

## RESEARCH ARTICLE

# The absorption and evaporation of water vapor by epiphytes in an old-growth Douglas-fir forest during the seasonal summer dry season: Implications for the canopy energy budget

Thomas G. Pypker<sup>1</sup> | Michael H. Unsworth<sup>2</sup> | John T. Van Stan II<sup>3</sup> | Barbara J. Bond<sup>4</sup>

<sup>1</sup>Department of Natural Resource Sciences, Thompson Rivers University, Kamloops, BC, Canada

<sup>2</sup>College of Earth, Ocean, and Atmospheric Sciences, Oregon State University, Corvallis, OR, USA

<sup>3</sup>Department of Geology and Geography, Georgia Southern University, Statesboro, GA, USA

<sup>4</sup>Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR, USA

## Correspondence

Thomas G. Pypker, Department of Natural Resource Sciences, Thompson Rivers University, Kamloops, BC V2C 0C8, Canada. Email: tpypker@tru.ca

## Funding information

Sigma Xi; Oregon State University; US Forest Service Pacific Northwest Research Station; National Science Foundation's Long-Term Ecological Research Program, Grant/Award Number: DEB 1440409

## Abstract

Our goal was to determine how epiphytic lichens and bryophytes affect canopy latent heat fluxes in an old-growth Douglas-fir forest when the canopy was dry. The epiphyte water content ( $WC_e$  expressed as a percent of dry weight) of representative epiphytic foliose lichens, fruticose lichens, and bryophytes was measured in the laboratory after 1 to 12 hr of exposure at five different values of vapor pressure deficit (VPD). After 12 hr of exposure,  $WC_e$  increased fivefold to sixfold as VPD decreased from 1849 to 132 Pa. In addition, we measured  $WC_e$  in the field using strain gauges. These field measurements were used to calibrate the models described below. Two models were created to estimate the potential latent heat flux from epiphytes at the canopy scale ( $LE_e$ ). The first model combined measured total biomass of epiphytes with a model that estimated the laboratory determined VPD-dependent changes in  $WC_e$  of the lichens/bryophytes (VPD method). The second model estimated  $LE_e$  by scaling the change in  $WC_e$  of epiphyte-laden branches that were continuously monitored *in situ* in the canopy by a strain gauge (SG method). Both methods showed a strong diurnal trend in  $LE_e$  when VPD was less than 645 Pa. Prior to sunrise, the epiphytes absorbed water, corresponding to a latent heat flux of 5 to 15  $W/m^2$  per unit ground area, whereas after sunrise, the epiphytes lost water at a rate of  $-10$  to  $-20$   $W/m^2$ . For short periods, epiphytes may contribute a significant portion of the latent heat flux from Douglas-fir forests.

## KEYWORDS

bryophytes, canopy micrometeorology, latent heat flux, lichens, vapor pressure deficit

## 1 | INTRODUCTION

Accurate accounting of the temporal dynamics in evapotranspiration (and its associated energy, or latent heat flux) is necessary for describing and predicting land-atmosphere interactions important to natural and human ecosystem processes. Specifically, patterns of latent heat (LE) exchange drive a host of watershed hydrological processes (Donohue, Roderick, & McVicar, 2007) that must be considered during water resource management planning (e.g., Donohue, Roderick, & McVicar, 2012; Renner, Seppelt, & Bernhofer, 2012). LE dynamics, however, are difficult to estimate in topographically complex vegetated landscapes (McVicar et al., 2007; Mu, Heinsch, Zhao, & Running, 2007), and attributing LE dynamics to specific ecosystem elements (e.g., transpiration, soil evaporation, or uptake/release of moisture from arboreal epiphytes) is even more challenging (Friesen,

Lundquist, & Van Stan, 2015; Wilson, Hanson, Mulholland, Baldocchi, & Wullschleger, 2001). Estimates of the effects of epiphytic lichens, bryophytes, and vascular plants on LE from forests are especially lacking in the current literature (Van Stan II & Pypker, 2015). This is unfortunate as forest epiphytes can store 200% to >1,000% of their dry weight in water (Pypker, Unsworth, & Bond, 2006a), thereby substantially influencing rainfall interception loss processes in tropical cloud forests, boreal forests, and temperate rain forests (Van Stan II & Pypker, 2015). The actual impact of epiphytes on water storage is often less than its potential maximum as antecedent rainfall and meteorological conditions that limit evaporation can reduce the available water storage (Hölscher, Köhler, van Dijk, & Bruijnzeel, 2004; Pypker, Unsworth, & Bond, 2006b). However, impact of the epiphytes community on canopy water storage is often considerable. In addition, the effect of epiphytes on forest canopy hydrology may

not be limited to rainfall events, as it has long been recognized that epiphytes have the ability to absorb water vapor from the atmosphere (e.g., Bertsch, 1966; Blum, 1973; Kolumbe, 1927). In fact, many lichens can increase the amount of water stored in their thalli by eightfold relative to their dry weight when the surrounding atmospheric vapor pressure deficit (VPD) approaches 0 Pa (Blum, 1973; Schlenz, Schroeter, & Green, 2000). Because diurnal microclimatological trends can create varying VPD conditions with strong consistency (e.g., Unsworth et al., 2004), could arboreal epiphytes alter the temporal dynamics of latent heat flux in forests? If so, ignoring epiphyte-related latent heat fluctuations may confound forest energy balances.

Quantifying epiphyte hydration in a field setting is challenging (Van Stan II & Pypker, 2015). Past researchers have used impedance techniques or weighing techniques to quantify epiphyte water content. When using the impedance technique, two alligator clips are clamped at a known distance apart on a lichen thallus or bryophyte leaf. A small voltage is applied, and the change in the electric current, as a result of the resistance of the gap between the two wires, is correlated to changes in water content of the lichen or bryophyte (e.g., Coxson, 1991). Alternatively, past work has weighed samples in the field using a portable scale to quantify water storage by epiphytes, but this has been limited to mostly rainfall interception studies (e.g., Hölscher et al., 2004; Köhler, Tobon, Frumau, & Bruijnzeel, 2007; Martin & Schmitt, 1989). An alternative method is to quantify the changes in epiphyte-laden branch weight using strain gauges. This methodology has been used in the past to quantify rainfall interception by tree branches and epiphytes in the field (Hancock & Crowther, 1979; Pypker et al., 2006b) and in the laboratory (Keim, Skaugset, & Weiler, 2006; Pypker et al., 2006a). The authors are not aware of any past studies that have used strain gauges to quantify atmospheric water uptake during rain-free periods by epiphytic lichens or bryophytes.

The Pacific Northwest (PNW) has a long summer dry season that can be a challenge to the survival of all plant species, including epiphytes. Despite having little or no vascular system, the biomass of epiphytic lichens and bryophytes in old-growth forests of the PNW can exceed 2000 kg/ha (McCune, 1993; Pike, Denison, Tracy, Sherwood, & Rhoades, 1975; Sillett & Rambo, 2000). To thrive under these conditions, lichens and bryophytes must absorb water vapor from the atmosphere (e.g., Bertsch, 1966; Blum, 1973; Kolumbe, 1927). Hence, the absorption of water vapor by the large populations of epiphytic lichens and bryophytes may be a significant component of the energy budget of the forest during the summer dry season. A substantial epiphyte effect on LE is made even more possible by the summer dry season's characteristic diurnal relative humidity (RH) trends, which typically range between 20% and 30% (VPD >2,600 Pa) during the day and above 80% (VPD <400 Pa) at night (Unsworth et al., 2004). This change in RH could result in the water content of many lichens varying between 10% and 80% of their dry weight in a diurnal cycle (Blum, 1973; Schlenz et al., 2000). If epiphytic bryophytes in these forests absorb a similar amount of water vapor, the diurnal absorption/evaporation in an old-growth Douglas-fir forest could exceed 1300 kg/ha (see Appendix A). To put this in perspective, if this water was absorbed/evaporated in 1 to 3 hr in the morning/evening, the latent heat flux associated with the phase

change would be equivalent to 31 to 95 W/m<sup>2</sup>, a significant quantity compared with forest transpiration. To examine these possibilities more rigorously, the goal of this study was to determine the magnitude and temporal variation of the absorption/evaporation of water vapor by epiphytic lichens and bryophytes in old-growth Douglas-fir forests.

