AN ABSTRACT OF THE DISSERTATION OF

<u>Thomas G. Pypker</u> for the degree of <u>Doctor of Philosophy</u> in <u>Forest Science</u> presented on <u>December 20, 2004</u>. Title: <u>The Influence of Canopy Structure and Epiphytes on the Hydrology of Douglas-fir Forests</u>

Abstract
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Barbara J. Bond

Canopy structure has a significant impact on the canopy hydrology of Douglas-fir forests in the Pacific Northwest (PNW). Whole canopy rainfall interception was measured for young Douglas-fir forest and compared to an old-growth Douglas-fir forest. The old-growth forest had significantly greater canopy water storage capacity (S) and direct throughfall fraction (p). However, the interception loss (I_n) for the old-growth forest was only slightly larger than the young forest due to the similar ratios of evaporation to rainfall intensity ($\bar{\bar{E}}/\bar{R}$). The spatial distribution of throughfall was more right-skewed in the old-growth forest; with many locations receiving throughfall in excess of gross precipitation (P_G). Despite differences in the spatial distribution of throughfall, the spatial distribution of soil moisture did not differ between the two forests. Because the S was significantly greater in the old-growth forest, the influence of epiphytic lichens and bryophytes on S was examined. The maximum water content (MWC_x) of individual samples of fruticose lichens, foliose lichens, and bryophytes from an old-growth Douglas-fir forest were measured in the laboratory and the field. The laboratory results indicate that typical epiphytic

fruticose lichens, foliose lichens and bryophytes for old-growth Douglas-fir forests in the PNW could store 2.23, 3.42 and 9.99 times their dry weight in water, respectively.   Although these values could be used to predict the maximum epiphyte-laden branch water storage under laboratory conditions, they were unable to do so under field conditions. In the field the biomass on the branch could not predict the maximum branch water storage because the branches: 1) were partially saturated for most of the measurement period; and 2) required greater than 30 mm of rain to saturate due to preferential flow routing water through the epiphyte mats. The frequent storms and the slow saturation of the canopy resulted an underestimation of S and an overestimation of $\overline{E}/\overline{R}$ by standard regression based techniques for estimating canopy variables. Lastly, the water stored on epiphyte-laden branches after exposure to natural rainfall was positively associated with rainfall intensity. The absorption of atmospheric water vapor by epiphytes in old-growth Douglas-fir forests in the PNW may have facilitated carbon uptake by green lichens and altered the energy budget of the forest during the seasonal summer drought. During the summer months the green lichens absorb sufficient quantities of atmospheric water to reactivate their photosystems. The diurnal absorption/evaporation of atmospheric water will result in significant uptake of water at night and may account for 5 to 21% of the canopy latent heat flux in the early morning (600 to 1000 h).

The Influence of Canopy Structure and Epiphytes on the Hydrology of
Douglas-fir Forests

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CONTRIBUTION OF AUTHORS

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SYMBOLS AND DEFINITIONS

A	Projected surface area of a branch (m^2)
B_{br}	Dry-weight biomass of bryophytes in the canopy (kg ha^{-1})
B_{fo}	Dry-weight biomass of foliose lichens in the canopy (kg ha^{-1})
B_{fr}	Dry-weight biomass of fruticose lichens in the canopy (kg ha^{-1})
b_{br}	Dry-weight biomass of bryophytes on a branch (kg)
b_{fo}	Dry-weight biomass of foliose lichens on a branch (kg)
b_{fr}	Dry-weight biomass of fruticose lichens on a branch (kg)
c_p	Specific heat of air (J kg^{-1} K^{-1})
E	Total Evaporation (mm)
E/R	Total evaporation divided by total rainfall (P_G) (dimensionless)
$\overline{E}/\overline{R}$	Ratio of evaporation to rainfall under saturated canopy condition (dimensionless)
c	fraction of canopy cover (m^2 m^{-2})
c_p	Specific heat capacity (J kg^{-1} K^{-1})
d	Zero zone displacement (m)
d_b	Diameter of a branch (m)
d_s	Stopping distance for a raindrop hitting a branch surface (m)
D	Raindrop diameter (m)
DW	Epiphyte dry weight (g)
F_i	Force of impact of a raindrop (kg)
g	The acceleration due to gravity (m s^{-2})
g_b	Branch boundary layer conductance (m s^{-1})
I	Rainfall intensity (mm h^{-1})
I_a	Interception loss during canopy drying (mm)
I_c	Interception loss during canopy wetting for $P_G < P_s$ (mm)
I_s	Interception loss during saturated canopy conditions (mm)
I_w	Interception loss during canopy wetting for events $P_G \geq P_s$ (mm)
I_n	Net interception loss (mm)
I_t	Rainfall intensity (kg m^{-2} h^{-1})
k	von Karmen's constant (0.41, dimensionless)
LE	Latent heat flux (W m^{-2})
LE_e	Latent heat flux of the epiphytic lichens and bryophytes (W m^{-2})
LE_{ec}	Eddy covariance estimate of canopy latent heat flux (W m^{-2})
M	Instantaneous mass of raindrops hitting a branch (kg)
P_G	Gross precipitation for a single storm event (mm)
P_G	The cumulative gross precipitation during a single storm event (mm).
P_n	Net precipitation beneath the canopy (throughfall) for a single storm event (mm)
P_n	The cumulative net precipitation during a single storm event (mm).
P_s	Precipitation required to saturated the canopy (mm)
p_i	Rainfall interception efficiency (dimensionless

p	Direct throughfall fraction (dimensionless)
R	Number of raindrops hitting the branch at a given moment
r_a	Canopy aerodynamic resistance to latent heat transfer (s m^{-1})
r_{e-LE}	Resistance to latent heat transfer for epiphytes on a branch (s m^{-1})
r_s	Number of raindrops hitting a surface (Raindrops m^{-2} s^{-1})
S	Canopy water storage capacity (mm)
S_{bs}	Branch surface water storage (kg)
S_e	Epiphyte water storage (kg)
S_{e-b}	Epiphyte-laden branch water storage (kg)
S_m	Maximum water storage by a branch during a rainfall event
S_f	Field storage capacity of a branch
t_d	Decimal time
t_h	Time (h)
t_s	Time (s)
WC_{br}	Water content of a bryophyte ((bryophyte weight minus B_{fo})/B_{fo})
WC_{fo}	Water content of a fruticose lichen ((lichen weight minus B_{fo})/B_{fo})
WC_{fr}	Water content of a foliose lichen ((lichen weight minus B_{fo})/B_{fo})
WW	Epiphyte wet weight (g)
u	Windspeed (m s^{-1})
V_T	Terminal velocity (m s^{-2})
w_b	Branch weight at given time during a rainfall event
z_0	Roughness length (m)
γ	Psychrometric constant (Pa K^{-1})

a.s.l.	Above sea level
LAI	Leaf area index (m^2 m^{-2})
RH	Relative humidity (%)
PNW	Pacific Northwest
WRCCRF	Wind River Canopy Crane Research Facility

Canopy water storage (S) – is as the quantity of water the canopy can store prior to saturating (mm)

Direct throughfall fraction (p) – the fraction of rainfall that passes directly to the floor

Field storage capacity – The amount of water a single branch stored after the rainfall stopped and the dripping from the branch ceased.

Interception loss (I_n) – The intercepted canopy and lost to the atmosphere via evaporation ($P_G - P_n$)

Maximum water storage – The maximum amount of water a branch held during a single rainfall event. Water-holding capacity

Chapter 1 - Introduction

The interception and evaporation of water by forest canopies strongly influences the hydrology of a forest. In the early to mid portion of the 20th century scientists monitored the impact that forest canopies had on the interception loss (I_n) of rainfall (e.g. Helvey and Patric, 1965; Horton, 1919; Rothacher, 1963; Voigt, 1960; Zinke, 1967). It was quickly recognized that forest canopies can reduce the amount of rainfall reaching the forest floor by 10 to 40% (Hörmann et al., 1996; Zinke, 1967). Later in the century, technology permitted the measurement of the water fluxes above a plant canopy (e.g. aerodynamic method, Bowen Ratio systems, eddy covariance systems) (Monteith and Unsworth, 1990). Research indicates that water vapor losses from forests typically range between 1 and 5 mm d^{-1}, depending on forest type and season (Larcher, 1995). Management of forests alters the hydrology of the ecosystem by changing the evaporation and transpiration (e.g. Harr, 1982; Hicks et al., 1991; Keppeler and Ziemer, 1990; Moore et al., 2004), rainfall interception loss (I_n) (e.g. Zinke, 1967) stream peak discharges and base flows (e.g. Harr et al., 1975; Hicks et al., 1991; Jones and Grant, 1996; Thomas and Megahan, 1998). In the Pacific Northwest (PNW) the hydrology of old-growth Douglas-fir forests has received attention over the past half century.

Although historically old-growth Douglas-fir forests in the PNW were extensively harvested, more recently land managers are attempting to

preserve these ecosystems or manage younger forests to mimic the complex structure of old-growth canopies (Franklin and Van Pelt, 2004; Sessions et al., 2004; Spies, 2004).   To understand how forest management will affect the hydrology of a forest or watershed, it is necessary to first improve our understanding of how the structure of old-growth Douglas-fir forest canopies affects the hydrology of the forest.

Douglas-fir forests of the Pacific Northwest

Douglas-fir forests in the PNW stretch from California to British Columbia and are exposed to cool/wet winters and warm/dry summers (Preston Jr. and Braham, 2002). In general, the canopy of a Douglas-fir forest develops from a monoculture young forest to a vertically and horizontally heterogeneous old-growth forest (>450 y-old) (Franklin et al., 2002). Old-growth Douglas-fir forest canopies differ from a young Douglas-fir forest because they have large canopy gaps (Gray and Spies, 1996), a diversity of tree species (Shaw et al., 2004), high canopy water storage capacity (S) (Link et al., 2004) and large epiphyte populations (McCune, 1993; Pike et al., 1975; Pike et al., 1977; Sillett and Rambo, 2000). These differences in canopy architecture will alter the quantity, distribution and timing of water delivered to the forest floor (e.g. Keim et al., 2004; Keim et al., in review; Link et al., 2004; Massman, 1983; Nadkarni and Sumera, 2004). The changes in canopy hydrology may influence the stability of hillslopes (Keim and Skaugset, 2003), change the quantity of water available for plants and streams (e.g. Ford and Deans, 1978; Jones, 2000), alter the latent heat fluxes from the forest canopy

(e.g. Moore et al., 2004; Unsworth et al., 2004) and if drastic enough, alter the regional climate (Bonan, 1999). Hence, forest canopy development may influence processes from the scale of the tree to the entire watershed.

Influence of canopy structure on rainfall interception loss (I_n)

As forests develop, the production of leaves, stems and boles increases the canopy surface area, thereby increasing the canopy water storage (S) and net interception loss of rainfall (I_n; gross precipitation above the canopy (P_G) minus net precipitation below the canopy (P_n)) (Aston, 1979; Keim, 2003). While the size of S is important in determining the I_n of a forest, a considerable portion of the rainfall is lost via evaporation during a storm (e.g. Gash, 1979; Rutter et al., 1971; Teklehaimanot et al., 1991). The structure of a forest canopy directly affects the ratio of evaporation to rainfall intensity after the canopy saturates ($\overline{E}/\overline{R}$) by altering the resistance to latent heat transfer (Jarvis and Fowler, 2001; Klaassen, 2001; Stewart and Thom, 1973; Teklehaimanot and Jarvis, 1991). For example Teklehaimanot et al. (1991) compared the I_n of four Sitka spruce forests that were a similar height, but had different spacing between the trees. The canopy with close spacing had the largest S, but the farthest spacing had the smallest resistance to latent heat transfer. This resulted in I_n decreasing with larger tree spacing, however the decrease was not proportional to the reduction in tree density. Thus, changes in the height, density, canopy roughness and S of the forest canopy will all influence the evaporation and I_n of a forest (Gash, 1979; Monteith and Unsworth, 1990).

The unique structure of old growth Douglas-fir canopies results in the S, direct throughfall fraction (p), $\overline{E}/\overline{R}$ and I$_n$ exceeding 3 mm, 0.3, 0.1 and 20%, respectively (Link et al., 2004; Rothacher, 1963).   The large S in old-growth Douglas-fir forests is generally attributed to: their high leaf area; storage of water in bark and dead wood; and large epiphytic populations (Keim, 2003; Levia Jr and Frost, 2003; Link et al., 2004; Rothacher et al., 1967; Waring and Running, 1998). When these old-growth forests are harvested, the peak discharge during a single storm event or the yearly water yield of the streams may increase (Harr et al., 1975; Hicks et al., 1991; Jones and Grant, 1996; Thomas and Megahan, 1998) or decrease (Harr and McCorison, 1979; Hicks et al., 1991). The increase or decrease in peak discharge or annual water yield in the period following harvesting has been attributed to changes in evapotranspiration, fog drip, and snow loads (Harr, 1982; Hicks et al., 1991; Keppeler and Ziemer, 1990). However, impacts of logging on peak flows and yearly discharge have been of debate (e.g. Jones and Grant, 1996; Thomas and Megahan, 1998) because of the interacting hydrological processes controlling stream discharge. Thus, to properly assess the influence of a forest on the hydrology of a watershed, all the hydrological processes must be understood; including the interception of rainfall by the forest canopy.

Role of lichens and bryophytes in canopy hydrology

In the recent past, the field of ecohydrology has received increasing attention (Rodriguez-Iturbe, 2000). Whereas, the study of the interaction between plants and hydrology is not novel (Bonnell, 2002), the renewed focus

provides a platform for collaboration between hydrologists and ecologists (Bond, 2003). For example, the effect of lichens and bryophytes on the hydrology of forests has received little attention, and to understand their effect requires collaboration between the two fields of hydrology and ecology.

The development of large epiphyte populations in old-growth Douglas-fir forests may significantly increase S (Keim, 2003; Levia Jr and Frost, 2003; Link et al., 2004; Rothacher et al., 1967; Waring and Running, 1998). Lichens and bryophytes are poikilohydric species that have a unique ability to survive long periods of desiccation (Kappen, 1973; Proctor, 1982; Proctor, 2000a). Lichens are the result of a symbiosis between a fungus (mycobiont) and one or more algae (photobiont). The mycobiont provides the structural support for the photobiont, and the photobiont in turn, provides energy via photosynthesis. Bryophytes include all hornworts, liverworts and mosses. Both lichens and bryophytes are cryptogamic and lack a true vascular system. To compensate for their inability to remove water from the soil, lichens and bryophytes have large maximum water contents (MWC_x) that range from 1.50 to 12.0 times their dry weight (Blum, 1973; Proctor, 2000b).   If the relative humidity (RH) of the atmosphere is high, lichens with a green algal symbiont also have the ability to absorb sufficient quantities of water vapor to reactivate their photosynthetic metabolism (Bertsch, 1966; Green et al., 2002; Lange et al., 1986; Schlensog et al., 2000).   Bryophytes may have the ability to absorb significant quantities of atmospheric water, but they are unable to reactivate their photosynthetic metabolism without liquid water (Proctor, 2000a).

The role of lichens and bryophytes in the hydrology of forest has received very little attention despite the fact that they may increase S (Keim, 2003; Levia Jr and Frost, 2003; Link et al., 2004; Rothacher et al., 1967; Waring and Running, 1998) and possibly alter the canopy's energy budget (Unsworth et al., 2004). With the warnings of higher temperatures due to global warming (Hamlet and Lettenmaier, 1999; Miles et al., 2000) and the rising population in the PNW (Brown, 2000), water issues will become more significant. Thus, it is important to understand what changes to the forests will influence the mechanisms that control the hydrology of the forest canopy.

The goal of this dissertation is to determine the effect of canopy structure on the hydrology of old-growth Douglas-fir forests in the PNW. More specifically, the dissertation focuses on how the development of large epiphyte populations in old-growth Douglas-fir forests will affect canopy hydrology.

Dissertation Structure

This dissertation contains an introduction, followed by 4 chapters written in manuscript form. The key results of the four manuscripts are summarized in a concluding chapter.

The rainfall interception by a young Douglas-fir forest in the Pacific Northwest is analyzed in Chapter 2 using a new method that provides information on the canopy water storage (S), ratio of evaporation to rainfall intensity ($\overline{E}/\overline{R}$) and the direct throughfall fraction changes (p) on a per-storm basis (Link et al., 2004). The results are compared to the rainfall interception by an old-growth forest that has a similar leaf area index (LAI), but different

canopy structure relative to the young forest. The chapter discusses how the development from a young forest canopy to an old-growth forest canopy will affect the S, I_n, $\overline{E}/\overline{R}$, p and spatial distribution of rainfall and soil moisture in the forest. Lastly, Chapter 2 explores the affect seasonal changes in the S, $\overline{E}/\overline{R}$ and p have on the accuracy of a commonly used analytical model (Gash, 1979).

In Chapter 3, the effect lichens and bryophytes have on the quantity of water storage on a branch was explored in the laboratory by exposing epiphyte-laden branches to different rainfall intensities under a rainfall simulator. The mass of water stored by individual samples of lichens and bryophytes commonly found in old-growth was determined in the laboratory. Epiphyte-laden branches were placed under a rainfall simulator and the water storage and the rainfall interception efficiency of the branches were determined.

Chapter 4 explores the impact that epiphytes have on the water storage of the branch and the whole canopy. It is determined whether laboratory estimates of the potential epiphyte-laden branch water storage (S_{e-b}) (Chapter 3) can predict the water storage by epiphyte-laden branches measured in the field. The chapter reports on how the distribution of the epiphytes increases the time the canopy remains wet following a storm event and the relationship between rainfall intensity and water storage by epiphyte-laden branches. The epiphytic lichens and bryophytes may alter S and influence the accuracy of commonly used regression based-models for calculating S, $\overline{E}/\overline{R}$ and p.

Chapter 5 presents the biomass and distribution of lichens and bryophytes in old-growth Douglas-fir forests in Central Oregon. The chapter presents a summary of the importance of the diurnal variation of RH on the ability of epiphytic lichens to absorb sufficient quantities of atmospheric water vapor to reactivate their photosynthetic metabolism. Furthermore, the chapter explores the impact that absorption/evaporation by epiphytic lichens and bryophytes may have on the energy budget of an old-growth Douglas-fir forest.

Chapter 6 summarizes the key findings of this study and discusses the future research that is needed to improve our understanding of the hydrology of Douglas-fir forests in the PNW.

Chapter 2 – The importance of canopy structure in controlling the interception loss and spatial distribution of rainfall: Examples from a young and old-growth Douglas-fir forests

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1.0 Abstract

The canopy water storage (S), direct throughfall fraction (p), the ratio of evaporation to rainfall intensity ($\overline{E}/\overline{R}$) and interception loss (I_n), of a Douglas-fir forest is influenced by short (seasonal) and long-term (decades to centuries) changes in the forest canopy. Gross precipitation (P_G), net precipitation (P_n) and soil moisture was measured in a young (25-y-old) Douglas-fir forest and compared the results with measurements previously made in an old-growth (>450-y-old) Douglas-fir forest (Link et al., 2004). Canopy rainfall variables were estimated using a regression-based method that estimates S, p and $\overline{E}/\overline{R}$ for individual storms using the relationship between P_G and P_n. The individual storm estimates of S, p and $\overline{E}/\overline{R}$ for the young forest were applied to a common rainfall interception model (Gash model (Gash, 1979)) to determine the effect of seasonal changes in canopy hydrologic variables have on estimates of I_n (young forest only). The Gash model was previously applied to the old-growth forest (Link et al., 2004).

The young forest had significantly different S (1.40 mm ±0.27) and p (0.12 ±0.07) relative to the old-growth forest (S = 3.32 ±0.35; p = 0.42 ±0.07). Seasonal variation in canopy structure, such as deciduous leaf senescence and coniferous needle drop, were correlated with decreases in S. The differences in S and p between the two forests resulted in an I_n that was only slightly larger in the old-growth forest because the $\overline{E}/\overline{R}$ for the two forests were similar (young = 0.18 ±0.06; old-growth = 0.17 ±0.08). $\overline{E}/\overline{R}$ in the young and old-growth forests may have been similar because developmental

changes associated with old-growth forest may alter the external resistance (r_a) and the effective area for evaporation. The old-growth forest has a large gap fraction (0.23 (Parker et al., 2004)) that resulted in a right skewed spatial distribution of the throughfall; with many locations receiving throughfall in excess of P_G. In contrast, the low gap fraction (0.11) found in the young forest produced more normally distributed throughfall. Despite differences in the spatial distribution of throughfall, the spatial distribution of soil moisture (depth = 0 to 31 cm) did not differ between the two forests. Bryophytes and litter on the forest floor, in conjunction with plant water uptake, may sufficiently alter the spatial distribution of soil moisture in the mineral soil.

The Gash model successfully predicted I_n for the young forest on a seasonal basis (3.29% error), but experienced larger errors (range = -91 to 36% error) for individual storms. The seasonal error and the error for individual storms improved when seasonal variations in canopy characteristics were incorporated in the model (seasonal error = 2.37%; individual storm error range = -12.0 to 21.7%). Therefore, short-term (seasonal) changes in phenology and long-term (decades to centuries) horizontal and vertical development of the forest canopy influence S, p, I_n and $\overline{E}/\overline{R}$ of Douglas-fir forests.

2.0 Introduction

Interception loss (I_n) of rainfall in temperate forests typically ranges between 9-48% of gross precipitation (P_G) and is influenced by canopy structure (Hörmann et al., 1996). Short (seasonal) and long-term (decades to

centuries) changes in canopy structure will alter the canopy water storage (S), direct throughfall fraction (p), and the ratio of evaporation to rainfall intensity ($\overline{E}/\overline{R}$), thereby influencing I_n. On the short-term, S may change seasonally with shoot elongation, deciduous tree leaf senescence and coniferous tree needle drop. Over the long-term, the quantity and spatial pattern of throughfall may be altered by changes in gap fraction, horizontal and vertical distribution of foliage and epiphytes, and changes in species composition. Hence, the canopy structure that influences I_n is a function of tree phenology, long-term changes in species composition, and the stage of forest development (Franklin et al., 2002; Ishii and McDowell, 2002; Ishii and Wilson, 2001; Zimmerman and Brown, 1971).

Tree phenology alters the surface area of the forest canopy thereby, influencing S and I_n. Not surprisingly, S and I_n in deciduous forests change dramatically between periods of growth and dormancy (e.g. Helvey and Patric, 1965; Leyton et al., 1967; Zinke, 1967). For example, S in a mixed hardwood forest in West Virginia decreased by 60% between summer and winter (Zinke, 1967). Coniferous forests may also experience seasonal differences in S. Link et al. (2004) found that S in an old-growth Douglas-fir forest decreased by approximately 0.5 mm subsequent to coniferous needle drop and deciduous plant senescence.

Long-term changes in species composition may alter the leaf area index (LAI; one-sided leaf surface area per unit ground area) and canopy architecture. S increases with increasing LAI (e.g. Aston, 1979; Flerchinger et

al., 1996; Wigmosta et al., 1994).   However, the relationship between LAI and

S is species dependent (Llorens and Gallart, 2000; Keim, 2003), varies

between young and old-growth forests (Link et al., 2004) and between tropical

and temperate forests (Herwitz, 1985). The architecture of the canopy

influences how water is routed through the canopy to the forest floor. For

example, Ford and Deans (1978) found that Sitka spruce trees with a large

number of branches inclined above the horizontal routed 27% of the gross

precipitation (P_G) down the stem, whereas Rothacher (1963), reported

negligible stem flow in old-growth Douglas-fir forests that had horizontal

branch structure. Furthermore, how the water is routed through the canopy

has important implications on the biogeochemistry and the spatial distribution

of rainfall beneath a canopy (Ford and Deans, 1978; Levia Jr and Frost, 2003).

The parameters S, p, $\overline{E}/\overline{R}$ and I_n are influenced by developmental

changes in canopy structure. For example, Douglas-fir forests in the Pacific

Northwest (PNW) typically develop through a series of stages from cohort

establishment, canopy closure, stem exclusion, maturation, vertical

diversification, horizontal diversification and pioneer cohort loss (Franklin et

al., 2002). As a forest progresses through the different stages, changes in the

gap fraction, horizontal and vertical distribution of foliage and epiphytes and

species composition will influence S, p, $\overline{E}/\overline{R}$ and I_n.   The changes in the

hydrological cycle through forest development stages are of particular

importance in the PNW because rainfall is infrequent during the summer

months. During the summer, the water content of the soil (Unsworth et al.,

2004) and the transpiration rates of the trees (Moore et al., 2004) are reduced. If developmental changes in canopy structure result in changes in I_n, forests in different stages of development will have more or less water available for plant uptake and stream discharge. Thus, developmental changes in canopy structure may help mitigate or exacerbate the stress of the dry summer months by altering the I_n of the forest, but few studies have investigated how rainfall interception is influenced by short or long-term changes in forest canopy structure.

Most studies on rainfall interception use one of two indirect techniques to quantify S, p, and $\overline{E}/\overline{R}$. The first indirect technique generates one (minimum method) or two (mean method) linear regressions between observations for multiple storms of P_G (x-axis) and net precipitation beneath the canopy (P_n) (y-axis) (e.g. Gash and Morton, 1978; Klaassen et al., 1998; Leyton et al., 1967). The minimum method provides an estimate of S by fitting a regression line to data from storms that saturate the canopy and have a low evaporation rate. The x-intercept of regression line provides the estimate of S. The mean method requires two regression lines relating P_G to P_n for storms that are either insufficient (R_1) or sufficient (R_2) to saturate the canopy. 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 $\overline{E}/\overline{R}$, the value of P_G at intersection point of R_1 and R_2 provides an estimate of the canopy saturation point (P_s) and, finally, the difference between P_G and P_n at the intersection point provides an estimate of S. An alternative technique to regression-based

methods is to measure rainfall interception of individual branches under rainfall simulator and to scale the results up to the stand using a variable such as LAI (e.g. Aston, 1979; Herwitz, 1985; Hutchings et al., 1988; Liu, 1998; Keim, 2003). The estimates of p, S, $\overline{E}/\overline{R}$ and P_s produced by these methods are often used in rainfall interception models, such as the Gash model, to estimate I_n for a forest (Gash, 1979; Rutter et al., 1971). The models must assume that seasonal changes in p, S and $\overline{E}/\overline{R}$ have little effect on estimates of I_n because the these indirect methods are unable to quantify changes in p, S , $\overline{E}/\overline{R}$ and P_s on a per storm basis. Recently, Link et al. (2004), proposed a new method that combines high-resolution data from an array of tipping bucket rain gauges with the mean method to estimate S, p and $\overline{E}/\overline{R}$ for each individual storm (we term this method for individual storms the IS method).

The goal of this project was to use the IS method to quantify and contrast the canopy water budgets of young and old-growth Douglas-fir forests. The two forests we studied are only about 4 km apart, and have similar LAI (about 10). The young forest is a 20 m tall, 25-y-old, even-aged, homogeneous Douglas-fir forest in the stem exclusion stage with a low gap fraction and small epiphyte population. In contrast, the old-growth forest is a 65 m tall, >450-y-old, uneven aged, heterogeneous Douglas-fir/Western Hemlock forest with a large gap fraction, large epiphyte population and is in the vertical or horizontal diversification stage. Functional attributes of these forests have been described in previous studies (e.g. Chen et al., 2004; McDowell et al., 2002; Phillips et al., 2003). This paper focuses on how short

(seasonal) and long-term (young vs. old-growth) developmental changes in canopy structure affected the S, p, $\overline{E}/\overline{R}$, I_n and spatial distribution of throughfall and soil moisture in Douglas-fir forests in the PNW using high-resolution rainfall data. More specifically the objectives of this study were to: 1) estimate the seasonal changes in S, p, $\overline{E}/\overline{R}$, I_n and spatial variability of throughfall and soil moisture for a young Douglas-fir forest; 2) compare the results with variables derived for an old-growth Douglas-fir forest with a similar LAI but different canopy structure; and 3) explore the effect seasonal changes in S, p and $\overline{E}/\overline{R}$ have on estimates of I_n produced by the Gash model (Gash, 1979).

3.0 Material and methods

3.1 Site description

The young 20 m, 25-y-old, planted Douglas-fir forest and the old-growth Douglas-fir forest (>450-y-old) (Link et al., 2004) are both located within the Gifford Pinchot National Forest and are approximately 4 km apart. The young forest (45º49'07.89" N, 121º59'38.95" W) is adjacent to the T.T. Munger Research Natural Area (elevation = 558 m a.s.l.) and was planted with Douglas-fir (*Pseudotsuga menziesii*) in 1977. The dominant understory woody species are western hemlock (*Tsuga heterophylla*) and vine maple (*Acer circinatum*).   The basal area of the Douglas-fir, western hemlock and vine maple was 29.5, 1.7 and 0.5 m^2 ha^{-1}, respectively. The forest floor was dominated by salal (*Gaultheria shallon*) (percent cover = 15%) and twin flower

(*Linnaea borealis* (percent cover = 4%), but the majority of forest floor was unvegetated (53% bare). Fourteen species of shrubs and herbs covered the remaining 28% of the forest floor. The litter depth on the forest floor was measured as 2.3 cm (n = 25 95%CI (1.8, 2.8)) by inserting pins vertically into the litter and measuring the depth at which the pin hit the mineral soil.

The old-growth forest is in Wind River Canopy Crane Research Forest (45º49'13.76" N, 121º54'06.88'W) at 368 m a.s.l.. A complete description of the forest and research facility can be found in Shaw et al. (2004). In short, the old-growth forest has a basal area of 70.98 m^2 ha^{-1} and 441 stems ha^{-1}. The majority of the trees are western hemlock (basal area 31.32 m^2 ha^{-1}; 244 stems ha^{-1}; average height 19.4 m; tallest tree 55.7 m) and Douglas-fir (basal area 29 m^2 ha^{-1}; 50 stems ha^{-1}; average height 52.2 m, tallest tree 64.6 m) (Shaw et al., 2004). There is an abundance of epiphytic lichens and bryophytes in the canopy (McCune, 1993). The understory is mostly vegetated (only 3% bare ground) and was dominated by bryophytes (27% cover), salal (15% cover), Oregon grape (14% cover) and vine maple. The litter depth on the forest floor was measured to be 8.1 cm (n = 50 95%CI (7.3, 8.9)). The forests have a temperate climate, wet winters, dry summers and receive over 2500 mm of annual precipitation.

3.2 Leaf area index (LAI) and gap fraction

LAI was measured in July 2002 using an LAI-2000 Plant Canopy Analyzer (LICOR, Inc., Lincoln, NE, USA). We made 50 measurements in the late evening in the young and old-growth forests and adjusted the LAI

estimates for clumping (Frazer et al. 2000) (LAI was adjusted by 1.89 for the young forest and 2.03 for the old forest).   The LAI for the young and old Douglas-fir forests was 10.2 (n = 73, 95%CI (9.0, 11.1)) and 9.6 (n = 26, 95%CI(9.0, 10.2)), respectively. In 2002, the LAI for the young forest was not statistically different from the average of for the old-growth forest (p-value = 0.17). The estimate of 9.6 was similar to the estimate of 8.6 by Thomas and Winner (2000) for 1997-99, using a line intercept method with estimates ranging between 8.2 and 9.3.

Gap fraction was calculated at the young forest using hemispherical photographs produced by a 180º fish-eye lens (Camera - Canon AE-1; Lens - 7.5 mm Cannon Fish-eye lens 7.5 mm 1:5.6, Canon USA Inc., New York, NY, USA). All photographs were taken at low sun elevation in the late evening. The images were analyzed for the fraction of open pixels (CANOPY, Los Alamos National Laboratory, Los Alamos, New Mexico, USA). For an estimate of gap fraction in the old-growth forest we used values produced by hemispherical photographs and published in Parker et al. (2004). The gap fractions for the young (0.11, n = 18, 95% CI (0.07, 0.15)) and old-growth (0.23 (Parker et al., 2004)) forests were statistically different (p-value >0.001).

3.3 Theory and calculation of canopy hydrologic variables

Rainfall events in forests can be partitioned into two discrete periods; pre- and post- canopy saturation. Prior to saturation the rainfall reaching the forest floor is primarily comprised of drops that pass directly to the forest floor without encountering foliage. The drops that do not reach the forest floor are

intercepted and temporarily stored by the canopy. The cumulative throughfall

during the storm (P_n (mm)) prior to canopy saturation rises less rapidly than

the cumulative gross precipitation during the storm (P_G (mm)) (i.e. P_n/P_G at

any time prior to canopy saturation is <1 and equal to p). Once the canopy

water storage (S) is filled (i.e. P_s= P_G, where P_S is the accumulated

precipitation that corresponds to canopy saturation), increases in P_n will

closely follow increases in P_G (Figure 1), and P_n will be less than or equal to

P_G unless there are other sources of water such as fog drip. If the slope of the

relationship between P_n and P_G is less than one, the difference from one is the

ratio of evaporation to rainfall intensity, or $\overline{E}/\overline{R}$.   Once the rain event is

finished, I_n can be calculated by dividing P_n by P_G.

The Individual Storm method (IS method) was applied to estimate S,

direct throughfall fraction (p), $\overline{E}/\overline{R}$ and interception loss (I_n) (see Link et al.,

2004). In brief, S, p, $\overline{E}/\overline{R}$, and I_n were calculated using the cumulative

relationship between P_n and P_G over discrete 10-minute intervals (Figure 1).

Prior to canopy saturation the relationship between P_G and P_n is calculated as:

$P_n = pP_G$ (1)

where p is the proportion of rainfall that passes through the canopy prior to

canopy saturation (Figure 1 – prior to inflection point). Prior to saturation

rainfall either directly reaches the forest floor or is intercepted by canopy.
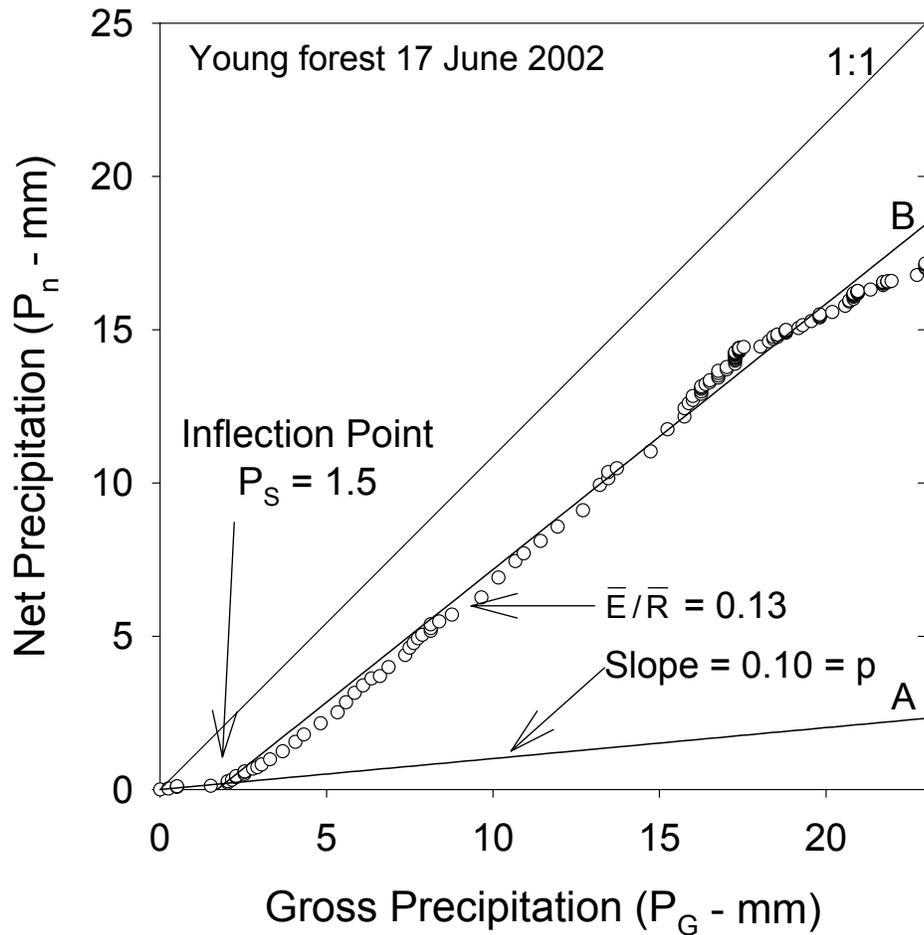
Figure 1 - The relationship between cumulative gross precipitation (P_G) and net precipitation (P_n) during a storm in the young forest (17 June 2002). The slope of regression "A" represents the direct throughfall (p = 0.10), the difference between P_G and P_n at the inflection point represents the canopy storage (S), the value of P_G at the inflection point is the canopy saturation point (P_S) and one minus the slope of regression "B" represents the ratio of evaporation to rainfall intensity ($\overline{E}/\overline{R}$ = 1-0.87).

