 20.3 cm and a resolution of 0.254 mm. Two tipping bucket rain gauges were placed in a clearing (30 m × 40 m) adjacent to the forest to measure P_G . Twenty-three tipping bucket rain gauges were placed randomly throughout a 2 ha area in the old-growth forest to measure P_n . Placing the array across a range of variability (Kimmins 1973; Puckett 1991) and relocating the collectors on a regular basis (every 4–6 weeks) reduces errors in the throughfall estimates by increasing the number of sampling points in the plot (Lloyd and Marques filho 1988; Wilm 1943). A second array consisted of 48 manual throughfall collectors (10.9 cm diameter) that were spaced 8 m apart along a 200 m transect and were not relocated during the measurement period. The second array was used to verify throughfall estimates and to confirm that there was no relocation bias in the data from the tipping bucket array. The manual throughfall collectors and tipping buckets were cleaned and leveled every 4 weeks.

Calculation of canopy variables

The mean, minimum, and IS methods were used to estimate S , p , and \bar{E}/\bar{R} from 30 March to 9 November 2003 and from 18 March to 19 May 2004. For these periods the cumulative net precipitation measured by the tipping bucket array under the canopy was within 1% of the value recorded by the manual throughfall collectors. In the intervening period, about 25% of the tipping buckets malfunctioned because of freezing temperatures, excess litter deposition in the funnels, and datalogger failure, so the methods were not applied to this period.

For the minimum method, S was estimated as outlined by Leyton et al. (1967). A linear regression relating P_G and P_n was fitted through data from all storms where P_G was greater than 10 mm and evaporation was small (the slope relating P_n to P_G for the storms was required to be within 0.1 of unity). We used a threshold of 10 mm because past research suggested that this was sufficient to saturate an old-growth Douglas-fir canopy (Link et al. 2004). The x -intercept for the regression provided the estimate of S .

With the mean method, S , p , and \bar{E}/\bar{R} were estimated by creating two regression lines (R_1 and R_2) that related P_n to P_G (Klaassen et al. 1998). The first regression line (R_1) was fit to all the storm events where P_G was insufficient to saturate the canopy. The second regression line (R_2) was fit to all storm events where P_G was sufficient to saturate the canopy. To determine which storm events were applied to R_1 or R_2 , the fits of the regression lines were optimized to minimize the mean square error of the two regression lines. When using the mean method, the slope of R_1 provides the estimate of p ; one minus the slope of R_2 provides an estimate of \bar{E}/\bar{R} ; the value of P_G at the intersection point of R_1 and R_2 provides an estimate of the canopy saturation point (P'_G); and

the difference between P_G and P_n at the intersection point provides an estimate of S .

Values of S , p , \bar{E}/\bar{R} , and I_w were calculated on a per-storm basis using the IS method, as described in Link et al. (2004). The IS method partitions each rainfall event into two discrete periods; pre- and post-canopy saturation. For each period a linear regression was established that related the cumulative below-canopy (net) precipitation during the storm (P_{cn} (mm)) to the cumulative gross precipitation (P_{cG} (mm)) during the storm. As with the mean method, the two regressions were optimized to minimize the mean square error of the two regression lines. Prior to canopy saturation the relationship between P_{cn} and P_{cG} is calculated as

$$[1] \quad P_{cn} = pP_{cG}$$

where p is the proportion of rainfall that passes through the canopy prior to canopy saturation (Fig. 1, line A).

Prior to saturation, it is assumed that intercepted water will either remain in the canopy as stored water or evaporate back to the atmosphere. Following saturation, intercepted rainfall will either drip to the forest floor or evaporate (Fig. 1, line B). The rainfall beneath the canopy can be computed using

$$[2] \quad P_{cn} = pP_{cG} + \left(1 - \frac{\bar{E}}{\bar{R}}\right)(P_{cG} - P'_G)$$

After optimizing the fit of eqs. 1 and 2, p was calculated using the slope of eq. 1 and \bar{E}/\bar{R} was calculated as one minus the slope of eq. 2. Then S is computed by

$$[3] \quad S = (1 - p)P'_G - I_w$$

where I_w is the rainfall that is evaporated during canopy wet-up. I_w was estimated by

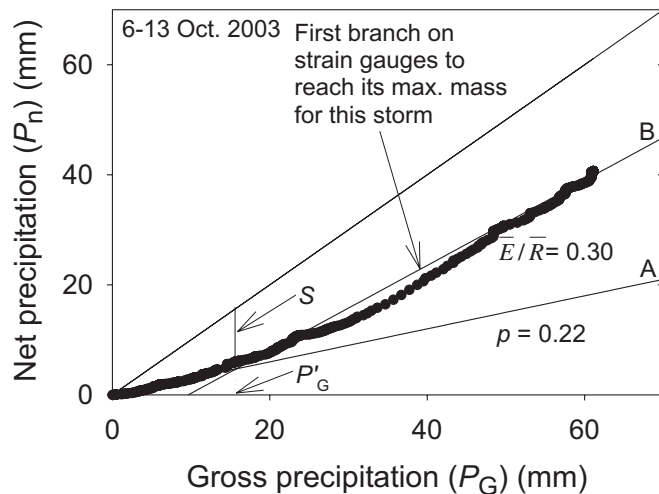
$$[4] \quad I_w = \left(1 - \frac{\bar{E}}{\bar{R}}\right)P'_G$$

Because Link et al. (2004) found that the use of \bar{E}/\bar{R} to calculate I_w frequently resulted in an overestimation of evaporation for an old-growth Douglas-fir forest, S was estimated both with I_w (S_w) and ignoring I_w (S_{wo}), and the difference was compared. Overestimation of I_w can occur if rainfall during canopy wet-up is infrequent. In these instances the intermittent rainfall will increase the time required for the canopy to saturate and the use of \bar{E}/\bar{R} in eq. 4 can overestimate I_w (Link et al. 2004).

Meteorological data and measurement of branch mass

To measure epiphyte rainfall interception under field conditions, we rigged two Douglas-fir trees (>60 m tall) 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 (Ultralight cup anemometer, Thornwaite Associates, Centerton, New Jersey, USA), a quantum sensor (LI-190SA quantum sensor, LI-COR, Lincoln, Nebraska, USA), and a relative humidity and temperature probe (HMP 45C, Vaisala Inc., Woburn, Massachusetts, USA). At each meteorological station a dead epiphyte-laden branch (>80% epiphyte cover) was cut from a nearby location in the tree

Fig. 1. The relationship between cumulative gross precipitation (P_G) and cumulative net precipitation (P_{cn}) during a storm (6–13 October 2003). Each solid dot represents a 10 min interval. The slope of regression A represents the direct throughfall ($p = 0.3$), the difference between P_G and P_n at the inflection point represents the canopy water storage (S), the value of P_G at the inflection point is the canopy saturation point (P'_G), and one minus the slope of regression line B is the ratio of evaporation to rainfall intensity ($\bar{E}/\bar{R} = 1 - 0.78$). There is no distinct inflection point to indicate where the canopy saturates. The IS method predicts that the canopy saturates after 15 mm of rainfall, whereas the branches on the strain gauges reached their maximum mass after 39–55 mm of rainfall.



and attached to a strain gauge (L2336, Futek Advanced Sensor Technology, Irvine, California, USA), which monitored branch mass continuously (Table 1). All meteorological and strain gauge data were recorded at 15 s intervals and averaged over 15 min using dataloggers (CR10X, Campbell-Scientific Inc., Logan, Utah, USA) with attached multiplexers (AM16/32, Campbell Scientific). The stations were installed in the summer of 2003 and the branches were replaced every 2–4 months. While changing the branches, the strain gauges were recalibrated using steel weights. The calibration did not change by more than 4% during any measurement period, so no adjustment was made for drift.

Branch descriptions

The epiphyte-laden branches were photographed and then destructively sampled after their removal from the field. A photograph of each epiphyte-laden branch was taken from above, and the projected area was determined using image processing software (Vegmeasure 1.6, D. Johnson, Department of Rangeland Science, Oregon State University, Corvallis, Oregon). The dry mass of fruticose lichens (hairy structure) (w_{fr}), foliose lichens (plate-like structure) (w_{fo}), and bryophytes (w_{br}) on each branch was determined by removing the epiphytes from the branch, separating them from the litter, and then sorting them into their functional groups. The branch dimensions (volume, surface area, and length) and the litter (needles, dirt) present on the branch were also determined. The dry masses of the branch, litter, and epiphytes were measured after drying at 70 °C for 72 h.