## 2 | MATERIALS AND METHODS

### 2.1 | Study site

The study area was in "Watershed 2" of the H.J. Andrews Experimental Forest, located within the western Cascades of central Oregon, USA (44.2°N, 122.2°W). The watershed is dominated by old-growth Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) and western hemlock (*Tsuga heterophylla* [Raf.] Sarg.). The canopies of the dominant and codominant trees were between 40 and 80 m, and the overall canopy had a leaf area index (LAI) of approximately 12.1 (±0.3 SE; Moore, Bond, Jones, Phillips, & Meinzer, 2004) and had large canopy gaps that are typical of old-growth Douglas-fir forests in the Pacific Northwest (Franklin et al., 2002; Gray & Spies, 1996). The region has mild, wet winters and warm, dry summers. The mean air temperatures for this forest (1958 to 2003) are 4.5 and 16°C for the periods of October to April and May to September, respectively (H.J. Andrews LTER long-term data set). The mean annual precipitation for this forest is 2,300 mm, with more than 95% falling between October and May (Rothacher, Dyrness, & Fredriksen, 1967). The soils are described as gravelly clay loam (Swanson & James, 1975).

### 2.2 | Lichen and bryophyte biomass and distribution

Epiphytic lichen biomass was estimated using the relationship between the quantities of epiphytic lichens littered on the forest floor and the biomass of epiphytic lichens in the canopy (McCune, 1994). On September 1, 2003, 27 circular plots (4 m diameter) were established in the study area, and epiphytic lichen fragments found in the plot were collected following the guidelines outlined in McCune (1994). After collection, the lichens were cleaned of debris and were sorted into two functional groups: foliose lichens (plate-like structure) and fruticose lichens (hairy structure). The lichens from each plot were oven dried at 70°C for 72 hr, and the dry weights from all plots were averaged and then multiplied by an empirical factor 100 (McCune, 1994) to estimate the dry weight of epiphytic lichens in the canopy. Epiphytic bryophyte biomass is more difficult to estimate and generally requires the destructive harvest of trees (McCune, 1993). An estimate of epiphytic bryophyte biomass from a previous study that McCune (1993) conducted in a nearby old-growth forest was used (780 kg/ha) because tree harvesting was not permitted in the study area.

Forest floor bryophyte biomass was estimated by randomly selecting 20 plots along a 200-m transect through the study area. At each plot, a 0.12 m<sup>2</sup> quadrat was placed on the forest floor, and all bryophytes inside the plot were removed. The forest floor bryophytes were sorted into four categories: step moss (*Hylocomium splendens* [Hedwig]), electrified cat's tail (*Rhytidiadelphus triquetrus*

[Hedw.] Warnst.), Oregon beaked moss (*Kindbergia oregona* [Sull.] Ochyra), and other bryophytes. The bryophytes were separated from forest floor litter and dried at 70°C for 72 hr to determine dry weight.

The vertical distribution of epiphytes in the canopy was estimated along two vertical transects (47 m). Along each transect, visual estimates of epiphyte surface cover were recorded at 5 m intervals at three randomly selected cardinal directions. The observations were made by a single observer who climbed a fixed rope, and, using a 0.2 × 0.5 m quadrat held horizontally at eye level and arm's length, visually estimated the percent cover of foliose lichens, fruticose lichens, and bryophytes within the two-dimensional view (McCune et al., 1997). This method has been demonstrated to be a satisfactory predictor of the relative abundance of different epiphytes (McCune et al., 1997).

### 2.3 | The use of VPD or RH to predict epiphyte water content ( $WC_e$ )

It is common within the lichen literature to relate the  $WC_e$  of a lichen sample to the RH of the air (e.g., Blum, 1973; Green et al., 2002; Lange, Green, & Ziegler, 1988; Lange, Kilian, & Ziegler, 1986; Matthes-Sears, Nash, & Larson, 1987). While the use of RH to predict  $WC_e$  is appropriate in a closed system under isothermal conditions (Monteith & Unsworth, 1990), the driving force for the vapor flux between the lichen or bryophyte and the atmosphere will ultimately be controlled by the VPD of the environment (Monteith & Campbell, 1980; Rundel, 1988). Within a closed pore space of a lichen thallus, the atmospheric water content of the air must come into equilibrium with the liquid water clinging to the pore surface. If the closed pore space was isothermal, it would be appropriate to use atmospheric RH to predict the equilibrium  $WC_e$  of the lichen. However, when considering the water relations of lichens *in situ* (open system), the exchange of the water between the lichen thallus and the atmosphere will depend on the gradient of water vapor between the pore spaces in the lichen and the surrounding air (Monteith & Campbell, 1980; Rundel, 1988). Therefore, in an open system, it is not appropriate to use RH to predict the exchange of water because RH is dependent on temperature (Monteith & Campbell, 1980; Rundel, 1988). Thus, to properly assess the flux, one must determine the VPD and the resistance to the exchange of water vapor between the lichen and the atmosphere. In most situations, the VPD over an evaporating surface can be assumed to be zero, but this may not be the case with lichens during the summer dry season (Rundel, 1988). The equilibrium vapor pressure within the pore spaces will not be saturated and may have a VPD of up to 30 MPa (Rundel, 1988). Therefore, a model that only uses atmospheric VPD to predict  $WC_e$  will be empirical because the VPD within the lichen pore space is unknown. However, in comparison to using RH, using atmospheric VPD in an evaporation model provides a more mechanistic determination of the exchange of water between a lichen and the atmosphere. Further research into the resistance to evaporation from the pore space is required to accurately predict the exchange of water between a lichen (or bryophyte) and the atmosphere.

### 2.4 | Laboratory measurements

The variation in water contents ( $WC_e$ ) of a foliose lichen ( $WC_{fo}$ ), fruticose lichen ( $WC_{fr}$ ), and bryophyte species ( $WC_{br}$ ) with VPD were measured in the laboratory. In this study,  $WC_e$  was expressed as the quantity of water stored by a thallus/leaf as a percent of its dry weight. The fruticose lichen, witch's hair (*Alectoria sarmentosa* [Ach.] Ach.); foliose lichen, lettuce Lung (*Lobaria oregano* [Tuck.] Mull. Arg.); and the bryophyte, cattail moss (*Isoetecium myosuroides* Brid.) were chosen because they represent 36%, 94%, and 36%, respectively, of epiphytic fruticose lichens, foliose lichens, and bryophytes found in old-growth Douglas-fir forests (McCune, 1994; Pike, Rydell, & Denison, 1977; Sillett, 1995).

To determine the dependence of  $WC_e$  of lettuce lung, witch's hair, and cattail moss on VPD, a dewpoint hygrometer (LI-910, LI-COR, Inc., Lincoln, Nebraska) was used to circulate air of fixed VPD at 200 cm<sup>3</sup>/min through a closed circuit loop that contained a small plastic chamber (volume 3,780 cm<sup>3</sup>). Samples of lettuce lung, witch's hair, and cattail moss were first stored at 0% RH for 48 hr and then placed in the chamber and exposed to a range of VPDs (158, 264, 528, 1057, and 1849 Pa, corresponding to 30%, 60%, 80%, 90%, and 94% RH, respectively) at 22°C for 12 hr ( $n = 10$  for each species at each VPD). The RH and temperature of the chamber were monitored every second (HMP45C, Campbell Scientific, Logan, Utah), and the data were averaged and stored on a data logger at 10-min interval (CR10X, Campbell Scientific). To monitor the incremental rate of water absorption at a given VPD, the lichen/bryophyte samples were weighed at 1, 2, 4, 8, and 12 h intervals (0.1 mg resolution, Explorer Pro, Ohaus, Pine Brook, NJ, USA). The dependence of  $WC_e$  of the thallus/leaf on VPD was modeled for each time interval using the following equation:

$$WC_x = (c \cdot d) / (d + VPD) \quad (1)$$

where  $c$  and  $d$  are fitting parameters.

