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The importance of canopy structure in controlling the interception loss of rainfall: Examples from a young and an old-growth Douglas-fir forest

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Abstract

The canopy water storage capacity (*S*), direct throughfall fraction (*p*), the ratio of evaporation to rainfall intensity ($\bar{E}/\bar{R}$) and interception loss (I_n), of a Douglas-fir forest are influenced by short (seasonal) and long-term (decades to centuries) changes in the forest canopy. Gross precipitation (P_G) and net precipitation (P_n) were measured in a young (25-year-old) Douglas-fir forest and the results compared with measurements previously made in a nearby old-growth (>450-year-old) Douglas-fir forest [Link, T.E., Unsworth, M.H., Marks, D., 2004. The dynamics of rainfall interception by a seasonal temperate rainforest. Agric. Forest Meteorol. 124, 171–191.]. Canopy rainfall variables were estimated using a regression-based method that estimates *S*, *p* and $\bar{E}/\bar{R}$ for individual storms using the relationship between P_G and P_n. The individual storm estimates of *S*, *p* and $\bar{E}/\bar{R}$ for the young forest were applied to a rainfall interception model (Gash model [Gash, J.H.C., 1979. An analytical model of rainfall interception by forest. Q. J. R. Meteorol. Soc. 105, 43–55.]) 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, T.E., Unsworth, M.H., Marks, D., 2004. The dynamics of rainfall interception by a seasonal temperate rainforest. Agric. Forest Meteorol. 124, 171–191.].

The young forest had significantly different *S* (1.40 mm ± 0.27) and *p* (0.12 ± 0.07) relative to the old-growth forest ($S = 3.32 \pm 0.35$; $p = 0.42 \pm 0.07$). 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 $\bar{E}/\bar{R}$ for the two forests were similar (young = 0.18 ± 0.06; old-growth = 0.17 ± 0.08). $\bar{E}/\bar{R}$ 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 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

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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 $\bar{E}/\bar{R}$ of Douglas-fir forests.
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1. Introduction

Interception loss (I_n) of rainfall in temperate forests typically ranges between 9 and 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 capacity (S), direct throughfall fraction (p), and the ratio of evaporation to rainfall intensity ($\bar{E}/\bar{R}$), thereby influencing I_n. In 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 after 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; Fleischbein et al., 2005). However, the relationship between LAI and S is species dependent (Llorens and Gallart, 2000; Keim, 2003), and varies between young and old-growth forests (Link et al., 2004) and between tropical and temperate forests (Herwitz, 1985).

The parameters S, p, $\bar{E}/\bar{R}$ 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, $\bar{E}/\bar{R}$ 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. 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 $\bar{E}/\bar{R}$. 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 estimates S by fitting a regression line to data from storms that saturate the canopy and have a low evaporation rate. 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. The estimates of p, S and $\bar{E}/\bar{R}$ produced by these methods are often used in rainfall interception models to estimate I_n for a forest (Gash, 1979; Rutter et al., 1971). The models must assume that variations in p, S and $\bar{E}/\bar{R}$ have little effect on estimates of I_n because the these indirect methods are unable to quantify changes in p, S, and $\bar{E}/\bar{R}$ 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 $\bar{E}/\bar{R}$ 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 about 4 km apart, and have similar LAI (about 10). The young forest is a 20 m tall, 25-year-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-year-old, uneven aged, heterogeneous Douglas-fir/Western Hemlock forest in the vertical or horizontal diversification stage, with a large gap fraction and epiphyte population. 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; Shaw et al., 2004). This paper focuses on how short (seasonal) and long-term (young versus old-growth) developmental changes in canopy structure affected S, p, $\bar{E}/\bar{R}$ and I_n in the forests using high-resolution rainfall data. More specifically the objectives of this study were to: (1) estimate the seasonal changes in S, p, $\bar{E}/\bar{R}$ and I_n 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 that seasonal changes in S, p and $\bar{E}/\bar{R}$ have on estimates of I_n produced by the Gash model (Gash, 1979).