Potential epiphyte-laden branch water storage capacity (m_{be})

The potential epiphyte-laden branch water storage capacity (m_{be}) was predicted by adding the estimated water storage by the fruticose lichens, foliose lichens, and bryophytes to an estimate of the water storage on the branch surface (m_{bs}) (eq. 5). The dry masses of the fruticose lichens, foliose lichens, and bryophytes on the branch were multiplied by each epiphytes' maximum water storage (internal and external water storage; $f_{(x)max}$) (fruticose lichens, 2.23; foliose lichens, 3.42; bryophytes, 9.99) (Pypker et al. 2006). After removing all the epiphytes from the branch and immersing the branch in water, the difference between the branch mass before and after immersion provided the estimate of m_{bs} . The m_{be} of an epiphyte-laden branch was calculated as

$$[5] \quad m_{be} = 2.23 w_{fr} + 3.42 w_{fo} + 9.99 w_{br} + m_{bs}$$

During rainfall, the strain gauges also recorded the force imparted to each branch by impacting raindrops. We performed a sensitivity analysis to determine whether the masses provided by the strain gauges required a correction for the force imparted by the impacting raindrops for storms ranging between 1 and 10 $\text{mm}\cdot\text{h}^{-1}$. A nonlinear empirical relationship presented in van Dijk et al. (2002) was used to estimate the fall velocity of a water droplet in still air based on droplet diameter:

$$[6] \quad v_T = 0.0561 D^3 - 0.912 D^2 + 5.03 D - 0.254$$

where v_T is the terminal velocity ($\text{m}\cdot\text{s}^{-1}$) and D is the diameter of the raindrop (mm). An exponential function is frequently used to estimate median drop size (D_{50}) from rainfall intensity (R):

$$[7] \quad D_{50} = \alpha R^\beta$$

where α and β are fitting coefficients (van Dijk et al. 2002). We used the fitting parameters presented by Laws and Parsons (1943), where $\alpha = 1.28$ and $\beta = 0.173$. These fitting coefficients provide median droplet sizes that are larger than many other coefficients found in the literature (van Dijk et al. 2002) and therefore provide an upper estimate of force of the drops on the branches. Since droplet size is positively skewed during rainfall, the median droplet size may be inappropriate for estimating the force of the rain on the branch. Therefore, a second equation was used to estimate the effective droplet size (D_e) that would result in the same force on the branch if all the droplets were the size of D_e :

$$[8] \quad D_e = \gamma D_{50}^\delta$$

where γ and δ are fitting coefficients (van Dijk et al. 2002). The fitting parameters used to estimate D_e from D_{50} were $\gamma = 1.12$ and $\delta = 0.85$ (van Dijk et al. 2002).

The force imparted by the impacting raindrops was estimated using Newton's second law:

$$[9] \quad F_i = \frac{0.5 m v_T^2}{d_s g} \times \frac{D_e / 1000}{v_T}$$

where F_i is the force of impact (in kg), m is the mass of water per second (in $\text{kg}\cdot\text{s}^{-1}$), d_s (in m) is the stopping distance of the raindrop, and g (in $\text{m}\cdot\text{s}^{-2}$) is the acceleration due to gravity. To estimate F_i it was assumed that (1) all the rain-

Table 1. Descriptions of the 20 branches placed on strain gauges from June 2003 to June 2004.

| Tree | Sampling dates | Species | Height (m) | Dry mass (g) | | | | |
|------|-----------------------------|-------------|------------|--------------|---------|------|--------|--------|
| | | | | Fruticose | Foliose | Moss | Litter | Branch |
| 1 | 27 June – 19 Aug. 2003 | Hemlock | 3.1 | 0 | 0 | 54.3 | 10.6 | 274.5 |
| 1 | 19 Aug. – 17 Oct. 2003 | Hemlock | 3.1 | 0 | 0.3 | 23.9 | 3.5 | 40.6 |
| 1 | 17 Oct. 2003 – 24 Mar. 2004 | Hemlock | 3.1 | 0 | 0 | 20.6 | 5.1 | 50.1 |
| 1 | 24 Mar. – 2 June 2004 | Hemlock | 3.1 | 0 | 0 | 13.7 | 9.4 | 129.7 |
| 2 | 22 July – 19 Aug. 2003 | Hemlock | 3.1 | 0 | 0 | 34 | 11.3 | 175.8 |
| 2 | 19 Aug. – 8 Oct. 2003 | Hemlock | 3.1 | 0 | 0 | 36.6 | 8.2 | 96.6 |
| 2 | 8 Oct. 2003 – 24 Mar. 2004 | Hemlock | 3.1 | 0.3 | 0 | 47.8 | 20.5 | 295 |
| 2 | 24 Mar. – 3 June 2004 | Hemlock | 3.1 | 0 | 0 | 20.9 | 13.7 | 110 |
| 1 | 27 June – 19 Aug. 2003 | Douglas-fir | 24.8 | 0.3 | 0 | 25.1 | 28.5 | 300.9 |
| 1 | 19 Aug. – 5 Nov. 2003 | Douglas-fir | 24.8 | 0.5 | 17.1 | 4.4 | 4.3 | 243.1 |
| 1 | 5 Nov. 2003 – 9 Apr. 2004 | Douglas-fir | 24.8 | 0.3 | 7.9 | 8 | 17.5 | 789.6 |
| 1 | 9 Apr. – 2 June 2004 | Douglas-fir | 24.8 | 0.4 | 8.4 | 13.2 | 6 | 427.9 |
| 2 | 22 July – 19 Aug. 2003 | Douglas-fir | 24.8 | 0.4 | 16.5 | 35.2 | 9.5 | 412.8 |
| 2 | 19 Aug. – 8 Oct. 2003 | Douglas-fir | 24.8 | 0.2 | 12.8 | 30.2 | 13.7 | 37.9 |
| 2 | 8 Oct. 2003 – 12 Apr. 2004 | Douglas-fir | 24.8 | 0.05 | 15.6 | 9.6 | 11.9 | 351.3 |
| 2 | 12 Apr. – 3 June 2004 | Douglas-fir | 24.8 | 0.05 | 10.7 | 10.3 | 10.3 | 463.5 |
| 1 | 27 June – 19 Aug. 2003 | Douglas-fir | 46.5 | 0 | 9 | 21.4 | 8 | 111.7 |
| 1 | 19 Aug. – 5 Nov. 2003 | Douglas-fir | 46.5 | 0.6 | 20 | 4.5 | 7.2 | 230.9 |
| 1 | 5 Nov. 2003 – 9 Apr. 2004 | Douglas-fir | 46.5 | 1.7 | 10.7 | 3.2 | 5.6 | 275 |
| 1 | 9 Apr. – 2 June 2004 | Douglas-fir | 46.5 | 0 | 17.3 | 0.4 | 0.2 | 80.6 |
| 2 | 22 July – 19 Aug. 2003 | Douglas-fir | 46.5 | 8.4 | 16.5 | 0.7 | 6.7 | 132.6 |
| 2 | 19 Aug. – 8 Oct. 2003 | Douglas-fir | 46.5 | 0.1 | 20.5 | 8.7 | 5.9 | 87.6 |
| 2 | 8 Oct. 2003 – 12 Apr. 2004 | Douglas-fir | 46.5 | 0.05 | 9.2 | 0.5 | 1 | 47.4 |
| 2 | 12 Apr. – 3 June 2004 | Douglas-fir | 46.5 | 0.1 | 10.7 | 11 | 2.5 | 224.5 |

Note: The branches were placed on one of two trees at 3.1, 24.8, or 46.5 m and their mass was monitored using a strain gauge. Tabulated masses are dry masses of each component.

drops had a diameter D_c ; (2) the stopping distance of the raindrops was D_c ; (3) m was determined by assuming the density of water was always $1000 \text{ kg}\cdot\text{m}^{-3}$ (therefore $1 \text{ mm}\cdot\text{h}^{-1}$ equals $1 \text{ kg}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$); and (4) the time required for impact could be determined as the diameter of the drop divided by its velocity.