### 2.5 | Field meteorological measurements

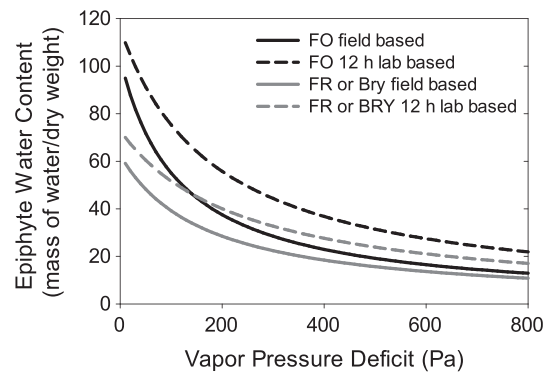
The microclimate of the canopy and the diurnal change in weight of epiphyte-laden branches were monitored at three stations in each of two Douglas-fir trees at 3.1, 24.8 and 46.5 m above the ground from July 22 to October 31, 2003. Each station consisted of a cup anemometer (Ultra-light cup anemometer, Thornwaite, USA), a quantum sensor (LI-190SA quantum sensor, LI-COR, Lincoln, NE, USA), an RH/temperature probe (HMP 45C, Vaisala Inc, Woburn, MA, USA), and a strain gauge (L2336, Futek Advanced Sensor Technology, Irvine, CA, USA). At each station, the instrumentation was attached to a 2 m metal pipe orientated horizontally to the ground. One end of the pipe was fixed to the tree and a chain connected the other end of the pipe to the tree at a 45° angle. A dead, epiphyte-laden branch (>80% epiphyte cover) was cut from the tree and suspended from the strain gauge by two strands of fishing wire, spaced on the branch to maintain its balance. In this way, the branch weight was continuously monitored by the strain gauge. Using a dead branch avoided the problem of the branch mass changing because of needle death and abscission. However, the use of dead wood did introduce some (assumedly negligible) error as the

wood may have absorbed some atmospheric moisture. All data were recorded at 15-s interval and averaged over 15 min using dataloggers (CR10X, Campbell-Scientific Inc.) with attached multiplexers (AM16/32, Campbell Scientific). The stations were installed in June 2003, and the branches were replaced every 2 to 4 months at which time the strain gauges were recalibrated using steel weights. The strain gauge calibrations did not change by more than 1% throughout the measurement period. The sensitivity of each strain gauge to changes in temperature was tested, and corrections were applied to the mass measurements.

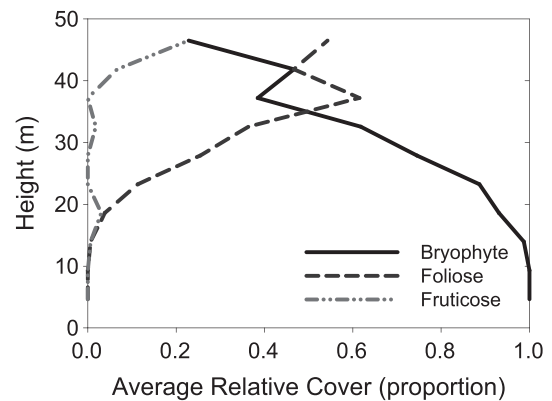
To determine whether the dependence of  $WC_e$  on VPD from laboratory measurements of lichen/bryophytes agreed with field measurements, three more Douglas-fir trees were rigged for climbing, and a pulley was fixed to each tree at 3.1, 24.8, and 46.5 m. On eight different days, individual samples of lettuce lung ( $n = 34$ ), witch's hair ( $n = 25$ ), and cattail moss ( $n = 37$ ) were weighed and then suspended at the three different heights starting between 1500 and 1600 hr. The lichen and bryophyte samples were allowed to equilibrate with the atmosphere for 14 to 15 h. Between 0500 hr and 0600 hr the following morning, the lichen and bryophytes samples were lowered to the ground and weighed. The samples were then dried for 72 hr at 70°C to attain dry weight. The measured  $WC_e$  of the epiphytes in the field were compared with estimates from the laboratory data by substituting the mean VPD measured on the two Douglas-fir trees at 0600 hr into Equation 1.

## 2.6 | Calculation of the latent heat flux ( $LE_e$ ) associated with lichen and bryophyte mass exchange

Two methods were used to estimate the  $LE_e$  associated with changes in water content of lichens and bryophytes in the old-growth Douglas-fir canopy over four 4-day ensemble period (day of year [DOY]: 206–209, 225–228, 244–247, and 274–277). These ensemble periods were chosen because (i) there were no precipitation events measured at the nearby weather station (<1 km away) or beneath the canopy (Pypker et al., 2006b), (ii) VPDs at all heights in the canopy were greater than 0 for at least 1 week prior to the ensemble period, and (iii) they represented periods with contrasting temperatures and VPDs. The first technique estimated the  $WC_e$  of the lichens and bryophytes by substituting the VPD measured at 15-min interval on the two trees at 3.1, 24.8, and 46.5 m into Equation 1 (VPD method [ $LE_{e-VPD}$ ]). Because the laboratory and field measurements of water absorption did not match, we applied the fitting parameters from the field measurements (Table 2 and Figure 1; see Discussion section, 4.2). This method assumed that (i) the responses of the  $WC_e$  of lettuce lung, witch's hair, and cattail moss to changes in VPD were representative of all foliose lichens, fruticose lichens, and bryophytes in the canopy; (ii) there was sufficient time during each 15-min interval for the lichens and bryophytes to come into mass equilibrium with their environment; (iii) the boundary layer conductance was constant; (iv) because the foliose lichens predominately occupied the mid to upper portion of the canopy (Figure 2), the change in the water content of two thirds and one third of foliose lichens for each 15-min interval ( $\Delta WC_{fo}$ ; kg) could be estimated using the VPD measured at the 24.8 and 46.5 m meteorological stations, respectively; (v) because the fruticose lichens



**FIGURE 1** The association between lichen and bryophyte water content ( $WC_e$ ) and vapor pressure deficit (VPD) for measurements made in the field and laboratory for foliose (FO) lichens, fruticose (FR) lichens, and bryophytes (BRY). The field measurements were made in the early morning after exposing the lichens and bryophytes to atmospheric conditions for 14 to 15 hr. In the laboratory, the  $WC_e$  of lichens and bryophytes was estimated after being exposed for 12 hr to a range of VPD (1849 Pa). The field samples absorbed less moisture than under laboratory conditions. The equation for the different lines are found in Table 2



**FIGURE 2** The vertical variation of biomass distribution of the epiphytic lichens and bryophytes during the summer months for an old-growth Douglas-fir forest in the Central Cascades of Oregon

predominantly occupied the top of the canopy (Figure 2), the change in the water content of the fruticose lichens for each 15-min interval ( $\Delta WC_{fr}$ ; kg) could be estimated using the VPD measured at the 46.5 m meteorological station; and (vi) because the bryophytes occupied the bottom portion of the canopy (Figure 2), the change in the water content of half of the bryophytes for each 15-min interval ( $\Delta WC_{br}$ ; kg) could be estimated by each of the VPD measurements at the 3.1 and 24.8 m meteorological stations. The  $WC_e$  of the different functional groups was estimated by Equation 1 and multiplied by the biomass of the foliose lichen, fruticose lichen, and bryophytes in the canopy.

$$LE_{e-VPD} = \frac{(\Delta WC_{fo} \cdot B_{fo} + \Delta WC_{fr} \cdot B_{fr} + \Delta WC_{br} \cdot B_{br}) \cdot \lambda}{s} \quad (2)$$

where  $\lambda$  is latent heat flux of vaporization (J/kg);  $s$  is time duration (15 min = 900 s); and  $B_{fo}$ ,  $B_{fr}$ , and  $B_{br}$  represent the biomass of the foliose lichens, fruticose lichens, and bryophytes, respectively ( $kg/m^2$ ), in the canopy.

The second method (SG method [ $LE_{e-SG}$ ]) used the weight change of the branches on the strain gauges to estimate  $LE_e$ . The dry weight of foliose lichens, fruticose lichens, and bryophytes on each branch was measured (Pypker et al., 2006b). For each 15-min interval, the change in weight of each branch ( $\Delta W_b$ ) was subdivided into the change in weight for each functional group (foliose lichen, fruticose lichen, and bryophyte) by assuming that the change in  $WC_e$  is represented by Equation 1 and then distributed as follows:

$$M_{fo} = \frac{\Delta W_b}{WC_{fr}/WC_{fo} \cdot (B_{fr} + B_{br}) + B_{fo}} \quad (3)$$

where  $M_{fo}$  is weight change of water per gram of foliose lichen (kg/kg);  $B_{fr}$  is the biomass of fruticose lichens on the branch (kg);  $B_{br}$  is the biomass of bryophytes on the branch (kg);  $B_{fo}$  is the biomass of foliose lichens on the branch (kg); and  $WC_{fr}$  and  $WC_{fo}$  were estimated using Equation 1. Equation 3 groups the biomass of fruticose lichens and bryophytes together by assuming that the relationships between their  $WC_e$  and VPD are the same (see Results section, 3.2).

For each tree, the  $LE_{e-SG}$  was estimated by assuming that a proportion of the weight change of the foliose lichens, fruticose lichens, and bryophytes in the canopy ( $a_{fo}$ ,  $a_{fr}$ , and  $a_{br}$ , respectively) was represented by the weight change of each branch. It was assumed that  $a_{fo}$ ,  $a_{fr}$ , and  $a_{br}$  were, respectively, 0, 0, and 0.5 for the branch at 3.1 m; 0.33, 0, and 0.5 for the branch at 24.8 m; and 0.67, 1, and 0 for the branch at 46.5 m.  $LE_{e-SG}$  was estimated by summing the latent heat flux for each branch:

$$LE_{e-SG} = \sum_i^n \left( M_{fo}(a_{fo} \cdot B_{fo}) + M_{fo} \cdot \frac{WC_{fr}}{WC_{fo}} (a_{fr} \cdot B_{fr} + a_{br} \cdot B_{br}) \right) \cdot \frac{\lambda}{s} \quad (4)$$

where  $n$  represents the number of branches monitored on the tree ( $n = 3$ ) and  $B_x$  represents biomass of species "x." The estimates of  $LE_{e-SG}$  produced for each tree were averaged to provide an estimate for the whole canopy.