Intercepted rainfall will either drip to the forest floor or evaporate back to the atmosphere (Figure 1 – after the inflection point). Hence, following saturation, the rainfall beneath the canopy is described as:

$$P_n = pP_s + (1 - \overline{E}/\overline{R})(P_G - P_S) \quad (2)$$

S is then computed by:

$$S = (1-p)P_S - I_W \quad \text{or} \quad S = (1-p)P_S \quad (3)$$

where I_W is the rainfall that is evaporated during canopy wet-up. Because Link et al. (2004) found I_w overestimated evaporation for an old-growth Douglas-fir, S was estimated with (S_w) and without I_w (S_{wo}). I_W was estimated by:

$$I_W = (\overline{E}/\overline{R})P_S \quad (4)$$

We used a second method (Subtraction method) to verify the estimates of E by the IS method (Horton, 1919). To allow for a comparison with the evaporation rate produced by the IS method, $\overline{E}/\overline{R}$ can be estimated by dividing E by P_G (E/R). The subtraction method estimates evaporative loss using a mass balance approach (Equation 5).

$$E = P_G - S - P_n \quad (5)$$

Here E is assumed to represent any rainfall that is not accounted for by S or P_n.

3.4 Throughfall measurement

Throughfall was measured 2002 using a roving array of 23 tipping bucket rain gauges (TE-525I, Texas Electronics Inc., Dallas, TX, USA) from 17

June to 30 November 2002. Each tipping bucket rain gauge has a collection area of 325 cm^2 and a resolution of 0.254 mm. The gauges were placed 1 m above the ground and the data were stored on individual microdataloggers (HOBO event, Onset Computer Corp., Pocasset, MA, USA). Two roughly perpendicular 70 m transects were established, and half of the tipping bucket array were randomly placed on each transect. A second array of 48 manually measured throughfall collectors complemented the tipping bucket array. Each manual throughfall collector had a 94 cm^2 collection area; the array was used to verify the estimates provided by the tipping bucket array (15 September to 30 November 2002). By placing the array across a range of variability (Kimmins, 1973; Puckett, 1991) and relocating the collectors on a regular basis (every 4-6 weeks) the errors in the throughfall estimates were reduced by increasing the number of sampling points in the plot (Lloyd and Marques Filhode, 1988; Wilm, 1943). The manual throughfall collectors and tipping buckets were cleaned and leveled every 4 weeks.

3.5 Stemflow

Stemflow was not measured directly at either the young or old-growth forests because rough-barked species typically have low stem flow values (Geiger, 1965; Helvey and Patric, 1965). For example, Rothacher (1963) found stemflow to be negligible in an old-growth forest Douglas-fir forest in the PNW (<0.27% of P_G), and a watering experiment by Hutchinson and Roberts (1981) demonstrated that stemflow was less than 2% of P_G for a young (9-y-old) Douglas-fir tree. However, Aussenac and Boulangeat (1980), Iroumé and

Huber (2002), and Mitscherlich and Moll (1970), found that stemflow could

range between 3 and 11% of P_G in young (<30-y-old) Douglas-fir forests. It is

difficult to infer stemflow values from one forest to another even if they are the

same forest type (Levia Jr and Frost, 2003). Stemflow values greater than 5%

of P_G are unlikely at the Wind River forest; to maintain mass balance with

stemflow greater than 5% of P_G, it would be necessary for the evaporative loss

to be negative for several of the storms in the young forest.   Fog drip is the

only likely mechanism that could account for evaporative loss being less than

zero (P_n>P_G). However, there was no evidence of fog drip in this forest during

the measurement period. Therefore, to test the sensitivity of the results to

changes in stemflow, we present two possible stemflow scenarios for the

young forest: stemflow = 0 and 5% of P_G for storms sufficient to saturate the

canopy (P_G > 5 mm).

3.6 Meteorological and soil moisture data

Gross precipitation was measured at the young site using two tipping

bucket rain gauges (TE-525I, Texas Electronics Inc., Dallas, TX, USA) with

individual microdataloggers (HOBO event, Onset Computer Corp., Bourne,

MA) placed at the top of a 25 m tower located within the study plot. The error

associated with measurements at this height are probably low because the

average windspeed during storm events was less than 0.7 m s^{-1}, with

maximum gusts that rarely exceeded 3 m s^{-1} (K Bible, Wind River Canopy

Crane Research Facility, unpublished data). Based on the typical rainfall

intensities (0.25 to 2 mm h^{-1}) and windspeeds (0 to 1 m s^{-1}) that occurred

during the measurement period, past work on other unshielded rain gauges indicates that the error in P_G should range between 1 and 6% (Michelson, 2004). The maximum error during the short periods where the windspeed exceeded 3 m s^{-1} and the rainfall intensity was low (0.25 mm h^{-1}) would be approximately 17% (Michelson, 2004). To complement the rainfall data, we monitored volumetric soil moisture using time domain reflectometry (TDR) (Model 1502C, Tektronix, Inc., Beaverton, OR). 20 pairs of TDR rods, 45 cm long, were inserted at 45° (integrated depth – 31 cm) at random locations along a 70 m transect at both sites (minimum spacing of 2 m), and measured every two weeks. The TDR observations were converted to estimates of volumetric soil moisture using site-specific calibrations (Czarnomski et al., in review).

3.7 Evaluation of the Gash model

The Gash model is a powerful tool for estimating I_n because of its simple requirements of S, p, and $\overline{E}/\overline{R}$. 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:

$$I_c = (1-p)\sum_{j=1}^{m} P_{G,j} \quad (6)$$

The amount of interception for n storms sufficient to saturate the canopy (i.e. $\geq$ the amount of rainfall to saturate the canopy - P_S) is calculated as the amount of water lost during wet up (I_w), the evaporation subsequent to canopy saturation (I_S) and the evaporation after the storm ceases (I_a). These interception variables are calculated as:

$$I_w = n(1-p)P_S - nS \quad (7)$$

$$I_S = (\overline{E}/\overline{R})\sum_{j=1}^{n}(P_G - P_S) \quad (8)$$

$$I_a = nS \quad (9)$$

P_S, S and $\overline{E}/\overline{R}$ were derived by averaging the values calculated from storms sufficient to saturate the canopy. The model was used on a per storm basis.

4.0 Results

4.1 Historical rainfall pattern

The summer and fall months of 2002 were dry (446 mm) relative to the average precipitation (1978-2001) at a meteorological station located approximately 6 km from the research site (NOAA National Climate Data Center (NCDC), data not shown). The only month where rainfall exceeded the historical average was in June (80 mm (2002) vs. 58 mm (historical)). During the spring, summer and fall of 2002, rainfall at the young forest was fairly

similar to that at the old-growth forest in 2000, but with substantially more

rainfall in October and less rainfall in November relative to 2002.

4.2 Canopy water capacity storage (S)

When evaporation prior to canopy to saturation (I_w) is included, S for

the young forest averaged 1.3 mm (95% CI (0.89,1.6), for all storms sufficient

to saturate the canopy - P_G > 5 mm) (Table 1). Without incorporating I_w, the

average S increased by 0.3 mm to 1.6 mm (95% CI (1.3,1.8) (Table 1).

Regardless of whether I_w was used in the calculation, there was considerable

seasonal variation in S during the study period (Figure 2). Following canopy
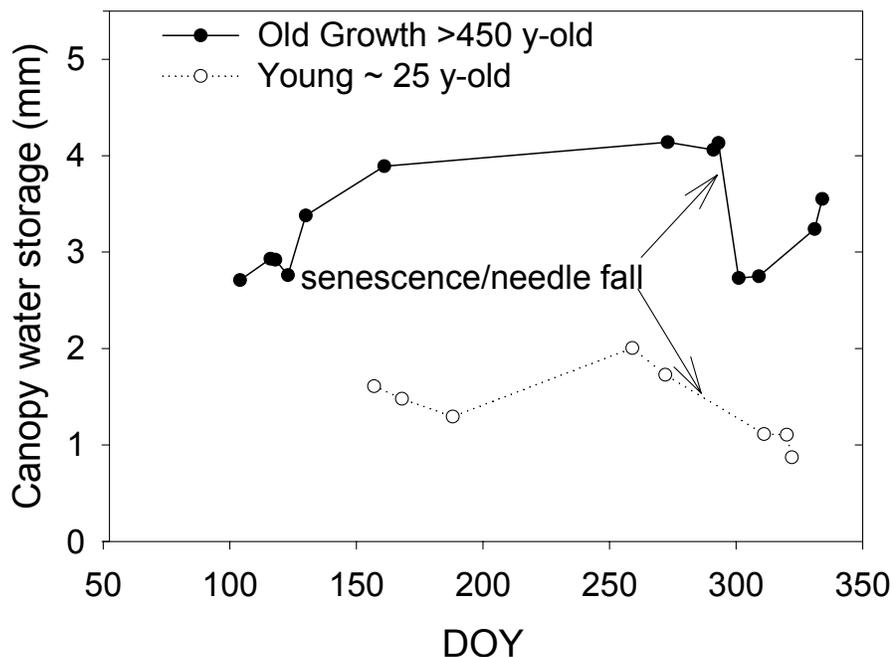
Figure 2 – The seasonal changes in canopy water storage for a young (25-y-old) and old-growth (>450-y-old) Douglas-fir forests in South Central Washington.

Table 1 – Gross precipitation (P_G), net throughfall (P_n), interception loss (I_n), ratio of evaporation to rainfall intensity ($\bar{E}/\bar{R}$), canopy water storage capacity with (S) and without including evaporation prior to saturation (S_{wo}) and direct throughfall fraction (p) for a young Douglas-fir forest.

Event	DOY	Duration (h)	P_G (mm)	P_n (mm)	I_{net} (mm)	I_{net} % loss	$\bar{E}/\bar{R}$ [1]	E/P_G [2]	S_w (mm)	S_{wo} (mm)	p (dimensionless)
1	157	29.67	22.99	17.16	5.83	25.4	0.13	0.19	1.48	1.74	0.10
2	168	16.67	57.66	47.31	10.35	18.0	0.16	0.16	1.33	1.63	0.13
3	188	4.67	5.08	2.57	2.51	49.5	0.31	0.29	1.02	1.57	0.12
4	216	6.33	4.32	1.93	2.39	55.3					
5	259	24.17	15.11	12.23	2.12	14.8	0.01	0.05	1.99	2.02	0.04
6	272	37.5	38.35	33.74	4.11	10.8	0.05	0.06	1.68	1.78	0.08
7	276	9.83	2.54	1.04	1.50	59.0					
8	311	137.8	198.25	160.96	37.29	18.8	0.18	0.18	0.97	1.26	0.23
9	320	22.83	39.12	26.42	12.70	32.5	0.30	0.30	0.88	1.33	0.10
10	322	24.83	35.31	25.80	9.51	26.9	0.25	0.25	0.71	1.03	0.18
Total			418.73	329.16	88.31	21.4					
Mean		31.43	41.75	32.92	8.84	31.1	0.18	0.19	1.26	1.55	0.12
Max		137.8	198.25	160.96	37.29	59.0	0.31	0.30	1.99	1.81	0.23
Min		4.67	2.54	1.04	1.50	10.8	0.01	0.05	0.71	1.28	0.04

[1] IS method
[2] Subtraction method

Table 2 - Forest characteristics for a young (25-y-old) and old-growth (>450-y-old) Douglas-fir forest in South Central Washington.

Variable	Young Forest	Old-growth Forest
Age (yr)	25	>450
Height (m)	20	65
Dominant tree species	Douglas-fir	W. Hemlock/Douglas-fir
LAI (m^2/m^{-2})	10.2 ±1.1	9.6 ±0.52
Litter depth (cm)	2.32 ±0.50[*]	8.1 ±0.80
Bare ground (%)	53	3
Epiphytes (kg ha^{-1})	Negligible	1780
Canopy water storage (mm)	1.4 ±0.27[*,$]	3.32±0.35[*]
Direct throughfall faction	0.12 ±0.07[*]	0.42 ±0.07[*]
Interception loss (proportion)	0.25 ±0.10[!,*] 0.20 ±0.10[#,*]	0.24 ±0.08[*]
Canopy saturation point (mm)	1.75 ±0.23[*]	
Spatial distribution of throughfall	Normal	Right-Skewed
$\bar{E}/\bar{R}$ (proportion)	IS method: 0.18 ±0.09[!,*] 0.12 ±0.09[#,*] Subtraction method: 0.19 ±0.08[!,*] 0.14 ±0.08[#,*]	IS method: 0.17 ±0.06[*] Subtraction method: 0.10 ±0.05[*]

[!] no stemflow
[#] 5% stemflow
[*] for storms > 5 mm in the young stand and >10 mm in the old-growth stand.
[$] calculated using the average of S_w and S_{wo} (see methods)

senescence and needle drop, S dropped from 2.0 mm to 1.0 mm in the young forest.

The mean and minimum methods estimated S to be 1.6 and 1.2, respectively, which is similar to the estimates from the IS method. In contrast, S was nearly twice as large in the old-growth Douglas-fir forest relative to the young forest (average = 3.3 95% CI (2.8,3.7), for storms >10 mm) for the entire measurement period in 2000 (Figure 2; Table 2) (p-value < 0.001). Storms with less than 10 mm of rainfall were not used to calculate canopy variables because of the larger S in the old-growth forest.

4.3 Direct throughfall (p)

From June to November 2002, p averaged just 0.12 (95%CI (0.07, 0.17) for storms>5 mm) for the young Douglas-fir forest (Figure 3). In the young forest, p was significantly smaller compared to the average of 0.42 (95% CI(0.35, 0.50) for storms>10 mm) for the old-growth Douglas-fir forest in 2002(p-value < 0.001) (Figure 3).

4.4 Net precipitation, interception loss (I_n) and evaporative loss

For the young forest the P_n was 329 mm for storms measured from 17 June to 22 November 2002. Therefore, for all storms at the young forest I_n was 21% and 16% for the scenarios of no stemflow and 5% stemflow, respectively. The P_n estimated by the 48 manual collectors corroborated the tipping bucket estimates (Table 3). For the three periods when the manual collectors were measured, the measurements of the two collector arrays did not differ by more than 2.4%.

The average I_n for storms sufficient to saturate the young Douglas-fir forest's canopy (P_G > 5mm) was 25% (n=8, 95%CI(14, 35) no stemflow) or 20% (n=8, 95%CI(12,32), 5% stemflow) (Figure 5; Table 1, 4). The I_n for storms greater than 10 mm for the old-growth forest averaged 24% (n=13, 95%CI (16, 32)), and was not significantly different from the I_n for the young Douglas-fir forest (p-value > 0.7475). However, if the Gash model is applied to the canopy parameters for the young and old-growth forests for a set of hypothetical storms ranging from 0.5 to 200 mm (Table 1), the I_n is slightly larger for the old-growth forest for storms between 10 and 100 mm (Figure 4).
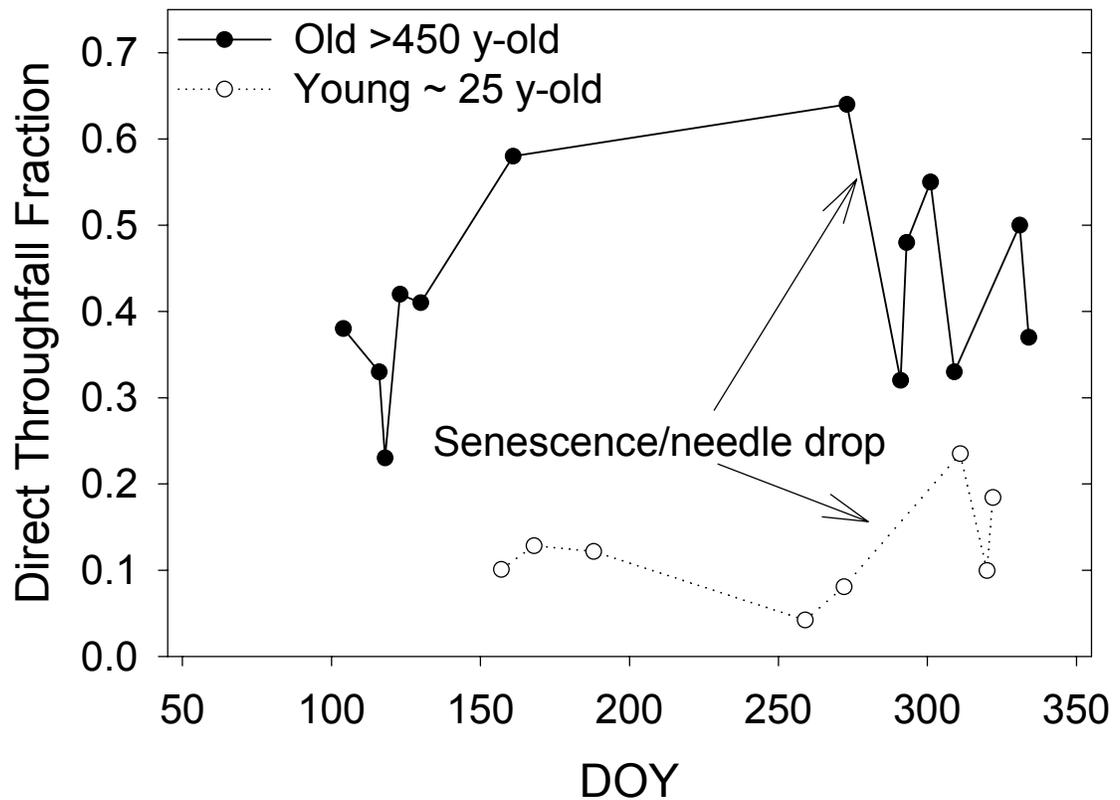
Figure 3 – Inter-storm differences in direct throughfall for a young (25-y-old) and old-growth (>450-y-old) Douglas-fir forest in South Central Washington.

Table 3 – Comparison between 48 manual throughfall collectors and 24 tipping bucket rain gauges for three periods between 15 September to 27 November 2002. % Error is calculated as ((TB-MC)/TB)*100, where TB is the throughfall measured by the tipping buckets and MC is the throughfall measured by the manual collectors.

Measurement period		Manual Collectors			Tipping Buckets			Error
Start	End	mm	SE	95% CI	mm	SE	95% CI	%
15 Sept.	17 Sept.	12.18	0.44	0.88	12.38	0.76	1.53	1.6
17 Sept.	5 Oct.	34.43	1.26	2.53	34.8	1.82	3.68	1.0
17 Nov	27 Nov	26.42	1.12	2.25	25.8	2.37	4.78	-2.4
Totals		73.03			72.98			<0.01

E/R for the young forest averaged between 19% (no stem flow scenario) (n = 8, 95% CI(11,26)) and 14% (5% stemflow scenario) (n = 8, 95% CI(8,23)) of P_G using the Subtraction method and $\bar{E}/\bar{R}$ was 18% (no stem flow) (n = 8, 95% CI(8,27)) and 12% (5% stemflow scenario) (n = 8, 95% CI(3,22)) using the IS method (Table 1 and 4). When estimated using the IS method, $\bar{E}/\bar{R}$ in the old-growth forest was 17 % (n = 13, 95% CI(10, 24)), but E/R was lower when estimated by the Subtraction method 11% (n=13, 95% CI (5,17)). The young forest evaporative losses during the storms are similar to the evaporative losses from the old-growth forest (no comparison produced a p-value < 0.05).

Table 4 – Interception loss (I_n) and the ratio of evaporation to rainfall intensity ($\bar{E}/\bar{R}$) for storms from 17 June to 22 November 2002 using two scenarios: no stemflow; 5% stemflow.

Event	DOY	No Stemflow			5% Stemflow		
		I_n (mm)	$\bar{E}/\bar{R}$ [1]	E/P_G [2]	I_n (mm)	$\bar{E}/\bar{R}$ [1]	E/P_G [2]
1	157	5.83	0.13	0.19	4.68	0.08	0.14
2	168	10.35	0.16	0.16	7.77	0.11	0.11
3	188	2.51	0.31	0.29	2.26	0.26	0.24
4	216	2.39	-	-	2.39	-	-
5	259	2.12	0.01	0.05	1.98	-0.04	0.00
6	272	4.11	0.05	0.06	2.69	0.00	0.01
7	276	1.50	-	-	1.50	-	-
8	311	37.29	0.18	0.18	27.38	0.13	0.13
9	320	12.70	0.30	0.30	10.74	0.25	0.25
10	322	9.51	0.25	0.25	7.74	0.20	0.20
Totals		88.31			69.13		
Mean			0.18	0.19		0.12	0.14

[1] Calculated using the IS method
[2] Calculated using the Subtraction method
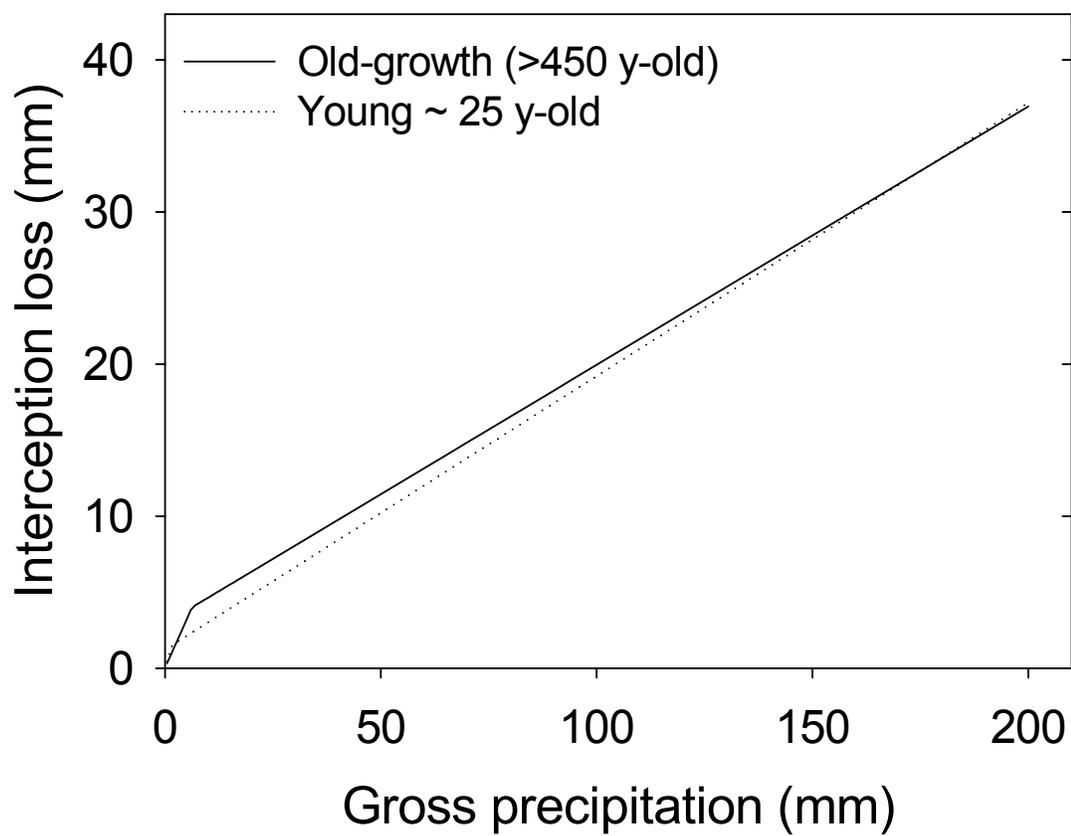
Figure 4 – The Gash model was applied to the canopy variable from the young and old-growth Douglas-fir forest (Table 2). The interception loss (I_n) is similar for the two forests after both canopies saturate.
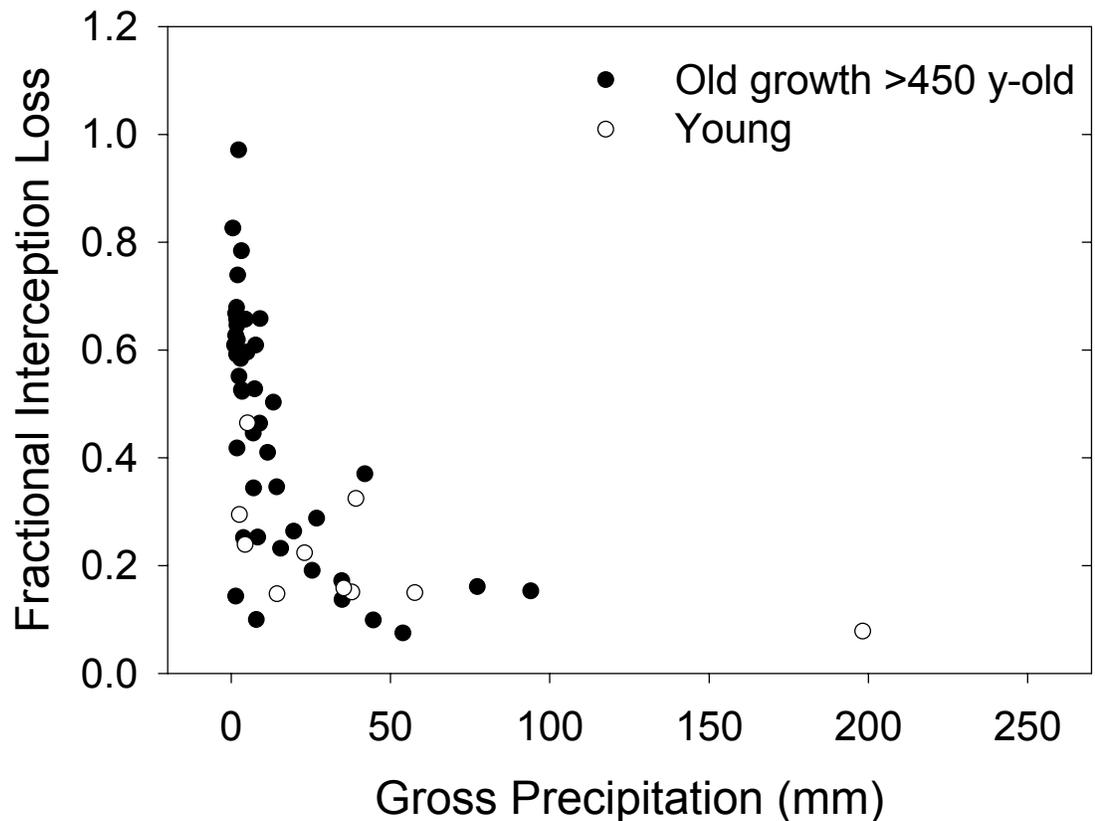
Figure 5 – The interception loss for a young (25-y-old) and old-growth (>450y-old) Douglas-fir forests relative to gross precipitation (P_G). The interception loss for storms >10 mm did not statistically differ (p-value<0.74).

4.6 Spatial variability of throughfall and soil moisture content

The rainfall was spatially distributed more normally in the young forest than in the old-growth forest (Figure 6). The old-growth forest had a greater proportion of the gauges than the young forest where $P_n>P_G$ (0.23 and 0.14, respectively). Furthermore, a larger number of gauges received <20% of P_G in the old-growth forest than in the young forest (0.04 and 0.01, respectively). The soil moisture for the young and old-growth forests did not differ throughout the 2002 growing season for any date (p-values between 0.12 and 0.92)
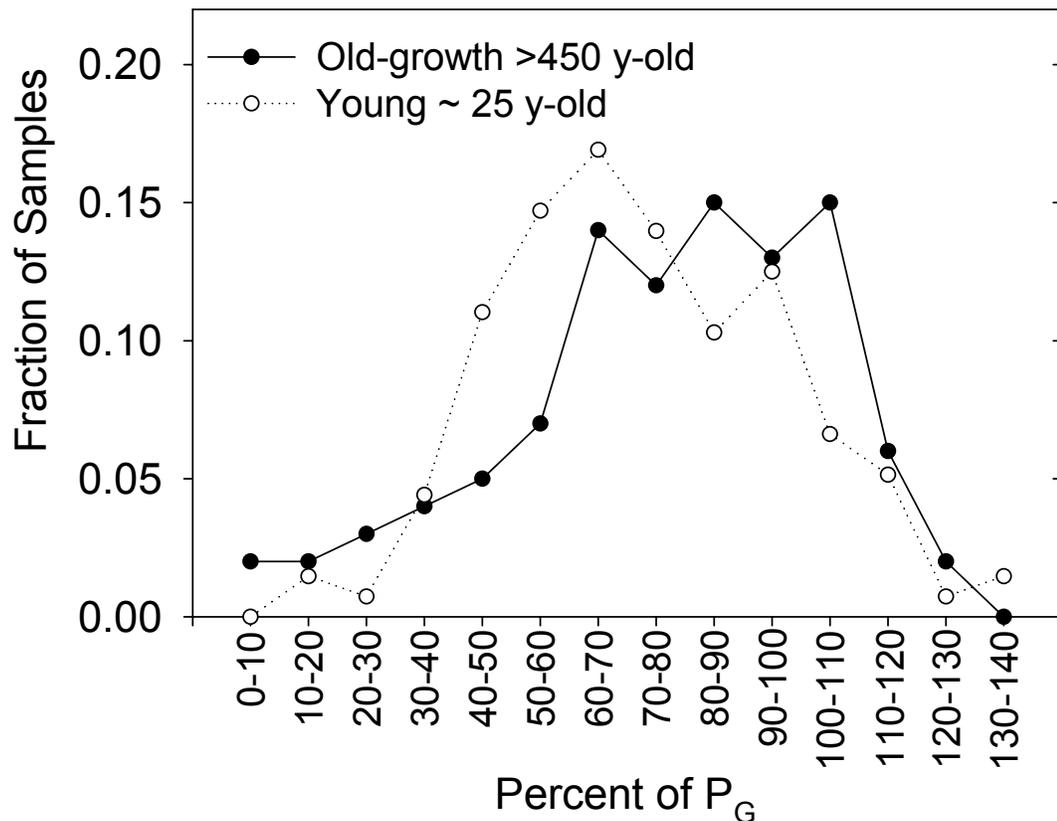
Figure 6 – The spatial distribution of net precipitation (P_n) under the young (25-y-old) and old-growth (>450-y-old) canopies (old-growth – n = 237; young – n =136).

(Figure 7). Furthermore, the variability in soil moisture values only differed on

DOY 191, 199 and 331 (Levene's test: p-value <0.05, <0.01, <0.05,

respectively). On those dates the soil moisture at the young forest was more

variable than at the old-growth site. Lastly, there was a weak, but significant,

negative relationship between time since last rainfall and the variability found

at the young and old forests (p-value = 0.02 and 0.05 for the young and old

forests, respectively).
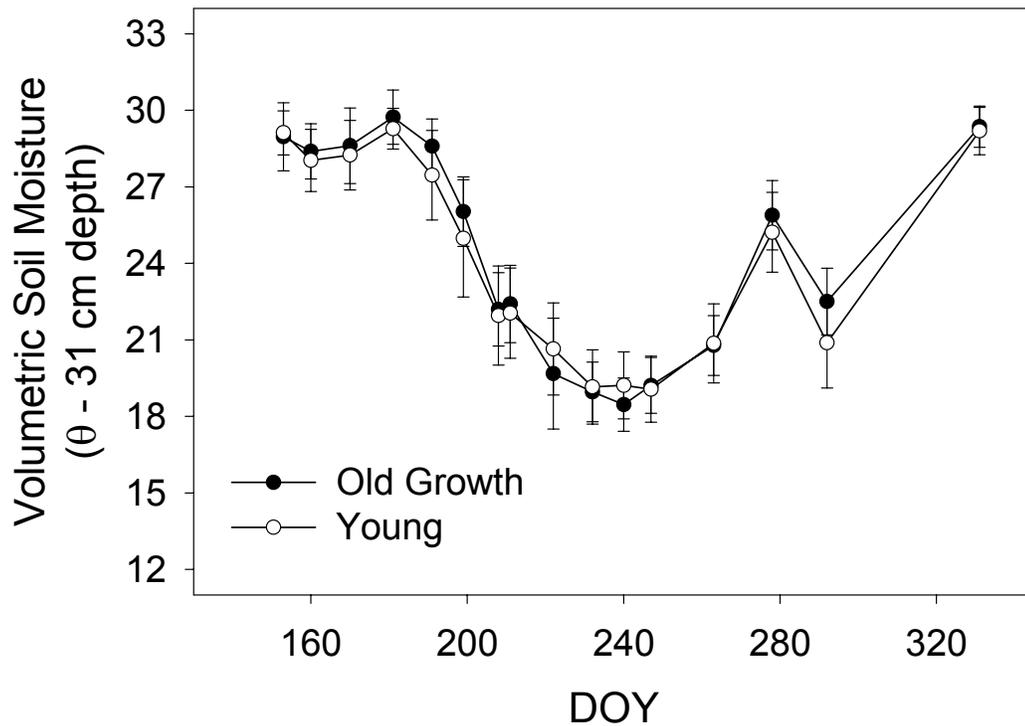
Figure 7 – The soil moisture content for the summer of 2002 in a young (25-y-old) and old-growth (>450-y-old) Douglas-fir forest in South Central Washington.

4.7 Gash Model

The simplified Gash model predicted values very similar to the

measured values for all storms at the young site (Table 5) and the predicted

seasonal total for I_n did not differ statistically from the estimates from the

tipping buckets (Table 5, p-value=0.92). The Gash model predicted the I_n to

be 83.4 mm, or 20%, of P_G from June through November. When the Gash

model incorporated the seasonal variation of p, S and $\overline{E}/\overline{R}$ determined from

use of the IS Method, the errors associated with the seasonal totals were

slightly reduced from 3.3% to 2.4%. However, when seasonal variation in p, S

and $\overline{E}/\overline{R}$ were incorporated on a per storm basis, the errors decreased for all but one storm (Table 5).