Evaluation of the effect of epiphytes on interception loss using the Gash model

The Gash model is a powerful tool for estimating I_n because of its simple requirements of S , p , and \bar{E}/\bar{R} . The model is, however, limited by the following assumptions outlined in Gash (1979): (1) rainfall is represented by a series of discrete storms separated by periods long enough to allow the canopy to completely dry; (2) the meteorological conditions are constant throughout the storm; and (3) there is no drip from the canopy during wet-up. The following model is a simplified version of the Gash model (Gash 1979; Link et al. 2004). The interception (I_c) during m small storms that were insufficient to saturate the canopy is described by

$$[10] \quad I_c = (1 - p) \sum_{j=1}^m P_{G,j}$$

The amount of interception for n storms sufficient to saturate the canopy (i.e., greater than or equal to the amount of rainfall to saturate the canopy — P'_G) is calculated as the amount of water evaporated during wet up (I_w), the evaporation after canopy saturation (I_s), and the evaporation after the storm ceases (I_a). These interception variables are calculated as

$$[11] \quad I_w = n(1 - p)P'_G - nS$$

$$[12] \quad I_s = \frac{\bar{E}}{\bar{R}} \sum_{j=1}^n (P_{G,j} - P'_G)$$

$$[13] \quad I_a = nS$$

To parameterize the model we calculated the mean of p (0.35), S (4.26 mm), P'_G (6.79 mm), and \bar{E}/\bar{R} (0.27) for every other storm as estimated by the IS method (Table 2, starting with storm 3). The model was then applied to all storms from 7 April to 9 November 2003 and from 25 March to 9 May 2004 that were not used to generate the parameters.

Results

Canopy variables

The IS method estimated that S_w , S_{w0} , \bar{E}/\bar{R} , and p for this old-growth forest averaged 2.9 mm, 4.9 mm, 0.24, and 0.35, respectively (Table 2). The estimates of S_w , \bar{E}/\bar{R} , and p are very similar to the values of S (3.3 mm), \bar{E}/\bar{R} (0.18), and p (0.36) estimated by the IS method for an old-growth Douglas-fir forest in south-central Washington (Link et al. 2004). However, when I_w (evaporation from the canopy during wet-up) is excluded from the calculation, the mean and range of S is much larger (Fig. 2). When I_w is included, S is likely underestimated for most of the storms because past research indicates that the use of \bar{E}/\bar{R} to estimate I_w (eq. 4) overestimates the effect of evaporation prior to canopy satu-

Table 2. Gross precipitation (P_G), net throughfall (P_n), interception loss (I_n), evaporation/rainfall ratio (\bar{E}/\bar{R}), canopy water storage capacity (S), and direct throughfall fraction (p) for an old-growth Douglas-fir forest in the Western Cascades (30 March – 1 December 2003; 22 March – 1 December 2003; 22 March – 14 May 2004).

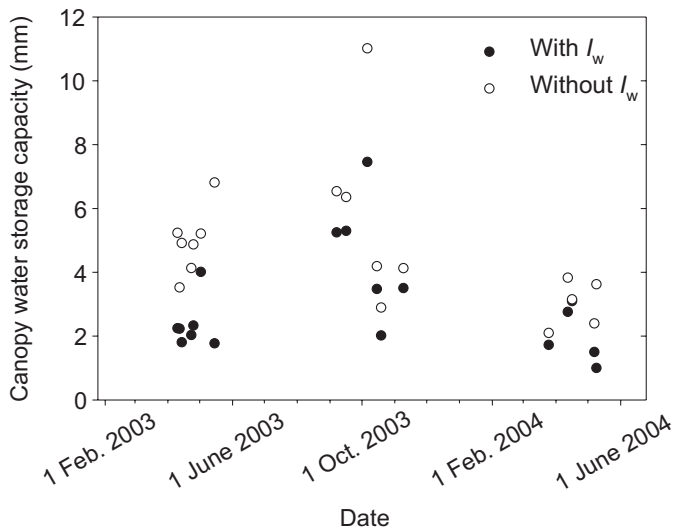
| Event | Location | Start | Duration (h) | P_G (mm) | P_n (mm) | I_n (% loss) | \bar{E}/\bar{R} | S (mm) | p | P'_G |
|-------|----------|---------------|--------------|------------|------------|----------------|-------------------|----------|------|--------|
| 1 | A | 7 Apr. 2003 | 7.77 | 1.78 | 0.63 | 64.6 | | | | |
| 2 | A | 9 Apr. 2003 | 15.6 | 2.67 | 1 | 62.5 | | | | |
| 3 | A | 10 Apr. 2003 | 43.5 | 19.8 | 9.7 | 51 | 0.37 | 5.24 | 0.35 | 8.07 |
| 4 | A | 12 Apr. 2003 | 37.6 | 21.8 | 12.8 | 41.3 | 0.3 | 3.53 | 0.18 | 4.29 |
| 5 | A | 14 Apr. 2003 | 85.8 | 35.9 | 19.7 | 45.1 | 0.41 | 4.92 | 0.35 | 7.54 |
| 6 | B | 21 Apr. 2003 | 22.7 | 3.56 | 0.97 | 72.8 | | | | |
| 7 | B | 23 Apr. 2003 | 42.8 | 27.2 | 16.2 | 40.4 | 0.31 | 4.13 | 0.39 | 6.74 |
| 8 | B | 25 Apr. 2003 | 27.7 | 13.3 | 7.41 | 44.3 | 0.29 | 4.87 | 0.45 | 8.89 |
| 9 | B | 28 Apr. 2003 | 6.9 | 1.27 | 0.24 | 81.1 | | | | |
| 10 | B | 29 Apr. 2003 | 15.6 | 6.6 | 2.92 | 55.8 | | | | |
| 11 | B | 2 May 2003 | 64.4 | 47.9 | 34.2 | 28.6 | 0.18 | 5.21 | 0.19 | 6.47 |
| 12 | C | 7 May 2003 | 27.3 | 5.97 | 2.06 | 65.5 | | | | |
| 13 | C | 9 May 2003 | 2.05 | 0.38 | 0.07 | 81.6 | | | | |
| 14 | C | 10 May 2003 | 9.94 | 4.32 | 1.28 | 70.4 | | | | |
| 15 | C | 11 May 2003 | 23.6 | 3.05 | 1.05 | 65.6 | | | | |
| 16 | C | 15 May 2003 | 58.7 | 15.4 | 6.14 | 6.1 | 0.49 | 6.82 | 0.34 | 10.3 |
| 17 | D | 25 May 2003 | 11.3 | 4.7 | 1.77 | 62.3 | | | | |
| 18 | D | 28 May 2003 | | 0.25 | 0.01 | 96 | | | | |
| 19 | D | 30 May 2003 | 2.2 | 4.32 | 1.64 | 62 | | | | |
| 20 | E | 13 June 2003 | 3.2 | 1.14 | 0.21 | 81.8 | | | | |
| 21 | E | 20 June 2003 | 20.3 | 3.81 | 0.73 | 80.8 | | | | |
| 22 | E | 22 June 2003 | | 0.25 | 0 | 100 | | | | |
| 23 | F | 2 Aug. 2003 | 10.6 | 0.38 | 0 | 100 | | | | |
| 24 | F | 6 Aug. 2003 | 3.42 | 5.46 | 1.68 | 69.2 | | | | |
| 25 | F | 22 Aug. 2003 | | 0.25 | 0 | 100 | | | | |
| 26 | F | 7 Sept. 2003 | 65.3 | 58.2 | 44.8 | 23 | 0.14 | 6.54 | 0.27 | 8.95 |
| 27 | F | 11 Sept. 2003 | 4.37 | 0.89 | 0.16 | 82 | | | | |
| 28 | F | 16 Sept. 2003 | 35.1 | 19.6 | 12.4 | 36.7 | 0.1 | 6.36 | 0.39 | 10.5 |
| 29 | G | 6 Oct. 2003 | 93.1 | 61.1 | 40.6 | 33.6 | 0.22 | 11 | 0.3 | 15.8 |
| 30 | G | 14 Oct. 2003 | 0.87 | 2.03 | 0.68 | 66.5 | | | | |
| 31 | G | 15 Oct. 2003 | 6.9 | 21.1 | 15 | 28.9 | 0.14 | 4.19 | 0.2 | 5.22 |
| 32 | G | 16 Oct. 2003 | 1.73 | 1.14 | 0.6 | 47.4 | | | | |
| 33 | G | 19 Oct. 2003 | 11.8 | 10.4 | 6.39 | 38.6 | 0.21 | 2.9 | 0.31 | 4.22 |
| 34 | G | 22 Oct. 2003 | 10.2 | 2.67 | 2.31 | 13.5 | | | | |
| 35 | G | 28 Oct. 2003 | 10.1 | 7.62 | 3.05 | 60 | | | | |
| 36 | H | 2 Nov. 2003 | 4.95 | 6.6 | 3.54 | 46.4 | | | | |
| 37 | H | 3 Nov. 2003 | 5.17 | 2.03 | 0.58 | 71.4 | | | | |
| 38 | H | 5 Nov. 2003 | 4.88 | 3.56 | 1.65 | 53.7 | | | | |
| 39 | H | 7 Nov. 2003 | 19 | 1.78 | 0.73 | 59 | | | | |
| 40 | H | 9 Nov. 2003 | 48.1 | 24.8 | 16 | 35.5 | 0.25 | 4.13 | 0.48 | 10.47 |
| 41 | H | 14 Nov. 2003 | 78.8 | 80.3 | 59.6 | 25.8 | na | na | na | |
| 42 | H | 19 Nov. 2003 | 36 | 29.7 | 14.2 | 52.2 | na | na | na | |
| 43 | H | 21 Nov. 2003 | 9.2 | 6.1 | 4.1 | 32.8 | | | | |
| 44 | H | 22 Nov. 2003 | 1 | 0.25 | 0.06 | 76 | | | | |
| 45 | H | 23 Nov. 2003 | 22.2 | 22.4 | 11.4 | 49.1 | na | na | na | |
| 46 | H | 25 Nov. 2003 | 36.6 | 43.4 | 33.9 | 21.9 | | | | |
| 47 | H | 27 Nov. 2003 | 5.52 | 1.27 | 1 | 21.3 | | | | |
| 48 | H | 28 Nov. 2003 | 10.57 | 76.6 | 66.7 | 12.9 | na | na | na | |
| 49 | I | 18 Mar. 2004 | 14.8 | 1.52 | 0.44 | 71.8 | | | | |
| 50 | I | 24 Mar. 2004 | 4.4 | 9.78 | 6.42 | 34.4 | | | | |
| 51 | I | 25 Mar. 2004 | 7 | 44.6 | 39.1 | 12.3 | 0.09 | 2.1 | 0.5 | 4.22 |
| 52 | I | 30 Mar. 2004 | 16.8 | 6.86 | 3 | 56.3 | | | | |
| 53 | J | 12 Apr. 2004 | 13 | 57.2 | 44.8 | 21.7 | 0.17 | 3.83 | 0.39 | 6.28 |
| 54 | J | 16 Apr. 2004 | 14.5 | 10.2 | 7.06 | 30.8 | 0.01 | 3.5 | 0.44 | 5.62 |