### 3 | RESULTS

#### 3.1 | Lichen and bryophyte biomass and distribution

Lichens and bryophytes occupied specific niches within the forest canopy. The bryophytes dominated below 30 m; the surface area of foliose and fruticose lichens increased above 30 m (Figure 2). The forest canopy contained 1,273 and 780 kg/ha of epiphytic lichens and bryophytes, respectively (Table 1). The lichens in this forest are primarily epiphytic, with the foliose lichens comprising >97% of the biomass (Table 1). The estimate of lichen biomass maybe even higher as litter on the forest floor may rapidly decompose or could be eaten. The forest floor contained an additional 465 kg/ha of bryophytes, of which >95% of the biomass was composed of step moss, electrified cat's tail, and Oregon beaked moss (Table 1). The combined total for the forest floor and epiphyte bryophyte biomass nearly equaled the estimates for the epiphytic lichen biomass (Table 1).

**TABLE 1** The biomass of epiphytic and forest floor lichens and bryophytes in an old-growth Douglas-fir forest in the Pacific Northwest

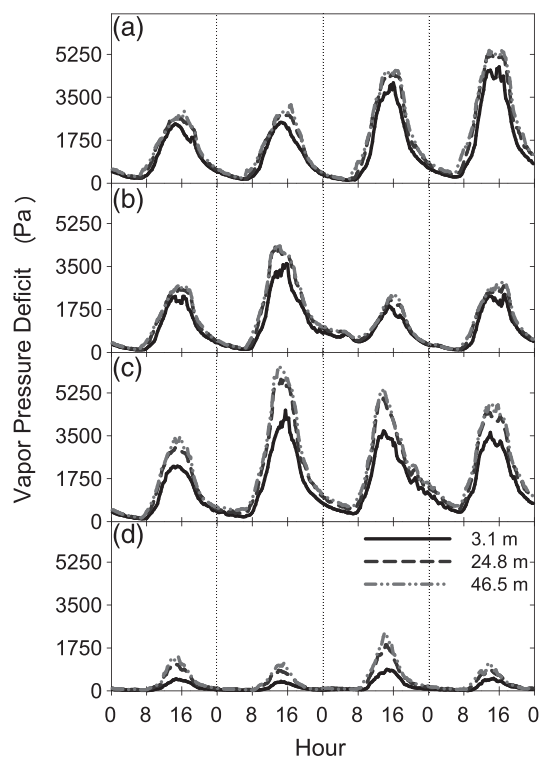
Group	Biomass (kg/ha)
Epiphytes	
Foliose lichens	1242 ± 452
Fruticose lichens	31.0 ± 22.0
Bryophytes	780 <sup>a</sup>
Forest floor bryophytes	
Oregon beaked moss	345 ± 177
Elect. Cat's Tail	68.0 ± 68.8
Step Moss	26.2 ± 27.9
Other moss	25.6 ± 53.5
Total	2518 ± 494

<sup>a</sup>From McCune (1993).

#### 3.2 | VPD and lichen/bryophyte $WC_e$

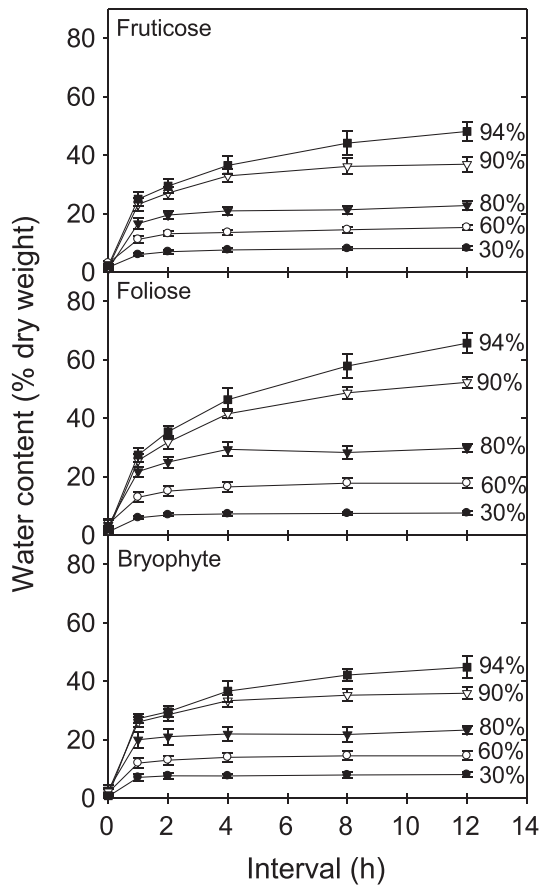
During the summer months, the VPD in the canopy diurnally ranged between 150 and 4000 Pa (RH ≈ 20% to 90%), with the VPD approaching 100 Pa (RH >95%) on some nights (Figure 3). For the four measurement periods, the VPD was generally lowest between 0600 and 0800 hr and peaked between 1300 and 1600 hr.

Under laboratory conditions, lichens and bryophytes experienced increases in  $WC_e$  as the VPD decreased (Figure 4). The water content of the lichens/bryophytes equilibrated within 2 hr at high VPD, but at low VPD, the lichens and bryophytes continued to absorb water after



**FIGURE 3** The vapor pressure deficit (VPD) at three heights (3.1, 24.8, and 46.5 m) during four ensemble periods during the summer/fall of 2003 (day of year: a = 206–209, b = 223–226, c = 244–247, and d = 274–277)

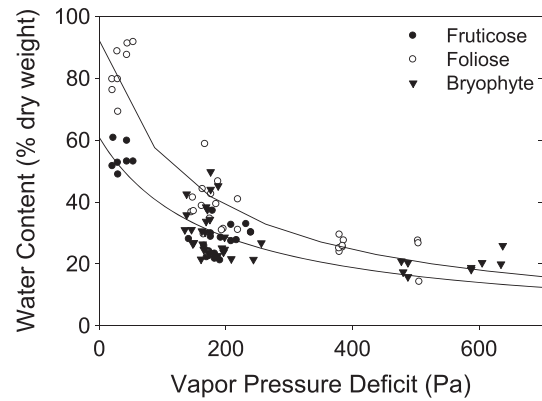




**FIGURE 4** The variation in water content ( $WC_e$ ) with exposure time for a fruticose lichen (witch's hair), foliose lichen (lettuce lung), and bryophyte (cattail moss) during exposure to six different relative humidity (RH) at 22°C. At 30, 60, 80, 90, and 94% RH and 22°C, the vapor pressure deficit is equivalent to 1849, 1057, 528, 264, and 158 Pa, respectively

12 hr (Figure 4). For many of the measurement intervals, the  $WC_e$  of witch's hair and cattail moss were statistically significantly different ( $p$ -values  $<.05$ ), but the difference between their mean  $WC_e$  at any given elapsed time/VPD combination was never greater than 3% (Figure 4). Thus, if equal masses of witch's hair and the cattail moss are exposed to the same VPD, it is reasonable to assume that they will absorb similar quantities of atmospheric water vapor. At a VPD above 1057 Pa (60% RH at 22°C), lettuce lung lichen had a similar  $WC_e$  to the witch's hair and cattail moss, but below a VPD of 1056 Pa, lettuce lung absorbed water more quickly and attained a greater  $WC_e$  than the other epiphytes. The rate of water uptake by lettuce lung lichen was generally more rapid than witch's hair or the cattail moss for time intervals less than 4 hr when the VPD was less than 1056 Pa (RH = 60%; Figure 4). The only exception was for first hour at 264 Pa (90% RH) where the water absorption by cattail moss was slightly more rapid than lettuce lung lichen ( $0.5 \text{ g}_{\text{water}} \text{ g}_{\text{dry weight}}/\text{h}$ ). Thus, the water absorption by lettuce lung was treated separately from the witch's hair and cattail moss (Figure 5).