5.0 Discussion

5.1 Canopy water storage capacity (S)

The IS method estimated S_w and S_{wo} for the young Douglas-fir forest to range between 1.3 and 1.6 mm, respectively (Table 1; Figure 2). Link et al. (2004) demonstrated that S is significantly reduced when I_w is included in the calculation of S (Equation 3). However, to assume that there is no evaporation when the canopy is wetting up is also unreasonable. The canopy typically required between 1 and 1.5 h to saturate and the difference between S_w and S_{wo} was 0.3 mm.   Therefore, the average evaporation rate was between 0.2 and 0.3 mm h^{-1}; more than twice that commonly found for temperate Douglas-fir forests (Klaassen et al., 1998).   Since there was no independent method for determining evaporation, and the I_w appeared to be too large, the average of S_{wo} and S_w was used to provide a seasonal estimate of S (S = 1.4 mm) (Table 1).

The values of S estimated by the IS method in the young forest were similar to estimates by the minimum method, mean method and past studies on young Douglas-fir forests. The estimate of S is very similar to the seasonal averages estimated by the minimum method (S = 1.2 mm) and mean method (S = 1.6 mm). Past studies on Douglas-fir forests in Europe found S ranged between 2.1 (Rutter et al., 1975) and 2.4 mm (Klaassen et al., 1998). S was

Table 5 – Estimates of I_c, I_w, I_S and I_a using a simplified version of the Gash model (1979) for a young Douglas-fir forests in south central Washington. The Gash model estimates are produced using either seasonal averages for canopy variables, or using variables produced by the IS method on a per storm basis. The estimates are compared with results from storm events measured using an array of tipping bucket rain gauges. Error (%) was calculated as ((MI-GI)/MI_ *100, where MI is measured interception loss (I_n) and GI is the Gash model estimates for I_n.

Event	DOY	Measured Variables			Gash Model – Average Seasonal Variables						Gash Model – Storm variables					
		P_G	P_n	I_n	I_c	I_w	I_s	I_a	Total	Error	I_c	I_w	I_s	I_a	Total	Error
		mm	mm	mm	mm	mm	mm	mm	mm	%	mm	mm	mm	mm	mm	%
1	168	22.99	17.16	5.83	0	0.14	3.72	1.4	5.26	9.83	0	0.26	2.82	1.48	4.56	21.7
2	179	57.66	47.31	10.35	0	0.14	9.78	1.4	11.32	-9.40	0	0.30	9.05	1.33	10.68	-3.22
3	188	5.08	2.57	2.51	0	0.14	0.58	1.4	2.12	15.5	0	0.55	1.02	1.02	2.59	-3.14
4	216	4.32	1.93	2.39	0	0.14	0.45	1.4	1.99	16.7	0	0.29	0.45	1.25	1.99	16.7
5	259	14.35	12.23	2.12	0	0.14	2.21	1.4	3.74	-76.8	0	0.03	0.15	1.99	2.16	-2.12
6	272	37.85	33.74	4.11	0	0.14	6.32	1.4	7.86	-91.5	0	0.10	1.91	1.68	3.69	10.16
7	276	2.54	1.04	1.50	0	0.14	0.14	1.4	1.68	-12.0	0	0.29	0.14	1.25	1.68	-12.0
8	311	198.3	161.0	37.29	0	0.14	34.39	1.4	35.93	3.66	0	0.30	35.37	0.97	36.63	1.77
9	320	39.12	26.42	12.70	0	0.14	6.54	1.4	8.08	36.4	0	0.45	11.37	0.88	12.70	0.02
10	322	35.31	25.80	9.51	0	0.14	5.87	1.4	7.41	22.0	0	0.32	9.49	0.72	9.52	-0.14
Total		417.4	329.2	88.31	0	1.4	69.99	14.0	85.39	3.29	0	2.88	70.75	12.56	86.20	2.37

I_c – Interception loss for storms insufficient to saturate the canopy
I_W – Interception loss due to evaporation prior to canopy saturation
I_S – Interception loss due to evaporation during the storm, but subsequent to canopy saturation
I_a – Interception loss due to evaporation following the completion of the storm

Table 6 – Canopy water storage capacity (S) and interception loss (In) values for Douglas-fir forests in Europe and North America.

Location	Age	Height	Density	Basal area	LAI	In	S	Reference
Wash., USA	25	20	2200	42	10.1	21.4[1]	1.26	This study
Britain	42	24	660	N/A	N/A	39	2.1	Robins, 1974; Rutter et al., 1975
Netherlands	27	18	800	N/A	9-13		2.4	Klaassen et al. 1998
Netherlands	29	18	992	33.4	8-12	38	N/A	Titak and Bouten, 1994
Oregon, USA	>400	N/A	N/A	33 and 47	N/A	20-30	N/A	Rothacher, 1963
Wash., USA	>450	65	441	67	9.6	25	2.71-4.17	Link et al., 2004

[1]Assumes no stemflow

slightly larger in these forests even though the LAI in the Klaassen et al.

(1998) study was similar to the LAI of the young forest in this study (Table 6).

However, as the following discussion illustrates, LAI may not be a good

predictor of S for Douglas-fir forests.

The greater S in the old-growth forest likely results from changes in

species composition and the colonization of old-growth forests by epiphytes

rather than from changes in LAI. S in the old-growth forest was nearly twice

the value found in the young forest even though the LAIs for the two forests

were very similar (young: 10.2 ±1.1 and old-growth: 9.6 ±0.61) (Figure 2). The

tree species compositions of the young and old-growth forests are not the

same; the young forest is almost entirely composed of Douglas-fir and the old-

growth forest is a mixture of Douglas-fir and western hemlock. As the forest

develops, more shade tolerant species, such as western hemlock, rise out of

the understory and become part of the forest canopy (Franklin et al., 2002).

Keim (2003) demonstrated that under similar simulated rainfall intensities

western hemlock stores 1.5 times more water per m^{-2} leaf surface area relative

to Douglas-fir, and he hypothesized that the different tree species composition

in the old-growth forest altered the magnitude of S. S in old-growth Douglas-fir

forest may also increase because they can contain approximately 1870 kg_{dry}

ha^{-1} of lichens and 780 kg_{dry} ha^{-1} bryophytes (McCune et al. 1993). The

maximum water contents of lichens and bryophytes range between 150 to

350% (Kershaw, 1985) and 500-1200% of their dry biomass (Proctor, 2000b),

respectively; implying that lichens and bryophytes in the old-growth forest may

account for between 0.67 to 1.6 mm of additional water storage. Hence, it

seems likely that the difference in S between these two forests may be

attributed to changes in species composition and canopy structure, not to

differences in LAI.   However, changes in LAI may be responsible for seasonal

variation in S.

Seasonal changes in S in the young forest coincided with phenological

changes of the forest canopy. In the fall, S decreased in the young forest

when deciduous leaf senescence and coniferous needle drop occurred (Table

1; Figure 2). This trend was present in the old-growth forest in 2000, but was

not as pronounced. During the period of needle drop in 2000, S in the old-

growth forest decreased from 4.1 mm to approximately 2.7-3.6 mm.

The magnitude of the seasonal change in S for both forests is difficult to

quantify because S varies with rainfall intensity (Calder et al., 1996) and

changing windspeed (Hörmann et al., 1996). Calder et al. (1996)

hypothesized that increasing rainfall intensity results in decreased S and

Hörmann et al. (1996) found that S was influenced by inter-storm variation in

windspeed and severity of wind gusts, which shake stored water off

leaves/branches. Measurements of windspeed, rainfall intensity and seasonal

variations in LAI are thus needed to properly assess the interactions. LAI was

measured LAI with a LI-Cor LAI 2000, which lacks the sensitivity to distinguish

seasonal changes in LAI in coniferous forests (Chen, 1996).   The change is

likely to be much more pronounced in deciduous forests, but needle drop and storm damage will likely change LAI seasonally in coniferous forests (Chen, 1996; Spanner et al., 1994). For example, Chen (1996) reported that the seasonal change in LAI was between 5 and 10% in stands of jack pine and black spruce in Saskatchewan, Canada. Hence, both short-term (seasonal) and long-term (canopy structural development) changes in canopy structure result in changes in S for Douglas-fir forests.

5.2 Direct throughfall fraction (p)

The floor of the young forest received less direct throughfall (p) than the floor of the old-growth forest because the gap fraction increases as Douglas-fir forests age. The gap fraction in the young forest was only 0.11 relative to 0.23 in the old-growth forest (Parker et al., 2004) (Table 1; Figure 3). Increasing gap fraction as Douglas-fir forests age is common because the large trees eventually die and fall out of the canopy (Franklin et al., 2002). In contrast, young Douglas-fir forests have small gaps and the vast majority of raindrops must strike the branches/foliage before reaching the forest floor.

5.3 Interception and evaporative loss

The young forest in 2002 had a similar I_n to that of the old-growth forest in 2000 despite the larger S in the old-growth forest (Table 1). However, if the Gash model is applied to the canopy parameters for the young and old-growth forests for a set of hypothetical storms ranging from 0.5 to 200 mm, the I_n for the old-growth forest is slightly smaller for storms ranging from 0 to 1.75 mm

and slightly larger for storms between 1.75 and 100 mm (Figure 4). The difference in I_n results from the larger S and p for the old-growth forest. For storms smaller than 1.75 mm the young forest has a greater I_n as 88% of the rainfall is intercepted by the canopy. For storms sufficient to saturate the young forest and insufficient to saturate the old-growth forest (between 1.75 and 6.3 mm) the larger S in the old-growth increases its I_n relative to the young forest. After both canopies saturated, the difference in the I_n of the young and old-growth forests will remain relatively constant because $\overline{E}/\overline{R}$ was similar in the two stands; with the I_n of the young forest exceeding the old-growth forest for storms greater than 100 mm (Table 1; Figure 4). Initially, it is counter-intuitive that the $\overline{E}/\overline{R}$ for a rougher canopy with a greater S would be similar to that of a shorter canopy with a smaller S.

The $\overline{E}/\overline{R}$ is large for PNW forests because the rainfall intensity is relatively low and the rainfall may be discontinuous during a single storm. Average rainfall intensities in the PNW for the measurement period in 2002 ranged between 0.25 and 3.45 mm h^{-1}. After canopy saturation $\overline{E}/\overline{R}$ in the young forest ranged between 0.01 and 0.30 and averaged 0.17. It is not uncommon for forests with low rainfall intensities to have $\overline{E}/\overline{R}$ ranging between 0.20 and 0.40 (e.g Gash et al., 1980; Zinke, 1967). The rate of evaporation depends on the canopy aerodynamic resistance to latent heat transfer (r_a) (Teklehaimanot and Jarvis, 1991; Teklehaimanot et al., 1991), so differences in r_a between these two forests will have a significant impact on the size of $\overline{E}/\overline{R}$.

It is well established that the magnitude of r_a depends on wind velocity (Monteith and Unsworth, 1990).   The importance of wind velocity on evaporation during storms has been both theorized and demonstrated by others (Link et al., 2004; Rutter et al., 1975). The above-canopy windspeeds for the forests in this study are typically three fold greater above the old-growth forest (65 m) relative to the young forest (20 m) (K. Bible, Wind River Canopy Crane Research Facility, data not shown). Despite the greater above-canopy windspeeds, the $\overline{E}/\overline{R}$ ratio in the old-growth forest is not greater than in the young forest. $\overline{E}/\overline{R}$ may be similar in these two forests because r_a depends not only on windspeed, but on the canopy structure (Monteith, 1965). r_a for a canopy in neutral stability is frequently calculated by:

$$r_a = \frac{1}{k^2 u}\left[\ln\left((z-d)/z_o\right)\right]^2 \quad (10)$$

where k is von Karman's constant (0.41), u is windspeed (m s^{-1}), z is the height of windspeed measurement, d is the zero plane displacement and z_o is the roughness length (where the z_o for momentum and sensible heat are assumed equal) (Gash et al., 1999; Monteith and Unsworth, 1990). For uniform canopies, values of d and z_o can be approximated as 0.75h and 0.1h, respectively, where h is canopy height. For the young and old-growth forests to have similar $\overline{E}/\overline{R}$, the combination of canopy structure and windspeed must act to produce a similar resistance to latent heat transfer.

The height of the Douglas-fir trees in old growth forest is substantially greater than in the young forest. Simply, given the average old-growth Douglas-fir heights (52.2 m) and assuming similar conditions above the two

forests, r_a would be smaller for the taller old-growth forest because of increased turbulence from the deeper roughness layer. Larger windspeeds over the taller forest would make r_a even smaller. However, the variable tree species composition may influence the r_a for the old-growth forest. Western hemlock occupy a significant portion of the canopy space, comprise >50% of the stems, have the greatest proportion of the basal area, and have an average height of only 19 m. Hence, old-growth Douglas-fir canopies predominately have a greater proportion of their foliage lower in canopy because of the emergence of shade tolerant trees from the understory and epicormic branches (Ishii et al., 2002; Ishii and Wilson, 2001; Parker et al., 2002; Parker and Russ, 2004; VanPelt and Franklin, 2000). Thus, the use of the average Douglas-fir height is likely inappropriate for calculating d and z_o (and hence, r_a) in the old-growth stand. We hypothesize that $\overline{E}/\overline{R}$ is similar in the young and old-growth forests because the greater gap fraction in the old-growth forest causes $\overline{E}/\overline{R}$ to be diminished.

The old growth forest has large gaps that reduce the area that can effectively exchange latent heat with the atmosphere. Sparse canopies result in suppressed evaporation during storms because of a reduction in the size of the effective area for evaporation (Gash et al., 1995; Gash et al., 1999). We suggest that the larger gap fraction (0.23) causes the old-growth forest to resemble a sparse canopy for evaporation. Link et al. (2004), used the methods from Gash et al. (1995) to predict evaporation from the old-growth forest by calculating the potential evaporation (E_p) using Penman-Monteith

equation (Monteith and Unsworth, 1990) and reducing it by the fraction of canopy cover (c).

$$E = E_p \cdot c \quad (11)$$

By assuming c=0.77 (one minus the gap fraction), the evaporative loss from the old-growth forest would be reduced by 23%.

If the canopy characteristics and the above canopy windspeeds are inserted into equation (10), and c is assumed to be 0.77 for the old-growth forest, the following shows that calculated estimates of $\overline{E}/\overline{R}$ for these two forests are similar. If one assumes that: 1) the windspeeds at the young forest are 1/3 of the windspeed at the old-growth forest; 2) the young forest has a canopy height of 20 m; 3) the old-growth forest has a effective height between the average height of the Douglas-fir and the western hemlock (39 m) 4) all other meteorological variables are identical, the calculated r_a values for the young and old-growth forest are approximately 6.2 and 4.4 s m^{-1}, respectively; i.e. r_a in the old-growth forest is 70% of the r_a for the young forest. The Penman-Monteith equation would therefore, estimate $E_{p(old-growth)}/E_{p(young)}$ = 1/0.7=1.4. Applying a gap-fraction correction c = 0.77 to the old-growth estimate would make $E_{p(old-growth)}/E_{p(young)}$ = 1.4*0.77=1.1, providing support for the similarity of $\overline{E}/\overline{R}$ between the two forests. Hence, developmental changes associated with old-growth canopy structure may mitigate evaporative losses by reducing z_o, d and the effective area for evaporation.

5.4 Spatial variability of throughfall and soil moisture

The greater p, S and gap fraction in the old-growth forest resulted in more spatially variable throughfall relative to the young forest (Figure 6). The value of p in the old-growth forest varied between 20-42% and the gap fraction was estimated at 23% (Parker et al., 2004). The large gap fraction implies that approximately 77% of the forested area stores a sufficient amount of rainfall to produce an average S of 3.3 mm for the old-growth forest. Furthermore, there are likely drip zones at the edges of the large canopy gaps because branches in the lower portion of an old-growth forest are typically horizontal or downward sloping (Zimmerman and Brown, 1971) and water will likely flow away from the bole of the tree. Conversely, the young forest has a low p and gap fraction and subsequently a more evenly distributed S. The more homogeneous young forest canopy will likely have fewer drip zones because the branches from different trees overlap. Consequently, the differences in the canopy structure results in skewed and normally-distributed throughfall in the old-growth and young forests, respectively (Figure 6), with many more locations beneath the old-growth forest, relative to the young forest, receive rainfall in excess of P_G.

The greater spatial variability of throughfall in the old-growth forest was expected to produce more heterogeneous soil moisture contents relative to the young forest. However, for most of the measurement period the spatial variability of soil moisture in the mineral soil was not statistically different in these two forests. This may be because of plant water uptake, forest floor

bryophyte cover and litter depth modulate potential impacts of the spatial variability of P_n. Eschner (1967) implied that the spatial distribution of soil moisture may depend on throughfall distribution, and Keim et al. (in review), found that the spatial pattern of throughfall was consistent from storm to storm. Given the consistent pattern, plants may place their roots in areas that receive more throughfall. Extraction of water via transpiration would then reduce the spatial variability of soil moisture. For example, Ford and Deans (1978) found that the biomass distribution of fine roots paralleled the spatial pattern of throughfall in a Sitka spruce forest. Bryophytes and litter on the old-growth forest floor may also alter the spatial variability in soil moisture. The TDR rods in this study were point samples that integrated the volumetric soil moisture for the top 31 cm of the mineral soil. Prior to reaching the mineral soil, throughfall in the old-growth forest may be intercepted by forest floor bryophytes (27% cover) and must pass through about 8 cm (range = 4 to 16 cm) of litter. Hence, the spatial distribution of throughfall measured at the forest floor cannot be directly applied to the distribution in the mineral soil; roots may modify the distribution of soil moisture via transpiration and hydraulic redistribution, and the forest floor litter and bryophytes may further modify the inputs into the mineral soil by intercepting and evaporating the throughfall.

5.5 Validity of the Gash Model

The Gash model worked well for the young forest because of sufficient drying time between storms (Table 5). The Gash model has successfully

estimated I_n for a range of coniferous and deciduous forests (e.g. Gash, 1979; Gash and Morton, 1978; Loustau et al., 1992a). However, the model has been unsuccessful when assumptions have not been fulfilled. For example, if there is insufficient time between storms for the canopy to dry, I_n is overestimated (Hutjes et al., 1990; Link et al., 2004). From 17 June to 22 November 2002, the Gash model and the throughfall array produced very similar estimates of I_n because there was sufficient drying time between storm events (Table 5). Whereas, the seasonal estimates of I_n were accurate, the errors on a 'per storm' basis were large.

Inter-storm variation in S, p and $\overline{E}/\overline{R}$ may contribute to larger errors in individual storm estimates. The individual storm errors ranged from -91 to 36% of the measured I_n for the young forest in 2002 (Table 5). The Gash model was originally created to estimate I_n on a seasonal basis (Gash, 1979); by applying the model seasonally, errors associated with the individual storms cancel each other out, thereby, improving the estimate. However, the larger error associated with individual storms highlight the inter-storm variability of S, p and $\overline{E}/\overline{R}$. If the inter-storm variation in S, p and $\overline{E}/\overline{R}$ were incorporated in the model, the individual storm estimates would improve.

When the Gash model incorporates the S, p and $\overline{E}/\overline{R}$ calculated by the IS method for each individual storm, the range of errors reduces to -12.0 to 21.7% of I_n and the error decreased for all but one storm (Table 5). Changes in rainfall intensity, drop size, windspeeds and rainfall duration can influence the values of S, p and $\overline{E}/\overline{R}$ on a per storm basis (Calder, 1996; Keim, 2003;

Link et al., 2004). Hence, it would be difficult to apply inter-storm variability to a site without constantly measuring the throughfall. However, changes in S correlate with seasonal changes in canopy structure (Figure 2), so, incorporating seasonal change in S may improve Gash model estimates for individual storms.

6.0 Conclusions

The IS method worked well on a young Douglas fir forest in the PNW. The canopy of the young forest is uniform, closed, and the spatial variability of canopy water storage (S) is reduced relative to an old-growth forest.   The values of S and the direct throughfall fraction (p) changed seasonally in the young forest and were significantly smaller relative to the old-growth forest. The higher S occurred in the old-growth forest despite both forests having nearly identical LAI. The increased S likely results from the presence of epiphytes, differences in canopy species and increased surface area of boles and branches. The value, p, was greater in the old-growth forest due to the increased gap fraction.   The high S and p in the old-growth resulted in a more skewed spatial distribution of throughfall relative to the young forest. However, in the old-growth forest, the increased skewness of the spatial distribution of the throughfall did not result in greater spatial variability in soil moisture in 2002. It is likely that other factors such as water uptake by roots and rainfall interception by litter and bryophytes on the forest floor modified the relationship between throughfall and soil moisture. Lastly, even though the values of p and S were very different between the two forest ages, the

evaporative fraction ($\overline{E}/\overline{R}$) was not. As Douglas-fir forests develop, changes in the p, S and gap fraction may act to mitigate changes in I_n and $\overline{E}/\overline{R}$, by influencing the aerodynamic resistance (r_a) and the effective area for latent heat transfer. Seasonally, the Gash model successfully predicted I_n for the young forest. However, on a storm-by-storm basis the errors associated with using the Gash model were fairly high. When the inter-storm variation in S, p and $\overline{E}/\overline{R}$ were applied to the Gash model, the seasonal and the individual storm estimates were improved. Hence, both short (seasonal) and long-term (decades to centuries) developmental changes in the canopy structure significantly influence the S, p and I_n of a Douglas-fir forest.

Acknowledgements

Chapter 3 - The role of epiphytes in the interception of rainfall in old-growth Douglas-fir forests of the Pacific Northwest: Part I – Laboratory analysis

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1.0 Abstract

Colonization of old-growth Douglas-fir forest canopies and forest floor by lichens and bryophytes have a considerable impact on the hydrology of a forest by altering rainfall interception and storage. The maximum water content (MWC_x) of individual samples of fruticose lichens, foliose lichens, bryophytes and dead canopy branches from an old-growth Douglas-fir forest were measured in the laboratory. Epiphyte-laden branches were exposed to three rainfall intensities (11.3, 16.1 and 39.8 mm h^{-1}) under a rainfall simulator. The MWC_x of the lichens, bryophytes and dead branches were measured in the laboratory were combined with the results from the rainfall simulator to determine: 1) whether the lichen and bryophyte biomass present on the branch could be used to predict epiphyte water storage and; 2) the water storage and interception efficiency (p_i) (total rainfall stored by a branch divided by the total rainfall intercepted by a branch) of epiphyte-laden branches.

Epiphytic fruticose lichens, foliose lichens and bryophytes that are typical for old-growth Douglas-fir forests in the Pacific Northwest could store 2.23 $\pm$0.35, 3.42 $\pm$0.64 and 9.99 $\pm$0.48 times of their dry weight in water (MWC_x), respectively. Step moss (*Hylocomium splendens*), electrified cat's tail (*Rhytidiadelphus triquetrus*) and Oregon beaked moss (*Kindbergia oregona*) are abundant on the forest floor of old-growth Douglas-fir forests and have a MWC_x of 8.38 $\pm$0.43, 11.50 $\pm$0.90 and 14.0 $\pm$0.77, respectively. Therefore, an old-growth Douglas-fir forest that contains 1242 kg ha^{-1}, 31 kg ha^{-1} and 780 kg ha^{-1}, of epiphytic foliose lichens, fruticose lichens and

bryophytes, respectively, has the potential to store approximately 1.3 mm of water in the canopy. The potential water storage of the forest is significantly increased if water storage by the forest floor bryophytes (0.6 mm) and dead branches in the canopy (1.06 mm) is included.

The water stored by an epiphyte-laden branch during and after rainfall could be predicted if the biomass of the epiphytic lichens and bryophytes was known (R^2 = 0.80, p-value <0.0001). For all three rainfall intensities, the branches required greater than 6 mm of rainfall to saturate. For each branch the maximum water storage (S_m) during the rainfall simulation and the water stored on the branch after the rainfall simulator was turned off (field storage capacity, S_f) did not differ for the three rainfall intensities (all p-values>0.05). Lastly, the p_i averaged between 0.5 and 0.7 after 2 mm of rain and did not differ among the three intensities (all p-values>0.05). The low p_i indicates that water is not rapidly absorbed by epiphytes and may flow off the branches along preferential flow routes. Therefore, the large MWC_x of epiphytic lichens and bryophytes will increases the canopy water storage, which will decrease the quantity of water available for plants during the seasonal summer drought, and the occurrence of preferential flow will delay canopy saturation, thereby altering the rainfall intensity at the forest floor relative to open areas, or canopies without large epiphyte populations.

2.0 Introduction

Old-growth Douglas-fir forests in the Pacific Northwest (PNW) have a large canopy water storage capacity (S) relative to younger Douglas-fir forests

(Link et al., 2004). Where canopy water storage capacity is defined as the quantity of water a canopy can hold when saturated. The change in S as a forest matures may have important implications for the forest water budget. For example, the PNW typically has summer droughts that result in reduced soil moisture and transpiration (Moore et al., 2004; Unsworth et al., 2004). The effect of the drought may be exacerbated in old-growth forests/watersheds due to the large value of S and the interception of summer rainfall by forest floor bryophytes.

Researchers have hypothesized that changes in tree species composition, increased wood surface area/deadwood, and the development of large epiphyte populations are responsible for the greater S in old-growth Douglas-fir forests (Chapter 2; Keim and Skaugset, 2003; Link et al., 2004; Rothacher, 1963). Old-growth Douglas-fir forests in the PNW have large populations of epiphytic lichens and bryophytes. McCune (1993) estimated that an old-growth forest in the Oregon Cascades contained 1870 kg ha^{-1} and 780 kg ha^{-1} (dry mass) of epiphytic lichens and bryophytes, respectively. This epiphyte biomass in old-growth Douglas-fir forests consists of approximately 74 species of lichens and 32 species of bryophytes (Pike et al., 1975). Bryophytes are also common on the forest floor of old-growth Douglas-fir forests. While they are not usually accounted for in the calculation of S, these species along with the litter and deadwood on the forest floor (Harmon and Sexton, 1995; Helvey and Patric, 1965), may considerably decrease the quantity of water that enters the organic layer/mineral soil. In old-growth

Douglas-fir forests located in Oregon, greater than 93 species of forest floor

bryophytes cover between 25 to 50% of the forest floor (Rambo and Muir,

1998; Shaw et al., 2004). The percent of the forest floor that is covered varies

greatly between forests (Rambo and Muir, 1998).

Lichens and bryophytes both have the ability to store large quantities of

water. Fruticose and foliose lichens have the capacity to rapidly absorb

between 150 to 350% of their dry weight in water (Blum, 1973; Kershaw,

1985). Bryophytes have an even larger range of water storage, between 500

to 1200% of their dry weight (Proctor, 2000b). Therefore, an old-growth

Douglas-fir forest that contains 1870 kg ha^{-1} of lichens and 780 kg ha^{-1} of

bryophytes should have the capacity to store between 0.67 and 1.6 mm of

water in the epiphyte biomass.

Past research has assumed that the large maximum water content

(water stored divided by its dry weight; MWC_x) of epiphytic lichens and

bryophytes influences rainfall interception by increasing S (Keim, 2003; Levia

Jr and Frost, 2003; Link et al., 2004; Rothacher et al., 1967; Waring and

Running, 1998). For example, Rothacher (1963) assumed that the absence of

stemflow in an old-growth Douglas-fir forest was the result of epiphytes storing

water on the tree boles. However, there has been no direct research on the

relationship between the MWC_x of epiphytes and forest floor bryophytes and

their rainfall interception efficiency (p_i) (the rainfall stored on a branch divided

by the rainfall intercepted by a branch). The goal of this study was to: 1)

Determine the MWC_x for common lichens and bryophytes in old-growth

Douglas-fir forests and 2) Determine the water storage and p_i of epiphyte-laden branches under a rainfall simulator.

3.0 Materials and methods

3.1 Lichen and bryophyte samples

Epiphytic and forest floor lichen and bryophyte samples (epiphyte-laden branches and individual samples) were removed from an old-growth Douglas-fir/western hemlock forest (> 400 y) located within the H J Andrews Experimental Forest in the western Cascades of Central Oregon (44.2°N, 122.2°W). Five old-growth Douglas-fir trees were rigged for climbing and 3 or 4 dead epiphyte-laden branches were removed per tree (n=18) for analysis. Dead western hemlock branches were removed from locations that were accessible near the forest floor (n = 10). The dead branches were required to be less than 2 m in length and have greater than 80% epiphyte cover. Dead branches allow for a more direct analysis of the effect of epiphytic lichens and bryophytes on rainfall interception and storage because they can be covered by large populations of epiphytes and they do not have any needles. The epiphytes in this stand were classified into three functional groups: foliose lichens, fruticose lichens and bryophytes. Individual samples of healthy foliose lichens, fruticose lichens and bryophytes were removed from the five Douglas-fir trees or were removed from the boles and stems of trees 0 to 2 m above the forest floor. Forest floor bryophytes were randomly collected along a 200 m transect. The epiphytic lichen biomass was dominated by foliose lichens

(1242 kg ha^{-1}) with a small portion in fruticose lichens (31 kg ha^{-1}, mostly

alectroid species) (Chapter 5). Field measurements of rainfall interception by

the forest canopy and individual epiphyte-laden branches are reported in

Chapter 4.

3.2 Lichen, bryophyte and dead branch maximum water content

Epiphyte samples were initially sorted into foliose lichens (plate-like

structure), fruticose lichens (hairy structure) and bryophytes. The foliose

lichen, lettuce lung (*Lobaria oregana*), and the fruticose lichen, witch's hair

(*Alectoria sarmentosa*), were chosen to represent their respective functional

groups because they comprise greater than 94 and 36% of the foliose and

fruticose lichen biomass in old-growth Douglas-fir forests, respectively

(McCune, 1994; Pike et al., 1977). The bryophyte functional group was

dominated by Dicranum moss (*Dicranum fuscescens*), Hypnum moss

(*Hypnum circinale*) and cattail moss (*Isothecium myosuroides*) (greater than

12, 11 and 36% of bryophyte biomass, respectively) (McCune, 1994; Pike et

al., 1977).   These three species were selected to represent the epiphytic

bryophytes.   The bryophytes were further sorted into the dominant forest floor

species (step moss (*Hylocomium splendens*), electrified cat's tail

(*Rhytidiadelphus triquetrus*), Oregon beaked moss (*Kindbergia oregona*))

present in the forest.   Thirty samples (approximately 1 g) of each group were

cleaned of litter and submerged in water for 30 minutes. The sample was

removed from the water and suspended in a sealed container at 22°C for 24 h

to allow excess water to drip off. To prevent evaporation from the sample, a

layer of water was maintained at the bottom of each container. The saturated

samples were then weighed to the nearest milligram and placed in an oven at

70°C for 72 h to attain dry weight.

The maximum water content of dead branches in the canopy (S_{db})

(internal storage only) was determined by placing 37, 5 cm samples of dead

branch (27 Douglas-fir and 10 western hemlock samples) in water for 30 days.

The dead branches came from 19 branches collected for this study and

from18 branches (n = 18; 12 Douglas-fir and 4 hemlock) used in a field study

on rainfall interception by epiphytic branches (Chapter 4). After being

immersed in the water for 30 days the branch samples were blotted dry,

weighed and then dried at 70°C for 168 h to attain dry weight.

The MWC_x of the lichens, bryophytes and the S_{db} of the dead branches

were calculated as:

$$MWC_x = \frac{(WW - DW)}{DW} \,(1)$$

where WW (g) was the sample's wet weight after immersion in the water, DW

(g) was the samples dry weight after 72 and 168 h at 70°C in a drying oven for

lichens/bryophytes and branches, respectively.

3.3 Rainfall Simulator

The water storage and rainfall interception efficiency (p_i) (rainfall stored

on a branch divided by the rainfall intercepted by a branch) of the epiphyte-

laden branches were determined using a rainfall simulator (A. Skaugset,

Department of Forest Engineering, Oregon State University). For a full

description of the rainfall simulator see Keim (2003). In brief, the rainfall simulator was equipped with three different nozzles (Model # G2.8W, G5.6W and G25 Spray Systems Inc., Wheaton, Illinois, USA) placed 4.9 m above the ground and capable of generating multiple intensities and drop sizes (Table 7). To estimate rainfall interception and storage, each air-dried branch was suspended on a supporting cable that was attached to a scale (Mettler-Toledo SR32001, Columbus, OH, USA) housed in a box located directly above the spray nozzles. The weight of the sample was recorded at 5 Hz on a desktop computer and the specimen remained under the rainfall until its weight stabilized. The range of intensities produced by the simulator is in the upper range of what can be expected in a typical storm in the PNW (Table 8).

Two corrections were applied to the raw data prior to estimating the water storage and p_i. First, for each rainfall intensity, the mass of water stored on the supporting cable was estimated by running the rainfall simulator with only the cable attached. The mass stored on the cable was subtracted from the raw data. Second, the force imparted by the rate change of momentum as the raindrops struck the specimen was subtracted. This force varied for each specimen because the angle of impact for the droplets differed between specimens. This force was estimated by turning the rainfall off for four 10-second intervals and estimating the instantaneous change in weight when the rainfall was turned back on (Keim, 2003).

Table 7 – A comparison between the rainfall intensities and related mean drop size produced by the rainfall simulator to the expected mean drop size for a storm at the same rainfall intensity in the Pacific Northwest.

Rainfall Intensity	Rainfall Simulator Mean Drop Size	Range of Expected Mean Drop Sizes
(mm h^{-1})	(mm)	(mm)[x]
11.28	1.1	1.5-1.9
16.1	1.0	1.6-2.1
39.8	1.3	2.0-2.6

[x] from (Best, 1950; Laws and Parsons, 1943; Mason and Andrews, 1960)

Table 8 – The 2 and 100 year return interval for the maximum length of time a single storm will produce a given rainfall intensity.

Rainfall Intensity	The maximum length of time a single storm will produce a given rainfall intensity[!]	
(mm h^{-1})	2 return interval	100 return interval
11.28	0.5 h	2.5 h
16.1	1/3 h	1.5 h
39.8	<1/10 h	1/3 h

[!] from (Chow, 1964)

Fourteen Douglas-fir branches were exposed once at each of three rainfall intensities (11.28, 16.1, 39.8 mm h^{-1}). Six hemlock branches were exposed only to the lowest rainfall intensity. Each branch was saturated at the given intensity and stored at room temperature for at least one week to allow it to return to its original weight. After being exposed to the final rainfall intensity, each branch was photographed from above and the vertical

projected area was determined using image processing software (Vegmeasure 1.6, D Johnson, Department of Rangeland Science, Oregon State University). The branch volume and surface area was estimated by measuring the branch diameter at 5 cm intervals and treating each section as a cylinder.   The epiphytes were removed from the branches and were sorted into foliose lichens, fruticose lichens, bryophytes and litter. Dry weights of epiphytes, branches and litter were determined by placing them in an oven at 70°C for 72 h.

3.4 Branch biomass description

The branches placed under the rainfall simulator contained between 7.2 and 70.2 g of epiphytes (Table 9). The epiphytes were predominately foliose lichens and bryophytes, with the fruticose lichens representing very little of the biomass (Table 9).