Table 2 (concluded).

| Event | Location | Start | Duration (h) | P_G (mm) | P_n (mm) | I_n (% loss) | \bar{E}/\bar{R} | S (mm) | p | P'_G |
|-------|----------|--------------|--------------|------------|------------|----------------|-------------------|----------|------|--------|
| 55 | J | 17 Apr. 2004 | 33.2 | 11.4 | 7.11 | 37.6 | | | | |
| 56 | J | 19 Apr. 2004 | 12.8 | 57.2 | 46.6 | 18.5 | | | | |
| 57 | J | 7 May 2004 | 11 | 12.2 | 7.25 | 40.6 | 0.27 | 2.4 | 0.27 | 3.28 |
| 58 | J | 8 May 2004 | 23.5 | 2.54 | 2.07 | 18.5 | | | | |
| 59 | J | 9 May 2004 | 46.5 | 10.7 | 5.48 | 48.8 | 0.39 | 3.63 | 0.46 | 6.74 |
| Total | | | | 939.2 | 632.2 | 51 | | | | |
| Avg. | | | | | | | 0.24 | 4.74 | 0.35 | 7.42 |

Note: Values of S were calculated with the assumption that the evaporation during canopy wet-up was negligible. \bar{E}/\bar{R} , S and p were estimated using the IS method and are only provided for storms with >10 mm of precipitation. A change in character in the location column indicates when the tipping bucket array had been relocated. na, not applicable.

Fig. 2. The estimates of canopy water storage capacity (S) by the individual storm method for an old-growth Douglas-fir forest (>450 years old) with and without the assumption that evaporation prior to canopy saturation (I_w) was negligible. The large S on 6 October 2003 (11.0 mm) likely results from a long wet-up period (>50 h) (see Discussion).



ration (Link et al. 2004). However, excluding I_w will inflate the estimate of S when rainfall is intermittent during the wet-up period. For example, on 6–13 October 2003 the IS method estimated S to be 11.0 mm, nearly two times greater than any other estimate of S (Fig. 2). This estimate of S was large because the rainfall intensity was intermittent during the wet-up period and the IS method estimated that it took more than 57 h for the canopy to saturate. If there are adequate meteorological measurements available, a more reasonable estimate of I_w could be generated using the Penman–Monteith equation (Link et al. 2004).

Estimates of S , p , and \bar{E}/\bar{R} by the mean method (3.1 mm, 0.41, and 0.21, respectively) were similar to the mean values from the IS method if I_w ($S = 2.9$ mm) was included in the calculation of S . In contrast, the S estimated by the minimum method ($S = 5.0$ mm) was similar to the mean value provided by the IS method when I_w was excluded (4.7 mm) (Table 2).

In general, the IS method underestimated the rainfall required for the branches to reach their maximum mass for

each storm (Table 3). The mass at the time of P'_G was usually less than 75% of the maximum branch mass (Table 3). For example, during a storm on 19 October 2003 the canopy was estimated to saturate after 5.22 mm of rainfall (Table 3). However, after 5.22 mm of rainfall the canopy was not saturated because the epiphyte-laden branches were only at 40%–75% of their maximum mass (Table 3; Fig. 3). Therefore, the value of \bar{E}/\bar{R} was overestimated.

Branch rainfall interception and evaporation

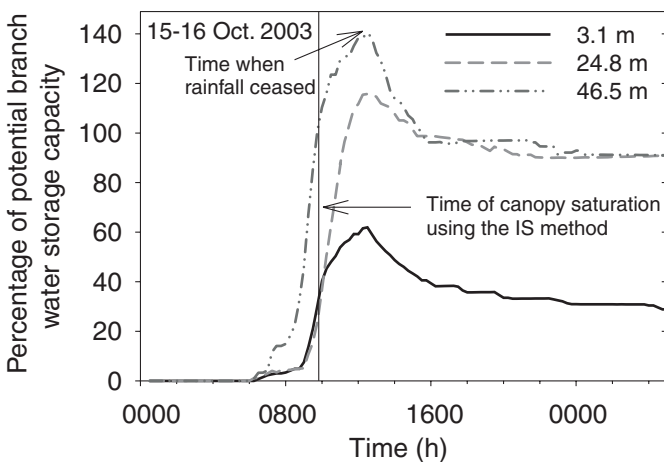
For most storm events under 30 mm the change in branch mass during the storm did not reach m_{be} , the predicted branch water storage capacity. The discrepancy was particularly large for branches placed at 3.1 and 24.8 m (Fig. 4a). Part of the difference may result from the branches being partially saturated prior to the rain event (Fig. 5). The canopy rarely dried between rain events, and this decreased the quantity of water that a branch could accumulate during the next storm. For example, branches at 3.1 and 24.8 m did not return to their prestorm masses 5 days after a 48 mm storm on 10 November 2004 (Fig. 5). To eliminate the portion of storms where there had been a very short period between rainfall events, only storms with more than 3 days of dry weather preceding the storm were analyzed (Fig. 4b). However, even with 3 days of dry weather, m_{be} was a poor predictor of branch water storage for storms less than 30 mm (Fig. 4b). For these small storms the predicted m_{be} was closer to the measured water storage for branches at 46.5 m than for those at 3.1 and 24.8 m. However, for storms greater than 30 mm the branch water storage was closer to m_{be} , and sometimes exceeded the m_{be} . We conclude that the quantity of lichens on a branch can be used to predict the epiphyte water storage only if the canopy is dry prior to the storm and the storm is large enough to saturate the entire canopy.

As the wet season progressed, the maximum branch mass during a storm was generally greater for each subsequent storm (Fig. 5). For example, during the month of November 2003 the branches at 3.1, 24.8, and 46.5 m showed an increase in their mass during storms; following each storm each branch would partially dry. Unless there was a long period of dry weather, the maximum mass of a branch in the following storm exceeded that of the previous storm (Fig. 5). The size of the increase in the maximum branch mass for a storm varied between the branches because each branch had different quantities of lichen, bryophyte, and deadwood biomass.