The relationship between VPD and the  $WC_e$  of lichens and bryophytes from laboratory measurements was not a good predictor of  $WC_e$  in field tests (Table 2). Therefore, to predict the  $WC_e$  of the lichens and bryophytes in the field, a relationship between VPD and



**FIGURE 5** Variation of lichen water content with the morning vapor pressure deficit for a fruticose lichen (witch's hair), foliose lichen (lettuce lung), and bryophyte (cattail moss) after exposure to atmospheric vapor pressure deficit overnight in the field. The water content ( $WC_e$ ) of the lichens and bryophytes can be described by  $WC_e = (c \cdot d)/(d + x)$  (Table 2). A single exponential function was used to describe the  $WC_e$  of the fruticose lichen and bryophyte because their  $WC$  never differed by more than 3.4% in the laboratory

**TABLE 2** The association between lichen and bryophyte water content ( $WC_e$ ) and vapor pressure deficit (VPD) for measurements made in the field and laboratory

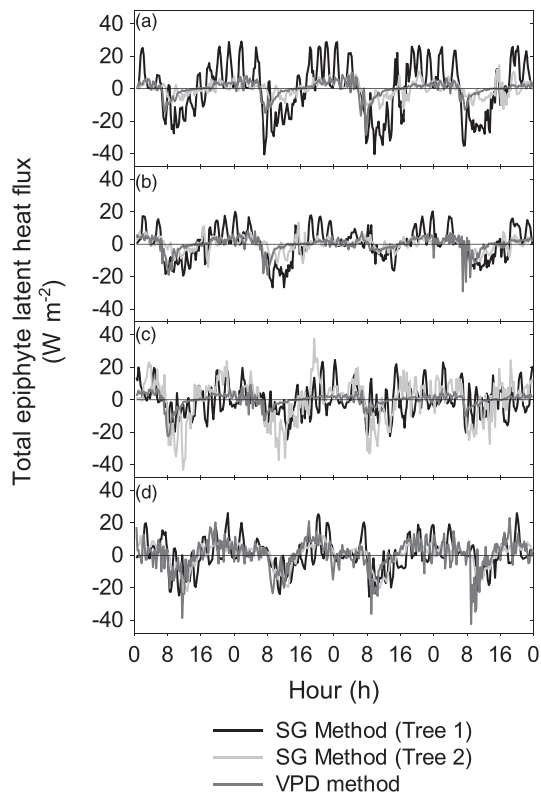
Measurement	Foliose lichens			Fruticose lichens and bryophytes		
	$c$	$d$	$R^2$	$c$	$d$	$R^2$
Field	103.3	114.1	0.84	62.67	166.7	0.63
1 hr	36.3	539.3	0.92	35.3	483.5	0.94
2 hr	48.3	442.9	0.94	40.1	469.4	0.94
4 hr	68.0	338.9	0.95	52.9	350.2	0.95
8 hr	94.9	228.6	0.97	66.5	264.4	0.97
12 hr	115.8	186.0	0.98	72.9	243.4	0.98

Note. The field measurements were made in the early morning after exposing the lichens and bryophytes to atmospheric conditions for 14 to 15 hr. In the laboratory, the  $WC_e$  of lichens and bryophytes were estimated after being exposed for 1, 2, 4, 8, and 12 hr to a range of VPD (158 to 1,849 Pa). The relationship between VPD and  $WC_e$  was described using  $WC_e = (c \cdot d)/(d + x)$ , where  $x$  is the VPD. The fruticose lichens and the bryophytes were grouped together because the difference in their  $WC_e$  at varying VPD was not statistically significant.

$WC_e$  was established using the field measurements (Figure 5). A single equation was used to estimate the  $WC_e$  of witch's hair and cattail moss as a function of VPD (Equation 1) because their  $WC_e$  values were always similar (Figure 5). The average differences between the estimates from Equation 1 and the measured morning  $WC_e$  of the individual samples of lettuce lung, witch's hair, and cattail moss were 7.3, 4.9, and 5.8%, respectively.

### 3.3 | Latent heat fluxes from epiphytic lichens and bryophytes

The VPD and SG methods for estimating epiphyte latent heat fluxes both estimated  $LE_e$  to range from  $-40$  to  $25 \text{ W/m}^2$  during the four ensemble periods (Figure 6). In the early morning hours when the VPD was low,  $LE_e$  was typically below  $10 \text{ W/m}^2$ , with periodic spikes above  $20 \text{ W/m}^2$  (Figure 6). The models suggest that lichens and



**FIGURE 6** The latent heat flux between epiphytic lichen and bryophytes ( $LE_e$ ) and the atmosphere in an old-growth Douglas-fir forest in the Oregon Cascades. The latent heat flux was estimated using the vapor pressure deficit (VPD) method and the strain gauge (SG) method during four ensemble periods during the summer/fall of 2003 (day of year: a = 206–209, b = 225–228, c = 244–247, and d = 274–277; see Methods section). Positive values represent latent heat gain (water uptake) and negative values represent latent heat loss (water loss) from the epiphytic lichens and bryophytes. The SG method was scaled to the canopy for each of the trees monitored (Trees 1 and 2)

bryophytes rapidly lost water in the morning after the VPD increased (0700 to 1200 hr), with the greatest losses occurring in the first few hours. The diurnal cycle of water absorption/evaporation was most pronounced when the VPD dropped below 200 Pa at night. For example, from DOY 274–277, the VPD frequently approached 0 Pa (100% RH) at night, and the diurnal variation in  $LE_e$  was well-defined. In contrast, during the last two days of the third ensemble period (DOY 244–247), the VPD did not drop below 320 Pa (or 80% RH) at any of the measurement heights (Figure 3), and  $LE_e$  was subsequently less periodic (Figure 6). The SG method provided a similar pattern, regardless of which tree was used to scale-up the measurements. However, estimated fluxes from Tree 1 were more variable, frequently reaching both greater positive and negative values (Figure 6).

## 4 | DISCUSSION

### 4.1 | Epiphyte biomass and distribution

In forests with abundant populations of epiphytes, it is common for lichens and bryophytes to be distributed in distinct horizontal layers

within the forest canopy (e.g., Campbell & Coxson, 2001; Ellyson & Sillett, 2003; McCune et al., 1997; Pike et al., 1975; Sillett & Rambo, 2000). As with other reports on epiphyte distribution in old-growth Douglas-fir forests (Clement & Shaw, 1999; Lyons, Nadkarni, & North, 2000; McCune et al., 1997; Pike et al., 1975; Pike et al., 1977; Sillett & Rambo, 2000), the epiphytic lichens in this study occupied the top of the forest canopy and epiphytic bryophytes the bottom portion (Figure 2). The biomass distributions of epiphytic lichens in the old-growth Douglas-fir forest in this study (Figure 1; Table 1) were similar to the distributions reported by McCune (1993) for a nearby 400-year-old forest. McCune (1993) estimated that the nearby forest contained 1,870 kg/ha of lichen biomass with the foliose lichens dominating (1,690 kg/ha).

### 4.2 | Atmospheric water vapor absorption

The time trends of increasing  $WC_e$  and the saturation values attained in this study (Figures 4 and 5) compare well with recent work seeking to model the  $WC_e$  dynamics of nonvascular epiphytes (Čabrajčić, Lidén, Lundmark, Ottosson-Löfvenius, & Palmqvist, 2010; Jonsson, Moen, & Palmqvist, 2008; Lakatos, 2011; Nardini, Marchetto, & Tretiach, 2013). The initial rapid uptake of water vapor is consistent with several studies examining lichen water relations after desiccation (Gauslaa, 2014). Continuous, slow uptake of water vapor under low VPD conditions (Figure 4) has been reported for green algal lichens and discussed as a contributing mechanism to these lichens' ability to survive under low liquid moisture availabilities (Čabrajčić et al., 2010; Gauslaa, 2014). A review of water exchange mechanisms in nonvascular epiphytes indicates that moisture held in external capillary spaces can contribute most significantly to the humidity responses of  $WC_e$  in foliose lichen, fruticose lichen, and bryophytes (Lakatos, 2011). Of course, under fully saturated conditions (i.e., after long periods of exposure to low VPD such as the night and early mornings in Figure 3), movement of external liquid water through capillaries can transport significant amounts of water to internal sinks (Lakatos, 2011). For example, several *Peltigera* lichen species at saturation  $WC_e$  were observed to hold large amounts of water as symplast (or osmotic) water (Nardini et al., 2013). These events of water uptake at night may activate lichen photosynthesis the following day (Lange, Schulze, & Koch, 1970).