3.5 Calculation of epiphyte-laden branch water storage

The maximum water storage (S_m) for each branch during a rainfall simulation was determined by fitting a hyperbolic curve to the change of storage, $S(t)$, with time (Figure 8).

$$S(t) = \frac{S_m t}{b + t} \quad (2)$$

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

Table 9 – Descriptions of the epiphyte biomass, litter biomass, branch biomass, branch surface water storage (S_b), maximum water content expressed as a percent of dry weight (S_{db}; equation 1) for the 20 branches exposed to the rainfall simulator.

Branch	Species	Fruticose g	Foliose g	Bryophyte g	Litter g	Branch g	S_{bs} g	S_{db} %	Projected Surface Area cm²
1	DF	0	12.1	0.6	0.1	84.3	19.6	178	246
2	DF	0.2	55.5	14.7	27.3	281.5	36.8	186	956
3	DF	0	12.6	2.5	1.9	40.8	14.3	188	367
4	DF	0	13.8	0.8	3.9	226.5	16.4	193	406
5	DF	0.6	19.3	14.7	22.4	369.7	55.8	166	737
6	DF	2.5	35.5	19	13.9	287.5	25	185	905
7	DF	0	15.7	1.9	1.2	313.4	14.5	178	299
8	DF	0.3	30.9	4	2.5	79.1	15.7	212	458
9	DF	1.3	8.4	37.2	32.3	351.3	65.5	224	877
10	DF	0.3	4.1	17.8	22.5	712	96.6	164	546
11	DF	0	0.2	21.4	10.2	222.7	38.5	171	570
12	DF	0.7	9.6	11	4.3	85.5	31.5	214	426
13	DF	0	12.3	22	13.6	106.9	21.9	202	429
14	DF	0.1	13.3	38.8	46.9	593.2	73.8	175	1000
15	HEM	0	0	19.7	9.5	52.5	16.8	224	913
16	HEM	0	0	38.4	14.5	736.9	11.6	156	739
17	HEM	0	0	20.1	4.3	49.8	15.2	164	972
18	HEM	0	0	7.2	2	74.1	20.9	146	606
19	HEM	0	0.3	23.9	3.5	40.6	11.1	242	1229
20	HEM	0	0	36.6	8.2	96.6	20.1	281	1201
Average		0.29	12.2	17.6	12.3	240	31.1	192	694

To determine how much water would remain on a branch after the rainfall simulator was turned off (field water storage capacity, S_f) a second regression was fitted to the portion of the data immediately after the rainfall ceased. We could not determine the field storage capacity by waiting for the water to stop dripping from the branch because evaporation immediately began to remove water from the branch after the rainfall simulator was turned off. Therefore, we took the first 3 minutes of the dry down curve (Figure 9) where water drip dominated the water loss from the branch and fit the following equation:

$$S(t) = S_m + \frac{ct}{d+t} \quad (3)$$

where c and d are fitting parameters. The derivative of this equation was used to determine the weight of the sample when the specimen was losing 0.01 g s^{-1}. This rate of water loss was considered a good estimate of S_f because it defines the point where dripping has nearly ceased but evaporation has not substantially altered the branch weight.

To provide an estimate of the potential epiphyte-laden branch water storage (S_{e-b}) the MWC_x of the epiphytes on the branch were combined with the water storage on the branch surface. The branch surface storage (S_{bs}) was estimated by weighing each branch before and after immersing the whole branch in water. The difference in the branch weight before and after immersion in water provided the estimate of S_{bs}. The S_{e-b} was estimated by

multiplying the biomass of epiphytic fruticose lichens (b_{fr}), foliose lichens (b_{fo})

and bryophytes (b_{br}) with their respective MWC_x (Table 10):

$$S_{e\text{-}b} = 2.23b_{fr} + 3.42b_{fo} + 9.99b_{br} + S_{bs} \quad (4)$$
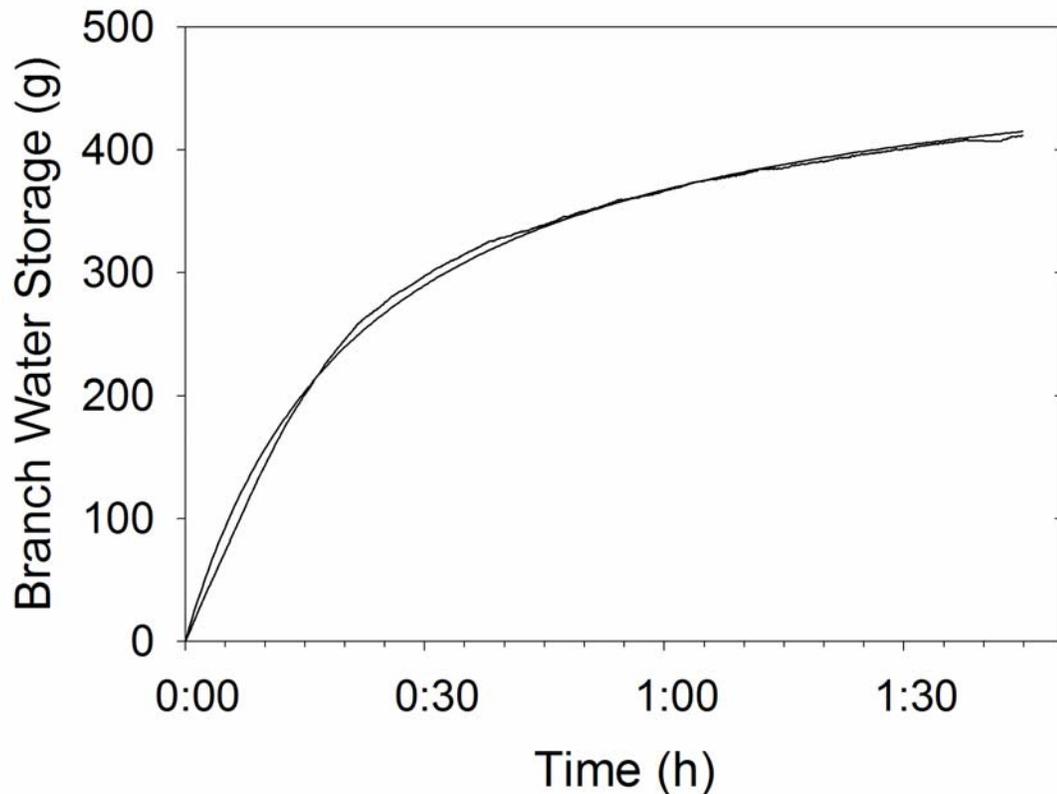
Figure 8 – Calculation of maximum water storage (S_m) of an epiphyte-laden branch using a rainfall simulator. A hyperbolic curve was fit to estimate the maximum water storage by the branch (Equation 2). For this branch S_m = 501.8 and b = 0.0153.
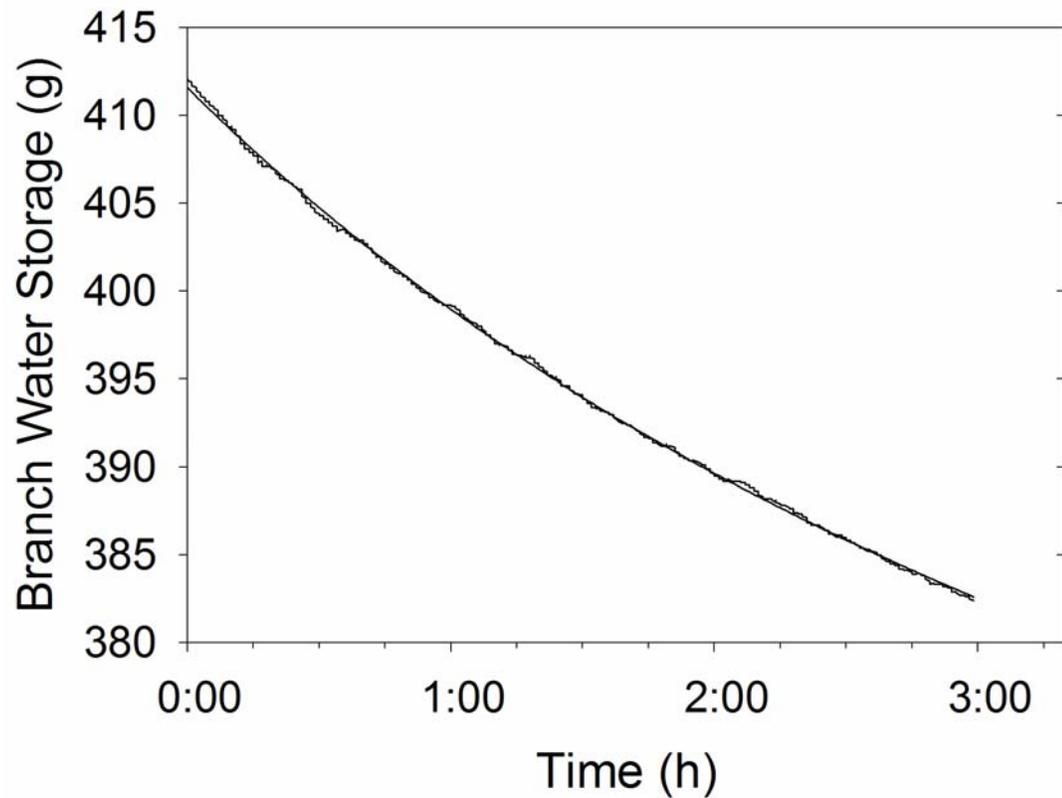
Figure 9 – Calculation of field water storage (Sf) for a branch after the rainfall ceased. A hyperbolic line was fit to the data following rainfall to estimate canopy water storage (S) after the branch stopped dripping (Equation 3). For this branch c = -83.3 ; and d = 0.0039.

Table 10 – The biomass and maximum water content (MWCx) of the
bryophytes and lichens for an old-growth forest in the Pacific Northwest. The
MWCx of the lichens and bryophytes were estimated by immersing the
lichen\bryophyte in water and representing the increase as a percentage of dry
weight (Equation 1). The potential storage is an estimate of the water storage
by lichens and bryophytes for the whole old-growth Douglas-fir forest.
Numbers behind the ± represent the 95% confidence interval.

Group	Biomass[!] kg ha^{-1}	Maximum Water Content (times dry weight)	Potential Storage (mm)
Epiphytes			
Foliose lichens	1242 ±452	3.42 ±0.35	0.42
Fruticose lichens	31.0 ±22.0	2.23 ±0.64	0.072
Bryophytes	780[#]	9.99 ±0.48	0.80
Forest Floor			
Oregon beaked	345 ±177	14.0 ±0.78	0.485
Elect. Cat's Tail	68.0 ±68.8	11.5 ±0.90	0.030
Step Moss	26.2 ±27.9	8.38 ±0.43	0.057
Other moss	25.6 ±53.5	11.30[*]	0.029
Total	2518±494	-	1.89

[!] From Chapter 5
[#] From (McCune, 1993)
[*] Estimated using the mean water-holding capacities of the three dominant
bryophytes on the forest floor.

3.6 Calculation of rainfall interception efficiency (p_i)

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

$$p_i = \frac{w_b}{b_s \cdot I_t \cdot t_h} \quad (5)$$

where w_b is the branch weight (kg) at time t_h (hours), b_s is the branch projected
surface area (m^2) and I_t is the rainfall intensity (kg h^{-1} m^{-2}).

4.0 Results

4.1 MWC$_x$ of lichens, bryophytes and dead branches

Table 6 summarizes the MWCx of the lichens and bryophytes after

immersion in water. The MWC$_x$ (intercellular and surface water storage) of the

dominant epiphytic bryophyte species (Dircranum moss, Hypnum moss and

cattail moss) were not significantly different (n=30 for each species, p-

value>0.05) and were therefore pooled. The MWC$_x$ of the epiphytic

bryophytes was significantly greater than that of the foliose and fruticose

lichens (p-values<0.001). In contrast, the MWC$_x$ of all the forest floor

bryophytes were statistically different from each other (Bonferonni multiple-

comparison test, all p-values>0.05) (Table 10). Lastly, the average S$_{db}$ for the

hemlock and Douglas-fir branches were not statistically different (p-

value>0.73) (Table 5).

4.2 Epiphyte-laden branch water storage under varying intensities

After allowing for water storage on the branch surface (S$_{bs}$; Table 5),

the S$_m$ and S$_f$ of the epiphyte-laden branches could be predicted using the

biomass of fruticose lichens, foliose lichens and bryophytes in conjunction with

the measured water-holding capacity of each epiphyte type (Equation 4;

Figure 10).   The MWC$_x$ of the dead branch was not included in the

measurements because the simulations ran for a maximum of two hours and,

therefore did not provide enough time for substantial amounts of water to
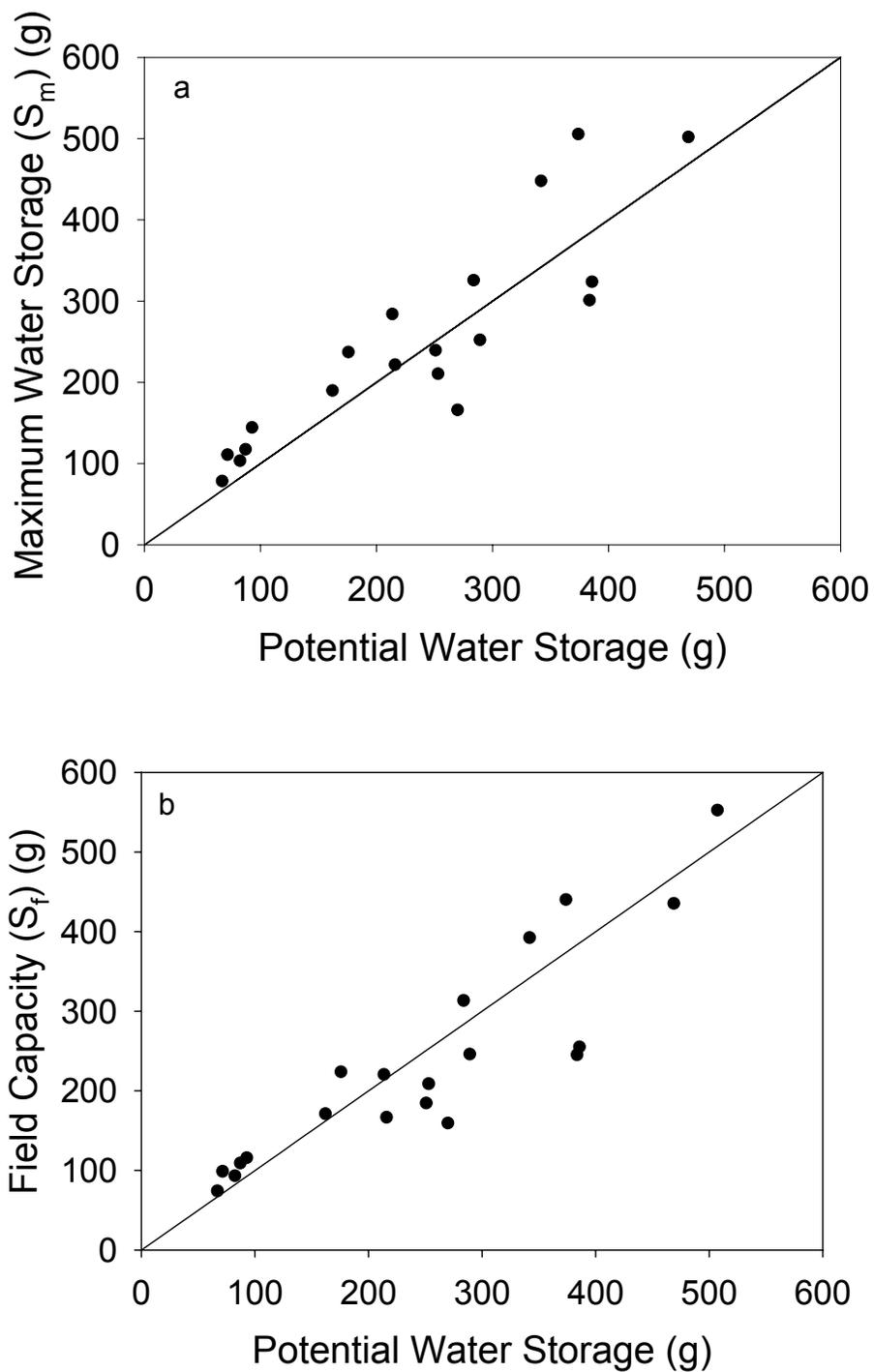
Figure 10 – The relationship between (a) the measured maximum water storage (S_m) and (b) the field water storage capacity (S_f) and the predicted potential water storage using the biomass and maximum water contents (MWC_x) of the three classes of epiphytes (Equation 4).

penetrate the dead branch. The S_{e-b} as estimated by Equation 4 and the

measured epiphyte-laden branch water storage did not differ significantly for

the estimates of S_m or S_f (p-values>0.05) (Figure 10).

For all of the rainfall intensities the S_m or S_f of the branches were not

statistically different (Bonferonni multiple comparisons, all p-values>0.05)

(Table 5). However, while not significant, the S_f for 12 of the 14 branches after

exposure to 39.8 mm h^{-1} was smaller than after exposure to 11.3 mm h^{-1} of

rainfall (Table 5). (Table 5). Finally, after accounting for the effect of the

epiphytic foliose lichens, fruticose lichens and bryophytes, the S_m and S_f of

epiphyte-laden hemlock branches did

Table 11 – The branch maximum water storage (S_m) and field water storage (S_f) for twenty branches exposed to three rainfall intensities.

Branch	S_m (g)			S_f (g)		
Rainfall Intensity mm h^{-1}	11.3	16.1	39.1	11.3	16.1	39.8
1	78.4	-	74.3	74.3	-	62.3
2	103.5	110.8	90.4	93.3	91.2	78.4
3	110.9	122.7	125.7	98.9	110.7	113.7
4	116.0	156.2	161.2	159.5	144.2	149.2
5	447.8	385.5	367.8	392.3	335.1	352.0
6	117.6	112.5	107.6	109.3	96.5	87.2
7	189.8	193.7	196.9	171.1	177.2	157.9
8	501.8	461.8	486.5	435.3	396.4	384.8
9	382.6	383.6	383.5	357.7	325.7	294.4
10	352.2	243.8	203.1	246.1	237.5	183.9
11	210.6	249.6	223.3	208.9	246.5	206.8
12	273.1	234.9	214.7	223.7	215.0	184.8
13	325.6	322.0	322.6	313.4	322.0	280.2
14	602.9	581.2	426.7	552.4	529.3	362.4
15	284.0			220.5		
16	301.2			245.2		
17	221.7			166.7		
18	144.5			116.0		
19	239.5			184.5		
20	323.8			255.2		

not differ statistically from values for the Douglas-fir branches (S_m – p-value>0.68; S_f – p-value>0.43).

4.3 Rainfall interception efficiency (p_i) under varying intensities

At rainfall intensities of 11.3, 16.1 and 39.8 mm h^{-1}, the p_i of the branches did not differ significantly (Bonferroni multiple comparisons all p-value>0.05) (Figure 11). After 2 mm of rainfall the branches had an average pi between 0.50 to 0.70.   The p_i for all branches gradually decreased to approximately 0.2 after 16 mm of rain. The relationship between the cumulative "rainfall" during the "storm event" (P_G) and p_i can be described by the hyperbolic equation:

$$p_i = \frac{0.90 \cdot 4.75}{4.75 + P_G} \quad (6)$$

5.0 Discussion

5.1 Lichen and bryophyte maximum water content (MWC$_x$)

When considering the influence of lichens and bryophytes on S, it is important to calculate both the water absorbed into the thallus/leaf and the water stored on the surface. The ability of lichens and bryophytes to store water is of importance to these species because they must collect the majority of their water from rainfall and dew (Blum, 1973; Proctor, 2000b). Past studies demonstrated that lichens and bryophytes store between 100 to 1200% of their dry weight in water (Blum, 1973; Proctor, 2000b). However, these values
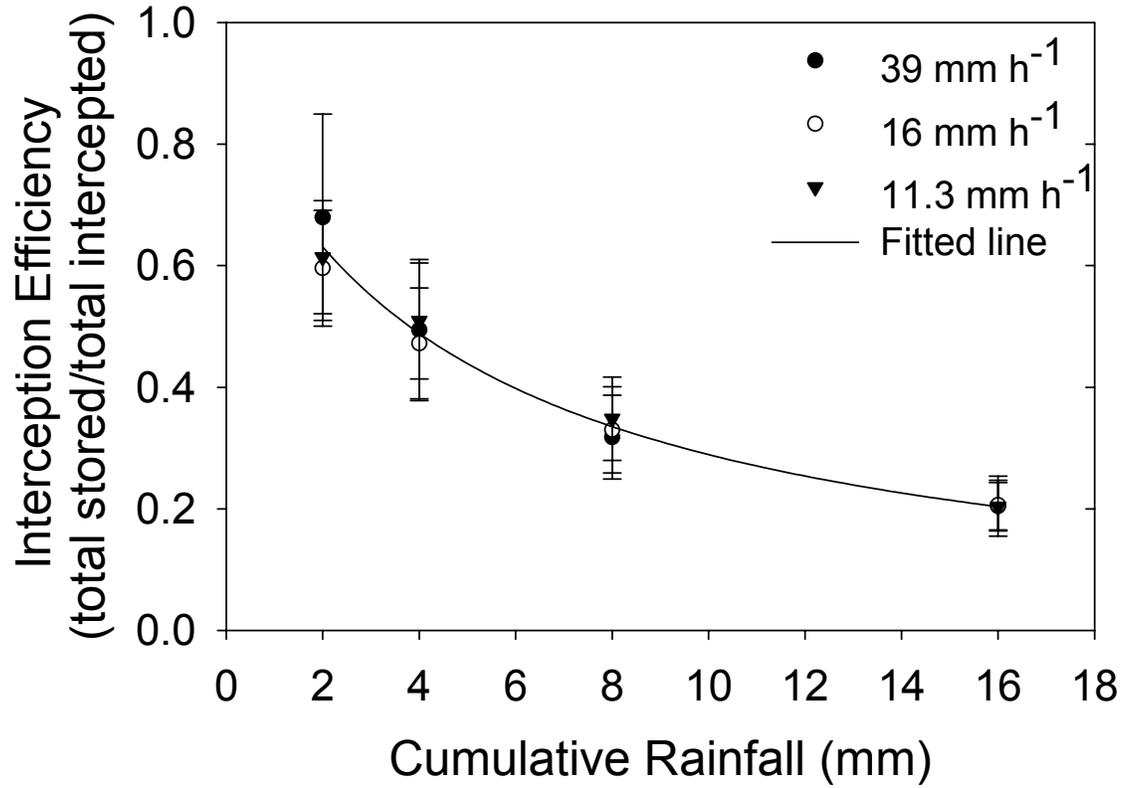
Figure 11 – The mean interception efficiencies (pi) of epiphyte-laden branches placed under a rainfall simulator at three different rainfall intensities.

are for specimens where surface water storage was excluded because the

specimens were blotted dry. This study measured both the water absorbed

within and the water stored on the surface of the thallus/leaf. Hence, the

MWC_x of the lichens and bryophytes reported here are higher than the

average water-holding capacities reported in the literature. For example, Blum

(1973) found that *Lobaria pulmonaria* stored 190% of its dry weight in water.

In contrast, the results from this study indicate that lettuce lung, a close

relative *L. pulmonaria,* can store 342% of its dry weight in water. Thus, the

potential water storage of the epiphytes increases when both the internal and surface water storage are considered.

5.2 Epiphyte-laden branch water storage

S_m and S_f of the branches can be predicted if the biomass of foliose, fruticose and bryophytes on the branch is known (Figure 10). The water storage by epiphytic lichens and bryophytes on Douglas-fir and western hemlock branches did not statistically differ between the species. Hence, if the quantities of lichens and bryophytes in the canopy are known, their potential contribution to S in old-growth Douglas-fir forests can be calculated. However, this estimate is useful only for predicting the total potential water storage of the epiphytes. If the epiphytes are not dry at the start of the storm, they will store less of the intercepted rainfall because a portion of their MWC_x is already filled.

In a typical old-growth Douglas-fir forest in the PNW there are two or three times more lichen biomass than bryophyte biomass in the canopy (Chapter 5; McCune, 1993). In terms of water storage the greater biomass of epiphytic lichens is offset by the larger water-holding capacity of the bryophytes. For example, the forest that provided the branches for this study was estimated to contain 1242 kg ha^{-1}, 31 kg ha^{-1}, 780 kg ha^{-1} of foliose lichens, fruticose lichens and bryophytes, respectively (Chapter 5). This is similar to the quantity of epiphytic foliose lichens (1690 kg ha^{-1}), fruticose lichens (180 kg ha^{-1}) and bryophytes (780 kg ha^{-1}) found in another old-growth Douglas-fir forest in the PNW (McCune, 1993). By multiplying the biomass of

epiphytic lichens and bryophytes with their respective water-holding capacities, an old-growth Douglas-fir forest could store between 1.2 to 1.4 mm of water in epiphytes alone. Thus, the water stored by epiphytic lichens and bryophytes in an old-growth Douglas-fir forest is comparable to the S reported for many young, closed canopied coniferous forests that do not have significant epiphyte populations (e.g. Chapter 2; Klaassen et al., 1998; Rutter et al., 1975; Tiktak and Bouten, 1994; Zinke, 1967).

The quantity of water storage by bryophytes increases when the water storage by forest floor bryophytes is accounted for. Forest floor bryophytes in a typical old-growth Douglas-fir forest cover 25 to 50% of the ground area (Rambo and Muir, 1998; Shaw et al., 2004), provide 485 kg ha^{-1} of biomass (Chapter 5) and absorb between 8-14 times their dry weight in water (Table 10). If the biomass of the forest floor bryophytes is multiplied by their respective water-holding capacities, forest floor bryophytes provide an additional 0.60 mm of potential water storage (Table 6).

5.3 Dead branch water storage

Water storage in dead branches also contributes to the large S observed in old-growth Douglas-fir forest canopies. Based on the allometric equations provided by Grier and Logan (1977) for a nearby old-growth Douglas-fir forest, the forest canopy in this study is expected to contain 551 kg ha^{-1} of dead branches. Assuming that these dead branches have an S_{db} of 1.92 (Table 5), the dead branches in this canopy will store an additional 1.06 mm of water. Dead branches do not represent the majority of wood biomass

in the canopy. For example, the same allometric equations estimate that the

canopy has 10698 kg ha^{-1} of bark.   The storage in this bark may be

considerable because Herwitz (1985), estimated water storage by bark

accounted for 30 to 50% of S for a tropical rainforest northeast Queensland,

Australia. Furthermore, storage in dead plant material is not limited to the

forest canopy.

The water stored in dead plant material on the forest floor may

contribute to water storage in old-growth Douglas-fir forests.   The forest floor

in old-growth Douglas-fir forests generally contain between 4-8 mm of litter

(Chapter 2; Shaw et al., 2004) and have 25% of its surface area covered by

deadwood (Harmon and Sexton, 1995).   Forest floor litter is estimated to store

between 100 and 150% of its dry weight in water (Helvey and Patric, 1965)

and the deadwood on the forest floor is estimated to intercept and store 2-5%

of P_n (Harmon and Sexton, 1995). Thus, the storage water by deadwood and

litter may be important in old-growth Douglas-fir forests and requires further

research.

5.4 Rainfall storage and preferential flow

When exposed to the rainfall simulator the epiphyte-laden branches

took up to 9 h to saturate. Generally, lichens and bryophytes immersed in

water become saturated within 5 minutes (Blum, 1973). However, for 19 of the

20 branches, only 50-79% of the initial 2 mm of water intercepted was stored

(Figure 11). Based on the products provided by applying Equation 2, the

branches required between 0.5 and 9 h at 11.3 mm h^{-1} to reach 95% of S_m

(Figure 8). In contrast, foliage samples placed under a rainfall simulator at 20 mm h^{-1} typically saturate after less than 8 minutes (Keim et al., in review). A closed-canopy coniferous forest that does not contain significant populations of epiphytes and has a leaf area index (LAI) between 8 and 12 will saturate after 1.4 to 4 mm of rainfall (Chapter 2; Klaassen et al., 1998). Thus, a single epiphyte-laden branch requires a greater quantity of rainfall to saturate than the canopy of a young coniferous forest with a small epiphyte population. The low p_i of the epiphyte-laden branches indicates that intercepted rainfall is not absorbed by the lichens/bryophytes (Figure 11), rather it may be following preferential flow routes off the branch.

Water that is intercepted by an epiphyte-laden branch may establish preferential flow routes through the epiphyte mats, just as water commonly follows preferential flow routes in soils (e.g. Hill and Parlange, 1972; McDonnell, 1990; Weiler and Naef, 2003). In soil, once water has an established a route, there is less resistance to further flow along that pathway. Epiphyte-laden branches form a 3-dimensional structure that intercepted rainfall must infiltrate and flow through. It is highly probable that as the rainfall infiltrates the epiphyte mats it will be routed along preferential flow routes. If preferential flow routes are present in epiphyte-laden branches, the saturation of a branch would be delayed because water would have difficultly reaching all of the epiphyte and branch surfaces.   Thus, the occurrence of preferential flow will alter the rainfall intensity and spatial variability at the forest floor,

which may decrease the probability of slope failure (Keim and Skaugset, 2003).

The slow saturation by the branches may not be entirely from preferential flow. Equation 6 indicates that as P_G approaches zero the p_i for an epiphyte-laden is 0.9. This suggests that when P_G is small, 10% of the rainfall striking a branch is not absorbed. It is possible that 10% of the rain striking a branch splashes off the surface on impact. Raindrop splash has been implicated in changing the water stored on a branch (Calder, 1996; Calder and Wright, 1986). Thus, a portion of the p_i may result from raindrop splash.

5.5 Rainfall intensity and interception efficiency (p_i)

Past research states that S is negatively associated with increasing windspeeds and rainfall intensities (Calder, 1996; Calder and Wright, 1986; Hörmann et al., 1996; Rutter et al., 1971). Greater windspeeds shake the branches and dislodge the stored water. Higher rainfall intensities have larger drop sizes (Best, 1950; Laws and Parsons, 1943; Mason and Andrews, 1960). It is hypothesized that the larger raindrops impart more force on the surface as they impact, thereby splashing water off of the surface (Calder et al., 1996; Rutter et al., 1971). There is some debate over whether this hypothesis is true (see Keim, 2003), but it is generally accepted that changes in rainfall intensity alters S. For example, Link et al. (2004), directly measured rainfall interception and storage in an old-growth Douglas-fir forest and found an association between S and rainfall intensity/wind speed.

The branches in this study did not have a greater p_i or water storage at lower rainfall intensities. The lack of association between water storage and rainfall intensity may result, in part, because the raindrop sizes generated by the simulator did not mimic what would be expected under natural rainfall (Table 7). However, the drop size did increase by 30% as rainfall intensity increased from 16.1 mm h^{-1} to 39.8 mm^{-1} and this increase was expected to result in less water storage. The morphology of the epiphytes, most notably the bryophytes, may dampen the effect changes in rainfall intensity have on epiphyte-laden branch water storage. When compared to with surface of a leaf/branch, the surface of the bryophytes on the branch is very rough. Hence, a droplet might be absorbed more easily because the probability of the droplet splashing off the surface may be decreased.

6.0 Conclusions

Lichens and bryophytes substantially increase the interception and storage of rainfall in old-growth forests. The MWC$_x$ of lichens and bryophytes are significantly different, with the epiphytic bryophytes storing three times more water per unit dry weight than the lichens. Because of their high water-holding capacity the epiphytic fruticose lichens, foliose lichens and bryophytes have the potential to increase the canopy water storage (S) in the old-growth Douglas-fir forests by about 1.3 mm. However, this study showed that all the epiphyte-branches require greater than 6 mm of rainfall to saturate. The water required to saturate an epiphyte-laden branch exceeds the quantity of rainfall required to saturate the canopy of a young closed-canopied Douglas-fir forest

with a small epiphyte population (Chapter 2; Klaassen et al., 1998). A large

amount of rainfall is required to saturate a branch because the rainfall

interception efficiency (p_i) of a branch was typically less than 0.7 after only 2

mm of rain. The low p_i likely occurs because water is following preferential

flow routes off the branch. Therefore, the large MWC_x of epiphytic lichens and

bryophytes increases canopy water storage capacity (S) and may exacerbate

water stress of the trees during summer drought.   The low p_i may influence

slope stability by delaying the saturation of the canopy and altering the rainfall

intensity at the forest floor.

Acknowledgements

Chapter 4 – The role of epiphytes in the interception of rainfall in old-growth Douglas-fir forests of the Pacific Northwest: Part II – field analysis

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1.0 Abstract

Epiphytic lichens and bryophytes alter the hydrology of old-growth Douglas-fir forests by increasing the canopy water storage (S) and prolonging the time required to both saturate and dry the canopy. Rainfall interception and storage were measured at the scale of the branch and forest stand from 30 March 2003 to 14 May 2004 in an old-growth Douglas-fir forest in the Pacific Northwest (PNW). The rainfall interception measurements were used to determine: 1) whether the potential maximum epiphyte-laden branch water storage (S_{e-b}), as estimated by the biomass of lichens/bryophytes on the branch, could predict the water stored on a branch during a storm event measured in the field; 2) the effect epiphyte distribution has on the time the canopy remains wet following a storm event; 3) how the estimate of S by three commonly used regression based techniques is influenced by epiphytic lichens and bryophytes; and 4) the relationship between rainfall intensity and the water storage on an epiphyte-laden branch.

During a storm, the S_{e-b} for an epiphyte-laden branch could not be used to predict the maximum branch water storage because the branches: 1) were partially saturated for most of the measurement period; and 2) required greater than 30 mm of rain to saturate due to preferential flow routing water through the epiphyte mats. The canopy remained partially saturated during for most of the wet season, in part, because water was not evenly distributed throughout the canopy. For example, bryophytes help prolong the time required to dry the

canopy because they store a large amount of water (>7800 kg ha^{-1}) and are located lower in the canopy where evaporative demand is diminished.

The mean, minimum and Individual Storm (IS) methods are indirect regression based techniques that estimate S for plant canopies by relating the gross precipitation (P_G) to the net precipitation (P_n) for multiple (minimum, mean) or individual (IS method) storms. All these methods assume that the canopy is completely dry prior to the storm and that it simultaneously saturates during the storm. 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, these methods underestimated the S of the old-growth forest.

The water stored on epiphyte-laden branches after exposure to natural rainfall was positively associated with rainfall intensity. The rough 3-dimensional structure of the lichen and bryophyte mats may limit water loss from raindrop splash and impede the drainage of water from the branch.

2.0 Introduction

The quantity of rainwater an old-growth Douglas-fir forest canopy can store during a storm (canopy water storage capacity (S)) is at least two fold greater than the S of a young Douglas-fir forest canopy with a similar LAI but few epiphytes (Chapter 2; Link et al., 2004). Epiphytic lichens and bryophytes can store large quantities of water (Chapter 3; Blum, 1973; Proctor, 2000) and are abundant in the old-growth Douglas-fir forests of the PNW (McCune, 1993; Pike et al., 1975; Sillett and Rambo, 2000). However, the significance of

epiphytic lichens and bryophytes on the hydrology of these forests is not well understood.