2. Material and methods

2.1. Site description

The young 20 m, 25-year-old, planted Douglas-fir (*Pseudotsuga menziesii*) forest and the old-growth Douglas-fir forest (>450-year-old) (Link et al., 2004) are both located within the Gifford Pinchot National Forest in southern WA, USA, and are approximately 4 km apart. The young Douglas-fir forest (45°49′07.89″N, 121°59′38.95″W) is adjacent to the T.T. Munger Research Natural Area (elevation = 558 m a.s.l.). 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 most common forest floor shrubs and herbs were 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 other species of shrubs and herbs covered the remaining 28% of the forest floor. The litter depth on the forest floor was 2.3 cm (n = 25, 95% CI (1.8, 2.8)), measured 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 Facility (45°49′13.76″N, 121°54′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 summary, the old-growth forest has 441 stems ha^{-1} with a basal area of 70.98 $m^2\ ha^{-1}$. 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 (>2000 kg ha^{-1}) (McCune, 1993). These epiphytes can store between 1.5 and 15 times their dry weight in water (Blum, 1973; Proctor, 2000). 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 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.

2.2. Leaf area index (LAI) and gap fraction

LAI was measured in July 2002 using a 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 LAIs for the young and old Douglas-fir forests were 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 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 1997–1999, 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 180° fish-eye lens (Camera: Canon AE-1; Lens: 7.5 mm Canon 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, NM, USA). For an estimate of gap fraction in the old-growth forest, we used values deduced from 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).

2.3. Theory and calculation of canopy hydrologic variables

To determine the canopy water storage capacity (S), direct throughfall fraction (p) and ratio of evaporation to rainfall intensity ($\bar{E}/\bar{R}$), past researchers have used regression based techniques (e.g. minimum method, mean method) that partition rainfall events into storms that are either insufficient or sufficient to saturate the forest canopy (e.g. Klaassen et al., 1998; Leyton et al., 1967; Llorens and Gallart, 2000). The minimum method provides an estimate of S by fitting a regression line relating P_n to P_G for storms sufficient to saturate the canopy and have minimal evaporation (Leyton et al., 1967; Llorens and Gallart, 2000). The x-intercept of the regression line provides the estimate of S. The mean method estimates S, p and $\bar{E}/\bar{R}$ by creating two linear regressions (R_1 and R_2) that relate P_n to P_G (Klaassen et al., 1998). The first regression line (R_1) is fit to all the storm events where P_G was insufficient to saturate the canopy. The second regression line (R_2) is fit to all storm events where P_G was sufficient to saturate the canopy. To determine which storm events were applied to R_1 or R_2, the fits of the regression lines are optimized to minimize the mean square error of the two regression lines. When using the mean method, the slope of R_1 provides the estimate of p, one minus the slope of R_2 provides an estimate of $\bar{E}/\bar{R}$, the value of P_G at intersection point of R_1 and R_2 provides an estimate of the canopy saturation point (P'_G) and, finally, the difference between P_G and P_n at the intersection point provides an estimate of S.

The IS method uses a similar approach as the mean method, but relates the cumulative net precipitation (P_n (mm)) to the cumulative gross precipitation (P_G (mm)) during a single storm event. Therefore, unlike the mean method, the IS method provides an estimate of S, p, $\bar{E}/\bar{R}$ and P'_G on per storm basis (Link et al., 2004). The IS method fits a regression line between P_n and P_G for the periods pre-(Line "A") and post-(Line "B") saturation (Fig. 1). As with the mean method, the slope of Line "A" provides the estimate of p, one minus the slope of Line "B" provides an estimate of $\bar{E}/\bar{R}$, the value of P_G at intersection point of Line "A" and Line "B" provides an estimate of P'_G and, finally, the difference between P_G and P_n at the intersection point provides an estimate of S. Once the rain event is finished, I_n can be calculated by subtracting as:

$$I_n = 1 - \frac{P_n}{P_G} \quad (1)$$

The line prior to saturation (Line "A", Fig. 1) was calculated as:

$$P_n = pP_G \quad (2)$$

The line post-canopy saturation (Line "B") was calculated as:

$$P_n = pP'_G + \left(1 - \frac{\overline{E}}{\overline{R}}\right)(P_G - P'_G) \quad (3)$$