Our field measurements demonstrate that lichens and bryophytes in the forest attained a lower  $WC_e$  relative to those placed under similar VPD in controlled laboratory conditions (Figures 4 and 5). It is not surprising that the field measurements did not replicate the laboratory measurements because water vapor absorption is not immediate and is a function of variables other than just VPD. In the laboratory, the lichens and bryophytes did not rapidly reach equilibrium at lower VPD (RH >90%); instead, they continued to accumulate water after 12 hr of continuous exposure (Figure 4). This is not unusual, as past research indicates that some lichens can continue to increase their  $WC_e$  for more than 22 days during exposure to high RH (low VPD; Blum, 1973). Thus, the time during which lichens are exposed to low nighttime VPD may not be sufficient to reach their potential  $WC_e$ . Furthermore, in the field, the wind speed and turbulence will be different than under laboratory conditions. Changing wind speeds will affect the boundary layer resistance of the lichens and bryophytes, thereby

increasing or decreasing the rate at which  $WC_e$  adjusts to the humidity of the surrounding air. Hence, the field relationship between VPD and lichen/bryophyte water content was used in the VPD model as it more likely represented actual lichen and bryophyte water content (Table 2). However, it is also possible that sample locations experienced greater radiative cooling than average, which would result in lower VPD values than those measured at the three heights in the canopy. Thus, spatial variability in microclimate makes it possible for some locations to have had greater water uptake than others.

### 4.3 | Comparison of the VPD and SG models

The two models were not always in agreement during the ensemble periods. The estimates of  $LE_e$  by the SG method likely differed, in part, from the VPD method because the VPD method provided an average for the whole canopy, whereas the SG method scaled the weight change of three branches on each of the two trees to estimate whole canopy exchange. The rate of absorption/evaporation of water by lichens/bryophytes will depend on their boundary layer resistance to latent heat transfer ( $r_{e-LE}$ ) and the surface temperature of the epiphyte. The magnitude of  $r_{e-LE}$  is a function of wind speed and the morphology of the epiphyte (Kershaw, 1985; Monteith & Unsworth, 1990). The irradiance and wind speed are highly variable throughout the canopy. Because the SG method depends on only six-point samples on two trees, it is likely that its estimates of  $LE_e$  are influenced by systematic biases. The systematic bias arises because the three branches on each tree are assumed to represent the entire canopy. If boundary layer resistances at these locations are consistently lower or higher than the appropriate canopy value because of microclimate variability, a systematic bias will result. For example, the latent heat flux from Tree 1 was consistently greater than from Tree 2 (Figure 6). When averaged, this bias would be reduced, but the sample size is still small. In addition, the methods assumed there was sufficient time during each 15-min interval for the lichens and bryophytes to come into mass equilibrium with their environment. The laboratory results demonstrate that the epiphytes require long periods (>12 hr) to equilibrate to their environment (Figure 3). The VPD method tends to increase or decrease the epiphyte biomass more quickly than the SG method (Figure 5). The discrepancy may result from parameters for the SG method being quantified using smaller time steps (15 min) relative to the VPD method (>12 hr). Hence, the magnitude of the estimates by the  $LE_{e-VPD}$  and the  $LE_{e-SG}$  differed throughout the day.

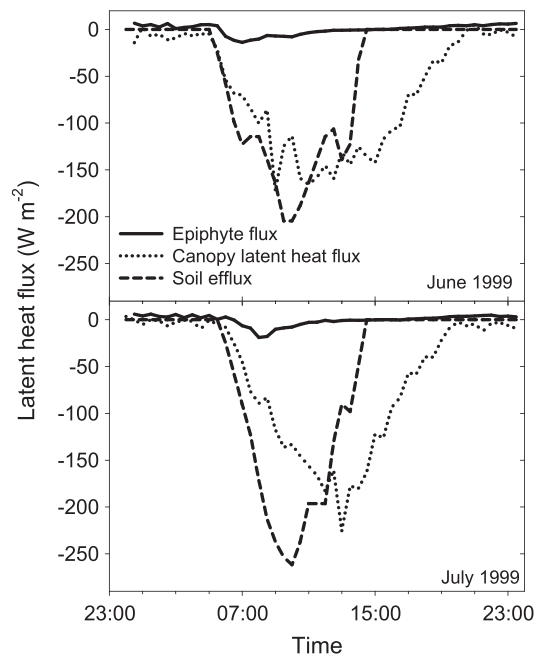
Despite not always being in agreement, the SG and VPD methods did have similar predictions of the magnitude and timing of water absorption and evaporation by the epiphytes. For all the ensemble periods, the two methods track each other fairly well (Figure 6). Both methods show that the diurnal cycle of absorption and evaporation is most distinguishable when the VPD drops below 200 Pa at night. This is not surprising, because the relationship between the  $WC_e$  of the lichens/bryophytes rapidly changes between 0 and 200 Pa (Figure 5). Thus, during nighttime periods that have low VPD, the epiphytes will absorb/evaporate greater quantities of water, and the diurnal variation in  $LE_e$  will increase.

### 4.4 | The effect of lichens and bryophytes on forest canopy latent heat fluxes

Absorption/evaporation of atmospheric water by lichens and bryophytes had its greatest effect on the energy budget of the forest in the early morning. Prior to sunrise, the VPD of air in the canopy generally reached its minimum (Figure 3), and the lichens/bryophytes continued to absorb water. When the VPD increased, the lichens and bryophytes rapidly lost moisture to the atmosphere (Figure 6). The latent heat flux (per unit ground area) associated with absorption of moisture by lichens and bryophytes prior to sunrise ranged between 1 and 20 W/m<sup>2</sup> but was usually between 5 and 15 W/m<sup>2</sup>. When the VPD increased in the morning, the lichens/bryophytes rapidly lost their absorbed water in 1 to 4 hr (Figure 6). Thus,  $LE_e$  can be a significant component of the forest energy budget over periods when the net available energy is still small.

To test the relative importance of  $LE_e$  during the summer dry season in an old-growth Douglas-fir forest, we applied the VPD model to an old-growth forest (Wind River Canopy Crane, south central Washington, USA) where an eddy covariance system was in place that quantified LE exchange above the forest canopy ( $LE_{ec}$ ). We applied the model using average diurnal VPD measurements from the Wind River tower, and we assumed that the epiphyte community was identical to H J Andrews because the age of the forests is similar, and both have well-developed epiphyte communities. While caution should be taken when evaluating the exact value of  $LE_e$ , the presence of an eddy covariance system allows for a direct comparison of  $LE_e$  estimates and  $LE_{ec}$ . Data from June and July 1999 was selected because Unsworth et al. (2004) reported on a discrepancy between soil moisture loss and canopy latent heat fluxes for this forest during that time. The researchers compared the moisture loss from the soil, using an array of soil moisture probes, with the  $LE_{ec}$  measured with an eddy covariance system. During the early morning hours, the soil moisture loss exceeded the above canopy latent heat flux by 0.04 to 0.12 mm/h (approximately 27 to 82 W/m<sup>2</sup>), suggesting sinks in the canopy were absorbing water.  $LE_e$  represented 5% to 21% of  $LE_{ec}$  for part of the morning (Figure 7) and 1% to 8% of net radiation. However, the exchange of water by lichens/bryophytes cannot explain the large 27 to 82 W/m<sup>2</sup> discrepancy reported by Unsworth et al. (2004; Figure 7). To explain the discrepancy, the lichens/bryophytes would need to absorb atmospheric water between 0600 and 1200 hr. Figure 7 shows that when the VPD method was applied to the same data set presented in Unsworth et al. (2004), the estimated  $LE_e$  at the time of the discrepancy (0600 to 1200 hr) was negative, indicating that the epiphytes would be losing water to the atmosphere. Prior to 0600 hr, the  $LE_e$  was positive (gaining water), but at that time, there was no discrepancy between the soil efflux and  $LE_{ec}$ . Therefore,  $LE_e$  represents a significant portion of the  $LE_{ec}$  for short periods, but the discrepancy between the soil efflux and the eddy covariance system likely resulted from the deposition of water on thermally massive objects (e.g., tree stems for which surface temperature lagged behind the increasing air temperature), an increase in atmospheric water vapor content from advection, instrument error, and/or inappropriate assumptions (Unsworth et al., 2004).