Lichens and bryophytes can rapidly absorb large quantities of liquid water (Blum, 1973; Proctor, 2000b). For example, the maximum water content (MWC_x) of epiphytic foliose lichens, fruticose lichens and bryophytes that are typical of an old-growth Douglas-fir forest are 2.23, 3.42 and 9.99 times of their dry weight in water, respectively (Chapter 3). The potential branch water storage of an epiphyte-laden branch (S_{e-b}) can be estimated by multiplying the biomass of the three epiphytic groups by their respective MWC_x. The S_{e-b} has successfully predicted the water storage of epiphyte-laden branches exposed to different rainfall intensities under a rainfall simulator (Chapter 3). Assuming that epiphytic lichens and bryophytes will saturate in a similar manner *in situ*, a typical old-growth Douglas-fir forest will store 1.4 mm of rainfall (14 000 kg ha^{-1}) in epiphytic lichens and bryophytes (assuming 180, 1650 and 780 kg ha^{-1} of fruticose, foliose and bryophytes, respectively (McCune, 1993)). This is a significant amount of storage as the S of many mature, closed canopied coniferous forests without large populations of epiphytic lichen/bryophytes ranges between 1 and 2.5 mm (e.g. Chapter 2; Gash et al., 1980; Rutter et al., 1975; Zinke, 1967).

The large MWC_x and physical structure of epiphytic lichens and bryophytes is likely to influence the interception efficiency (p_i) of a branch (total rainfall stored on a branch divided by the total rainfall intercepted by the branch). To saturate an epiphyte-laden branch, the rainfall must infiltrate the

mats of lichens and bryophytes. But, as the water infiltrates through the mats, preferential flow routes form, and water moves off the branch before it can be absorbed (Chapter 3). 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 that are commonly used for estimating S, the proportion of direct throughfall (p) and the ratio of evaporation to rainfall intensity after canopy saturation ($\overline{E}/\overline{R}$) 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 of 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 $\overline{E}/\overline{R}$ using multiple storm events and the IS method estimates them on a 'per storm' basis (see section 3.3 for a complete description of each technique). The minimum, mean and IS methods may be inaccurate in old-growth Douglas-fir forests because they assume that the entire canopy is dry prior to the storm and that the canopy saturates simultaneously during the storm. A monoculture forest with a spatially uniform LAI may satisfy the 'simultaneous saturation' assumption. However, typical old-growth Douglas-fir forests may not satisfy this assumption because they are strongly heterogeneous (Franklin et al., 2002; Franklin and Van Pelt, 2004).

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. It has often been reported that branch water storage is negatively associated with increasing rainfall intensity (e.g. Calder, 1996; Calder and Wright, 1986; Price and Carlyle-Moses, 2003). As rainfall intensity increases the size of the raindrops increase (Best, 1950; Laws and Parsons, 1943; Mason and Andrews, 1960). At terminal velocity, these larger raindrops will impart a greater force when impacting on a surface. It has been hypothesized that the increase in force associated with larger raindrops will splash a greater quantity of water off of a leaf/branch, thereby reducing the leaf/branch water storage (Calder, 1996; Calder and Wright, 1986).   Although epiphytic lichens and bryophytes can resemble leaves (e.g. foliose lichens), they often have a different structure than leaves and branches. For example, the thalli of lichens can be hairy/pendulous (e.g. fruticose lichen) and the leaves of bryophytes frequently form mats that have a very rough surface relative to a tree leaf. Hence, the water storage capacity of epiphyte-laden branches may differ from that of tree leaves/branches.

Despite the large MWC_x of lichens and bryophytes we do not know of any studies that specifically discuss their effect on rainfall interception and storage. If hydrological modeling of forests in the PNW is to be improved, the influence of epiphytic lichens and bryophytes on canopy hydrology must be understood. This study uses a combination of stand and branch scale measurements of rainfall interception in an old-growth Douglas-fir forest to

determine: 1) whether laboratory based estimate of S_{e-b} (Chapter 3) 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 a storm event; 3) whether 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.

3.0 Materials and methods

3.1 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 (*Psuedostuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterphylla* (Raf.) Sarg.) forest that is greater than 450 y-old. The canopy is greater than 60 m tall, has an LAI of approximately 12.1 (Moore et al., 2004) and has large canopy gaps that are typical for old-growth Douglas-fir forests in the Pacific Northwest (PNW) (Franklin et al., 2002; Gray and Spies, 1996). There are approximately 1242 kg ha^{-1} of epiphytic foliose lichens, 31 kg ha^{-1} of epiphytic fruticose lichens 780 kg ha^{-1} epiphytic bryophytes, and 465 kg ha^{-1} of forest floor bryophytes (Chapter 5; McCune, 1993). 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).

3.2 Gross precipitation and throughfall measurement

Gross precipitation (P_G) and net precipitation below the forest canopy (P_n) were measured from 30 March to 1 December 2003 and 22 March to 14 May 2004 using tipping bucket rain gauges (TE-525I, Texas Electronics Inc., Dallas, TX, USA). The tipping buckets were placed approximately 1 m above the ground and monitored using individual dataloggers (HOBO event, Onset Computer Corp., Bourne, MA). Each tipping bucket rain gauge has a collection area of 325 cm^2 with a resolution of 0.254 mm. Two tipping bucket rain gauges were placed in a clearing adjacent (size = 30 m by 40 m) to the forest to measure P_G. An array of 23 tipping bucket rain gauges were randomly placed throughout a 2 ha area within the old-growth forest to measure P_n. By 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 the errors in the throughfall estimates by increasing the number of sampling points in the plot (Lloyd and Marques, 1988; Wilm, 1943). A second array of 48 manual throughfall collectors were spaced 8 m apart along a 200 m transect. Each manual throughfall collector had a 94 cm^2 collection area and was used to verify the estimates provided by the tipping bucket array. The manual throughfall collectors and tipping buckets were cleaned and leveled every 4 weeks.

3.3 Calculation of canopy variables

The mean, minimum and IS methods were used to estimate S, p, and $\overline{E}/\overline{R}$ or the measurement period. To be accurate, bucket type models such

as the IS, mean and minimum methods must assume that: 1) the entire canopy simultaneously saturates during the storm event; and 2) the canopy is dry prior to a storm event. If these assumptions are violated the accuracy of the methods should be diminished.

We estimated S using the minimum method as outlined by Leyton et al. (1967). In short, a linear regression relating P_G (x-axis) and P_n (y-axis) was fitted through data from all storms that were greater than 10 mm (P_G) and were visually determined to have minimal evaporation. 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.

The mean method was used to estimate S, p and $\overline{E}/\overline{R}$ 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 fit of the regression lines was 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 $\overline{E}/\overline{R}$, the value of P_G at intersection point of R_1 and R_2 provides an estimate of the canopy saturation point (P_s) and, finally, the difference between P_G and P_n at the intersection point provides an estimate of S.

The S, p, $\overline{E}/\overline{R}$ and I_n were calculated on a 'per storm' basis using the IS method as outlined in Link et al. (2004). The IS method partitions each rainfall event in forests into two discrete periods; pre- and post- canopy saturation. For each period a linear regression was created that related the cumulative net precipitation during the storm (P_n (mm)) to the cumulative gross precipitation (P_G (mm)) during the storm. As with the mean method, the two regressions are optimized to minimize the mean square error of the two regression lines. Prior to canopy saturation the relationship between P_G and P_n is calculated as:

$$P_n = pP_G \quad (1)$$

where p is the proportion of rainfall that passes through the canopy prior to canopy saturation (Figure 12 – Line "A"). Prior to saturation, it is assumed that the intercepted water will either remain in the canopy as stored water or will be evaporated back to the atmosphere. Following saturation, intercepted rainfall will either drip to the forest floor or evaporate back to the atmosphere (Figure 12 – Line "B"). The rainfall beneath the canopy can be computed using:

$$P_n = pP_G + (1 - \overline{E}/\overline{R})(P_G - P_S) \quad (2)$$
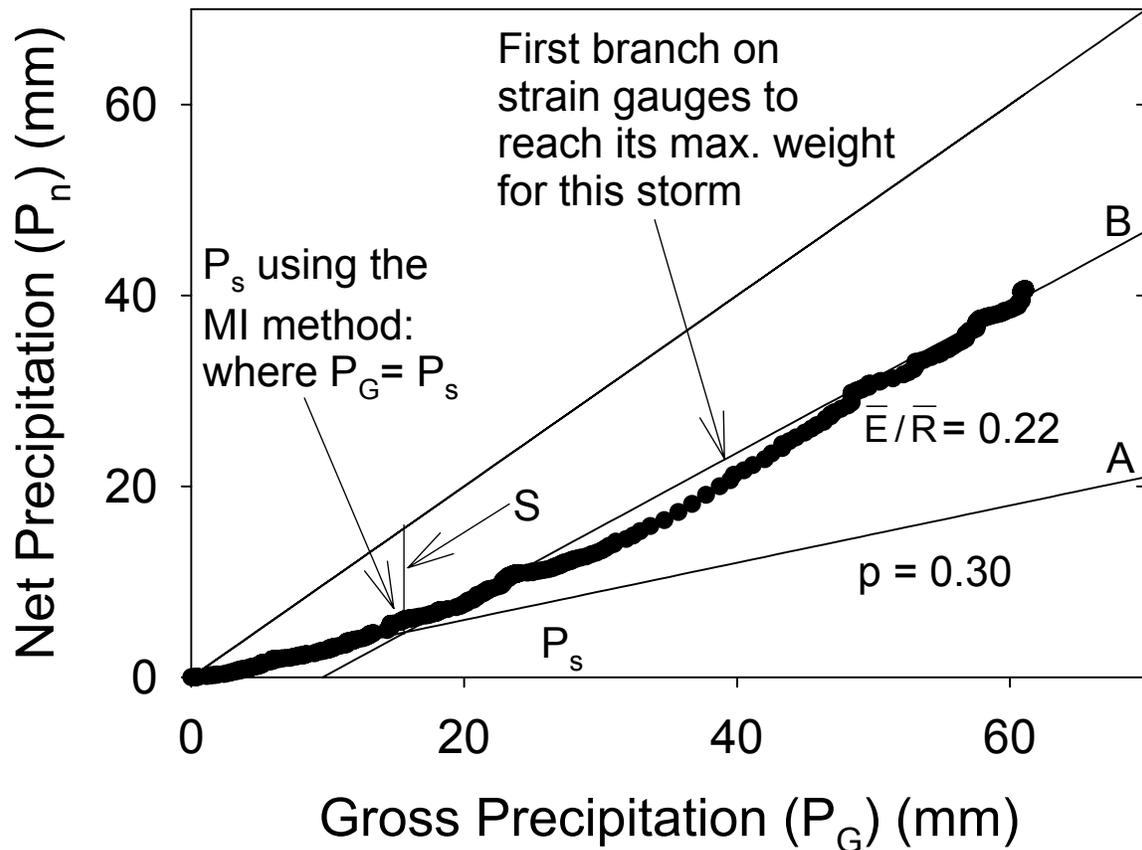
Figure 12 – The relationship between cumulative gross precipitation (*P_G*) and net precipitation (*P_n*) during a storm (6-13 October 2003). Each solid dot represents a 10-minute interval. The slope of regression "A" represents the direct throughfall (p = 0.10), the difference between *P_G* and *P_n* 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_S) and one minus the slope of regression line "B" is the ratio of evaporation to rainfall intensity ($\bar{E}/\bar{R}$ =1-0.87). There is no distinct inflection point to indicate where the canopy saturates. The IS method predicts the canopy saturates after 15 mm of rainfall, whereas the branches on the strain gauges reached their maximum weight after 39 to 55 mm of rainfall.

As with the mean method, one minus the slope of Equation 2 provides the estimate of $\overline{E}/\overline{R}$. S is then computed by:

$$S = (1-p)P_S - I_W \quad (3)$$

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

$$I_W = (\overline{E}/\overline{R})P_S \quad (4)$$

Because Link et al. (2004) found the use of $\overline{E}/\overline{R}$ to calculate I_w frequently resulted in an overestimation of evaporation for an old-growth Douglas-fir, S was estimated with (S_w) and without I_w (S_{wo}) and the difference compared. The overestimation of I_w can occur if rainfall during canopy wet-up is infrequent. In these instances the sporadic rainfall will increase the time required for the canopy to saturate and the use of $\overline{E}/\overline{R}$ in Equation 4 can overestimate I_w (Link et al. 2004).

3.4 Meteorological data and measurement of branch weight

To measure epiphyte rainfall interception under field conditions, we rigged two Douglas-fir trees for climbing and installed meteorological stations at 3.1, 24.8 and 46.5 m above the ground. Each station consisted of a cup anemometer (Ultra-light cup anemometer, Thornwaite, USA), a quantum sensor (LI-190SA quantum sensor, LI-COR, Lincoln, NE, USA), a relative humidity/temperature probe (HMP 45C, Vaisala Inc, Woburn, MA, USA), and a strain gauge (L2336, Futek Advanced Sensor Technology, Irvine, CA, USA). At each meteorological station a dead epiphyte-laden branch (>80% epiphyte

cover) was cut from a nearby location in the tree and attached to the strain gauge, which monitored its weight continuously. All data were recorded at 15 s intervals and averaged over 15 minutes using dataloggers (CR10X, Campbell-Scientific Inc., Logan, UT, USA) with attached multiplexers (AM16/32, Campbell Scientific). The stations were installed in the summer of 2003 and the branches were replaced every two to four months. While changing the branches, the strain gauges were recalibrated using steel weights. Between the recalibrations it was not necessary to adjust for a drift in the output from the strain gauges because the calibration did not change by more than 3.9% during the measurement period. The surface temperature of the lichen or bryophyte was measured on each branch using a thermistor (0.5 cm diameter) placed in contact with the underside of the lichen thallus or bryophyte leaf. Surface temperature was recorded at 5-minute intervals and stored on a datalogger (HOBO Pro Series, Onset Computer Corp.).

3.5 Branch descriptions

The epiphyte-laden branches were photographed and then destructively sampled after their removal from the field. A photograph of each the epiphyte-laden branch was taken from above and the vertical projected area was determined using image processing software (Vegmeasure 1.6, D Johnson, Department of Rangeland Science, Oregon State University). The dry weight of fruticose lichens (hairy structure) (b_{fr}), foliose lichens (plate-like structure) (b_{fo}) and bryophytes (b_{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 weights of the branch, litter and epiphytes were measured after drying at 70°C for 72 h.

3.6 Potential epiphyte-laden branch water storage (S_{e-b})

The potential epiphyte-laden branch water storage (S_{e-b}) was predicted by adding the estimated water storage by the fruticose lichens, foliose lichens and bryophytes with an estimate of the water storage on the branch surface (S_{bs}) (Equation 5). The dry weight of the fruticose, foliose and bryophytes on the branch were multiplied by each group's MWC_x (fruticose lichens = 2.23; foliose lichens = 3.42; bryophytes = 9.99) (Chapter 3). After removing all the epiphytes from the branch and immersing the branch in water, the difference between the branch weight before and after immersion provided the estimate of S_{bs}. The S_{e-b} of an epiphyte-laden branch was calculated as:

$$S_{e-b} = 2.23b_{fr} + 3.42b_{fo} + 9.99b_{br} + S_{bs} \quad (5)$$

During rainfall events the weight of the branch was adjusted for the force imparted to the branch by impacting raindrops. Gunn and Kinzer (1949) found a non-linear empirical relationship between the fall velocity of a water droplet in stagnant air and the droplet diameter:

$$V_T = 9.40 \cdot (1 - \exp(-1.57 \cdot 10^3 \cdot D^{1.15})) \quad (6)$$

where V_T is the terminal velocity (m s^{-1}) and D is the diameter of the raindrop (m). Best (1950), estimated that the average size of a raindrop could be predicted using the rainfall intensity:

$$D = (1.3 \cdot I^{0.232}) \cdot (-\ln(0.5))^{1/2.25} \quad (7)$$

where I is the rainfall intensity (mm h^{-1}). Equations (6) and (7) were combined to estimate the average fall velocity of the drops at different rainfall intensities.

The force imparted by the impacting raindrops was removed from the branch weight by using Newton's second law:

$$F_i = \frac{1/2 \cdot m \cdot v_T^2}{d_s \cdot g} \quad (8)$$

where F_i is the force of impact (kg), m is the instantaneous mass of raindrops hitting the branch (kg), and d_s (m) is the stopping distance of the raindrops and g (m s^{-2}) is the acceleration due to gravity. To estimate F_i it was assumed that: 1) all the raindrops had a diameter that equaled the mean raindrop size 2) the stopping distance of the raindrops equaled the mean diameter of the raindrops 3) the number of raindrops hitting the branch at a given moment (R) was equal to:

$$R = \frac{D}{v_T} \cdot r_s \cdot A \quad (9)$$

where number r_s is the number of raindrops hitting the branch every second (raindrops m^{-2} s^{-1}) and A is the branch surface area (m^2).

4.0 Results

4.1 Branch rainfall interception and evaporation

For most storm events under 30 mm the $S_{e\text{-}b}$ overestimated the maximum branch water storage during a single storm event and was particularly inaccurate for branches placed at 3.1 m and 24.8 m (Figure 13).

Part of the inaccuracy may result from the branches being partially saturated prior to the rain event (Figure 14). The canopy rarely dried between rain events and this decreased the quantity of water a branch could store during the next storm event. For example, branches at 3.1 and 24.8 m did not return to their prestorm weight 5 days after a 48 mm storm on 10 November 2004. To eliminate the portion of storms with a very short period between events, only storms with more than three days of dry weather preceding the storm were analyzed. However, even with three days of dry weather the S_{e-b} was still unable to predict branch water storage for storms less than 30 mm (Figure 13). For storms with less than 30 mm of rainfall the S_{e-b} was more accurate for branches at 46.5 m than those at 3.1m and 24.8m. However, for storms greater than 30 mm the branch water storage was closer to the S_{e-b}, but sometimes exceeded the S_{e-b}. Hence, the quantity of lichens on a branch can only be used to predict the epiphyte water storage 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 weight during a storm was generally greater for each subsequent storm (Figure 15). For example, during the month of November 2003 the branches at 3.1, 24.8 and 46.5 m, increased their weight during storm events; following the storm event, each branch would partially dry. Unless there was a long period of dry weather, the maximum weight a branch in the following storm exceeded that of the previous storm (Figure 15). The size of the increase in the maximum

branch weight for a storm varied between the branches because each branch had different quantities of lichen, bryophyte and deadwood biomass.

4.2 Canopy variables

The IS, mean and minimum methods were applied to storm events from 30 March to 9 November 2004 and from 18 March to 19 May 2004.   For this period the tipping bucket array under the canopy exceeded the manual throughfall collectors by only 0.9%. From 10 November to 1 December 2003 greater than 25% of the tipping buckets malfunctioned because of freezing temperatures, excess litter deposition in the funnels and logger failure. This resulted in the estimates of P_n by the tipping bucket array being 25% less than the estimate by the array of manual throughfall collectors. Thus, the IS, mean or minimum methods were not applied to rainfall events during latter period.
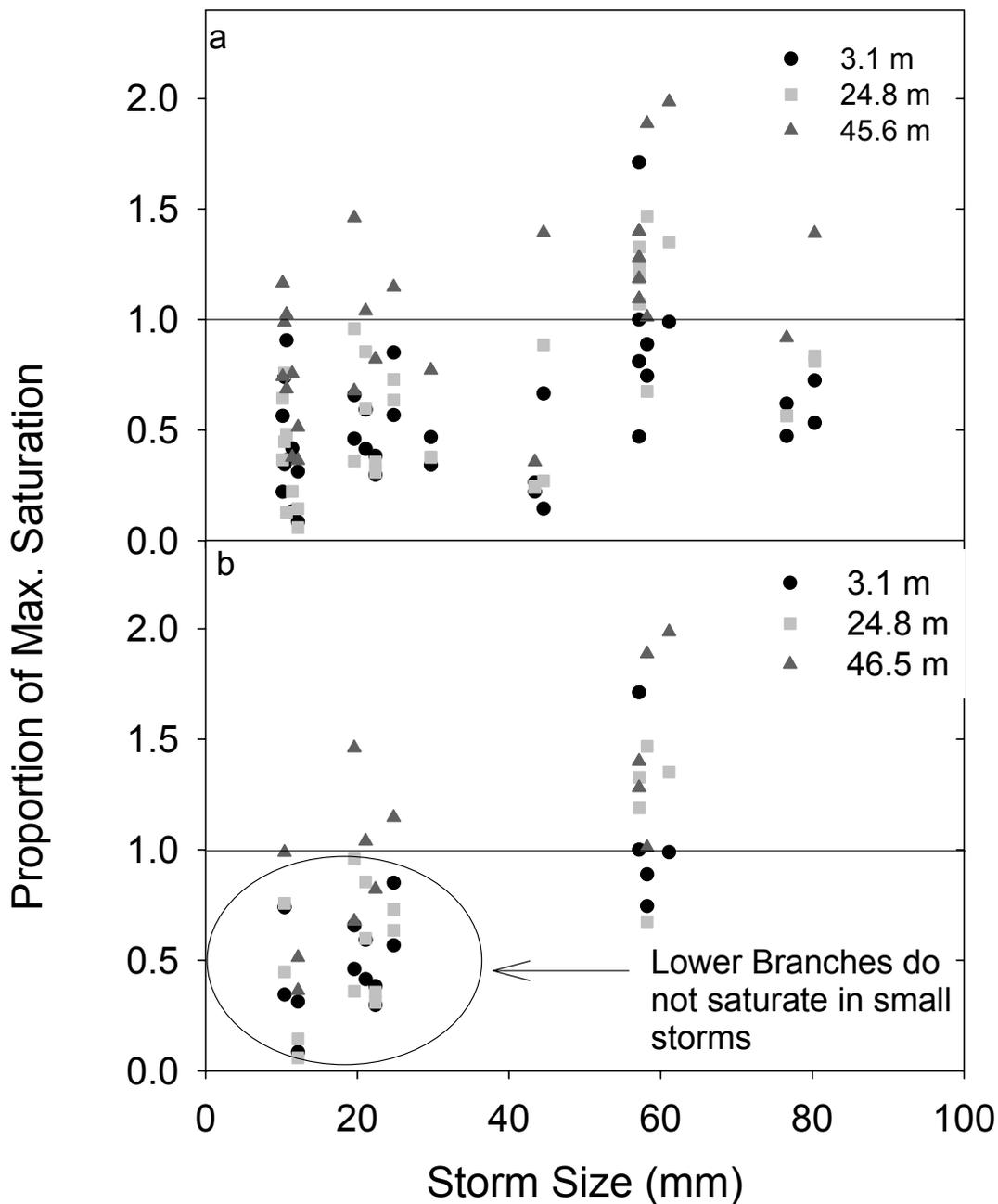
Figure 13 – The relationship between the storm size and the maximum branch weight for the storm normalized by the branch's potential water storage (Equation 5). Plot "a" presents the data for storm events from 7 Sept. 2003 to 11 May 2004. Whereas plot "b" presents data for storms from the same period that had at least three days of dry weather prior to the storm event. The branches were hung at three different heights (3.1 m, 24.8 m and 46.5 m).
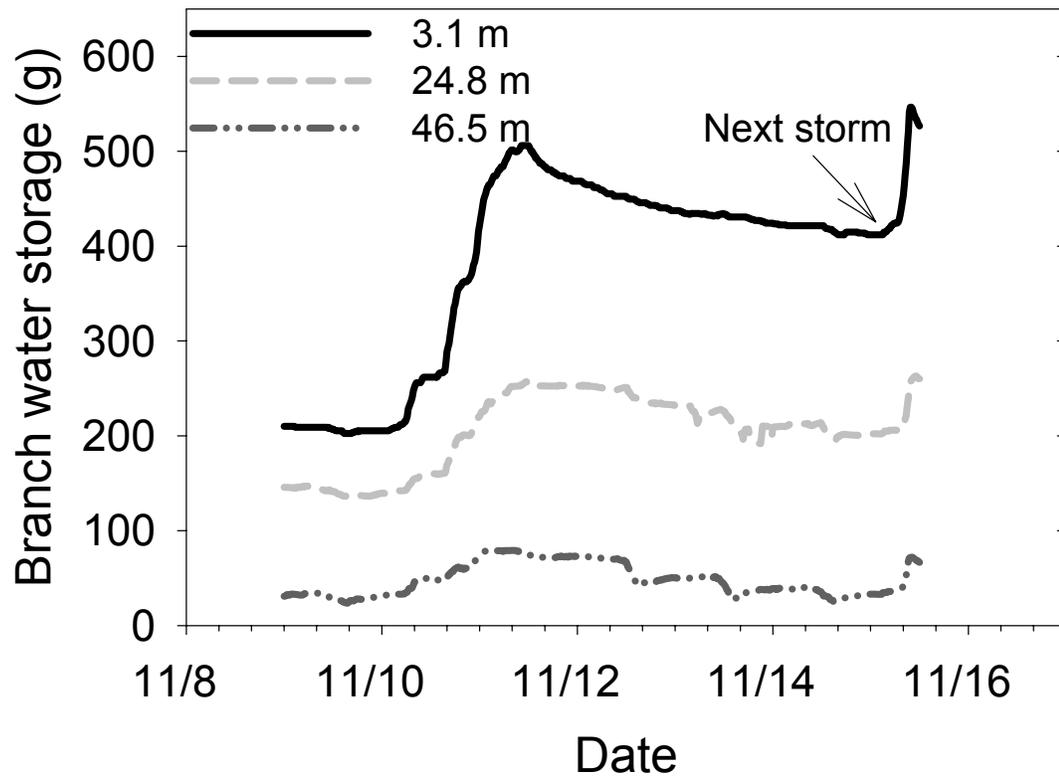
Figure 14 – After a storm event, branches at all measurement heights (3.1, 24.8 and 46.5 m) had protracted drying times. Even after 5 days with no rainfall many of the branches rarely dried. The branches at the three heights have different water storage because each branch had a different surface area, branch biomass and epiphyte biomass.
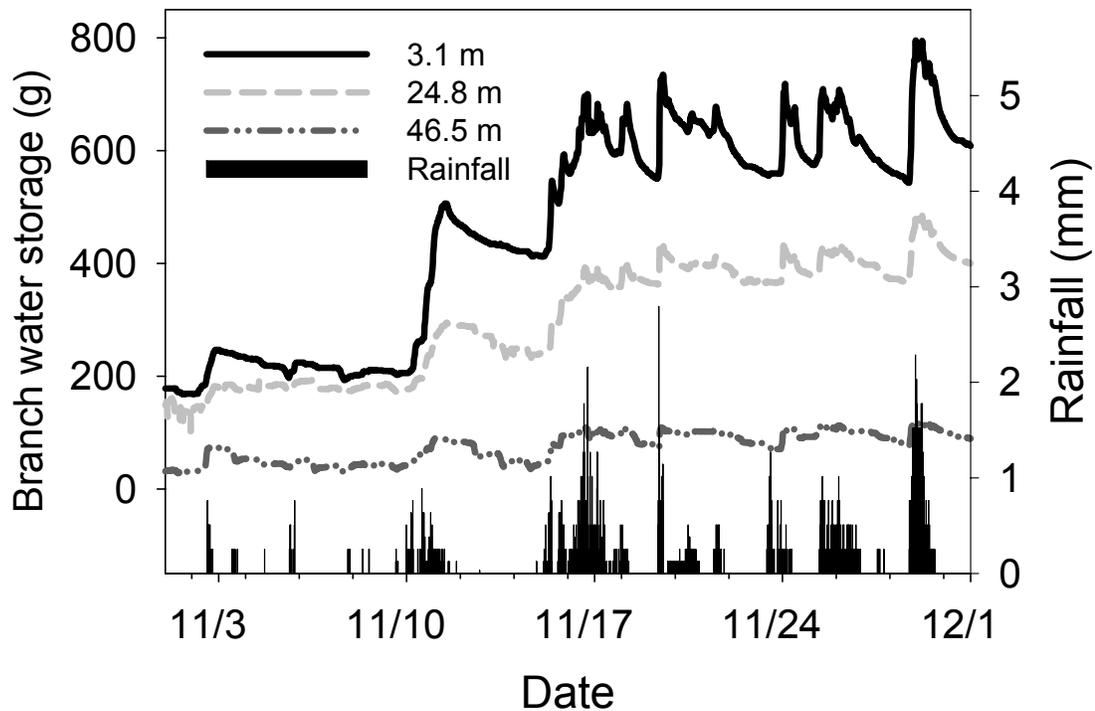
Figure 15 – After a storm event the branches would partially dry and some of the water likely migrated into the deadwood.   The transfer of water to the deadwood resulted in the maximum branch weight increasing for each subsequent storm.

The IS method estimates of S in the old-growth forest ranged between 1.00 and 7.5 mm when I_w was included and between 2.1 and 11.0 when I_w was excluded in the calculation of S (Figure 16). In both calculations the S was greatest after the summer drought. Values of p and $\overline{E}/\overline{R}$ also varied significantly throughout the measurement period, ranging between 0.18 to 0.50 and 0.01 to 0.49, respectively (Table 12).

The estimates of S, p and $\overline{E}/\overline{R}$ provided by the mean method (3.1, 0.41 and 0.21, respectively) were similar to the mean values provided by the IS method if I_w (S = 2.94 mm) is included in the calculation of S. In contrast, the S estimated by the minimum method (S = 5.0 mm; Table 13) was similar to the mean value provided by IS method when I_w was excluded (4.74 mm) (Table 14).

In general, the IS method underestimated the rainfall required for the branches to reach their maximum weight (Table 15). If the weight of the monitored branches at the time of P_s (as derived by the IS method) is compared to their maximum branch weight during the same storm event, the weight is usually less than 75% of the maximum branch weight (Table 15). For example, during a storm on 15 October 2003 the IS method predicted that the canopy saturated after 5.21 mm of rainfall (Table 15). However, the canopy was not saturated because the epiphyte-laden branches were only at 40 to 75% of their maximum weight for the storm when P_G equaled 5.21 mm (Table 15; Figure 17). Therefore, the $\overline{E}/\overline{R}$ would be overestimated.

Table 12 – Descriptions of the 20 branches placed on strain gauges from June 2003 to June 2004. The branches were placed on one of two trees at 3.1, 24.8 or 46.5 m and their weight was monitored by a strain gauge.

Sampling Dates	Species	Height	Fruticose g	Foliose g	Moss g	Litter g	Branch g
6/27/03 – 19/8/03	Hemlock	3.1	0	0	54.3	10.6	274.5
19/8/03 – 17/10/03	Hemlock	3.1	0	0.3	23.9	3.5	40.6
17/10/03 – 24/3/04	Hemlock	3.1	0	0	20.6	5.1	50.1
24/3/04 – 2/6/04	Hemlock	3.1	0	0	13.7	9.4	129.7
22/7/03 – 19/8/03	Hemlock	3.1	0	0	34	11.3	175.8
19/8/03 – 8/10/03	Hemlock	3.1	0	0	36.6	8.2	96.6
8/10/03 – 24/3/04	Hemlock	3.1	0.3	0	47.8	20.5	295
24/3/04 – 3/6/04	Hemlock	3.1	0	0	20.9	13.7	110
6/27/03 – 19/8/03	Doug.-F	24.8	0.3	0	25.1	28.5	300.9
19/8/03 – 5/11/03	Doug.-F	24.8	0.5	17.1	4.4	4.3	243.1
5/11/03 – 9/4/04	Doug.-F	24.8	0.3	7.9	8.0	17.5	789.6
9/4/04 – 2/6/04	Doug.-F	24.8	0.4	8.4	13.2	6.0	427.9
22/7/03 – 19/8/03	Doug.-F	24.8	0.4	16.5	35.2	9.5	412.8
19/8/03 – 8/10/03	Doug.-F	24.8	0.2	12.8	30.2	13.7	37.9
8/10/03 – 12/4/04	Doug.-F	24.8	0.05	15.6	9.6	11.9	351.3
12/4/04 – 3/6/04	Doug.-F	24.8	0.05	10.7	10.3	10.3	463.5
6/27/03 – 19/8/03	Doug.-F	46.5	0	9.0	21.4	8.0	111.7
19/8/03 – 5/11/03	Doug.-F	46.5	0.6	20	4.5	7.2	230.9
5/11/03 – 9/4/04	Doug.-F	46.5	1.7	10.7	3.2	5.6	275
9/4/04 – 2/6/04	Doug.-F	46.5	0	17.3	0.4	0.2	80.6
22/7/03 – 19/8/03	Doug.-F	46.5	8.4	16.5	0.7	6.7	132.6
19/8/03 – 8/10/03	Doug.-F	46.5	0.1	20.5	8.7	5.9	87.6
8/10/03 – 12/4/04	Doug.-F	46.5	0.05	9.2	0.5	1	47.4
12/4/04 – 3/6/04	Doug.-F	46.5	0.1	10.7	11	2.5	224.5

Table 13 – The estimates of canopy water storage capacity (S), the ratio of evaporation to rainfall intensity ($\bar{E}/\bar{R}$) and the direct throughfall fraction (p) for an old-growth Douglas-fir forest using the mean and minimum (S only) methods.

| Method	S (mm)	$\bar{E}/\bar{R}$	p
Mean	3.09	0.21	0.41
Minimum	5.00	-	-
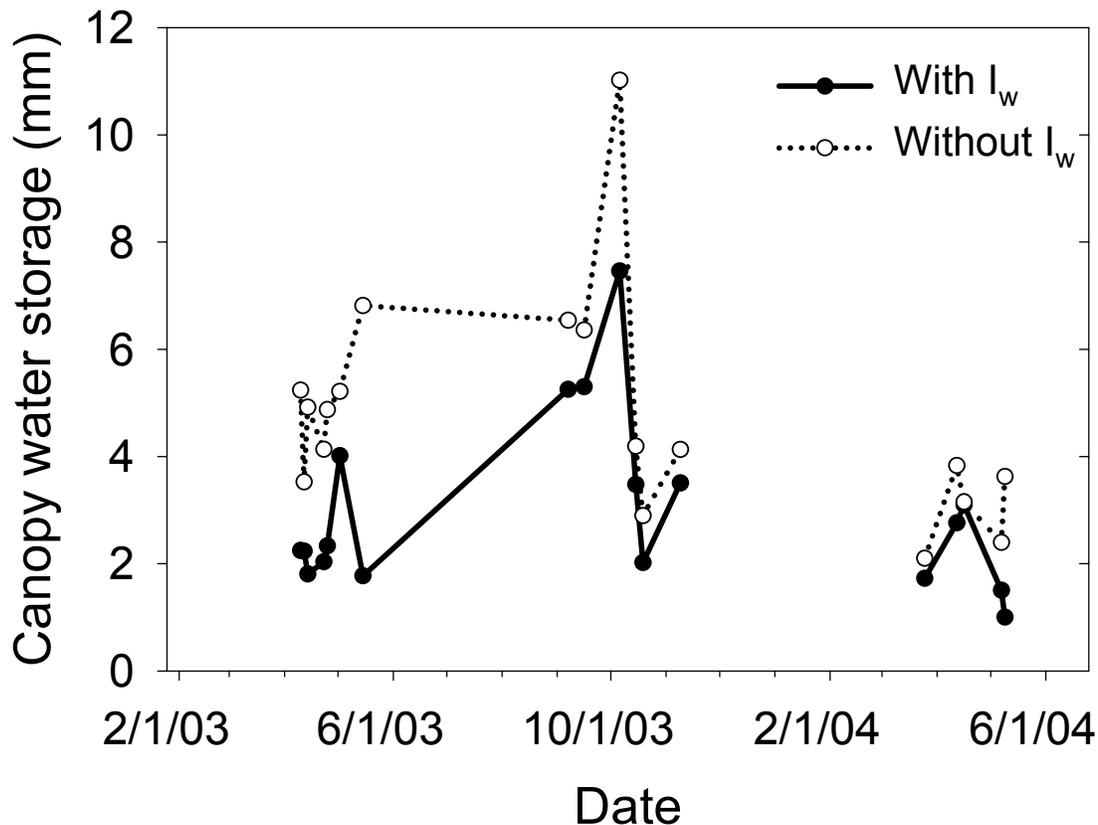
Figure 16 – The estimates of canopy water storage by the IS method for an old-growth Douglas-fir forest (>450 y-old) with and without assuming evaporation prior to canopy saturation (I_w) was negligible. The large S on 6 Oct 2003 (11.0 mm) likely results from a long wet up period (>50 h) (see discussion).