S was then computed by:

$$S = (1-p)P'_G - I_w \quad \text{or} \quad S = (1-p)P'_G \quad (4)$$

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-

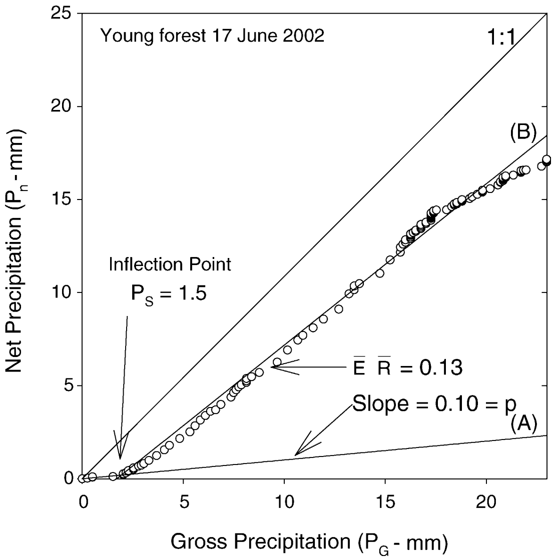

Fig. 1. The relationship between cumulative gross precipitation (P_G) and net precipitation (P_n) during a storm in the young forest (17 June 2002). The slope of regression "*A*" represents the direct throughfall ($p = 0.10$), the difference between P_G and P_n at the inflection point represents the canopy storage capacity (*S*), the value of P_G at the inflection point is the canopy saturation point (P'_G) and one minus the slope of regression "*B*" represents the ratio of evaporation to rainfall intensity ($\bar{E}/\bar{R} = 1-0.87$).

fir, S was estimated in two ways, with I_w (S_w) and without I_w (S_{wo}). I_w was estimated by:

$$I_w = \left(\frac{\bar{E}}{\bar{R}}\right) P'_G \quad (5)$$

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 $\bar{E}/\bar{R}$ can be estimated by dividing E by P_G (E/R). The subtraction method estimates evaporative loss using a mass balance approach (Eq. (6)).

$$E = P_G - S - P_n \quad (6)$$

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

2.4. Use of indirect methods for estimating canopy parameters

The use of indirect methods (mean and minimum methods) to estimate canopy variables has been criticized for underestimating S and overestimating $\bar{E}/\bar{R}$ (Klaassen et al., 1998; Llorens and Gallart, 2000). Past research also indicates that indirect methods can be inaccurate in areas with high spatial variability of throughfall (Lloyd et al., 1988) and do not always agree with direct measurements of canopy variables by microwave attenuation (e.g. Klaassen et al., 1998). We minimized the effect of spatial variability on the throughfall estimates by randomly relocating the gauges throughout the measurement periods (Lloyd and Marques Filhode, 1988; Wilm, 1943). The estimates of S by direct and indirect methods differ, in part, because past research has not used the same definition of S. For example, when Gash and Morton (1978) applied an indirect regression based technique to estimate S, they defined S as the minimum amount of water required to fill the canopy storage. In contrast, when using microwave attenuation to quantify S, Klaassen et al. (1998) defined S as the maximum amount of water the canopy will store during a storm event. Thus, the estimates of S using indirect and direct methods are unlikely to be similar because variables such as rainfall intensity and wind will alter the quantity of water stored in the canopy during a storm (Calder, 1996; Hörmann et al., 1996; Keim, 2003).