**FIGURE 7** The latent heat flux from the lichens and bryophytes modeled using the vapor pressure deficit method compared with the measured soil efflux using soil moisture probes and the canopy latent heat flux measured by eddy covariance for an old-growth forest in South Central Washington in June and July 1999. Positive values represent latent heat gain by the canopy (water uptake) and negative values represent latent heat loss by the canopy (water loss). The values for the soil efflux and eddy covariance were modified from the average daily values for June and July as presented by Unsworth et al. (2004)

The effect of lichens and bryophytes on LE has been reported for other forests (Betts, Ball, & McCaughey, 2001; Betts, Goulden, & Wofsy, 1999; Kershaw & Rouse, 1971). For example, the LE of a Boreal Jack pine forest increased significantly following a rainfall event (Betts et al., 1999). Betts et al. (1999) attributed a portion of the increase in LE to the flux of water from the forest floor bryophytes. The increased evaporation of water from the bryophytes and the intercepted canopy water altered the near-surface climate of the boreal forest, decreasing the depth of the planetary boundary layer (Betts et al., 2001). It is also likely that the effect of the latent heat flux from the lichens and bryophytes in old-growth Douglas-fir forests during the wet season will have a significant impact on the energy budget of the forest because lichens and bryophytes in these forests increase canopy water storage by 1 to 3 mm (Link, Unsworth, & Marks, 2004; Pypker, Bond, Link, Marks, & Unsworth, 2005; Pypker et al., 2006b). Further research is needed to determine the effect this may have on the local climate/microclimate during the wet season, as epiphytes in other ecosystems are known to reduce VPD and therefore moisture stress of plants (Stanton et al., 2014).

## 5 | CONCLUSIONS

We demonstrated that the large epiphyte biomass in old-growth Douglas-fir forests exerts an influence over diurnal LE dynamics ( $LE_e$ ) that has hitherto been unquantified. The field and laboratory measurements both indicate that the change in water content of the

epiphytes is directly related to the VPD of the air. However, the time response of  $WC_e$  to changing VPD is hyperbolic; at low VPD, the rate of water uptake causes  $WC_e$  to only slowly approach maximum water content. A VPD-based model agreed well with *in situ* strain gauge methods, with both indicating that the absorption/evaporation of water by the lichens and bryophytes alters the latent heat flux of the forest canopy (LE). We suggest that future research seek to address knowledge gaps limiting the estimation methods (e.g., characterizing controls over resistance to evaporation in lichen/bryophyte pore spaces), to investigate LE dynamics of other paraphyletic epiphyte groups in different forest types (e.g., vascular epiphytes in the tropics), and to assess how  $LE_e$  dynamics affect moisture stress for host plants.

## ACKNOWLEDGMENTS

We wish to thank J. Moreau, T. White, and T. Ocheltree for their assistance in the field. We thank Dr. J. McDonnell, Dr. T. Link, Dr. A. Meigs, and C. Tarasoff for their helpful comments on the manuscript. Lastly, we wish to thank the H.J. Andrews LTER staff for their provision of equipment and facilities. Data and facilities were provided by the H.J. Andrews Experimental Forest research program, funded by the National Science Foundation's Long-Term Ecological Research Program (DEB 1440409), US Forest Service Pacific Northwest Research Station, and Oregon State University. Funding for this project was provided by Sigma Xi and the Department of Forest Science, Oregon State University.

## REFERENCES

- Bertsch, A. (1966). Über den  $CO_2$ -Gaswechsel einiger flechten nach wasserdampfaufnahme. *Planta*, 68, 157–166.
- Betts, A. K., Ball, J. H., & McCaughey, J. H. (2001). Near-surface climate in the boreal forest. *Journal of Geophysical Research*, 106, 33529–33541.
- Betts, A. K., Goulden, M., & Wofsy, S. (1999). Controls on evaporation in a boreal spruce forest. *Journal of Climate*, 12, 1601–1618.
- Blum, O. B. (1973). Water relations. In V. Ahmadjian, & M. E. Hale (Eds.), *The lichens* (pp. 381–400). New York: Academic Press.
- Čabrajčić, A. V. J., Lidén, M., Lundmark, T., Ottosson-Löfvenius, M., & Palmqvist, K. (2010). Modelling hydration and photosystem II activation in relation to *in situ* rain and humidity patterns: A tool to compare performance of rare and generalist epiphytic lichens. *Plant Cell and Environment*, 33, 840–850. doi:10.1111/j.1365-3040.2009.02110.x
- Campbell, J., & Coxson, D. S. (2001). Canopy microclimate and arboreal lichen loading in subalpine spruce-fir forest. *Canadian Journal of Botany*, 79, 537–555.
- Clement, J. P., & Shaw, D. C. (1999). Crown structure and the distribution of epiphyte functional group biomass in old-growth *Pseudotsuga menziesii* trees. *Ecoscience*, 6, 243–254.
- Coxson, D. S. (1991). Impedance measurement of thallus moisture content in lichens. *Lichenologist*, 23, 77–84.
- Donohue, R. J., Roderick, M. L., & McVicar, T. R. (2007). On the importance of including vegetation dynamics in Budyko's hydrological model. *Hydrology and Earth System Sciences*, 11, 983–995.
- Donohue, R. J., Roderick, M. L., & McVicar, T. R. (2012). Roots, storms and soil pores: Incorporating key ecohydrological processes into Budyko's hydrological model. *Journal of Hydrology*, 436, 35–50. doi:10.1016/j.jhydrol.2012.02.033
- Ellyson, W. J. T., & Sillett, S. C. (2003). Epiphyte communities on sitka spruce in an old-growth redwood forest. *The Bryologist*, 106, 197–211.
- Franklin, J. F., Spies, T. A., Van Pelt, R., Carey, A. B., Thornburgh, D. A., Berg, D. R., ... Shaw, D. C. (2002). Disturbances and structural development of

- natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and Management*, 155, 399–423.
- Friesen, J., Lundquist, J., & Van Stan, J. T. (2015). Evolution of forest precipitation water storage measurement methods. *Hydrological Processes*, 29, 2504–2520. doi:10.1002/hyp.10376
- Gauslaa, Y. (2014). Rain, dew, and humid air as drivers of morphology, function and spatial distribution in epiphytic lichens. *Lichenologist*, 46, 1–16. doi:10.1017/s0024282913000753
- Gray, A. N., & Spies, T. A. (1996). Gap size, within-gap position and canopy structure effects on conifer seedling establishment. *Journal of Ecology*, 84, 635–645.
- Green, T. G. A., Schlenz, M., Sancho, L. G., Winkler, B., Broom, F. D., & Schroeter, B. (2002). The photobiont determines the pattern of photosynthetic activity within a single lichen thallus containing cyanobacterial and green algal sectors (photosymbiodeme). *Oecologia*, 130, 191–198.
- Hancock, N. H., & Crowther, J. M. (1979). A technique for the direct measurement of water storage on a forest canopy. *Journal of Hydrology*, 41, 105–122.
- Hölscher, D., Köhler, L., van Dijk, A. I. J. M., & Bruijnzeel, L. A. (2004). The importance of epiphytes to total rainfall interception by a tropical montane rain forest in Costa Rica. *Journal of Hydrology*, 292, 308–322.
- Jonsson, A. V., Moen, J., & Palmqvist, K. (2008). Predicting lichen hydration using biophysical models. *Oecologia*, 156, 259–273. doi:10.1007/s00442-008-0990-5
- Keim, R. F., Skaugset, A. E., & Weiler, M. (2006). Storage of water on vegetation under simulated rainfall of varying intensity. *Advances in Water Resources*, 29, 974–986.
- Kershaw, K. A. (1985). *Physiological ecology of lichens*. Cambridge: Cambridge University Press.
- Kershaw, K. A., & Rouse, W. R. (1971). Studies on lichen-dominated systems. I. The water relations of *Cladonia alpestris* in spruce-lichen woodland in northern Ontario. *Canadian Journal of Botany*, 49, 1389–1399.
- Köhler, L., Tobon, C., Frumau, K. F. A., & Bruijnzeel, L. A. (2007). Biomass and water storage dynamics of epiphytes in old-growth and secondary montane cloud forest stands in Costa Rica. *Plant Ecology*, 193, 171–184.
- Kolumbe, E. (1927). Untersuchungen über die Wasserdampfaufnahme der Flechten. *Planta*, 3, 734–757.
- Lakatos, M. (2011). Lichens and bryophytes: Habitats and species. In U. Lüttge, E. Beck, & D. Bartels (Eds.), *Plant desiccation and tolerance* (pp. 65–87). Berlin: Ecological Studies. Springer-Verlag.
- Lange, O. L., Green, T. G. A., & Ziegler, H. (1988). Water status related photosynthesis and carbon isotope discrimination in species of lichen genus *Pseudocyphellaria* with green and blue-green photobionts and in photosymbiodemes. *Oecologia*, 75, 494–501.
- Lange, O. L., Kilian, E., & Ziegler, H. (1986). Water vapor uptake and photosynthesis of lichens: Performance differences in species with green and blue-green algae as phycobionts. *Oecologia*, 71, 104–110.
- Lange, O. L., Schulze, E.-D., & Koch, W. (1970). Experimentall-ökologische untersuchungen an flechten der Negev-Wüste. II CO<sub>2</sub> – Gaswechsel und wasserhaushalt von *Ramalina maciformis* (Del.). Bor am natürlichen standort während der sommerlichen trochenperioide. *Flora (Jena)*, 159, 38–62.
- Link, T. E., Unsworth, M. H., & Marks, D. (2004). The dynamics of rainfall interception by a seasonal temperate rainforest. *Agricultural and Forest Meteorology*, 124, 171–191.
- Lyons, B., Nadkarni, N. M., & North, M. P. (2000). Spatial distribution and succession of epiphytes on *Tsuga heterophylla* (western hemlock) in an old-growth Douglas-fir forest. *Canadian Journal of Botany*, 78, 957–968.
- Martin, C. E., & Schmitt, A. K. (1989). Unusual water relations in the CAM atmospheric epiphyte *Tillandsia usneoides* L. (Bromeliaceae). *Botanical Gazette*, 150, 1–8 doi: 10.1086/337741
- Matthes-Sears, U., Nash, T. H. III, & Larson, D. W. (1987). The ecology of *Ramalina menziesii*. VI. Laboratory responses of net CO<sub>2</sub> exchange to moisture, temperature, and light. *Canadian Journal of Botany*, 65, 182–191.
- McCune, B. (1993). Gradients in epiphyte biomass in three *Pseudotsuga-Tsuga* forests of different ages in Western Oregon and Washington. *The Bryologist*, 96, 405–411.
- McCune, B. (1994). Using epiphyte litter to estimate epiphyte biomass. *The Bryologist*, 97, 396–401.
- McCune, B., Amsberry, K. A., Camacho, F. J., Clery, S., Cole, C., Emerson, C., ... Widmer, M. (1997). Vertical profile of epiphytes in Pacific Northwest old-growth forest. *Northwest Science*, 71, 145–152.
- McVicar, T. R., Van Niel, T. G., Li, L. T., Hutchinson, M. F., Mu, X. M., & Liu, Z. H. (2007). Spatially distributing monthly reference evapotranspiration and pan evaporation considering topographic influences. *Journal of Hydrology*, 338, 196–220. doi:10.1016/j.jhydrol.2007.02.018
- Monteith, J. L., & Campbell, G. S. (1980). Diffusion of water vapour through integuments – Potential confusion. *Journal of Thermal Biology*, 8, 7–9.
- Monteith, J. L., & Unsworth, M. H. (1990). *Principles of environmental physics*. New York: Edward Arnold.
- Moore, G. W., Bond, B. J., Jones, J. A., Phillips, N., & Meinzer, F. C. (2004). Structural and compositional controls on transpiration in a 40- and 450-yr-old riparian forest in western Oregon, USA. *Tree Physiology*, 24, 481–491.
- Mu, Q., Heinsch, F. A., Zhao, M., & Running, S. W. (2007). Development of a global evapotranspiration algorithm based on MODIS and global meteorology data. *Remote Sensing of Environment*, 111, 519–536. doi:10.1016/j.rse.2007.04.015
- Nardini, A., Marchetto, A., & Tretiach, M. (2013). Water relation parameters of six *Peltigera* species correlate with their habitat preferences. *Fungal Ecology*, 6, 397–407. doi:10.1016/j.funeco.2013.05.004
- Pike, L. H., Denison, W. C., Tracy, D. M., Sherwood, M. A., & Rhoades, F. M. (1975). Floristic survey of epiphytic lichens and bryophytes growing on old-growth conifers in western Oregon. *The Bryologist*, 78, 389–402.
- Pike, L. H., Rydell, R. A., & Denison, W. C. (1977). A 400-year-old Douglas fir and its epiphytes: biomass, surface area, and their distribution. *Canadian Journal of Forest Research*, 7, 680–699.
- Pypker, T. G., Bond, B. J., Link, T. E., Marks, D., & Unsworth, M. H. (2005). The importance of canopy structure in controlling the interception loss of rainfall: Examples from a young and old-growth Douglas-fir forests. *Agricultural and Forest Meteorology*, 130, 113–129.
- Pypker, T. G., Unsworth, M. H., & Bond, B. J. (2006a). The role of epiphytes in rainfall interception by forests in the Pacific Northwest. I. Laboratory measurements of water storage. *Canadian Journal of Forest Research*, 36, 808–818.
- Pypker, T. G., Unsworth, M. H., & Bond, B. J. (2006b). The role of epiphytes in rainfall interception by forests in the Pacific Northwest. II. Field measurements at the branch and canopy scale. *Canadian Journal of Forest Research*, 36, 819–832.
- Renner, M., Seppelt, R., & Bernhofer, C. (2012). Evaluation of water-energy balance frameworks to predict the sensitivity of streamflow to climate change. *Hydrology and Earth System Sciences*, 16, 1419–1433. doi:10.5194/hess-16-1419-2012
- Rothacher, J., Dyrness, C. T., & Fredriksen, F. L. (1967). *Hydrologic and related characteristics of three small watersheds in the Oregon cascades*. Portland, OR: USDA Forest Service.
- Rundel, P. W. (1988). Water relations. In M. Galun (Ed.), *Handbook of lichenology* (pp. 17–36). Boca Raton: CRC Press, Inc.
- Schlenz, M., Schroeter, B., & Green, T. G. A. (2000). Water dependent photosynthetic activity of lichens from New Zealand: Differences in the green algal and the cyanobacterial thallus parts of photosynthesis. *Bibliotheca Lichenologica*, 75, 149–160.
- Sillett, S. C. (1995). Branch epiphyte assemblages in the forest interior and on the clearcut edge of a 700-year-old Douglas fir canopy in Western Oregon. *The Bryologist*, 98, 301–312.

- Sillett, S. C., & Rambo, T. R. (2000). Vertical distribution of dominant epiphytes in Douglas-fir forests of the Central Oregon Cascades. *Northwest Science*, 74, 44–49.
- Stanton, D. E., Huallpa Chávez, J., Villegas, L., Villasante, F., Armesto, J., Hedin, L. O., & Horn, H. (2014). Epiphytes improve host plant water use by microenvironment modification. *Functional Ecology*, 28, 1274–1283. doi:10.1111/1365-2435.12249
- Swanson, F. J., & James, M. E. (1975). Geology and geomorphology of the H.J. Andrews Experimental Forest, Western cascades, Oregon. *Pacific Northwest Forest and Range Experiment Station, USDA Forest Service, Portland, OR Research Paper PNW-188*: 1–14.
- Unsworth, M. H., Phillips, N., Link, T., Bond, B. J., Falk, M., Harmon, M. E., ... Paw U, K. T. (2004). Components and controls of water flux in an old-growth Douglas-fir/western hemlock ecosystem. *Ecosystems*, 7, 468–481.
- Van Stan, J. T. II, & Pypker, T. G. (2015). A review and evaluation of forest canopy epiphyte roles in the partitioning and chemical alteration of precipitation. *Science of the Total Environment*, 236, 813–824.
- Wilson, K. B., Hanson, P. J., Mulholland, P. J., Baldocchi, D. D., & Wullschlegel, S. D. (2001). A comparison of methods for determining forest evapotranspiration and its components: Sap-flow, soil water budget, eddy covariance and catchment water balance. *Agricultural and Forest Meteorology*, 106, 153–168.

**How to cite this article:** Pypker, T. G., Unsworth, M. H., Van Stan, J. T., II, and Bond, B. J. (2016), The absorption and evaporation of water vapor by epiphytes in an old-growth Douglas-fir forest during the seasonal summer dry season: implications for the canopy energy budget, *Ecohydrology*, doi: 10.1002/eco.1801

## APPENDIX A

### The Potential Diurnal Water Absorption and Evaporation by Epiphytes

The large populations of epiphytes in old-growth Douglas-fir forests of the PNW may diurnally absorb and evaporate 1.3 tonnes/ha of atmospheric water vapor during the dry summer months. The potential diurnal water absorption/evaporation ( $\Delta WC$ ) by epiphytic lichens and bryophytes during the summer dry season was calculated by assuming the following: the canopy contained 1,870 kg/ha of lichens and 780 kg/ha of bryophytes (total =  $B_e = 2,650$  kg/ha; McCune, 1993); the RH of the air within the canopy diurnally ranged from 30% to 80%; the water content of the lichens/bryophytes at 30% RH ( $WC_{RH30\%}$ ) was 0.3 of their dry weight (Blum, 1973); and the water content of the lichens/bryophytes at 80% RH ( $WC_{RH80\%}$ ) was 0.8 of their dry weight (Schlensog et al., 2000).

$$\Delta WC = B_e \cdot WC_{RH80\%} - B_e \cdot WC_{RH30\%}$$

Under these assumptions, the diurnal absorption/evaporation of water vapor equals 1,325 kg/ha of water.