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

Event	Start	Duration h	P_G (mm)	P_n (mm)	I_n %loss	$\bar{E}/\bar{R}$	S (mm)	p
1	7/4/03	7.77	1.78	0.63	64.6			
2	9/4/03	15.6	2.67	1.00	62.5			
3	10/4/03	43.5	19.8	9.70	51.0	0.37	5.24	0.35
4	12/4/03	37.6	21.8	12.8	41.3	0.30	3.53	0.18
5	14/4/03	85.8	35.9	19.7	45.1	0.41	4.92	0.35
6	21/4/03	22.7	3.56	0.97	72.8			
7	23/4/03	42.8	27.2	16.2	40.4	0.31	4.13	0.39
8	25/4/03	27.7	13.3	7.41	44.3	0.29	4.87	0.45
9	28/4/03	6.90	1.27	0.24	81.1			
10	29/4/03	15.6	6.60	2.92	55.8			
11	2/5/03	64.4	47.9	34.2	28.6	0.18	5.21	0.19
12	7/5/03	27.3	5.97	2.06	65.5			
13	9/5/03	2.05	0.38	0.07	81.6			
14	10/5/03	9.94	4.32	1.28	70.4			
15	11/5/03	23.6	3.05	1.05	65.6			
16	15/5/03	58.7	15.4	6.14	6.1	0.49	6.82	0.34
17	25/5/03	11.3	4.70	1.77	62.3			
18	28/5/03		0.25	0.01	96.0			
19	30/5/03	2.20	4.32	1.64	62.0			
20	13/6/03	3.20	1.14	0.21	81.8			
21	20/6/03	20.3	3.81	0.73	80.8			
22	22/6/03		0.25	0	100			
23	2/8/03	10.6	0.38	0	100			
24	6/8/03	3.42	5.46	1.68	69.2			
25	22/8/03		0.25	0	100			
26	7/9/03	65.3	58.2	44.8	23.0	0.14	6.54	0.27
27	11/9/03	4.37	0.89	0.16	82.0			
28	16/9/03	35.1	19.6	12.4	36.7	0.10	6.36	0.39
29	6/10/03	93.1	61.1	40.6	33.6	0.22	11.0	0.30
30	14/10/03	0.87	2.03	0.68	66.5			
31	15/10/03	6.90	21.1	15.0	28.9	0.14	4.19	0.20
32	16/10/03	1.73	1.14	0.60	47.4			
33	19/10/03	11.8	10.4	6.39	38.6	0.21	2.90	0.31
34	22/10/03	10.2	2.67	2.31	13.5			
35	28/10/03	10.1	7.62	3.05	60.0			
36	2/11/03	4.95	6.60	3.54	46.4			
37	3/11/03	5.17	2.03	0.58	71.4			
38	5/11/03	4.88	3.56	1.65	53.7			
39	7/11/03	19.0	1.78	0.73	59.0			
40	9/11/03	48.1	24.8	16.0	35.5	0.25	4.13	0.48
41	14/11/03	78.8	80.3	59.6	25.8	na	na	na
42	19/11/03	36.0	29.7	14.2	52.2	na	na	na
43	21/11/03	9.20	6.10	4.10	32.8			
44	22/11/03	1.00	0.25	0.06	76.0			
45	23/11/03	22.2	22.4	11.4	49.1	na	na	na

Table 14 – (Continued)

46	25/11/03	36.6	43.4	33.9	21.9			
47	27/11/03	5.52	1.27	1.00	21.3			
48	28/11/03	10.57	76.6	66.7	12.9	na	na	na
49	18/3/04	14.8	1.52	0.44	71.8			
50	24/3/04	4.40	9.78	6.42	34.4			
51	25/3/04	7.00	44.6	39.1	12.3	0.09	2.10	0.50
52	30/3/04	16.8	6.86	3.00	56.3			
53	12/4/04	13.0	57.2	44.8	21.7	0.17	3.83	0.39
54	16/4/04	14.5	10.2	7.06	30.8	0.01	3.5	0.44
55	17/4/04	33.2	11.4	7.11	37.6			
56	19/4/04	12.8	57.2	46.6	18.5			
57	7/5/04	11.0	12.2	7.25	40.6	0.27	2.40	0.27
58	8/5/04	23.5	2.54	2.07	18.5			
59	9/5/04	46.5	10.7	5.48	48.8	0.39	3.63	0.46
	Totals		939.2	632.2	51.0			
	Averages					0.24	4.74	0.35
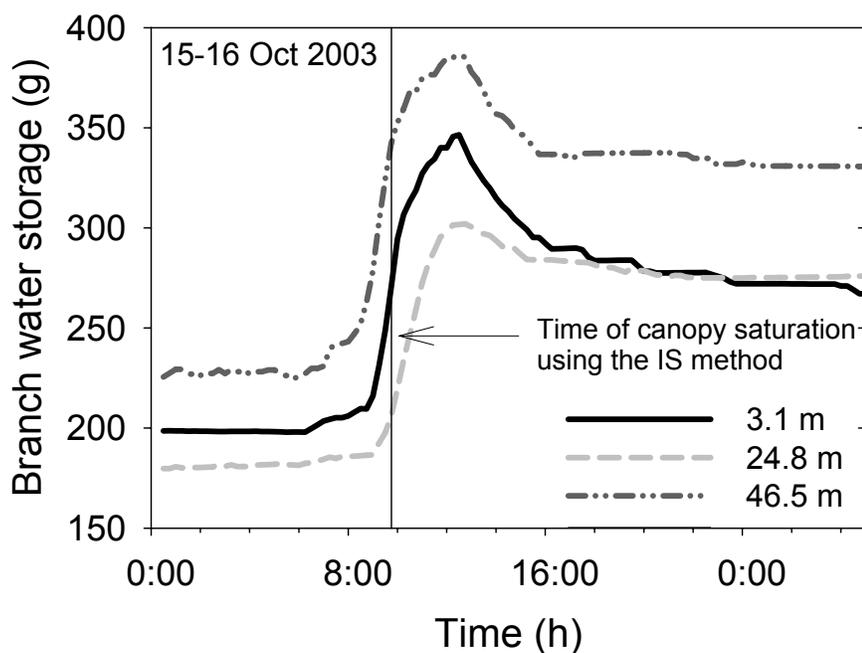

Figure 17 – The IS method underestimates the time required for the canopy to saturate. On 15-16 October 2003 three branches on Tree 1 were only 32 to 40% of their maximum weight for the storm when the IS method predicted the canopy saturated. The branches at the three heights have different water storage because each branch had a different surface area, branch biomass and epiphyte biomass.

Table 15 - A comparison between the IS estimates of canopy saturation point (P_S) and the proportion of the maximum weight for each branch at 3.1, 24.5, 45.6 m at the estimated time of P_S. The IS method underestimates the rainfall required to saturate epiphyte-laden branches.

Event Date	IS method P_S (mm)	Tree 1 Proportion of Maximum Branch Weight at P_s			Tree 2 Proportion of Maximum Branch weight at P_s		
		3.1 m	24.8 m	46.5 m	3.1 m	24.8 m	46.5 m
7/9/03	8.9	0.40	0.32	0.47	0.68	0.56	0.81
16/7/03	10.5	0.53	0.47	0.63	0.58	0.56	0.45
15/10/03	11.3	0.40	0.40	0.32	0.67	0.75	0.69
19/10/03	5.22	0.78	0.68	0.88	0.66	0.76	0.69
9/11/03	4.22	0.77	0.67	0.81	0.78	0.78	0.64
14/11/02	10.7	0.84	0.71	0.86	0.62	0.74	0.74
25/3/04	4.22	0.98	0.99	0.98	0.25	0.67	0.33
13/4/04	6.28	0.57	0.60	0.80	0.54	0.55	0.27
16/4/04	5.62	0.85	0.80	0.80	0.95	0.68	0.67
7/5/04	3.28	1.0	1.0	0.90	1.0	0.95	1.0
9/5/04	6.74	0.69	0.78	0.75	0.79	0.80	0.51

4.3 Maximum branch water storage and rainfall intensity

The water stored on a saturated epiphyte-laden branch was positively correlated with rainfall intensity. For example, the storm event on 28-29 November 2003 exceeded 76.6 mm (Table 14). After 28 mm of rainfall, all the branches on the strain gauges reached their maximum weight for the storm. After the branches reached their maximum weight the rainfall intensity fluctuated between 1 and 8 mm h^{-1} for 10 hours. During this period all the epiphyte-laden branches had a positive relationship between rainfall intensity and branch water storage (Figure 18) and the air temperature ranged between 2.5 and 7 °C.

5.0 Discussion

5.1 Epiphyte and canopy water storage

Unlike water storage by epiphyte-laden branches exposed to different rainfall intensities under a rainfall simulator (Chapter 3), the S_{e-b} was unable to predict the maximum water stored by the branches measured under field conditions (Figure 13). The S_{e-b} could not predict the water storage by a branch under field conditions because: 1) they were often partially saturated prior to a storm event; and 2) many of the rainfall events were smaller than the 30 mm required for the branches to approach S_{e-b}. If the branches are partially saturated prior to the storm event, their water storage capacity is partially filled and they will store less water. However, even if storms with three or more days of dry weather are excluded from the analysis, the S_{e-b} still could not predict the branch water storage (Figure 13).
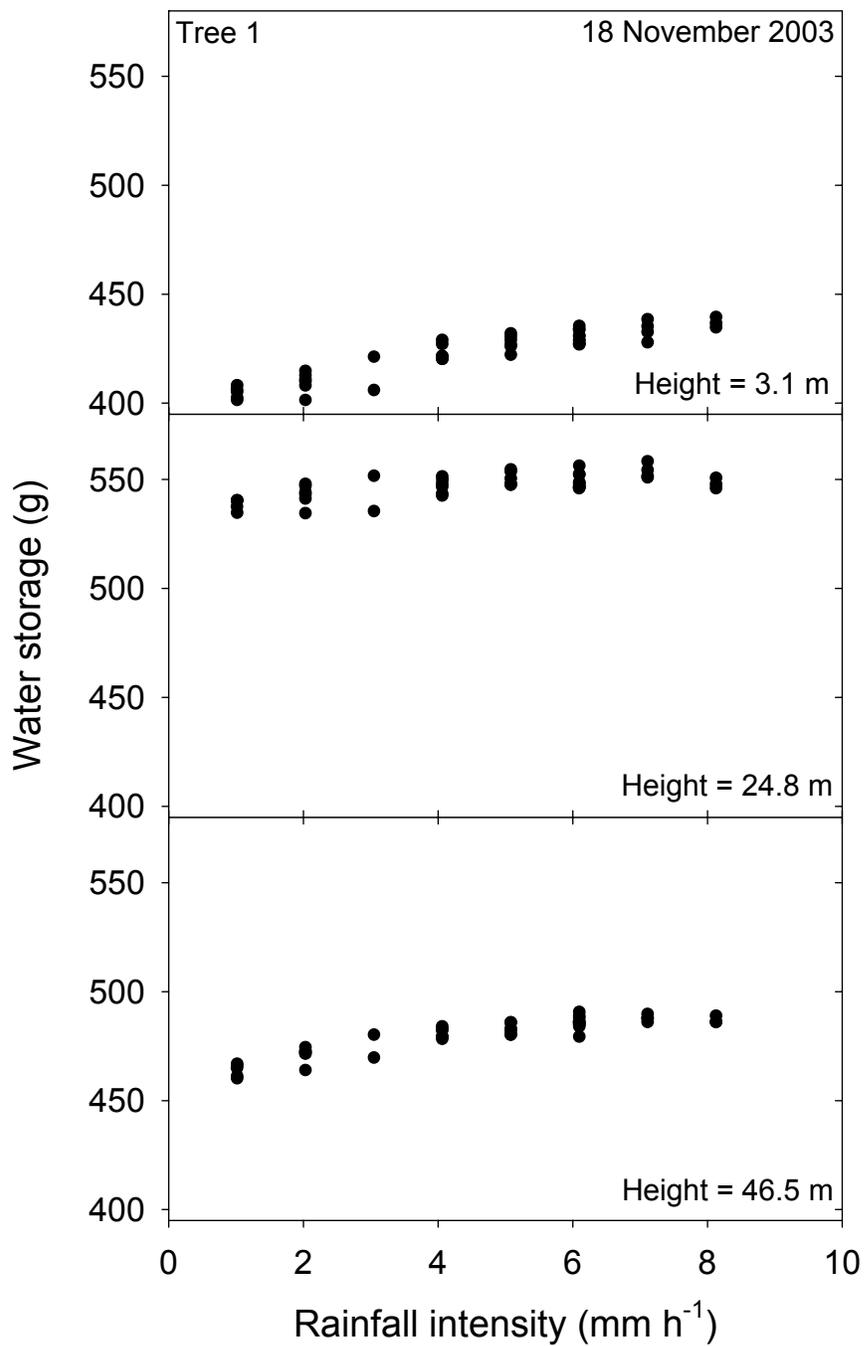
Figure 18 – The positive relationship between rainfall intensity and branch water storage at three different heights (3.1, 24.8 and 46.5 m) for epiphyte-laden branches on 28 November 2003.

In the field, most of the epiphyte-laden branches did not approach the S_{e-b} unless a storm exceeded 30 mm of rainfall (Figure 13). Even under controlled conditions using a rainfall simulator the weight of epiphyte-laden branches did not stabilize until they received at least 6 mm of rainfall (Chapter 3). Epiphyte-laden branches require a large amount of rainfall to saturate because water may preferentially flowed through the epiphyte mats and the MWC_x of the epiphytes is large (Chapter 3) (Figure 17; Table 15). In contrast, branches that have few epiphytes usually saturate with less than 2 mm of rainfall (Keim, 2003). Thus, epiphyte-laden branches will continue to store water throughout most storm events.

The epiphyte-laden branches continued to store water throughout the measurement period (Figure 15). 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 event (e.g. Chapter 1; Klaassen et al., 1996; Link et al., 2004). For example, Hancock and Crowther (1979) monitored the weight of individual branches in a Sitka spruce plantation and found that the branches returned to their prestorm weight less 12 hours after a storm. In contrast, following a storm in the old-growth Douglas-fir forest, the branches rarely dried to their prestorm weight because the S for the forest is large, the rain events were closely spaced, and water may have migrated into the deadwood (Figure 14).

Dead branches in the old-growth Douglas-fir canopy in this study are capable of storing 192% of their dry weight in water; and this accounts for 1.06

mm of canopy water storage (Chapter 3). The residence time of water that is stored in dead branches is likely longer than for lichen/bryophytes. Evaporation from the dead branches may be slow because absorption of solar radiation/sensible heat and the loss of latent heat should be 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/boles. The water storage in the bark and wood of live branches/boles may be considerable as simple allometric equations estimate that this forest contains 2156 kg ha^{-1} of bark (Chapter 3). 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/on the epiphytes and a longer-term storage pool in the livewood, deadwood and bark. Hence, the branches attain greater weights with each storm because the surface only partially dries between storms and the deadwood absorbs increasing amounts of water (Figure 15). However, more research is needed to estimate the total canopy storage and the residence time of water in old-growth Douglas-fir canopies.

5.2 Epiphyte distribution and water storage

Epiphytic lichens and bryophytes are not evenly distributed throughout the forest canopy. Epiphytic lichens in this forest dominate the upper portions of the canopy (above 35 m) where the evaporative demands are the greatest (Chapter 5; McCune et al., 1997; Pike et al., 1977). In contrast, bryophytes dominate lower in the canopy (i.e. <35 m) where wetting and drying cycles are

reduced (Chapter 5). The location of the lichens and bryophytes may have a significant role in the distribution of water in the forest canopy.

The abundance and distribution of lichens and bryophytes in the canopy should increase the time required for the canopy to dry after a storm. Based on their associated MWC_x, epiphytic foliose lichens, fruticose lichens and bryophytes in this forest can store 0.42, 0.072 and 0.78 mm of water, respectively (Chapter 3). While bryophytes have less biomass (780 kg ha^{-1}) relative to epiphytic fruticose and foliose lichens (31 and 1242 kg ha^{-1}, respectively), they can store three to four times more water 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 (or 14 000 kg ha^{-1}) (Chapter 3). The high MWC_x associated with bryophytes combined with their distribution shifts the distribution of 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 (Parker et al., 2002). Thus, the epicormic branches, western hemlock and bryophytes will store water lower in the canopy where the potential evaporation is decreased due to reduced wind speeds, solar radiation and vapor pressure deficits (Chapter 5). Thus, the forest canopy will remain

partially saturated for most of the wet season due to frequent storms and the water storage lower in the canopy.

5.3 Effectiveness of the mean, minimum and IS methods

The IS method estimated that the S_w, S_{wo}, $\overline{E}/\overline{R}$ and p for this old-growth forest averaged 2.94 mm, 4.92mm, 0.24 and 0.35, respectively. The estimates of S_w, $\overline{E}/\overline{R}$ and p are very similar to the S (3.3 mm), $\overline{E}/\overline{R}$ (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 is excluded in the calculation, the mean and range of S is much larger (Figure 16). When I_w is included, S is likely underestimated for most of the storms because past research indicates that the use of $\overline{E}/\overline{R}$ to estimate I_w (Equation 4) overestimates the effect of evaporation prior to canopy saturation (Link et al., 2004). However, excluding I_w will inflate the estimate of S when rainfall is sporadic 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 (Figure 16). The estimate of S was large because the rainfall intensity was sporadic 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).

In the present study, the mean method provided values of $\overline{E}/\overline{R}$ 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) the minimum method (5.0 mm)
are near the mean 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 simultaneously saturates and is dry prior to the storm.

It may be reasonable to assume that forest canopies that do not contain
epiphytes or other structures that slowly absorb water will simultaneously
saturate. However, this assumption is violated for old-growth Douglas-fir
forests because the saturation of the canopy will be delayed by preferential
flow of rainwater through the numerous epiphyte mats and the slow absorption
by other structures such as dead branches. It becomes apparent that the
canopy does not simultaneously saturate when observing individual branches
(Figure 17) or relating P_n and P_G (Figure 12). For an old-growth Douglas-fir
forest here is no distinct inflection point between P_n and P_G because the old-
forest canopy does not simultaneously saturate (Figure 12). In contrast,
rainfall interception by a young Douglas-fir forest canopy comes closer to
satisfy the "simultaneous saturation assumption" because the relationship
between P_n and P_G has a sharper inflection point (Chapter 2).

The delay in saturation will result in the IS, mean and minimum
methods underestimating total S and overestimating $\overline{E}/\overline{R}$ (IS and mean
methods only) in old-growth Douglas-fir forests.   Because the canopy will
continue to store water after the P_s provided by the IS (Figure 17) and mean
method, the slope of the second regression line (Equation 2) will be too
gradual and $\overline{E}/\overline{R}$ will be overestimated. Klaassen et al. (1998), reported a

similar problem when comparing direct measurements of S and $\overline{E}/\overline{R}$ by

microwave attenuation to the mean method for a young Douglas-fir forest in

the Netherlands. They found the mean method underestimated S by a factor

of 2 and overestimated $\overline{E}/\overline{R}$ by a factor of 3.

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 (Figure 16). After a 93 mm storm on the 6-13 October 2003,

estimates of S by the IS method decreased because the canopy was unable to

dry between storms.   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 will not provide an estimate of the maximum

canopy water storage, but at best, a functional water storage for the canopy on

a 'per storm' (IS method) or yearly (minimum and mean method) basis.

Where the functional water storage is defined as the maximum water storage

minus the portion of the storage already filled prior to the storm event.

5.4 Rainfall intensity and branch water storage

The positive relationship between rainfall intensity and branch weight

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 (Figure 18). The adjustment of the branch weight for the force of

the raindrops on the branch was small, ranging from 0.3 to 0.93 g for rainfall intensities of 1 to 8 mm h^{-1}. This change probably represents the upper limit of the force imparted to the branch as Equation 8 assumes the stopping distance to be equal to the raindrop diameter. In reality, the thalli/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 (Equation 7). 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 windspeed and branch weight (R^2<0.2). However, for the purpose of this analysis, the changes in windspeed were ignored because greater windspeeds should decrease branch water storage by shaking water off the branch (Hörmann et al., 1996). Water absorption by the deadwood could not be attributed to the greater branch weight because the rainfall intensity steadily decreased during the 10 h analysis period. The increase in branch water storage is therefore related to increasing rainfall intensities.

Based on previous research, it is generally accepted that the water storage on a branch decreases as the rainfall intensity increases (e.g. 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 will impart a greater force to the leaf/branch surface, thereby splashing greater quantities of water off of the surface. In contrast, Keim (2003) found that the branch water storage for a

variety of coniferous and deciduous branches commonly found in the PNW was positively correlated with rainfall intensity. He argued that the experiment presented by Calder (1996) only accounted for the effect of increasing drop size on water storage, but failed to account for the addition of rainwater to the branch. Keim (2003) asserts that the status of the storage on a branch depends on the ratio between the rate of drainage losses from the branch (e.g. splash from raindrops or dripping from the branch) and 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. The structure of epiphyte-laden branches favors increased storage with increasing rainfall intensity.

Epiphytic lichens and bryophytes create mats of thalli/leaves providing a rough, 3-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 may minimize splash formation by absorbing the energy from the impacting drop and of the water that is splashed a significant portion may be recaptured by the rough mat surface. The rainwater will instead 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/bryophyte mat, the water may pond in the mat air spaces or on the surface of the thalli/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 come

to an asymptote because the branch can no longer store increasing amounts of water. For the branches on 28 November 2003 the relationship between rainfall intensity and branch water storage appeared to asymptote as the rainfall intensity approached 8 mm h^{-1} (Figure 17). Chapter 3 shows that there is little increase in water storage for epiphyte-laden branches placed under a rainfall simulator at rainfall intensities of 11, 16 and 39 mm h^{-1}. At these rainfall intensities the water stored is may be similar because the air spaces and the thalli/leaf surfaces become fully saturated and the rainfall immediately drains from the branch. However, because rainfall intensities are usually below 11 mm h^{-1} in the PNW (Chow, 1964), water storage by saturated epiphyte-laden branches will be positively related to rainfall intensity.

6.0 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 (MWC$_x$) of lichens and bryophytes leads to increased potential water storage by an epiphyte-laden branch (S$_{e-b}$). Unlike laboratory experiments (Chapter 3), the water storage by epiphyte-laden branches during a single storm event did not equal S$_{e-b}$ because: 1) branches required greater than 30 mm of rainfall to saturate; and 2) branches were unable to dry between storm events.

The epiphytic lichens and bryophytes prolonged the time required for the canopy saturate during a storm and to dry after a storm. The saturation of the canopy was delayed because of preferential flow of water through epiphyte

mats and the high maximum water content (MWC_x) of the epiphytic lichens and bryophytes increased the canopy water storage (S). The bryophytes contributed to the canopy remaining partially saturated from much of the wet season because their distribution and large MWC_x resulted in larger water storage capacity lower in the canopy where evaporative demand is lower than upper canopy layers.

In old-growth Douglas-fir forests the occurrence of preferential flow and the inability of the canopy to dry between storm events results in bucket type models (e.g. IS, mean and minimum methods (Klaassen et al., 1998; Leyton et al., 1967; Link et al., 2004)) underestimating canopy water storage (S) and overestimating mean evaporation rate during storms ($\overline{E}/\overline{R}$). Lastly, in contrast with 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/bryophyte mats reduced the loss of water by raindrop splash and impeded the drainage of water from the branch.

Acknowledgements

Chapter 5 – The absorption of water vapor by epiphytic lichens and bryophytes in an old-growth Douglas-fir forest during the seasonal summer drought: Implications for green lichen photosynthesis and canopy energy budgets

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1.0 Abstract

The absorption of atmospheric water vapor by epiphytes in old-growth Douglas-fir forests in the Pacific Northwest (PNW) may facilitate carbon uptake by green lichens and alters the energy budget of the forest during the summer drought. This study used a combination of laboratory and field techniques to determine the effect that changes in vapor pressure deficit (VPD) have on the water content (WC_x; water content as a percent of dry weight) of epiphytic lichens and bryophytes. The diurnal change in the WC_x of the epiphytes was modeled to determine the effect on the energy budget of an old-growth Douglas-fir forest during the summer drought of 2003.

The old-growth Douglas-fir forest contained 1242, 31 and 780 kg ha^{-1} of epiphytic foliose lichens, fruticose lichens and bryophytes in the canopy, respectively.   Vertically, the bryophytes dominate below 30 m where the evaporative demand was significantly diminished, and the foliose and fruticose lichens became increasingly dominant above 30 m.

The WC_x of three representative epiphytic lichens/ bryophytes (lettuce lung (*Lobaria oregnana*), witch's hair (*Alectoria sarmetosa*) cattail moss (*Isothecium myosuroides*)) were measured at five different VPD (RH = 158, 264, 528, 1057 and 1849%) after 1, 2, 4, 8 and 12 h of exposure. The WC_x of the epiphytes rapidly increased at lower VPD ($WC_x = y_o + (a \cdot b)/(b + x)$). The WC_x of witch's hair and cattail moss at the different VPD were statistically different (p-values<0.05), but the difference was never greater than 3.4%. In contrast, lettuce lung absorbed water more quickly and attained a higher WC_x

relative to the witch's hair and cattail moss (p-value<0.05). Both lettuce lung

and witch's hair have a green algal symbiont and likely absorb sufficient

quantities of atmospheric water to reactivate their photosynthetic metabolism

on between 55 to 96% of the summer nights.

Two models were created to estimate the canopy scale latent heat flux

of the lichen/bryophytes (LE_e) in the Douglas-fir forest. The first model

combined the measured epiphyte biomass with a model that estimated the

VPD dependent changes in WC_x of the lichens/bryophytes (VPD method).

The second model estimated LE_e by scaling the change in WC_x of epiphyte-

laden branches that were continuously monitored *in situ* to the canopy (SG

method). Both methods showed a strong diurnal trend in LE_e. Prior to sunrise

the epiphytes absorbed water at a rate between 5 to15 W m^{-2}. After sunrise

the RH rapidly fell and the epiphytic lichens/bryophytes lost water rate of -10 to

-20 W m^{-2}; with some periods reaching -40 W m^{-2}. Between 600 and 1000 h

the latent heat flux from the epiphytes accounted for 5 to 21% of the canopy

latent heat flux. Therefore, the absorption of water vapor may directly benefit

green lichens in old-growth Douglas-fir forests and must be considered when

evaluating the LE of forests with large epiphyte populations.

2.0 Introduction

The large populations of epiphytes in old-growth Douglas-fir forests of

the Pacific Northwest (PNW) may diurnally absorb and evaporate 1.3 tonnes

ha^{-1} of atmospheric water vapor during the dry summer months (Appendix I).

The PNW typically has a long summer drought 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 these forests can exceed 2000 kg ha^{-1} (McCune, 1993; Pike et al., 1975; Sillett and Rambo, 2000) and these organisms have an impressive ability to survive droughts (Kappen, 1973; Proctor, 1982; Proctor, 2000a). We hypothesize that the absorption of large quantities of atmospheric water vapor by epiphytes beneficially enhances the survival of lichens during droughts and alters the energy budget of the old-growth Douglas-fir forest canopies.

It has long been recognized that lichens have the ability to absorb water vapor from the atmosphere (e.g. Bertsch, 1966; Blum, 1973; Kolumbe, 1927) (NOTE: While relative humidity has frequently been used to predict the water content of lichens (Blum, 1973; Green et al., 2002; Lange et al., 1988; Lange et al., 1986; Matthes-Sears et al., 1987), it is more appropriate to use vapor pressure deficit (VPD) to predict the flux of water vapor to and from epiphytic lichens and bryophytes (see methods)). Many lichens can increase the amount of water stored in their thalli by 8 fold when the relative humidity (RH) increases from 30 to 98% (Blum, 1973; Schlensog et al., 2000). Past research indicates that when the RH exceeds 80%, the water content (WC_x) of many lichens with a green algal symbiont (green lichens) will be greater than 20%, allowing these lichens will reactivate their photosystems (e.g. Bertsch, 1966; Green et al., 2002; Lange et al., 1988; Lange et al., 1986). However, this relationship is species specific, as some green lichens require a WC_x in

excess of 50% to reactivate their photosynthetic metabolism (Antoine, 2001).

It has been proposed that the absorption of water vapor facilitates the survival

of these lichens during a drought (Blum, 1973; Lange et al., 2001; Matthes-

Sears and Nash III, 1986). Cyanolichens are a second group of lichens that

have a blue-green algal symbiont and are abundant in old-growth Douglas-fir

forests in the PNW (McCune, 1993; Pike et al., 1977; Sillett and Rambo,

2000). Cyanolichens are unable to absorb sufficient quantities of water vapor

from the atmosphere to reactivate their photosynthetic metabolism (e.g. Green

et al., 2002; Lange et al., 1993; Lange et al., 1986). The reason for this

difference between green lichens and cyanolichens is still unknown (Lange et

al., 2001). In contrast with lichens, all bryophytes are unable to reactivate their

photosynthetic metabolism without liquid water (Proctor, 2000a). Thus, the

absorption of water vapor by bryophytes has received little attention.

However, the absorption of water vapor by the large populations of epiphytic

lichens and bryophytes may have a significant impact on the energy budget of

the forest during the summer drought.

During summer drought, the RH within the canopy typically ranges

between 20 to 30 % (VPD > 2600 Pa) during the day and above of 80% (VPD

< 400 Pa) at night. This change in RH results in the water content of many

lichens increasing from 10 to 80% of dry weight (Blum, 1973; Schlensog et al.,

2000). If epiphytic bryophytes absorb a similar amount of water vapor, the

diurnal absorption/evaporation in an old-growth Douglas-fir forest would total

1325 kg ha^{-1} (Appendix I). If this water were absorbed/evaporated in one to

three hours in the morning/evening, the latent heat flux associated with the phase change would be equivalent to between 31 to 95 W m^{-2}.

In an old-growth Douglas-fir forest in South Central Washington, Unsworth et al. (2004) measured the moisture loss from the soil using an array of soil moisture probes and the flux of water above the forest canopy using an eddy covariance system (LE$_{ec}$).   During the early morning hours, the soil moisture loss exceeded the flux of water vapor above the canopy between 0.04 to 0.12 mm h^{-1} (or approximately 27 to 82 W m^{-2}). Because the measurement periods occurred near the end of the summer drought when the soil water could not drain to deeper soil layers, it was concluded that the reduction in soil water content resulted from transpiration (Unsworth et al., 2004). The difference between the soil and canopy water fluxes was either the result of instrument error, incorrect assumptions about the source area or the storage of water within the forest canopy air space. Using a vertical transect of water vapor measurements in the canopy, Unsworth et al. (2004) determined that an increase in the water vapor content of the air within the canopy could only account for 0.02 mm h^{-1} of the missing water flux. Unsworth et al. (2004) hypothesized that, because the air temperature in the canopy during these periods approached the dewpoint temperature, the remaining difference between the soil and canopy water fluxes resulted from water deposition on thermally massive objects such as tree boles/stems or absorption by epiphytic lichens/bryophytes. However, to date there has been little research on the absorption of atmospheric water by epiphytic lichens and

bryophytes in old-growth Douglas-fir forests and the consequences for photosynthesis and the energy budget. The goal of this study was to: 1) determine whether the diurnal variation of VPD in an old-growth Douglas-fir forest allowed epiphytic lichens to absorb sufficient quantities of atmospheric water vapor to be likely to reactivate their photosynthetic metabolism; and 2) determine the impact of absorption/evaporation by epiphytic lichens and bryophytes on the latent heat flux of an old-growth Douglas-fir forest.

3.0 Materials and methods

3.1 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 forest is dominated by old-growth Douglas-fir (*Psuedostuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterphylla* (Raf.) Sarg.). The canopy is greater than 60 m tall, has an LAI of approximately 12.1 (Moore et al., 2004) and has large canopy gaps that are typical of old-growth Douglas-fir forests in the Pacific Northwest (Franklin et al., 2002; Gray and Spies, 1996). The region has mild winters and warm dry summers. The mean air temperature for this forest (1958 to 2003) is 4.5 and 16°C for the periods of October to April and May to September, respectively (HJ Andrews LTER long-term data set). The mean annual precipitation of for this forest is 2300 mm, with more than 95% falling between October and May (Rothacher et al., 1967). The soil is described as gravelly clay loam (Swanson and James, 1975).

3.2 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 established by McCune (1994). On 1 September 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 h and the dry weights from all plots were averaged and then multiplied by the 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^{-1}) 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^2 quadrat was placed on the forest floor and all bryophytes inside the plot were removed. The forest floor bryophytes were sorted into 4 categories: step moss (*Hylocomium splendens*), electrified cat's tail (*Rhytidiadelphus triquetrus*), Oregon beaked (*Kindbergia oregona*) and other bryophytes.   The

bryophytes were separated from forest floor litter and dried at 70°C for 72 h to

determine dry weight.

The relative abundance 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 3 randomly selected cardinal

directions. The observations were made by a single observer who climbed a

fixed rope, and using a 0.2 m by 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).

3.3 The use of vapor pressure deficit (VPD) or relative humidity (RH) to predict epiphyte water content (WC$_x$)

It is commonplace within the lichen literature to relate the WC$_x$ of the

lichen to the RH of the air (Blum, 1973; Green et al., 2002; Lange et al., 1988;

Lange et al., 1986; Matthes-Sears et al., 1987). While the use of RH to predict

WC$_x$ is appropriate in a closed system under isothermal conditions (Monteith

and Unsworth, 1990), the driving force for the flux between the lichen or

bryophyte and the atmosphere will ultimately be controlled by the VPD of the

environment (Monteith and 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. The

evaporation of the water into the pore space will require the latent heat of

vaporization and the energy to expand the partial pressure of water vapor to its larger volume. If the closed pore space were isothermal, it would be appropriate to use RH to predict the equilibrium WC_x 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 and 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 (i.e. the VPD at 90% RH is not the same when the air is at 10 and 20°C). Thus, to properly assess the flux one must determine 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 the case with lichens during the summer drought (Rundel, 1988). The equilibrium vapor pressure within the pore spaces will not be saturated and may have a VPD of up to 30 MPa above the surface (Rundel, 1988). Therefore, the use of atmospheric VPD will not be as precise because the VPD within the lichen pore space is unknown. However, relative to RH, using VPD 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 and the atmosphere.