Table 3. A comparison between the individual storm (IS) estimates of canopy saturation point (P'_G) and the proportions of the maximum mass for each branch at 3.1, 24.5, and 45.6 m at the estimated time of P'_G .

| Event date | IS method P'_G (mm) | Proportion of max. branch mass at P'_G | | | | | |
|--------------|--------------------------|--|--------|--------|--------|--------|--------|
| | | Tree 1 | | | Tree 2 | | |
| | | 3.1 m | 24.8 m | 46.5 m | 3.1 m | 24.8 m | 46.5 m |
| 7 Sept. 2003 | 8.9 | 0.40 | 0.32 | 0.47 | 0.68 | 0.56 | 0.81 |
| 16 July 2003 | 10.5 | 0.53 | 0.47 | 0.63 | 0.58 | 0.56 | 0.45 |
| 15 Oct. 2003 | 11.3 | 0.40 | 0.40 | 0.32 | 0.67 | 0.75 | 0.69 |
| 19 Oct. 2003 | 5.22 | 0.78 | 0.68 | 0.88 | 0.66 | 0.76 | 0.69 |
| 9 Nov. 2003 | 4.22 | 0.77 | 0.67 | 0.81 | 0.78 | 0.78 | 0.64 |
| 14 Nov. 2002 | 10.7 | 0.84 | 0.71 | 0.86 | 0.62 | 0.74 | 0.74 |
| 25 Mar. 2004 | 4.22 | 0.98 | 0.99 | 0.98 | 0.25 | 0.67 | 0.33 |
| 13 Apr. 2004 | 6.28 | 0.57 | 0.60 | 0.80 | 0.54 | 0.55 | 0.27 |
| 16 Apr. 2004 | 5.62 | 0.85 | 0.80 | 0.80 | 0.95 | 0.68 | 0.67 |
| 7 May 2004 | 3.28 | 1.0 | 1.0 | 0.90 | 1.0 | 0.95 | 1.0 |
| 9 May 2004 | 6.74 | 0.69 | 0.78 | 0.75 | 0.79 | 0.80 | 0.51 |

Fig. 3. Variation in branch water storage with time for branches at three heights during a storm on 15–16 October 2003. Also shown is the estimated time of canopy saturation using the individual storm (IS) method. The branches all reach their maximum mass for the storm at the same time because the rainfall ceased before all the branches could fully saturate.



Gash model estimates

When applied to the storms not used to parameterize the model, the Gash model estimated the cumulative I_n to be 294 mm, 53 mm greater than cumulative I_n inferred from the rain gauges (Fig. 6). The model appears more accurate for storms insufficient to saturate the canopy. After the canopy was assumed to reach its P'_G (6.79 mm), most model estimates exceeded the measured I_n . The model was more accurate for the storm events that immediately followed the summer drought. The inaccuracy in modeling the remaining larger storms resulted in the Gash model overestimating the cumulative I_n of the storms by 20%.

Maximum branch water storage and rainfall intensity

The water stored on each saturated epiphyte-laden branch was positively correlated with rainfall intensity. For example, gross precipitation over the storm of 28–29 November 2003 was 76.6 mm (Table 2). All the branches on the strain

gauges reached their maximum mass for the storm after 28 mm of rainfall. After the branches reached their maximum mass the rainfall intensity fluctuated between 1 and 8 mm·h⁻¹ for 10 h, while the air temperature ranged between 2.5 and 7 °C. During this period all the epiphyte-laden branches had a positive relationship between rainfall intensity and branch water storage (Fig. 7).

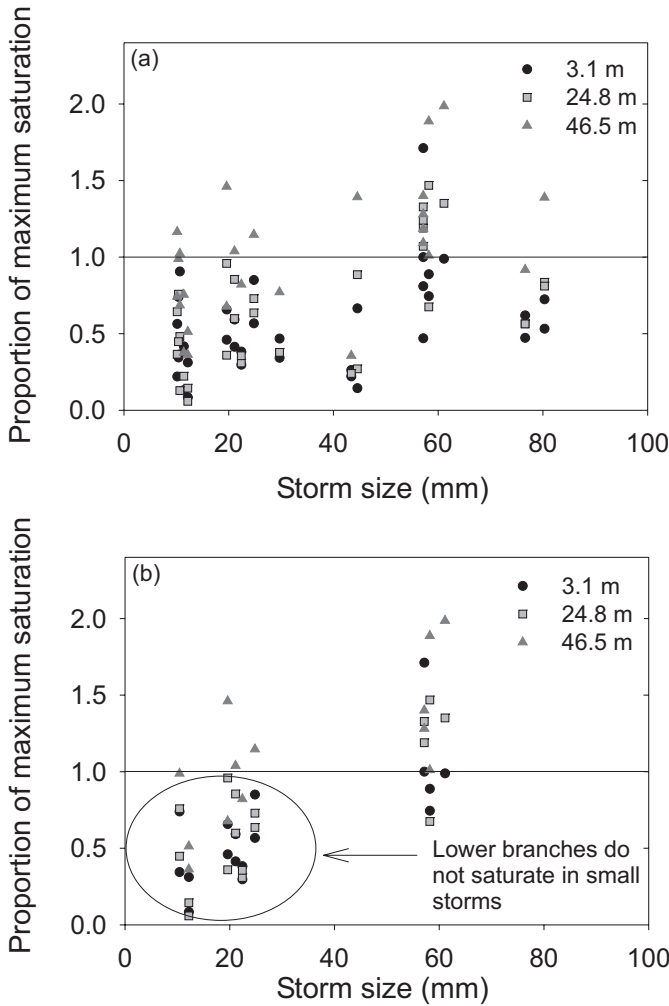
The positive relationship between rainfall intensity and branch mass resulted from increased water storage, not from changes in the force imparted by the impacting raindrops, changes in wind speed, or the storage of water in deadwood. The sensitivity analysis indicates that force imparted by the impinging raindrops on the branch would be small, ranging from 0.1 to 1.95 g·m⁻² for rainfall intensities of 1 to 20 mm·h⁻¹. If the effective raindrop size were twice the diameter estimated by eq. 8, the force on the branch for storms between 1 to 20 mm·h⁻¹ would still only range between 0.1 and 2.54 g·m⁻². This range probably represents the upper limit of the force imparted to the branch, as eq. 9 assumes the stopping distance to be equal to the raindrop diameter and all the branches had projected areas under 0.25 m². In reality, the thalli and leaves of the lichens and bryophytes are flexible and will move upon impact of the raindrops, thereby increasing the stopping distance and decreasing the force (eq. 9). There was no statistical relationship between the branch water storage and wind speed for four of the six branches (p value > 0.17). Two of the branches had a weak positive relationship between wind speed and branch mass ($R^2 < 0.2$). For the purpose of this analysis, changes in storage with wind speed were assumed negligible. Water absorption by the deadwood cannot explain the greater branch mass because the branch masses steadily decreased during the 10 h analysis period. We conclude that increase in branch water storage was therefore related to increasing rainfall intensities.

Discussion

Epiphyte distribution and water storage

Epiphytic lichens and bryophytes are not evenly distributed throughout the forest canopy. Epiphytic lichens in this

Fig. 4. The relationship between the storm size and the maximum branch mass for the storm normalized by the branch's potential water storage (eq. 5). (a) Data for all storm events from 7 September 2003 to 11 May 2004. (b) Data for storms from the same period that had at least 3 days of dry weather prior to the storm event. The branches were suspended at three different heights (3.1, 24.8, and 46.5 m).



forest dominate the upper portions of the canopy (above 35 m), and this is where the evaporative demands are the greatest (Pike et al. 1977; McCune et al. 1997; Pypker et al. 2006). In contrast, bryophytes dominate lower in the canopy (i.e., <35 m), where wetting and drying cycles are constrained by available energy and turbulent transfer (Pypker et al. 2006). The location of the lichens and bryophytes appears to have a significant role in the distribution of water in the forest canopy.