An alternative technique to regression-based methods is to measure rainfall interception by individual branches under a rainfall simulator, scaling 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). Scaling branch level measurements to the canopy requires precise knowledge of the forest canopy surface area and structure. Hence, this method usually assumes the canopy structure remains constant throughout the measurement period. Other researchers have used methods, such as the attenuation of microwaves (Bouten et al., 1991; Klaassen et al., 1998) or gamma rays (Calder and Wright, 1986), which are able to provide insight into seasonal changes in interception parameters. However, these systems have rarely been used because they are expensive and are not readily available. To summarize, the different techniques for determining S, p and $\bar{E}/\bar{R}$ all have strengths and weaknesses. The IS method is advantageous because the equipment necessary is affordable, it provides estimate of S, p and $\bar{E}/\bar{R}$ on a per storm basis and it does not assume constant canopy structure.

2.5. Measurement of gross precipitation (P_G) and net precipitation (P_n)

To measure P_G at the young site using we used 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 errors 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 rarely exceeding 3 m s^{-1} (K Bible, Wind River Canopy Crane Research Facility, unpublished data). Based on the typical rainfall intensities (0.25–2 mm h^{-1}) and windspeeds (0–1 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).

We measured P_n 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 was 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.

2.6. Stemflow

Stemflow was not measured directly at either the young or old-growth forests because rough-barked species typically have low stemflow 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-year-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-year-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).

2.7. Comparison of rainfall parameters from two different years

The measurements in the young stand from 17 June to 30 November 2002 are compared to measurements made in the old-growth forests from 30 March to 3 December 2000 because we did not have a sufficient number of tipping buckets to simultaneously estimate throughfall in both forests. The measurement periods are limited to the spring, summer and fall, because snowfall and freezing temperatures decrease the accuracy of the tipping bucket rain gauges. It is justifiable to compare the two datasets because the means of the canopy parameters are a sample of all possible storm events

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_w) and without (S_{wo}) including evaporation prior to saturation and direct throughfall fraction (p) for a young Douglas-fir

Event	DOY	Duration (h)	P_G (mm)	P_n (mm)	I_{net} (mm)	I_{net} (% loss)	$\bar{E}/\bar{R}$[a]	E/P_G[b]	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
Maximum		137.8	198.25	160.96	37.29	59.0	0.31	0.30	1.99	1.81	0.23
Minimum		4.67	2.54	1.04	1.50	10.8	0.01	0.05	0.71	1.28	0.04

[a] IS method.
[b] Subtraction method.

in each year (young, $n = 8$; old-growth, $n = 13$). The estimates come from a wide range of storms sizes (young = 10.4–198 mm; old-growth = 11.4–94.0 mm) and durations (young = 4.7–138 h; old-growth = 8.7–92.0 h) (Table 1). The wide range of storm events allow for the comparison of the canopy parameters, despite the short measurement period.

To allow for a more direct comparison between the two forests, the mean values of S, p and the $\bar{E}/\bar{R}$ for each forest were used in the Gash model (Gash, 1979) and I_n was estimated for a range of hypothetical storms (P_G = 0–200 mm) (See Section 2.8 for methods). The Gash model has been shown to predict I_n accurately in old-growth Douglas-fir forests, if there is sufficient time between storms for the canopy to dry (Link et al., 2004).

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

$$I_c = (1 - p)\sum_{j=1}^{m} P_{G,j} \quad (7)$$

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

$$I_w = n(1 - p)P'_G - nS \quad (8)$$

$$I_S = \left(\frac{\bar{E}}{\bar{R}}\right)\sum_{j=1}^{n}(P_G - P'_G) \quad (9)$$

$$I_a = nS \quad (10)$$

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

3. Results

3.1. Historical weather 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 June (80 mm (2002) versus 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 there was substantially more rainfall in October 2000 and less rainfall in November relative to 2002.

3.2. Canopy water storage capacity (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 0.3–1.6 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 (Fig. 2). Following canopy senescence and needle drop, S dropped from 2.0 to 1.0 mm in the young forest.