3.4 Laboratory measurements

The variation in water contents (WC_x) of a foliose lichen (WC_{fo}), fruticose lichen (WC_{fr}) and bryophyte species (WC_{br}) with VPD was measured in the laboratory. WC_x in this study 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 sarmetosa*), foliose lichen, lettuce Lung (*Lobaria oregnana*) and the bryophyte, cattail moss (*Isothecium myosuroides*), where 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 et al., 1977; Sillett, 1995). Witch's hair has a green algal symbiont. Lettuce lung is generally classified as a cyanolichen, but it actually has a tripartite symbiosis with a green and a blue-green alga (Antoine and McCune, 2004). In lichens that contain both green and blue-green alga, only the sectors with green alga can reactivate photosynthetic metabolism after absorbing sufficient quantities of atmospheric water vapor (Green et al., 2002; Lange et al., 1986). Lichens with a green algal symbiont typically can reactivate their photosynthetic metabolism when their WC_x exceeds 20%, but the relationship is species specific (e.g. Bertsch, 1966; Green et al., 2002; Lange et al., 1988; Lange et al., 1986). For example, Lettuce lung requires their WC_x to exceed 50% for reactivate their photosynthetic metabolism (Antoine, 2001). Thus, both lettuce lung and witch's hair can reactivate their photosynthetic metabolism if there is a sufficient quantity of water vapor in the air.

To determine the dependence of WC_x 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 $cm^3 min^{-1}$ through a closed circuit loop that contained a small plastic chamber (3780 cm^3). Samples of lettuce lung, witch's hair and cattail moss were first stored at 0% RH for 48 hours and then placed in the chamber and exposed to either a VPD of 158, 264, 528, 1057 and 1849 Pa (30, 60, 80, 90 and 94% RH, respectively) at 22°C for 12 hours (n = 10 for each species at each RH). The RH and temperature of the chamber was monitored every second (HMP45C, Campbell Scientific, Logan, Utah) and the data were averaged and stored on a data logger at 10 minute intervals (CR10X, Campbell Scientific, Logan, Utah). 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_x of the thallus/leaf on VPD was modeled for each time interval using the following equation:

$$WC_x = (a \cdot b)/(b + x) \quad (1)$$

where a and b are fitting parameters.

3.5 Field meteorological measurements

The microclimate of the canopy and the diurnal change in weight of epiphyte-laden branches were monitored at 3 meteorological stations in each of two Douglas-fir trees at 3.1, 24.8 and 46.5 m above the ground. 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). A dead epiphyte-laden branch (>80% epiphyte cover) was cut from the tree and its weight was continuously monitored by the strain gauge.   Using a dead branch avoided the problem of the branch mass changing because the needles died and fell off. All data were recorded at 15 s intervals and averaged over 15 minutes using dataloggers (CR10X, Campbell-Scientific Inc., Logan, UT, USA) with attached multiplexers (AM16/32, Campbell Scientific). The stations were installed in June of 2003 and the branches were replaced every two to four 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.

To determine whether the dependence of WC_x on VPD of lichen/bryophytes measured in the laboratory agreed with that measured in the field, 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 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 between 1500 and 1600 h. The lichen and bryophyte samples were allowed to equilibrate with the atmosphere for 14 to 15 h. Between 500 and 600 h the following morning, the lichen and bryophytes samples were lowered to the ground and weighed.

The samples were then dried for 72 h at 70°C to attain dry weight. The measured WC_x 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 600 h into Equation 1.

3.6 Calculation of the latent heat flux (LE_e) associated with lichen and bryophyte mass exchange

Two methods were used to estimate the latent heat flux (LE_e) associated with weight changes of lichens and bryophytes in the old-growth Douglas-fir canopy over four 4 day ensemble periods (Day of year (DOY): 206-209, 225-228, 244-247, 274-277). These ensemble periods were chosen because there were no precipitation events (rain or dew) for at least one week prior to the ensemble period and they represented periods with varying temperatures and VPD. The first technique estimated the WC_x of the lichens and bryophytes by substituting the VPD measured at 3.1, 24.8 and 46.5 m at 15 min intervals in the canopy into Equation 1 (VPD method ($LE_{e\text{-}VPD}$)). This method assumed that: 1) the responses of the WC_x of lettuce lung, witch's hair and cattail moss to changes in VPD were representative of all foliose lichens, fruticose lichen and bryophytes in the canopy; 2) there was sufficient time during each 15 minute interval for the lichens and bryophytes to come into mass equilibrium with their environment; 3) the change in the water content of two thirds and one third of foliose lichens for each 15 min interval (ΔWC_{fo}; kg) could be estimated using the VPD measured at the 24.8 and 46.5 m meteorological stations, respectively; 4) the change in the water content of the

fruticose lichens for each 15 min interval (Δ WC$_{fr}$; kg) could be estimated using

the VPD measured at the 46.5 m meteorological station; and 5) the change in

the water content of half of the bryophytes for each 15 min interval (ΔWC$_{br}$; kg)

could be estimated by each of the VPD measurements at the 3.1 and 24.8 m

meteorological stations. The prediction by the VPD method for the two trees

was averaged to provide an estimate of the LE$_{e\text{-VPD}}$ for the epiphytic lichens

and bryophytes. The use of the different stations for the different epiphyte

functional groups mimics the distribution of these epiphytes within the canopy

(Figure 19). The WC$_x$ of the different functional groups were estimated by

Equation 1 and multiplied by the biomass foliose lichen, fruticose lichen and

bryophytes in the canopy.

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

where λ is latent heat flux of vaporization (J kg^{-1}); s is time duration (15 min =

900 s); B$_{fo}$, B$_{fr}$, and B$_{br}$ represent of the biomass of the foliose lichens,

fruticose lichens and bryophytes, respectively (kg m^{-2}) in the canopy.

The second method (SG method (LE$_{e\text{-SG}}$)) 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

(Chapter 3). For each 15 min interval the change in weight of each branch

(ΔW_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$_x$ 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} in 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 the relationship between their WC_x and VPD are the same (see results).

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}, a_{br}, respectively) were 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:

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

Where n represents the number of branches monitored on the tree (n=3). The estimates of LE_{e-SG} produced for each tree were averaged to provide an estimate for the whole canopy.
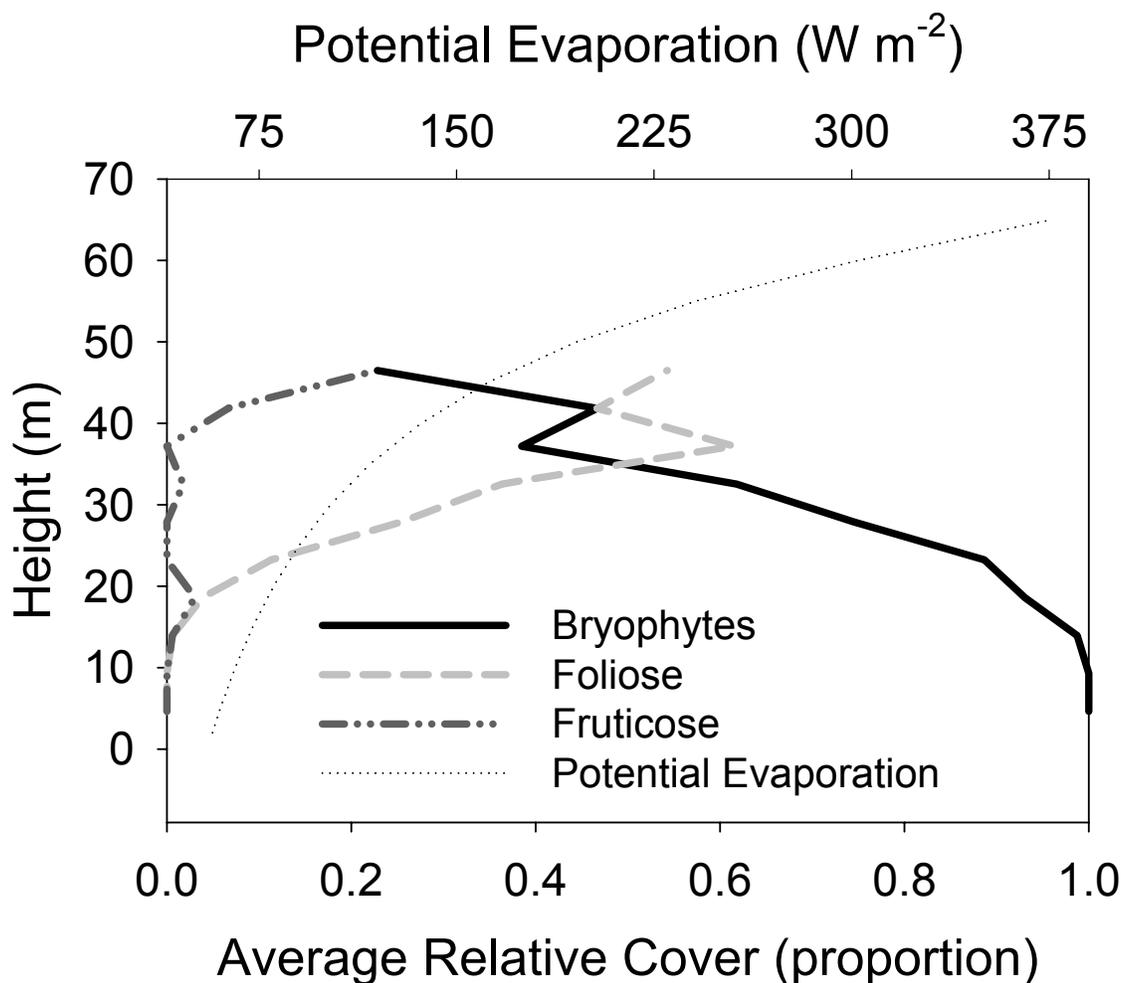
Figure 19 – The vertical variation of biomass distribution of the epiphytic lichens and bryophytes and the potential evaporation (see Appendix II) during the summer months for an old-growth Douglas-fir forest in the Central Cascades of Oregon.

4.0 Results

4.1 Lichen and bryophyte biomass and distribution

Lichens and bryophytes occupy specific niches within the forest

canopy. The bryophytes dominated below 30 m, with the surface area of

foliose and fruticose lichens increasing above 30 m (Figure 19).   The forest

canopy contained 1273 and 780 kg ha^{-1} of epiphytic lichens and bryophytes, respectively (Table 16). The lichens in this forest are primarily epiphytic with the foliose lichens comprising >97% of the biomass (Table 16). The forest floor contained an additional 465 kg ha^{-1} of bryophytes; of which greater than 95% of the biomass was comprised of step moss, electrified cat's tail and Oregon beaked moss (Table 16).   The combined total for the forest floor and epiphyte bryophyte biomass nearly equaled the estimates for the epiphytic lichen biomass (Table 16).

Table 16 – 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^{-1}
Epiphytes	
Foliose lichens	1242 ±452
Fruticose lichens	31.0 ±22.0
Bryophytes	780[1]
Forest Floor Bryophytes	
Oregon beaked	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

[1] From McCune (1993)

4.2 Canopy microclimate

The decrease in light intensity and wind speeds lower in the canopy resulted in lower surface temperatures and evaporative demand (Figure 19 and 20). For example, during a typical sunny summer day the evaporative

demand for an epiphyte-laden branch drops from 376 W m^{-2} at 65 m to 66 W

m^{-2} at 10 m (See Appendix II for details).

During the summer months the VPD in the canopy diurnally ranged

between 150 to 4000 Pa (RH $\approx$ 20 to 90%), with the VPD approaching 100 Pa

(RH>95%) on some nights (Figure 21).   For the four measurement periods

the VPD was generally lowest between 1300 and 1600 h and peaked between

600 and 800 h.
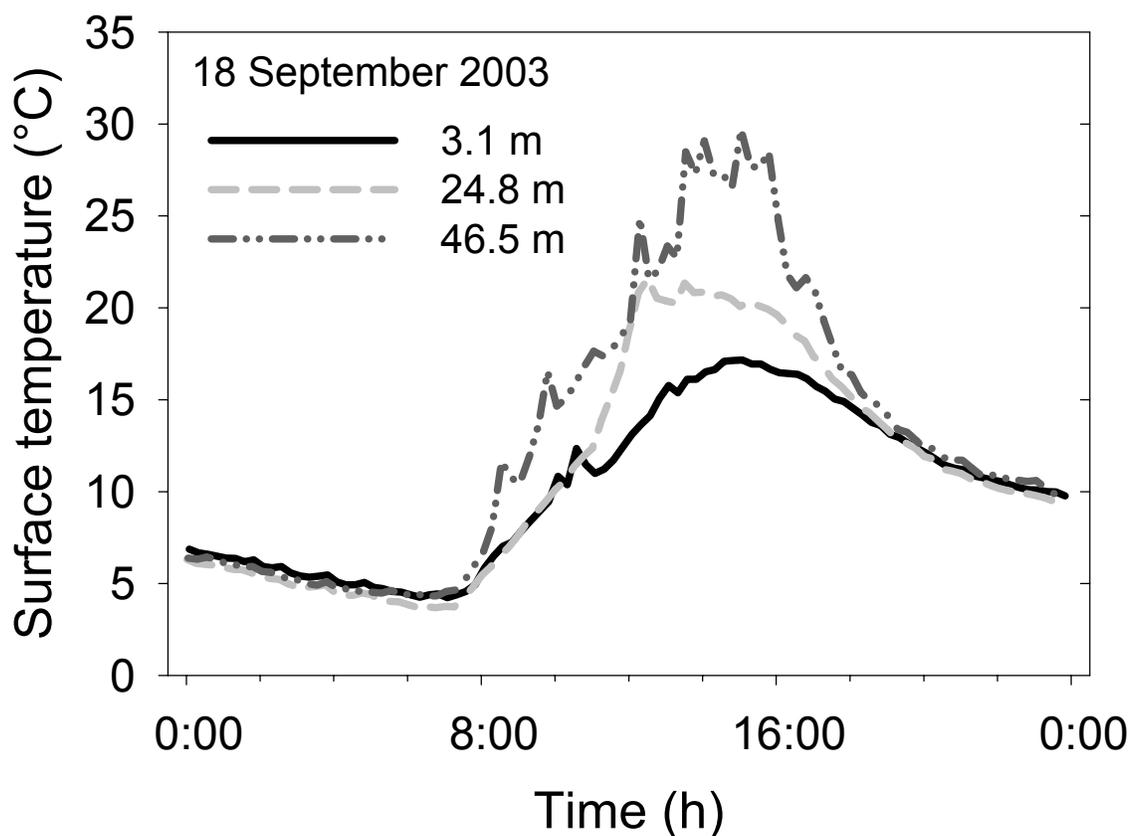
Figure 20 – Surface temperature of lichens/bryophytes at 3.1, 24.8 and 46.5 m above the forest floor.
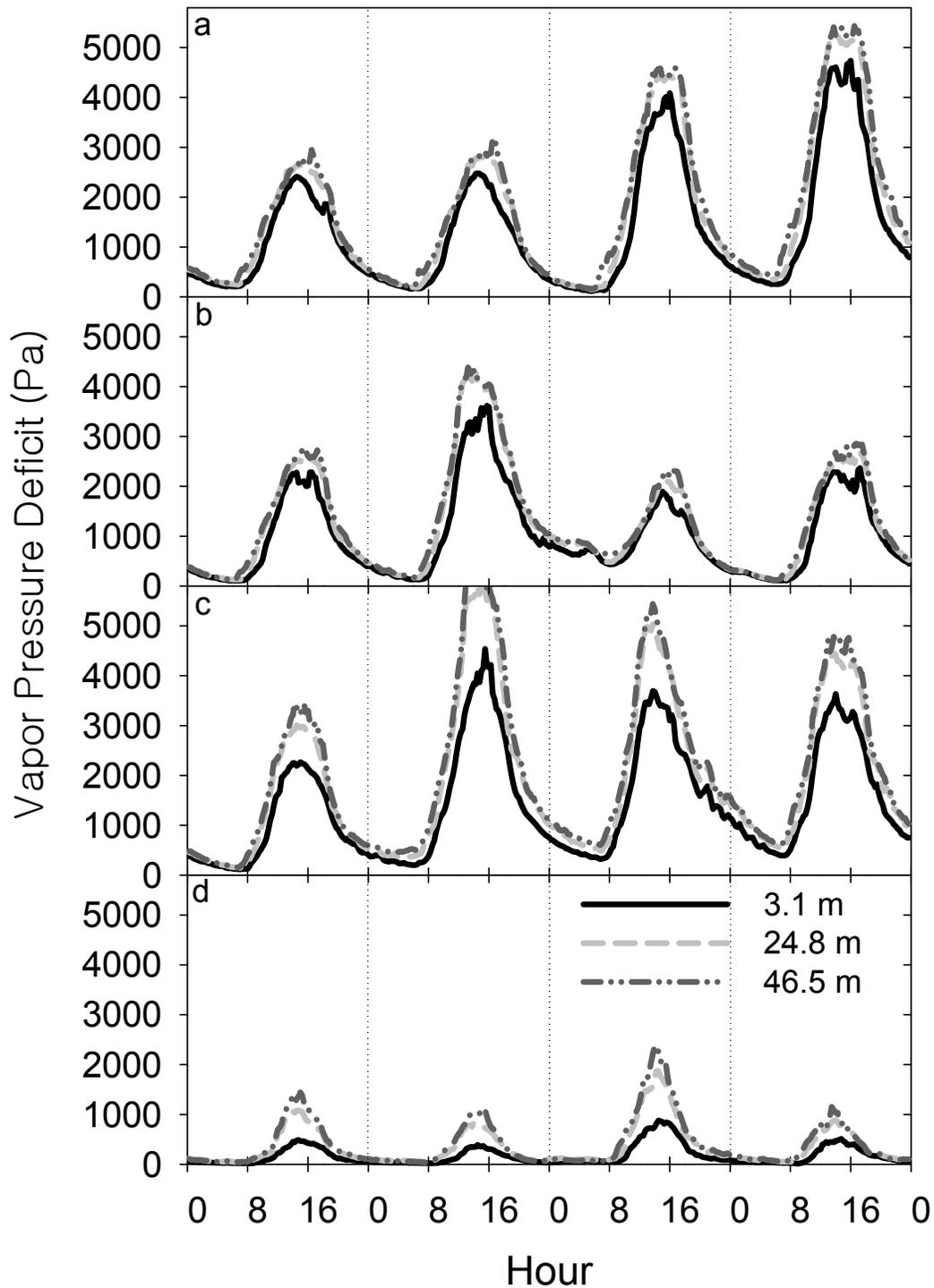
Figure 21 – The vapor pressure deficit (VPD) at three heights (3.1, 24.8 and 46.5 m) during four ensemble periods during the summer/fall of 2003 (Day of year (DOY): a = 206-209, b = 223-226, c = 244-247 and d = 274-277).
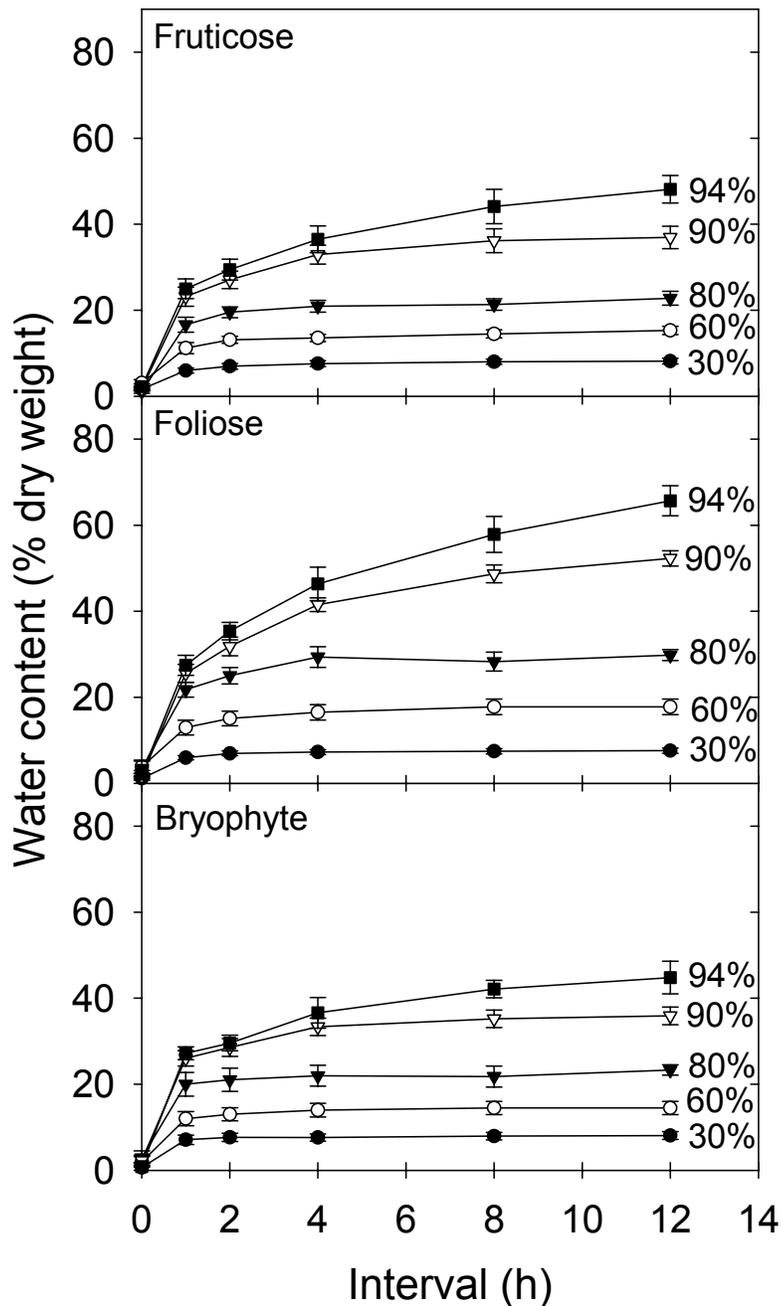
Figure 22 – The variation in water content (WCx) with exposure time for a fruticose lichen (witch's hair), foliose lichen (lettuce lung) and bryophyte (cattail moss) during exposure to six different RH at 22°C. At 30, 60, 80, 90 and 94% RH and 22 °C, the vapor pressure deficit is equivalent to 1849, 1057, 528, 264 and 158 Pa, respectively.
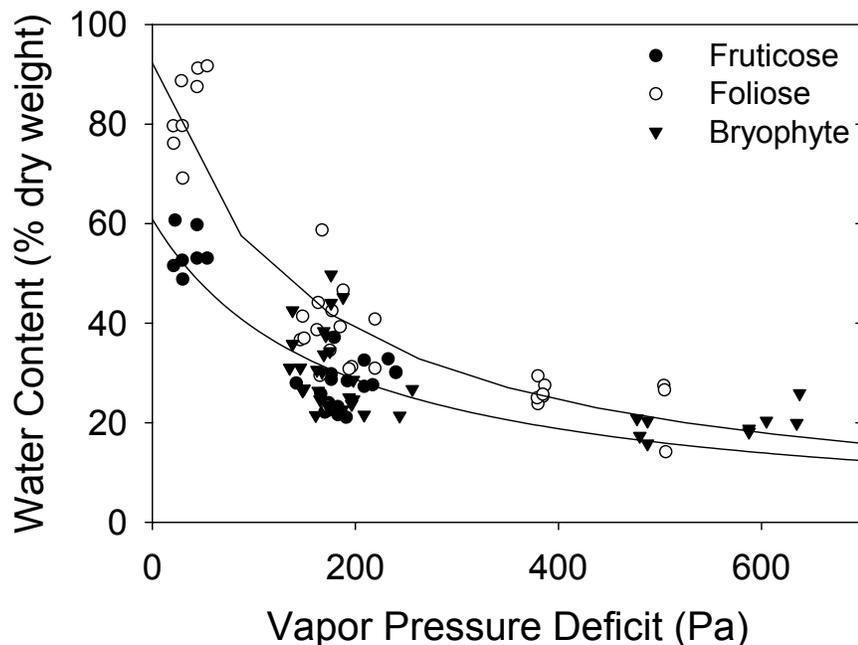
Figure 23 – Variation of lichen water content with the morning vapor pressure deficit for a fruticose lichen (witch's hair), foliose lichen (lettuce lung) and bryophyte (cattail moss) after exposure to atmospheric VPD overnight in the field. The water content (WC_x) of the lichens and bryophytes can be described by the $WC_x = (a \cdot b)/(b + x)$. A single exponential function was used to describe the WC_x of the fruticose lichen and bryophyte because their WC never differed by more than 3.4% in the laboratory. (Foliose lichens: a = 92.31, b = 145.1; Fruticose lichens/bryophytes: a = 60.89, b = 178.5).

4.3 Vapor pressure deficit (VPD) and lichen/bryophyte WC_x

Under laboratory conditions lichens and bryophytes experience increases in WC_x as the VPD decreased (Figure 22). The lichens/bryophytes equilibrated more rapidly as the VPD increases and at VPD less than 264 Pa (90% RH at 22°C), the lichens and bryophytes continued to store water after 12 h (Figure 22). For many of the measurement intervals, the WC_x of witch's hair and cattail moss were statistically different (p-values<0.05), but the difference between their mean WC_x at any given elapse time/VPD combination was never greater than 3.4% (Figure 22). Thus, if the 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) the lettuce lung lichen had a similar WC_x to the witch's hair and cattail moss, but below a VPD of 1056 Pa the lettuce lung absorbed water more quickly and attained a greater WC_x. Thus, the water absorption by lettuce lung was treated separately from the witch's hair and cattail moss (Figure 23).

The relationship between VPD and the WC_x of the lichen and bryophyte using the 4, 8 or 12 h elapsed time had difficulty predicting the WC_x of individual samples of lettuce lung, witch's hair and cattail moss that were placed for 14 to 15 h in the forest canopy (Table 17). Therefore, to predict the WC_x of the lichens and bryophytes in the field, a relationship between VPD and WC_x was established for the field measurements (Figure 23). A single equation was used to estimate the WC_x of witch's hair and cattail moss as a function of VPD (Equation 1) because their WC_x values were always similar (Figure 23). The values of WC_x calculated from the laboratory-derived equations were not significantly different from the WC_x of the individual samples of lichens and bryophytes measured in the field (all p-values>0.05). Values from the fitted equations for the field measurements were always within 24% of the measured lichen/bryophyte WC_x and the average difference between the estimates from equation and the measured morning WC_x of the individual samples of lettuce lung, witch's hair and cattail moss was 7.3, 4.9 and 5.8%, respectively.

Table 17 – The association between lichen and bryophyte water content (WC_x) and vapor pressure deficit (VPD) for measurements made in the field laboratory. The field measurements were made in the early morning after exposing the lichens and bryophytes to atmospheric conditions for 14 to 15 h. In the laboratory the WC_x of lichens and bryophytes were estimated after being exposed for 1, 2, 4, 8 and 12 h to a range of VPD (158 to 1849 Pa). The relationship between VPD and WC_x was described using: $WC_x = y_o + (a \cdot b)/(b + x)$, where x is the VPD. The fruticose lichens and the bryophytes were grouped together because their association between WC_x and VPD was not biologically significant.

Measurement	Foliose lichens			Fruticose lichens and Bryophytes		
	a	b	R^2	a	b	R^2
Field	103.3	114.1	0.84	62.67	166.7	0.63
1 h	34.80	642.5	0.94	33.55	579.4	0.97
2 h	46.11	520.5	0.97	38.09	565.3	0.98
4 h	64.97	387.3	0.97	50.36	405.8	0.98
8 h	90.93	253.6	0.98	63.37	299.4	0.99
12 h	92.31	145.1	0.99	60.89	178.51	1.0

4.4 Latent heat fluxes from epiphytic lichens and bryophytes

The VPD and SG methods both estimated LE_e between -40 to 25 W m^{-2} in the four ensemble periods (Figure 24). In the early morning hours when the VPD was low, the LE_e was typically below 10 W m^{-2}, with periodic spikes above 20 W m^{-2} (Figure 24). The lichens and bryophytes rapidly lost water in the morning after the VPD increased (700 to 1200 h), with the greatest losses occurring before noon. The diurnal cycle of water absorption/evaporation was most pronounced when the VPD dropped below 200 Pa at night. For example, 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 21) and LE_e was subsequently less periodic (Figure 24). In, contrast from DOY 274-277, the VPD frequently approached 0 Pa (100% RH) at night and the diurnal variation in LE_e was well defined (Figure 24).
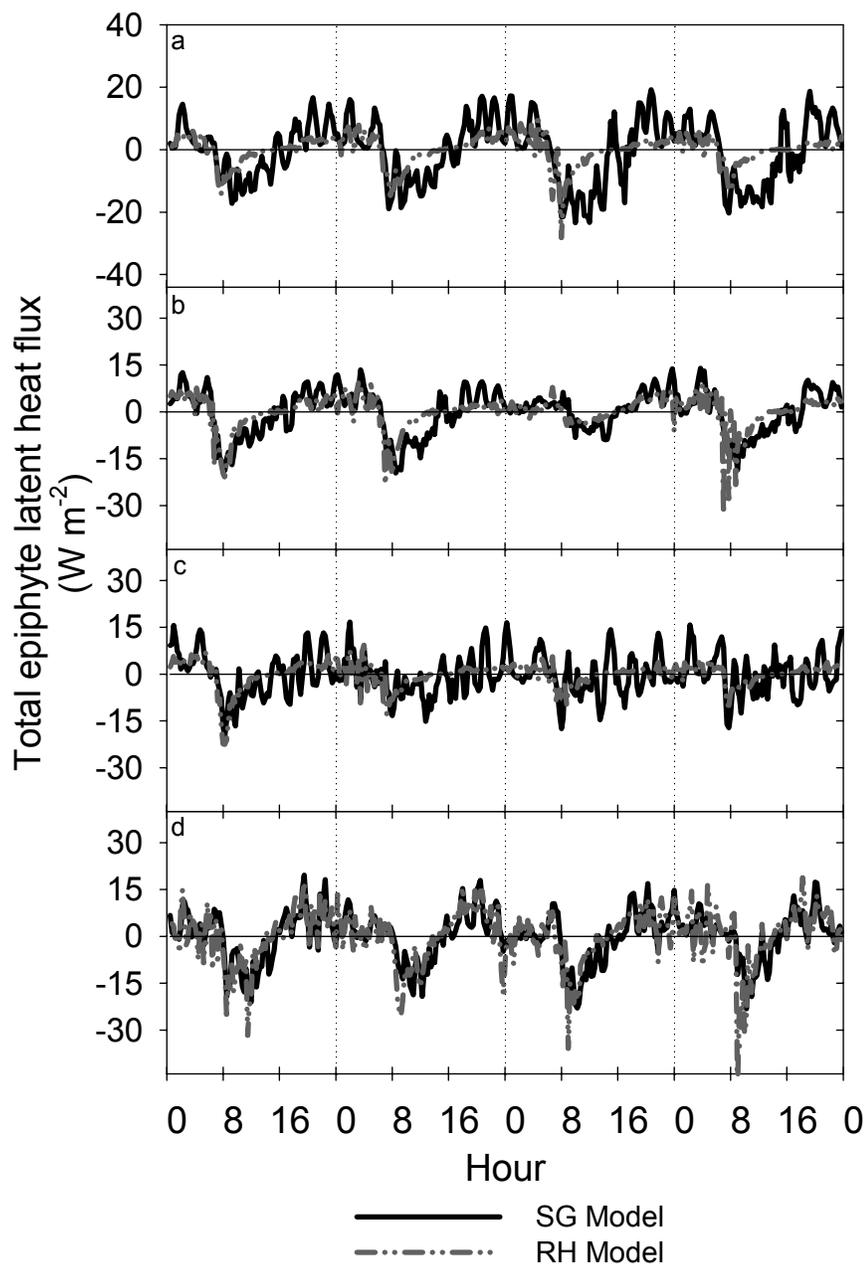
Figure 24 – The latent heat flux between epiphytic lichen and bryophytes (LE$_e$) and the atmosphere in an old-growth Douglas-fir forest in the Oregon Cascades. The latent heat flux was estimated using the VPD method and the Strain Gauge method during four ensemble periods during the summer/fall of 2003 (Day of year (DOY): a = 206-209, b = 225-228, c = 244-247 and d = 274-277) (see methods).   Positive values represent latent heat gain (water uptake) and negative values represent latent heat loss (water loss) from the epiphytic lichens and bryophytes.

5.0 Discussion

5.1 Epiphyte biomass and distribution

The biomass estimates for the old-growth Douglas-fir forest in this study (Table 16) are similar to those reported by McCune (1993), who estimated that a nearby 400 y-old forest to contained 1870 kg ha^{-1} of lichen biomass with the foliose lichens dominating (1690 kg ha^{-1}).

In forests with abundant populations of epiphytes it is common to have the lichens and bryophytes distributed in distinct horizontal layers within the forest canopy (e.g. Campbell and Coxson, 2001; Ellyson and Sillett, 2003; McCune et al., 1997; Pike et al., 1975; Sillett and Rambo, 2000). As with other reports on epiphyte distribution in old-growth Douglas-fir forests (McCune et al., 1997; Pike et al., 1977; Sillett and Rambo, 2000), the epiphytic lichens occupied the top of this forest canopy and epiphytic bryophytes the bottom portion of this forest canopy (Figure 19).

The distribution of lichens higher in the canopy and bryophytes lower in the canopy is generally attributed to changes in microclimate, nutrient availability and competition (e.g. Antoine and McCune, 2004; Campbell and Coxson, 2001; McCune et al., 1997). The stratification of the lichens and bryophytes in the canopy may, in part, result from microclimatic changes in light intensity, wind speeds and evaporative demand (McCune, 1993; McCune et al., 1997). For example, the diurnal range in surface temperatures of the epiphytes is larger higher in the canopy due to increased solar radiation (Figure 20). The greater evaporative demand (Figure 19) may preclude larger

populations of bryophytes higher in canopy because they cannot tolerate repeated wetting and drying cycles (Proctor, 1982; Proctor, 2000b). However, other factors such as competition may also influence the distribution of lichens and bryophytes.

Antoine and McCune (2004) transplanted several lichen species including an alectroid lichen (*Usnea scabrata*) and lettuce lung at different heights in the canopy and monitored their growth for one year. They demonstrated that the realized niche of these species did not necessarily match the location in the canopy where they had their greatest growth rates. For example, the biomass of lettuce lung peaked at 25-30 m while its growth rate peaked between 40-45 m. Thus, the distribution of lichens and bryophytes is complex as factors other than microclimate may be important in determining their distribution. Further research is needed to understand the interaction between competition, microclimate and nutrient availability on lichen and bryophyte biomass and distribution.