The abundance and distribution of lichens and bryophytes in the canopy is likely to increase the time required for the canopy to dry after a storm and may modify the spatial distribution of stored water. Based on storage capacity and abundance, epiphytic foliose lichens, fruticose lichens, and bryophytes in this forest can store approximately 0.4, 0.07, and 0.8 mm of water, respectively (Pypker et al. 2006). While the forest contained less bryophyte biomass (780 kg·ha⁻¹) relative to that of epiphytic fruticose and foliose lichens combined (31 and 1242 kg·ha⁻¹, respectively), bryo-

Fig. 5. Rainfall amount and change in branch water storage with time in November 20 03. After a storm each event, branches at all measurement heights (3.1, 24.8, and 46.5 m) had protracted drying times. The rainfall intensity was calculated by aggregating net precipitation over 15 min.

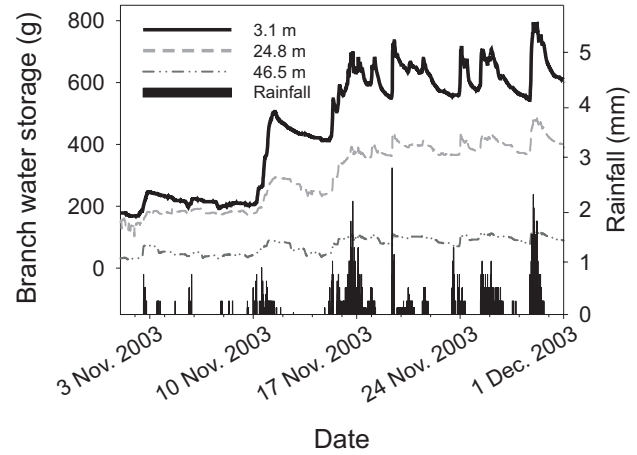
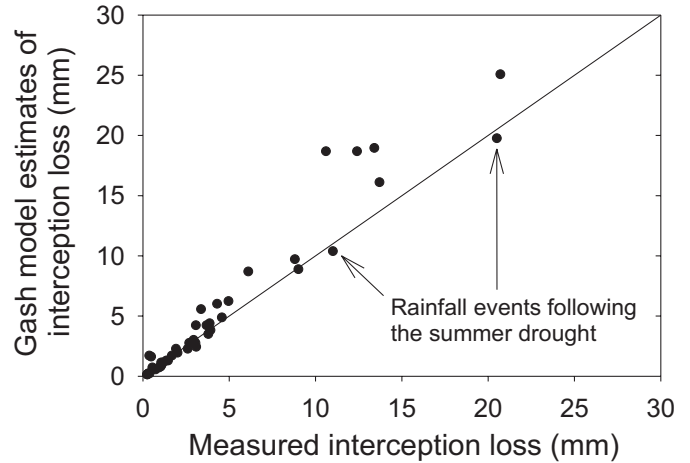
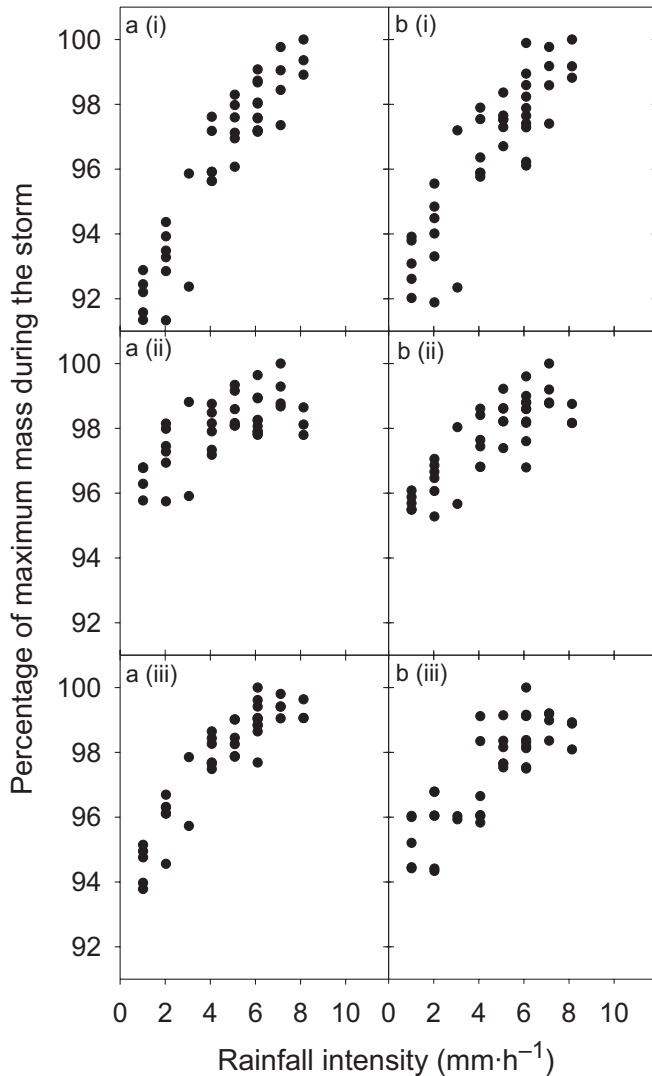


Fig. 6. Gash model estimates of interception loss (I_n) compared to the measured I_n provided by the throughfall collectors.



phytes can store three to four times more water per unit dry mass than foliose and fruticose lichens. If the forest-floor bryophytes are included, the potential water storage associated with bryophytes increases to 1.4 mm for this forest (14 000 kg·ha⁻¹) (Pypker et al. 2006). The high $f_{(x)\max}$ associated with bryophytes, combined with their location, shifts the distribution of stored water lower in the canopy. Furthermore, old Douglas-fir trees produce epicormic branches lower on their boles, and shade-tolerant western hemlock trees emerge from the forest floor in these old-growth ecosystems (Franklin et al. 2002; Ishii and McDowell 2002). The presence of epicormic branches and the shorter western hemlock trees increases the leaf surface area lower in the canopy (Nadkarni and Sumera 2004; Parker et al. 2002). The combination of epicormic branches, shorter western hemlock trees, and bryophytes results in a larger fraction of stored water lower in the canopy, where potential evaporation is decreased due to reduced wind speeds, solar radiation, and vapor pressure deficits (Pypker 2005). Thus, it can be inferred that the forest canopy will remain partially saturated for most of the wet season when there are frequent storms.

Fig. 7. The relationship between rainfall intensity and branch water storage of epiphyte-laden branches (28 November 2003). Branches were monitored on two trees (*a* and *b*) at three different heights (*i*, 3.1 m; *ii*, 24.8 m; *iii*, 46.5 m). All points presented occurred after the branches had reached their maximum mass for the storm. The mass of the epiphyte-laden branch is presented as a percentage of the maximum epiphyte-laden branch mass for the storm. The rainfall intensity was calculated by aggregating net precipitation over 15 min.



Epiphyte and canopy water storage

In contrast to its success in predicting water storage by epiphyte-laden branches exposed to different rainfall intensities under a rainfall simulator (Pypker et al. 2006), eq. 5 was unable to predict the water storage by the branches measured in the field during single storms (Fig. 4a). Reasons for this failure were (1) branches and epiphytes were often partially saturated prior to a storm and (2) many of the rainfall events were smaller than the 30 mm required for the branches to approach m_{be} . If saturated, the epiphyte-laden branches are expected to equal or exceed their m_{be} because this variable estimates the water stored after the branch has stopped dripping (analogous to canopy water storage capacity). If the

branches do not dry prior to the following rain event they will store less water from the following storm. However, even when storms preceded by 3 days or more of dry weather were excluded from the analysis, m_{be} still could not be used to predict the branch water storage (Fig. 4b).

In the field, most of the epiphyte-laden branches did not approach m_{be} unless a storm exceeded 30 mm of rainfall per unit ground area (Fig. 4b). Even under controlled conditions using a rainfall simulator, the mass of epiphyte-laden branches did not stabilize until they intercepted at least 6 mm of rainfall (Pypker et al. 2006). Epiphyte-laden branches require a large amount of rainfall to saturate because water may follow preferential flow paths through the epiphyte mats and the $f_{(x)max}$ of the epiphytes is large (Pypker et al. 2006) (Fig. 3; Table 3). In contrast, branches with few epiphytes that are placed under a rainfall simulator usually saturate after they intercept less than 2 mm of rainfall (Keim et al. 2005). Thus, epiphyte-laden branches will continue to store water throughout most storms (Fig. 5).