5.2 Atmospheric water vapor absorption and photosynthetic metabolism

The VPD of the canopy typically dropped below 690 Pa during the summer and early fall (Figure 21). The laboratory results indicate that at a VPD of 585 Pa, the WC_x of witch's hair will exceed 20% and at a VPD of 265 Pa, the WC_x of lettuce lung will exceed 50% (Figure 22). In general, green lichens require a WC_x of 20% to reactivate their photosynthetic metabolism (Bertsch, 1966; Blum, 1973; Kershaw, 1985; Matthes-Sears et al., 1987), but

the relationship is species specific (e.g. Antoine, 2001; Lange et al., 1970; Sundberg et al., 1997). Lettuce lung requires a WC_x of 50% to reactivate its photosynthetic metabolism (Antoine, 2001). However, the nighttime VPD required for the lichens to reactivate their photosynthetic metabolism is likely higher. The field measurements show a more conservative relationship between VPD and WC_x; with witch's hair requiring a VPD below 360 Pa and lettuce lung requiring a VPD below 120 Pa to reach a WC_x of 20 and 50%, respectively. It is not surprising that under field conditions, the lichens require a lower VPD to reach their metabolic thresholds. In the laboratory the lichens and bryophytes did not rapidly reach equilibrium at lower VPD (RH >90%); they continued to store water after 12 h of continuous exposure. This is not unusual, as past research indicates that lichens can continue to increase their WC_x for more than 22 days after exposure to high RH (Blum, 1973). Thus, the time the lichens are exposed to the low nighttime VPD may not be sufficient to reach their potential WC_x. Furthermore, under field conditions the velocity of the wind will be different than under laboratory conditions. The changing windspeeds will affect the boundary layer resistance of the lichens, thereby increasing or decreasing their WC_x. Thus, the lichens may not reach WC_x measured under laboratory conditions. Based on the WC_x measured in the field, the WC_x of witch's hair will exceed 20% on more than 96% of the nights and the WC_x of lettuce lung will exceed 50% on more than 55% of the nights.

Past research on other lichen species indicates that the carbon fixation by lichens may be significant in Douglas-fir forests during the summer drought

(Kershaw, 1985; Lange et al., 2001; Matthes-Sears and Nash III, 1986). For example, during a drought in coastal Northern California, Matthes-Sears and Nash III (1986) found 11% of the annual carbon gain by *Ramalina menziesii*, an alectroid species similar to witch's hair, resulted from the reactivation of its photosynthetic metabolism by absorption of water vapor alone. Likewise, Green et al. (2002) found that the green algal sections of a lichen with a tripartite symbiosis absorbed sufficient quantities of atmospheric water to reactivated the their photosystems on greater than 94% of the study days. Thus, the witch's hair and lettuce lung are likely to be fixing carbon because on at least 55% of the days during the summer these lichens could absorb sufficient quantities of water to allow for photosynthesis.

The carbon fixation by green lichens during the summer drought may be limited because they rapidly dry in the early morning hours. The WC_x of witch's hair generally will drop below 20% after less than 1 to 4 h after sunrise and the WC_x of lettuce lung dropped below 50% after only 1-2 h. Past reports on the carbon uptake by other lichens at low WC_x indicate these green lichens in Douglas-fir forests could assimilate 0.1 to 0.3 mg CO_2 $g_{dryweight}^{-1}$ h^{-1} (Kershaw, 1985). However, while these species may be able to photosynthesize for short periods, the respiratory cost must be considered when evaluating the benefit of absorbing atmospheric water vapor. When the WC_x of the lichen is sufficient to fix carbon, it will also respire at a faster rate (Antoine, 2001; Kershaw, 1985; Matthes-Sears et al., 1987). Prior to sunrise the lichens attain

high WC_x and will begin to respire, and if these losses are not replenished by photosynthesis after the sun rises, the lichen will perish.

The balance between respiration and photosynthesis during the summer months may partially explain the distribution of lichens within the canopy. Lichens typically are found higher in the canopy of old-growth Douglas-fir forests where the early morning light levels should be greater (Figure 19). With greater light the lichens may be able to fix sufficient quantities of carbon to balance their respiratory losses, whereas lower in the canopy the light levels are diminished and the lichens might not be able to fix sufficient quantities of carbon to balance their respiratory losses. However, the relationship of photosynthesis to microclimate variables and the time required for green lichens to reactivate their photosynthetic metabolism is species specific (Kershaw, 1985; Lange and Kilian, 1985; Lange et al., 1986). Therefore, further research is needed to determine the net photosynthesis of lichens during the summer drought.

5.3 The forest canopy energy budget

The estimates of LE_e by the SG method differs from the VPD method because the VPD method provides an average for the whole canopy and the SG method scales the weight change of six branches on a two trees to estimate 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 windspeed and the morphology of the

epiphyte (Kershaw, 1985; Monteith and Unsworth, 1990). The irradiance and windspeed are highly variable throughout the canopy. Since the SG method depends on only six point samples on two trees, it is likely that the estimates of LE_e are influenced by systematic biases. Hence, the magnitude of the estimates by the LE_{e-VPD} and the LE_{e-SG} will differ throughout the day.

Although the VPD and SG methods were not always in agreement, they were similar in their prediction of the timing of water absorption and evaporation by the epiphytes. For all the ensemble periods, the two methods track each other fairly well (Figure 24). Both methods show that the diurnal cycle of absorption and evaporation is most distinguishable when the VPD drops below 200 Pa at the night. This is not surprising because the relationship between the WC_x of the lichens/bryophytes and rapidly changes between 0 and 200 Pa (Figure 23). Thus, during nighttime periods that have high VPD, the epiphytes will absorb/evaporate greater quantities of water and the diurnal variation in LE_e will increase.

The absorption of atmospheric water by lichens/bryophytes cannot explain the 27 to 82 W m^{-2} discrepancy between the latent heat flux above the canopy (LE_{ec}) and the water loss from the soil as reported by Unsworth et al. (2004). To explain the discrepancy, the lichens/bryophytes need to absorb atmospheric water during the period in question. However, when the VPD method is applied to the same dataset presented in Unsworth et al. (2004), the estimated LE_e at the time of the discrepancy (600 h to 1200 h) is negative; indicating that the lichens are losing water to the atmosphere (Figure 25).

Prior to 600 h, the LE_e is positive (gaining water), but at that time, there is no discrepancy between the soil efflux and LE_{ec}. Therefore, the discrepancy between the soil efflux and the eddy covariance system should result from the deposition of water on thermally massive objects, the increase in atmospheric water vapor content, instrument error and/or inappropriate assumptions (Unsworth et al., 2004). For example, to compare the soil efflux with the eddy covariance measurements Unsworth et al. (2004) were required to assume that both flux estimates were of represented the same area. This may be a significant source of error because the area measured by an eddy covariance system varies with both wind speed and direction.

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 21) and the lichens/bryophytes continued to absorb water. When the VPD increased, the lichens and bryophytes rapidly lost moisture to the atmosphere (Figure 24).   The latent heat flux associated with absorption of moisture by lichens and bryophytes prior to sunrise ranged between 1 and 20 W m $^{-2}$, but was usually between 5 and 15 W m^{-2}. When the VPD decreased in the morning, the lichens/bryophytes rapidly lost their absorbed water in 3 to
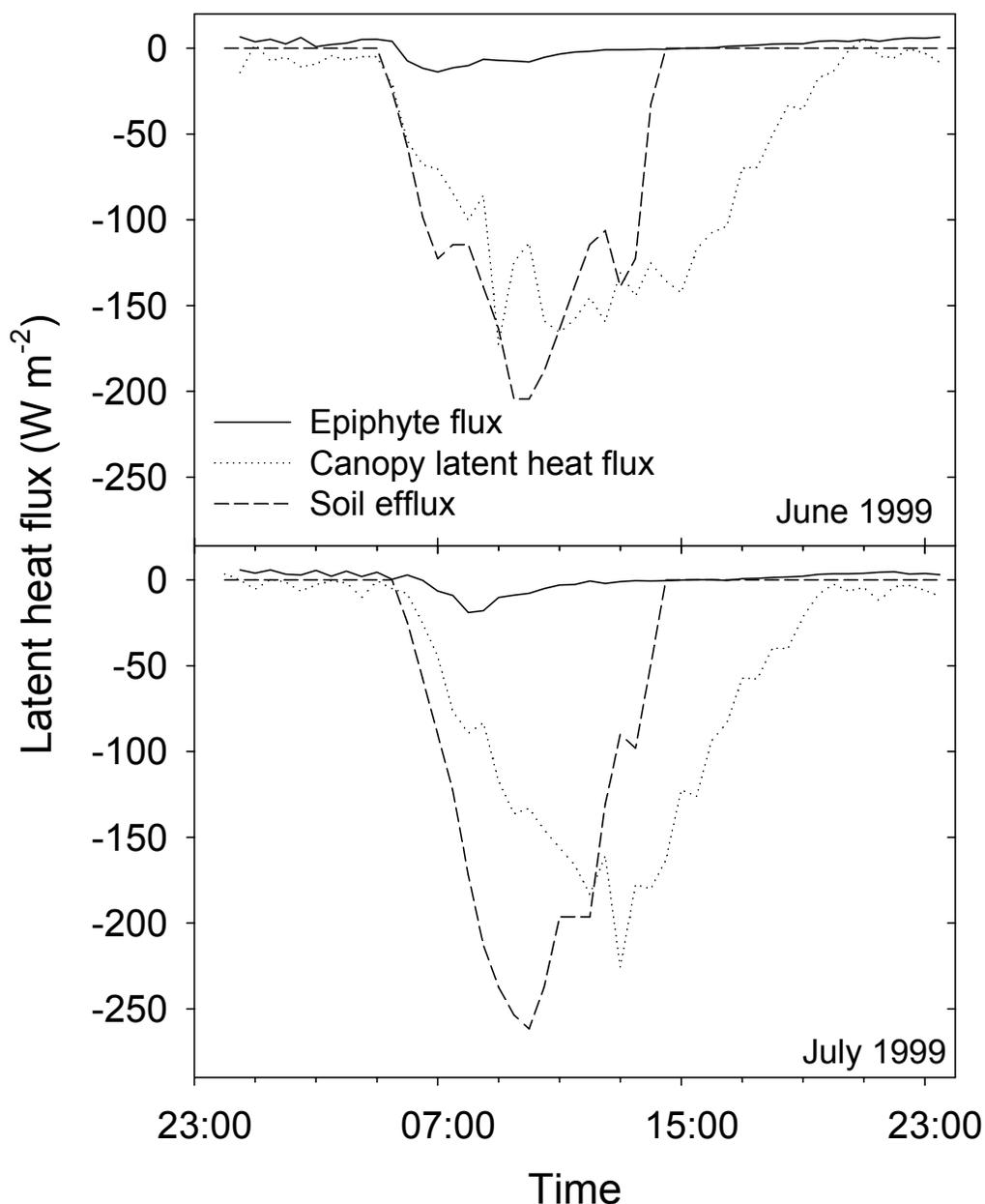
Figure 25 – The latent heat flux from the lichens and bryophytes modeled using the VPD method compared with the measured soil efflux using soil moisture probes and the canopy latent heat flux measured by eddy covariance for an old-growth forest in South Central Washington. Positive values represent latent 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 are the average daily values as presented by Unsworth et al. (2004).

4 hours (Figure 24, 25). Thus, the LE_e is significant because it is equivalent to 5 to 21% LE_{ec} (Figure 25).

The effect of lichens and bryophytes on LE has been reported for other forests of a Boreal Jack pine forest in central Manitoba, Canada (e.g. Betts et al., 2001; Betts et al., 1999; Kershaw and Rouse, 1971). For example, the LE of a Boreal Jack pine forest increased significantly following a rainfall event. 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 during the wet season may have a significant impact on the energy budget of the forest because there will be larger quantities of water stored in their thalli/leaves relative to the summer months. Further research is needed to determine the effect this may have on the local climate.

6.0 Conclusions

As with other old-growth Douglas-fir stands, there were abundant epiphyte populations (2053 kg ha^{-1}) at this study site and the epiphytic lichens and bryophytes occupied distinct niches (McCune et al., 1997; Pike et al., 1977; Sillett and Rambo, 2000). The bryophytes were more abundant lower in the canopy and the lichens were more abundant higher in the canopy. The partitioning of lichens higher in the canopy and bryophytes lower in the canopy

may result from vertical differences in microclimate, nutrient availability or competition.

The epiphyte foliose lichen, lettuce lung, the fruticose lichen, witch's hair and the bryophyte, cattail moss, absorbed greater quantities of water as the VPD of the air decreased. For a given VPD, the witch's hair and cattail moss attained a similar water content (WC_x) after 1, 2, 4, 8 and 12 h of exposure. In contrast, lettuce lung absorbed water more rapidly and attained a greater WC_x than to the other epiphytes. All three epiphytes exceeded 20% WC_x at 80% RH, a WC_x at which past research indicates that many green lichens can reactivate their photosynthetic metabolism at 80% RH (e.g. Bertsch, 1966; Green et al., 2002; Lange et al., 1988; Lange et al., 1986). Thus, atmospheric water absorption may be physiologically important for many green lichens because they may be able to photosynthesize for at least a fraction of the day on 80% of the days during the summer drought. However, the benefit of carbon fixation must be contrasted with the respiratory losses prior to sunrise. For example, if lichens are lower in the canopy they may respire more water than they gain by photosynthesis because light levels are too low. However, lichens higher in the canopy may receive enough light in the early morning to fix sufficient quantities of carbon to balance or exceed their respiratory losses prior to sunrise. However, further research is needed to explain how atmospheric water absorption affects the carbon budget of lichens and their distribution in the canopy.

The absorption/evaporation of water by the lichens and bryophytes significantly alters the latent heat flux of the forest canopy (LE) relative to canopies without large epiphytes populations. Prior to sunrise the RH of the canopy typically exceeded 80% and the flux of water to the lichens/bryophytes ranged between 5 to 10 W m^{-2}. After sunrise the lichens and bryophytes rapidly lost the nocturnally absorbed water in 1 to 4 hours. The rapid evaporation from the lichens/bryophytes accounted for 5 to 41% of the latent heat flux from the canopy. The absorption of atmospheric water by lichens and bryophytes could not account for the 27 to 82 W m^{-2} discrepancy between the water lost from the soil by transpiration and the latent heat flux above an old-growth Douglas-fir canopy as reported by Unsworth et al. (2004). To explain the discrepancy the lichens/bryophytes were required to absorb atmospheric water between 600 to 1200 h; however, they lost water during this period. Therefore, the discrepancy between the soil efflux and the eddy covariance system should result from the deposition of water on thermally massive objects, the increase in atmospheric water vapor content, instrument error or inappropriate assumptions.

Acknowledgements

Chapter 6 – Conclusions

This study investigated the influence of canopy structure on forest hydrology. Chapter 2 focused on the effects that whole canopy structural changes have on the interception loss of rainfall (I_n). The following chapters defined how the development of large populations of epiphytes in old-growth Douglas-fir forests affected the forest's hydrological cycle. Chapter 3 determined the maximum water contents (MWC_x) of representative foliose, fruticose and bryophyte species. The MWC_x of the representative lichens/bryophytes were used to determine whether the maximum water-holding capacity of an epiphyte-laden branch could be predicted when the biomass of epiphytes on the branch was known. Chapter 4 used the results from Chapter 3 to determine the role of lichens in the interception and storage of rainfall under field conditions. Lastly, Chapter 5 analyzed if absorption/evaporation of atmospheric water vapor by epiphytic lichens/bryophytes during the summer drought was sufficient to: 1) reactivate the photosynthetic metabolism of a typical green lichen and 2) alter the energy budget of the forest canopy.

Chapter 2 described the rainfall interception by a young Douglas-fir forest and contrasted this with an old-growth Douglas-fir forest. The young Douglas-fir forest was a closed-canopied Douglas-fir monoculture and had a small gap fraction (0.11). In contrast, the old-growth forest canopy consisted of both Douglas-fir and western hemlock, had large canopy gaps and a large population of epiphytes. The values of S and the direct throughfall fraction (p)

changed seasonally in the young forest and were significantly smaller relative

to the old-growth forest (Chapter 4; Link et al., 2004). The higher S occurred

in the old-growth forest despite both forests having nearly identical LAI.   The

larger canopy gaps, epiphyte populations, S and p in the old-growth resulted

in a more positively skewed spatial distribution of throughfall relative to the

young forest.   However, the skewed spatial variability of the throughfall in the

old-growth forest did not result in greater spatial variability in soil moisture. It

is likely that other factors such as water uptake by roots and rainfall

interception by forest floor litter and bryophytes modified the relationship

between throughfall and soil moisture. Lastly, even though the values of p

and S were very different between the two forest ages, values of the

evaporative fraction ($\overline{E}/\overline{R}$) were not. As Douglas-fir forests develop, changes

in the p, S and gap fraction may act to mitigate changes in $\overline{E}/\overline{R}$, by

influencing the aerodynamic resistance (r_a) and the effective area for latent

heat transfer. Thus, because of the larger S in the old-growth forest, the I_n of

the old-growth forest was only slightly larger than that of the young Douglas-fir

forest .

Seasonally, the Gash model successfully predicted I_n for the young

forest. However, on a storm-by-storm basis the errors associated with using

the Gash model ranged from -91 to 36% of the measured value. When the

inter-storm variation in S, p and $\overline{E}/\overline{R}$ were applied to the Gash model, the

seasonal and individual storm estimates were improved. Hence, both short

(seasonal) and long-term (decades to centuries) developmental changes in the canopy structure strongly influence the S, p and I_n of a Douglas-fir forest.

Chapter 3 demonstrated that lichens and bryophytes substantially increase interception and storage of rainfall in old-growth forests. The MWC_x of lichens and bryophytes were significantly different, with epiphytic bryophytes storing three times more water per unit dry weight than the lichens. Because of their large MWC_x, the epiphytic fruticose lichens, foliose lichens and bryophytes have the potential to increase the S of old-growth Douglas-fir forests by roughly 1.3 mm. However, when exposed to the rainfall simulator, the epiphyte-laden branches did not immediately store all the intercepted water as the branches required greater than 6 mm of rainfall to saturate. A large amount of rainfall is required to saturate an epiphyte-laden branch because the rainfall interception efficiency (p_i) of a branch is typically less than 0.7 after only 2 mm of rain. The low p_i likely occurs because water is following preferential flow routes off the branch.

In Chapter 4, epiphytic lichens and bryophytes were shown to significantly impact the hydrology of old-growth Douglas-fir forests by altering the rainfall interception and canopy water storage. The large MWC_x of lichens and bryophytes leads to increased potential epiphyte-laden branch water storage (S_{e-b}), but unlike laboratory experiments (Chapter 3) S_{e-b} could not be used to predict the water storage by epiphyte-laden branches that were measured in the field because: 1) the branches required greater than 30 mm

of rainfall to saturate; and 2) the branches were unable to dry between storm events.

The epiphytic lichens and bryophytes helped to prolong the time required for the canopy to saturate during a storm and to dry after a storm. The occurrence of preferential flow of water and high $S_{e\text{-}b}$ of epiphyte-laden branches resulted in the branches saturating very late during most storm events. Epiphytic lichens and bryophytes have a large MWC_x that increases the amount of water that must evaporate from canopy subsequent to a storm. Furthermore, bryophytes have a larger MWC_x relative to lichens and they are primarily located lower in the canopy where the energy for evaporation is reduced. Thus, epiphytic lichens and bryophytes contribute to the canopy remaining partially saturated for much of the wet season.

The occurrence of preferential flow routes and the inability of the canopy to dry between storm events results in bucket type models (e.g. MI , mean and minimum methods (Klaassen et al., 1998; Leyton et al., 1967; Link et al., 2004)) underestimating canopy water storage (S) and overestimating the ratio of evaporation to rainfall intensity ($\overline{E}/\overline{R}$) in old-growth Douglas-fir forests. Lastly, in contrast with the hypothesis presented by Calder (1996), the relationship between rainfall intensity and branch water storage is positive for epiphyte-laden branches. The rough surface of lichen/bryophyte mats may reduce loss of water by raindrop splash and impede the drainage of water off the branch.

Chapter 5 demonstrated that the absorption of atmospheric water by epiphytic lichens and bryophytes has the potential to reactivate the photosynthetic metabolism of green lichens and alters the energy budget of the forest canopy. A foliose lichen (lettuce lung), fruticose lichen (witch's hair), and bryophyte (cattail moss), were exposed to five different vapor pressure deficits (VPD) (158, 264, 528, 1057 and 1849 Pa) at 22°C for 1, 2, 4, 8 and 12 h. After exposing witch's hair to 528 Pa (80% RH) and lettuce lung to 264 Pa (90% RH) for 12 h, their water contents (WC_x) exceeded 20% and 50%, repectively . This is significant for lettuce lung and witch's hair because they both have a green algal symbiont that can reactivate their photosynthetic metabolism if their WC_x exceeds 20% (e.g. Bertsch, 1966; Green et al., 2002; Lange et al., 1988; Lange et al., 1986). However, when exposed to field conditions, witch's hair and lettuce lung required a lower VPD of 360 and 120 Pa, respectively, to attain a WC_x that may reactivate their photosynthetic metabolism   to reach their potential metabolic thresholds, witch's hair and lettuce lung required lower a VPD under field conditions; 360 and 120 Pa, respectively. However, even if a lower VPD is required to reactivate their photosynthetic metabolism under field conditions, green lichens should still be able to reactivate their photosynthetic metabolism on 55 to 96% of summer nights.

The diurnal change in WC_x was sufficient to alter the energy budget of the canopy. Both of the VPD and SG methods used to estimate the diurnal latent heat flux of the lichens/bryophytes showed strong diurnal trends; the

epiphytes absorbed water at night and evaporated water during the day. The net change in WC_x on each day was approximately zero. The nighttime absorption of water ranged from between 5 and 10 W m^{-2}. After sunrise, as the VPD within the canopy rapidly increased, the WC_x of the epiphytes rapidly decreased. This resulted in the LE_e ranging between 5 to 40 W m^{-2}, which would account for up to 21% of the canopy latent heat flux of an old-growth Douglas-fir canopy during a typical mid-summer morning. Therefore, the absorption/evaporation of water vapor by epiphytic lichens and bryophytes is important for the metabolism of green lichens and significantly affects the energy budget of old-growth Douglas-fir forests.

Future directions

The results of this research leads to many new exciting research questions. The most pressing questions include: the size of the different water storage pools in old-growth Douglas-fir forests and the residence time of the water those pools; how do the spatial inputs of throughfall affect the infiltration and distribution of water in the soil and how does that affect tree root distribution?; how does the ratio of evaporation to rainfall intensity change as Douglas-fir forests develop from young monoculture stands to mature old-growth forests?; what exactly is the relationship between rainfall intensity and branch water storage?; and can the amount of carbon fixed by green lichens during drought affect their survival and their distribution in the canopy.

Water storage by the canopy and forest floor litter/bryophytes

Chapters 3 and 4 demonstrated that the S of old-growth forests is significantly larger than previously reported. Standard regression based techniques underestimate the size of S because their underlying assumptions are violated. The absorption of water by deadwood and the large MWC_x of lichens and bryophytes significantly increased the size of S. However, the question still remains: "Exactly how large is the canopy water storage?" To understand the hydrology of a forest canopy it is necessary to determine the maximum water content and residence time of the different storage pools (i.e. deadwood, foliage, epiphytes). The fractionation of the different hydrogen and oxygen isotopes in water may be used to` determine the time required for water to cycle though the different canopy storage pools. Once the dynamics of the canopy water storage are understood, hydrologic models can be developed that accurately describe the dynamics of water storage in old-growth forests.

Water storage in a forest is not limited to the canopy. For example, water storage by the forest floor bryophytes and litter may significantly increase the storage of water above the mineral soil because they have significant capacity to store water. Chapter 3 reported that at an old-growth Douglas-fir forest contained 465 kg ha^{-1} of forest floor bryophytes that could store between 8 and 14 times their dry weight in water. In young Douglas-fir forest the forest floor litter was 1 to 2 cm versus 8 cm depth in the old growth forest (Chapter 2). Hence, the storage of water by the litter may be an

important variable, as conifer litter has been estimated to store 2-3 times its dry weight in water (Helvey, 1967). Furthermore, preliminary results indicate that a section of old-growth Douglas-fir forest floor litter exposed to a rainfall intensity of 15 mm h^{-1} for 2 h intercepted and stored 577 g of water (Figure 26, Pypker, unpublished data). Therefore, further research is needed to determine how the forest floor litter and bryophytes intercept rainfall and route the water through to the mineral soil.

Chapters 3 and 4 limited their discussion to the interception and storage of liquid precipitation. However, the large surface area provided by lichen thalli and bryophyte leaves may store significant quantities of ice/snow. For example, following several snow/ice storms in January 2004 the branches stored between 513 to 2287 g of ice/snow (Figure 27). These same branches only stored between 100 and 250 g of water during single liquid precipitation event. Thus, further research on multiple storms is needed to confirm the quantity of snow/ice stored by epiphytes.

Spatial variability of soil moisture

The results of Chapter 2 demonstrate that the spatial distribution of rainfall differed between young and old-growth Douglas-fir forests. The difference in spatial variability of the rainfall may influence the preferential flow of water through the soil during storm events. Weiler and Naef (2003), demonstrated that when water is uniformly sprinkled on the ground the water infiltrates the soil along preferential flow paths. The results of Chapter 2
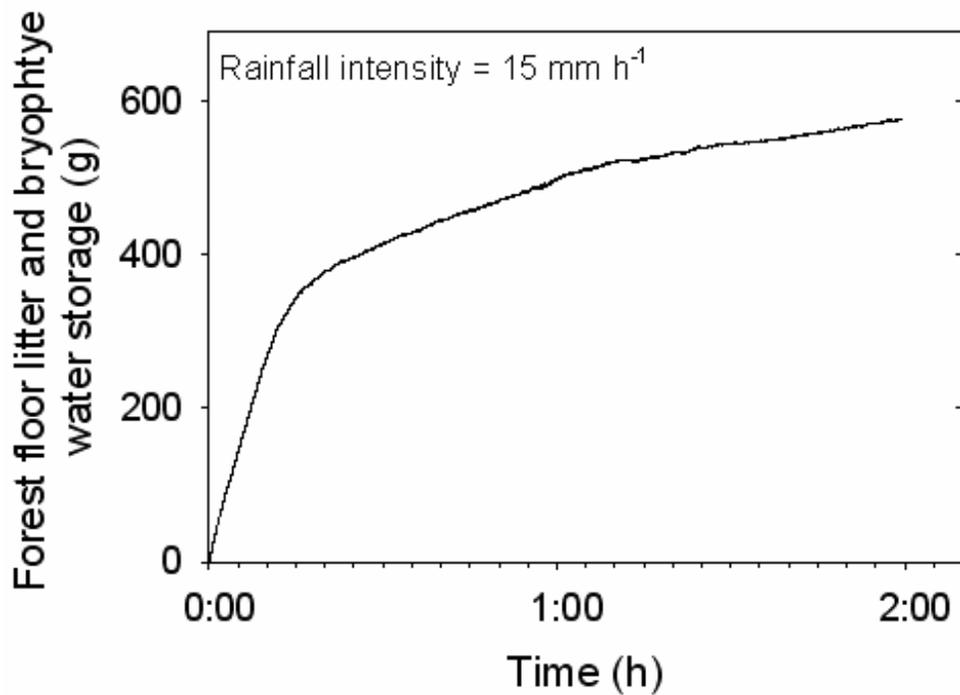
Figure 26 – The interception and storage of rainfall by forest floor litter (110 g) and bryophytes (56 g) exposed to 15 mm h⁻¹ under a rainfall simulator.
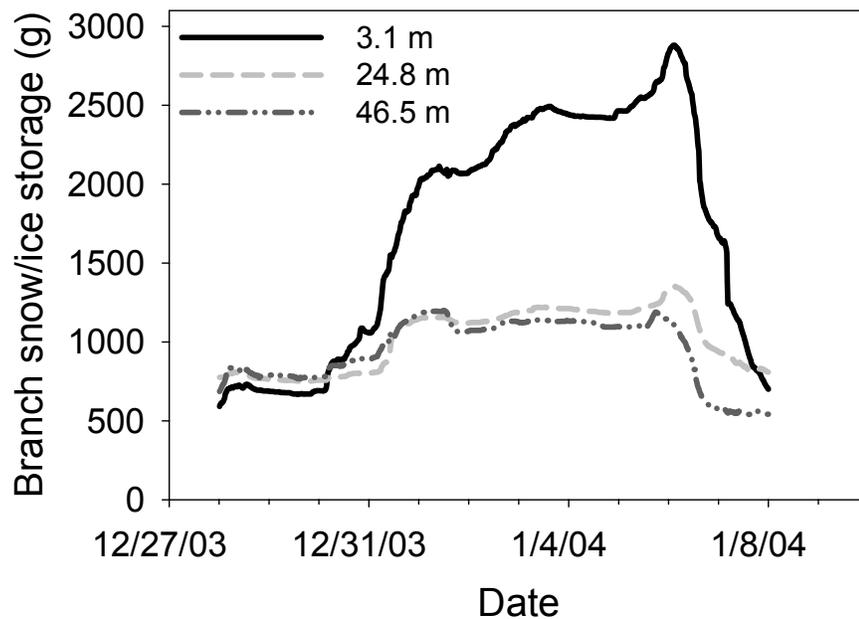

Figure 27 - The interception and storage of snow/ice by three epiphyte-laden branches at three different heights in an old-growth Douglas-fir forest.

demonstrates that the spatial input of rainfall is not homogenous and Keim and

Skaugset (2003) reported that rainfall interception by the canopy decreased

overall rainfall intensity at the forest floor. These changes in the spatial

variability and intensity of rainfall beneath a forest canopy may affect how and

where rainfall infiltrates into the soil. Further research is needed to determine

how the spatial inputs of water affect soil moisture distribution, hillslope

drainage and preferential flow paths.

If the inputs of the rainfall are spatially consistent for each storm event,

then the trees may place their roots within these areas to maximize water

uptake. Keim et al. (in review), demonstrated that over several storms there is

a temporal persistence in the spatial pattern of throughfall. The distribution of

tree roots may be influenced if this spatial pattern is maintained for long

periods. Further research is needed to determine the temporal persistence of

the spatial distribution of rainfall and if the root distribution in Douglas-fir

forests are associated with these spatial inputs. If the roots are placed in

these input locations, it may explain why Chapter 2 reported similar spatial

variability in soil moisture between the young and old-growth forests.

Ratio of evaporation to rainfall intensity

Chapter 2 reported that the changes in canopy structure resulted in

$\bar{E}/\bar{R}$ for the young and old-growth forests being very similar. However, the

effectiveness of the IS method or mean methods for estimating $\bar{E}/\bar{R}$ is subject

to question (Klaassen et al., 1998) as Chapter 4 demonstrated that their

underlying assumptions were violated. Thus, to accurately determine the size

of $\overline{E}/\overline{R}$ as a Douglas-fir forests develop it would be advantageous to measure the instantaneous flux of latent heat above the canopy during the storm event. Currently, eddy covariance systems have difficulty measuring the latent heat flux because rainwater disrupts the sensors. However, it is possible to discontinuously monitor LE for during a storm (Gash et al., 1999; Mizutani et al., 1997) and as technology improves a more accurate estimate of the latent heat flux may be determined.

Rainfall intensity and branch water storage

Keim (2003), and the results from Chapter 5, question Calder's hypothesis of decreasing branch storage with increasing rainfall intensity. However, the methods that provided the results for Keim (2003) and Chapter 5 are insufficient to absolutely disprove Calder's hypothesis. Keim (2003) presented results of branches exposed to rainfall intensities that were extreme (>20 mm h^{-1}) and contained drop sizes too small for the PNW. Furthermore, the rainfall simulator was placed in a dry warehouse, and it is possible that significant advection of heat to the branches affected branch water storage. Thus, it would be useful to create a simulation using intensities that are closer to those experienced in the PNW. Chapter 5 used rainfall measurements from a nearby clearing to generate the relationship between branch storage and rainfall intensity. The rainfall intensity within a forest canopy is highly variable; therefore, using rainfall measurements from a nearby clearing is unlikely to accurately represent rainfall intensity within the forest canopy. It would be useful to simultaneously measure branch water storage and rainfall intensity

under natural rainfall conditions.   Future work should involve a suite of branches (real and artificial) monitored by strain gauges, tipping bucket rain gauges and other meteorological instruments placed in an open field to determine the relationship of rainfall intensity to branch water storage under natural conditions.

Green lichen photosynthesis

Chapter 5 indicated that green lichens should be able to reactivate their photosynthetic metabolism on 80% of the nights during summer drought. The period of time available for the lichens to fix carbon is short; ranging between 1 and 3 hours. Direct measurements of green lichen photosynthesis are needed to quantify the significance of the carbon gain during the periods drought. The carbon uptake of the lichens could be modeled if their response to light, water content and temperature were known.

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Appendix I – The potential diurnal water absorption and evaporation by epiphytes

The large populations of epiphytes in old-growth Douglas-fir forests of the Pacific Northwest (PNW) may diurnally absorb and evaporate 1.3 tonnes ha^{-1} of atmospheric water vapor during the dry summer months. The potential diurnal water absorption/evaporation (ΔWC) by epiphytic lichens and bryophytes during the summer drought was calculated by assuming: the canopy contained 1870 kg ha^{-1} of lichens and 780 kg ha^{-1} of bryophytes (Total = B_e = 2650 kg ha^{-1}) (McCune, 1993); the relative humidity (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; Schlensog et al. 2000); and the water content of the lichens/brophytes at 80% RH ($WC_{RH80\%}$) was 0.8 of their dry weight (Blum 1973; 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 1325 kg ha^{-1} of water.

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Appendix II – Estimating potential evaporation from epiphytes

To estimate the potential evaporation (E_p) from epiphyte-laden branches at different heights in the canopy it was assumed that: the difference between the incoming and outgoing long-wave radiation for the branch was negligible (i.e. branch surface temperature equaled the air temperature); the solar radiation above the canopy equaled 440 W m^{-2}; the albedo of the forest was 0.15; the net radiation (R_n) was equal to the solar radiation multiplied by one minus the albedo; the above canopy windspeed (u) equaled 1.5 m s^{-1}; the air temperature was 20°C; and the vapor pressure deficit (VPD) equaled 1500 Pa.

The decline in u and net radiation through the canopy were estimated by applying the meteorological data measured at 3.1, 24.8 and 46.5 m on Tree 1 to the following equation:

$$\text{variable} = d_o \cdot e^{a(z/z_{top} - 1)} \quad (1)$$

where d_o is the value at the top of the canopy, a is a fitting parameter that was calculated by optimizing the fit of Equation 1 to the meteorological data measured on the two trees, z is the height in the canopy (m), and z_{top} is the height of the canopy (65 m).

The boundary-layer conductance (g_b) for the branch was estimated by assuming that: the branch and the overlying lichen/bryophyte mat had a cylindrical shape; the branch diameter (d_b) was 0.2 m; and the airflow was perpendicular to the branch. Using the equation outlined by Jones (1992), g_b was calculated as:

$$g_b = 1.5 \cdot 4.03 \cdot (\frac{u^{0.6}}{d_b^{0.4}})/1000 \quad (2)$$

The E_p was then calculated using the Penman equation:

$$E_p = \frac{s(Rn) + \rho \cdot c_p \cdot g_b \cdot vpd}{s + \gamma} \quad (3)$$

where s slope of the saturation vapor pressure curve at 20°C, p is the density

of air (kg m^{-3}), c_p is the specific heat capacity of air (J kg^{-1}), γ is the

psychrometric constant (Pa K^{-1}).

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