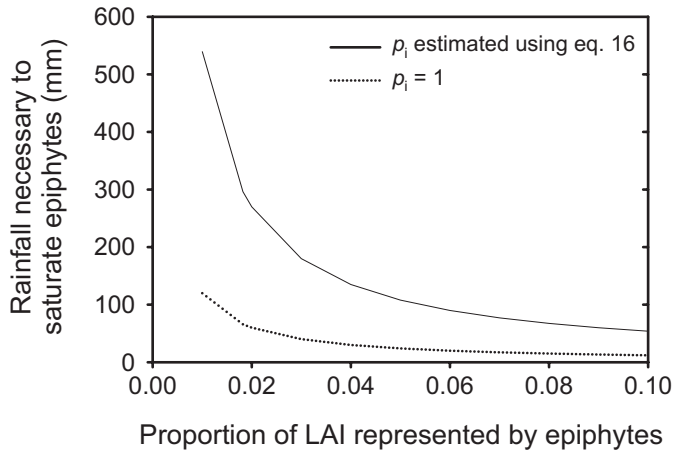
The low interception efficiency of epiphyte-laden branches will result in delayed saturation of the canopy (Pypker et al. 2006). The rainfall required to saturate the epiphytes in the canopy can be estimated using the following equation:

$$[14] \quad p_i = \frac{xy}{y + P_G}$$

where $x = 0.9$ and $y = 5.03$ (Pypker et al. 2006). Based on the biomass of lichens and bryophytes in this canopy and their associated water-holding capacities, the canopy epiphytes can store 1.2 mm of rainfall. Thus, the rainfall necessary to saturate the epiphytes (P_{Gsat}) can be calculated by multiplying both sides of eq. 16 by P_{Gsat} (where $P_{Gsat} - p_i = 1.2$ mm) and then rearranging the equation to solve for P_{Gsat} . Under these assumptions P_{Gsat} is estimated to be 5.4 mm of rainfall. These values are likely to be somewhat imprecise, as coefficients used in eq. 14 were for simulated rainfall at intensities greater than 11 mm·h⁻¹. However, to saturate all the epiphytes in the canopy, P_G must be greater than 5.4 mm because epiphytes represent only a small portion of the surface area in the canopy that intercepts rainfall. This canopy has an LAI = 12 (Moore et al. 2004), and most of that surface area is presumably in leaves. The rainfall required to saturate all the epiphytes can be estimated by assuming the epiphytes represent between 1% and 10% of the intercepting surface area (Fig. 8). Based on this assumption the epiphytes in this canopy will require P_G to be between 54 and 540 mm of rainfall to saturate. Even if the epiphytes have $p_i = 1$, they will still require between 12 and 120 mm of rainfall (Fig. 8). Therefore, while the value of 5.4 mm may be somewhat uncertain, Fig. 8 demonstrates most of epiphyte-laden branches continued to store water throughout a rainfall event.

Because past research indicates that canopies can dry rapidly, forest canopies have often been assumed to dry within a few hours or days after a storm (e.g., Klaassen et al. 1996; Link et al. 2004; Pypker et al. 2005). For example, Hancock and Crowther (1979) monitored the mass of individual branches in a Sitka spruce plantation and found that the branches returned to their prestorm mass less than 12 h after a storm. In contrast, canopies with large populations of epiphytes may not dry rapidly following a storm. For example, Hölischer et al. (2004) found that nonvascular epiphytes in a

Fig. 8. The quantity of gross precipitation (P_G) required to fully saturate all the epiphytes in the canopy for a range of leaf area index (LAI). Two scenarios are presented. The first scenario assumes that the interception efficiency (p_i) can be calculated using eq. 14. The second scenario assumes that all raindrops striking the branch are stored by the branch.



tropical montane forest could store 0.8 mm of rainfall. However, despite being able to store a considerable amount of water, these epiphytes rarely dried during the wet season and thus had a small effect on I_n (Hölscher et al. 2004). Similarly, in the present study, the branches measured in old-growth Douglas-fir forest rarely dried to their prestorm mass because the canopy storage for the forest is large, the rain events were closely spaced, and water may have migrated into the deadwood (Fig. 5).

Dead branches in the old-growth Douglas-fir canopy in this study are capable of storing 192% of their dry mass in water, and this accounts for 1.06 mm of canopy water storage (Pypker et al. 2006). The residence time of water that is stored in dead branches is likely longer than for lichens and bryophytes. Evaporation from the dead branches may be slow because absorption of solar radiation and the loss of latent heat probably decreased by the epiphytes covering the branch and with canopy depth.

Water storage in wood is not limited to the dead branches; it likely occurs in the bark (Herwitz 1985) and perhaps the wood of live branches and boles. Water storage in the bark and wood of live branches and boles may be considerable, since simple allometric equations estimate that this forest contains almost 11 000 kg·ha⁻¹ of bark (Pypker et al. 2006). The storage of water in live and deadwood likely creates two storage pools, a large shorter-term storage pool on the surface of the wood and in or on the epiphytes and a longer-term storage pool in the livewood, deadwood, and bark. Hence, the branches attain greater mass with each storm because the surface only partially dries between storms and the deadwood absorbs increasing amounts of water (Fig. 5). More research is needed to estimate the influence of these storage pools on the total canopy storage and the residence time of water in old-growth Douglas-fir canopies.

Effectiveness of the mean, minimum, and IS methods

In the present study, the mean method provided values of \bar{E}/\bar{R} and p that were similar to those from the IS method

(0.21 and 0.41, respectively), and the estimates of S by the mean (3.1 mm) and the minimum (5.0 mm) methods are near the means of S_w and S_{wo} , respectively. However, the estimates of S provided by these methods are likely too small because they assume that the canopy saturates at all levels simultaneously and is dry prior to the storm.

It may be a reasonable approximation to assume that forest canopies that do not contain epiphytes or other structures that absorb water slowly will saturate simultaneously. However, this assumption is not appropriate for old-growth Douglas-fir forests. For example, when observing individual branches (Fig. 3), it is apparent that the canopy does not reach saturation when the IS method predicts it should. Furthermore, for an old-growth Douglas-fir forest there is no distinct inflection point between P_{cn} and P_{cG} because the old-forest canopy does not simultaneously saturate (Fig. 1). In contrast, rainfall interception by a young Douglas-fir forest canopy comes closer to satisfying the “simultaneous saturation assumption”, as demonstrated by the sharper inflection point between P_{cn} and P_{cG} (Pypker et al. 2005).

The delayed achievement of maximum storage in epiphytes relative to foliage will result in the IS, mean, and minimum methods underestimating total S and overestimating \bar{E}/\bar{R} (IS and mean methods only) in old-growth Douglas-fir forests. Because the canopy will continue to store water after the value of P'_G provided by the IS (Fig. 3) and mean method is reached, the slope of the second regression line (eq. 2) will be too small and \bar{E}/\bar{R} will be overestimated.

The IS, mean, and minimum methods could not provide an accurate estimate of S for the forest because the canopy is partially saturated from October to May. For example, the greatest values of S provided by the IS method occurred when the canopy was extremely dry after the summer drought (Fig. 2). Estimates of S by the IS method prior to a 93 mm storm from 6 to 13 October 2003 were greater than estimates after the storm (Fig. 2). The estimates of S were smaller after the 6–13 October storm because the canopy was unable to dry between the subsequent storm events (Fig. 5). If capacity of the canopy to store water during a single storm event is considered analogous to a “bucket”, the “bucket” remains partially filled for most of the wet season in this forest. Hence, the estimate of S using the IS or mean methods is not a good estimate of S , but at best is a measure of the “functional water storage” of the canopy on a per-storm (IS method) or yearly (minimum and mean method) basis, where functional water storage is defined as the maximum water storage minus the portion of the storage already filled prior to the storm event.

To determine whether epiphytes have an affect on the ability of regression-based techniques to estimate p , S , and \bar{E}/\bar{R} , the Gash model was applied to a subset of the data (see Evaluation of the effect of epiphytes on interception loss using the Gash model section). The Gash model accurately predicted the interception loss for storms smaller than 7 mm, but had greater difficulty when the storms exceeded P'_G (Fig. 6). For the portion of storms larger than P'_G the estimate of I_n relies primarily on the value of \bar{E}/\bar{R} . If the IS method underestimates S and overestimates \bar{E}/\bar{R} because epiphytes saturate later in the storm, it would be expected that this would cause the Gash model to overestimate I_n for

large storms. For most storms greater than 10 mm the model did overestimate I_n . Although, it is possible that this is the result of random error (past research has demonstrated that the Gash model relies on errors in the calculation of I_n cancelling each other out when estimating I_n (Loustau et al. 1992)), the model overestimated I_n by 20% and it is more likely that the \bar{E}/\bar{R} used was too large.

For some storms the effect of overestimating \bar{E}/\bar{R} may be partially offset by underestimating S . These compensating errors would reduce the error in the Gash model. For example, the Gash model was the most accurate for the storms that immediately followed the summer drought (Fig. 6). During these storms the canopy was dry and any overestimation in \bar{E}/\bar{R} may have been compensated for by greater amounts of water being stored in the epiphyte mats.

Canopy water storage capacity is usually considered equivalent to the water that a canopy will store after rainfall has ceased and the canopy stops dripping (Gash 1979; Keim et al. 2005). This depth of water is then considered the quantity of water that is available for evaporation during a storm. Equation 5 calculates this value for the epiphyte-laden branches, but unlike other branches that are only broad-leaved or needle-leaved, all this water may not be readily available for evaporation. Epiphytes form large mats on branches and store water both externally and internally. The storage of water internally, coupled with storage within mats of epiphytes, will increase the resistance to evaporation and will limit the quantity of water available for evaporation. Therefore, the use of eq. 5 to estimate S of epiphytes in the canopy may be inaccurate, as all this water is not available for evaporation during the storm. As a consequence, the estimates of S by the IS and mean methods would be closer to the "true" quantity of water available for evaporation in the canopy, despite the canopy not saturating simultaneously. Therefore, it is plausible that while epiphytes increase the water storage in a canopy, their affect on I_n is reduced because much of the stored water will not be easily evaporated during or after the storm. Further research is needed to define how much of the water stored in epiphyte mats is actually available for evaporation during rainfall events.

Rainfall intensity and branch water storage

Based on previous research, it is generally accepted that the water storage on a branch decreases as the rainfall intensity increases (Calder 1996; Price and Carlyle-Moses 2003). However, this is not the case for epiphyte-laden branches. Calder (1996) hypothesized that the greater drop sizes associated with higher rainfall intensities impart a greater force to the leaf and branch surface, thereby splashing greater quantities of water off the surface. In his experimental work, Calder (1996) demonstrated that leaf water storage decreased when he increased drop size but held rainfall intensity constant. In contrast, Keim et al. (2005) found that the branch water storage for a variety of coniferous and deciduous branches commonly found in the Pacific Northwest was positively correlated with rainfall intensity. He argued that the experiment presented by Calder (1996) failed to account for the increase in rainfall intensity that is associated with greater drop size. Keim et al. (2005) asserted that the magnitude of the storage on a branch depends on the ratio of the rate of

drainage losses from the branch (e.g., splash from raindrops or dripping from the branch) and rate of the addition of water to the branch storage by incoming rainfall. This ratio depends on the structure of the branch and therefore varies between plant species. We postulate that the structure of epiphyte-laden branches favors increased storage with increasing rainfall intensity for the following reasons.

Epiphytic lichens and bryophytes create mats of thalli and leaves providing a rough, three-dimensional structure for the water to impact on and navigate through. A raindrop hitting a bryophyte mat on a branch may not splash water off the branch because the mat structure absorbs the energy from the impacting drop and of the water that is splashed; a significant portion of the water may be recaptured by the rough mat surface. Instead of splashing, the rainwater will infiltrate the mat and drip from the bottom of the branch. Just as with soil, if the rainfall intensity exceeds the infiltration capacity of the lichen or bryophyte mat, the water may pond in the mat air spaces or on the surface of the thalli and leaves. Hence, the branch water storage will increase as the rainfall intensity increases. However, at some point the relationship between rainfall intensity and branch water storage should approach an asymptote, because at high rainfall intensities the rate of water addition to the branch will equal the rate drainage from the branch. Pypker et al. (2006) demonstrated that there was little increase in water storage for epiphyte-laden branches placed under a rainfall simulator at large rainfall intensities of 11, 16, and 39 mm·h⁻¹. At these rainfall intensities the water stored may be maximized because the air spaces and the thalli and leaf surfaces become fully saturated and the continuing rainfall immediately drains from the branch. However, because rainfall intensities are usually below 11 mm·h⁻¹ in the Pacific Northwest (Chow 1964), water storage by saturated epiphyte-laden branches will be positively related to rainfall intensity.

Conclusions

Epiphytic lichens and bryophytes significantly impact the hydrology of old-growth Douglas-fir forests by altering the rainfall interception and storage of the forest canopy. The large maximum water content ($f_{(x)\max}$) of lichens and bryophytes leads to increased potential water storage capacity by an epiphyte-laden branch (m_{be}). Unlike laboratory experiments (Pypker et al. 2006), the water storage by epiphyte-laden branches during a single storm event was not equivalent to its potential water storage capacity because (1) branches required greater than 30 mm of rainfall to saturate and (2) branches were unable to dry between storm events.

Epiphyte-laden branches require a long period of time to saturate during a storm and to dry after a storm. The saturation of the canopy is probably delayed because of preferential flow of water through epiphyte mats and the high $f_{(x)\max}$ of the epiphytic lichens and bryophytes increased the canopy water storage capacity (S). The bryophytes contributed to the canopy remaining partially saturated for much of the wet season because their distribution and large $f_{(x)\max}$ resulted in the storage of water lower in the canopy, where evaporative rates are lower than in upper canopy layers.

In old-growth Douglas-fir forests the long period of time required for epiphyte-laden branches to reach maximum saturation and the inability of the canopy to dry between storm events may result in rainfall interception models (e.g., IS, mean, and minimum methods (Klaassen et al. 1998; Leyton et al. 1967; Link et al. 2004) underestimating S and overestimating mean evaporation rate during storms (\bar{E}/\bar{R}). In contrast to the hypothesis presented by Calder (1996), the relationship between rainfall intensity and branch water storage was positive for epiphyte-laden branches, probably because the rough surface of lichen and bryophyte mats reduced the loss of water by raindrop splash and impeded the drainage of water from the branch. Therefore, epiphytic lichens and bryophytes affect the hydrology of old-growth Douglas-fir forests by increasing S , prolonging the time required for the canopy to both saturate during a storm and dry following a storm, and altering the transfer of water through the canopy to the forest floor. These effects will likely reduce the precision of standard regression-based models for predicting rainfall variables.

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List of symbols

- C Canopy water storage (mm)
- D Droplet diameter (mm)
- D_{50} Median droplet diameter for a given rainfall intensity
- D_e Effective droplet size (mm)
- d_s Droplet stopping distance (m)
- \bar{E}/\bar{R} Ratio of mean evaporation to mean rainfall intensity during saturated canopy conditions (dimensionless)
- F_i Force of rain impinging on a branch ($\text{kg}\cdot\text{m}^{-2}$)
- $f_{(x)\text{max}}$ Maximum internal and external epiphyte water storage ($\text{g water}\cdot(\text{g epiphyte dry mass})^{-1}$)
- g Acceleration due to gravity ($\text{m}\cdot\text{s}^{-2}$)
- I_a Interception loss during canopy drying (mm)
- I_c Interception loss during canopy wetting ($P_G < P'_G$)
- I_n Interception loss (mm)
- I_s Interception loss during saturated canopy conditions (mm)
- I_w Interception loss during canopy wetting (mm)
- LAI Leaf area index (mm)
- m Mass of rainfall impinging on a surface ($\text{kg}\cdot\text{s}^{-1}$)
- m_{be} Potential epiphyte-laden branch water storage capacity (g)
- m_{bs} Potential water storage on the surface of a dead branch (g)
- P_G Gross rainfall (mm)
- P_{cG} Cumulative gross rainfall during a single storm (mm)
- P_n Net throughfall (mm)
- P_{cn} Cumulative net throughfall during a single storm (mm)
- P'_G Gross rainfall required to saturate the canopy (mm)
- P_{Gsat} Rainfall necessary to saturate the epiphytes (mm)
- p Direct throughfall portion (dimensionless)
- p_i Interception efficiency (dimensionless)
- R Rainfall intensity ($\text{mm}\cdot\text{h}^{-1}$)
- S Canopy water storage capacity (mm)
- S_w Canopy water storage capacity when I_w is included in the calculation
- S_{wo} Canopy water storage capacity when I_w is not included in the calculation
- v_T Terminal velocity of a falling raindrop ($\text{m}\cdot\text{s}^{-1}$)
- w_{br} Dry mass of bryophytes
- w_{fo} Dry mass of foliose lichens
- w_{fr} Dry mass of fruticose lichens