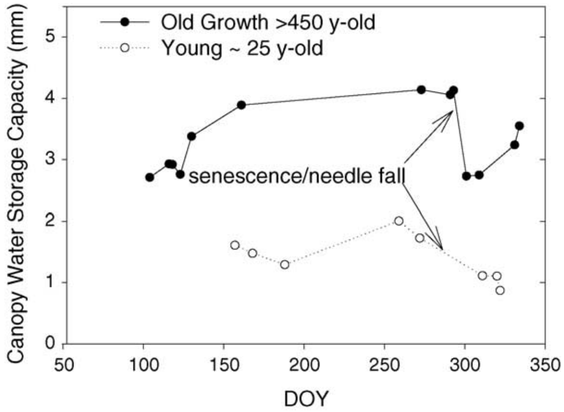

Fig. 2. The seasonal changes in canopy water storage capacity for a young (25-year-old) and old-growth (>450-year-old) Douglas-fir forests in South Central Washington.

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

Variable	Young forest	Old-growth forest
Age (year)	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[a]	8.1 ± 0.80
Bare ground (%)	53	3
Epiphytes (kg ha^{-1})	Negligible	1780
Canopy water storage capacity (mm)	1.4 ± 0.27[a,b]	3.32 ± 0.35[a]
Direct throughfall faction	0.12 ± 0.07[a]	0.42 ± 0.07[a]
Interception loss (proportion)	0.25 ± 0.10[a,c] 0.20 ± 0.10[a,d]	0.24 ± 0.08[a]
Canopy saturation point (mm)	1.75 ± 0.23[a]	
$\overline{E}/\overline{R}$ (proportion)		
IS method	0.18 ± 0.09[a,c] 0.12 ± 0.09[a,d]	0.17 ± 0.06[a]
Subtraction method	0.19 ± 0.08[a,c] 0.14 ± 0.08[a,d]	0.10 ± 0.05[a]

[a] For storms > 5 mm in the young stand and >10 mm in the old-growth stand.
[b] Calculated using the average of S_w and S_{wo} (see Section 2).
[c] No stemflow.
[d] 5% stemflow.

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 (Fig. 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.

3.3. 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 (Fig. 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) (Fig. 3).

3.4. Net precipitation, interception loss (I_n) and evaporative loss

For the young forest, 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 ($P_G > 5$ mm) was 25% ($n = 8$, 95% CI (14, 35) no stemflow) or 20% ($n = 8$, 95% CI (12, 32), 5% stemflow) (Fig. 4; Tables 1 and 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 (Fig. 5).

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 (Tables 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

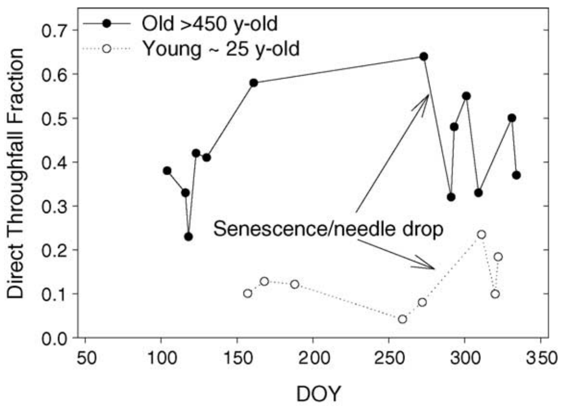

Fig. 3. Inter-storm differences in direct throughfall fraction for a young (25-year-old) and old-growth (>450-year-old) Douglas-fir forest in South Central Washington.

Table 3
Comparison between 48 manual throughfall collectors and 24 tipping bucket rain gauges for three periods between 15 September to 27 November 2002

Measurement period		Manual collectors			Tipping buckets			Error (%)
Start	End	mm	S.E.	95% CI	mm	S.E.	95% CI	
15 September	17 September	12.18	0.44	0.88	12.38	0.76	1.53	1.6
17 September	5 October	34.43	1.26	2.53	34.8	1.82	3.68	1.0
17 November	27 November	26.42	1.12	2.25	25.8	2.37	4.78	−2.4
Totals		73.03			72.98			<0.01

% 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.

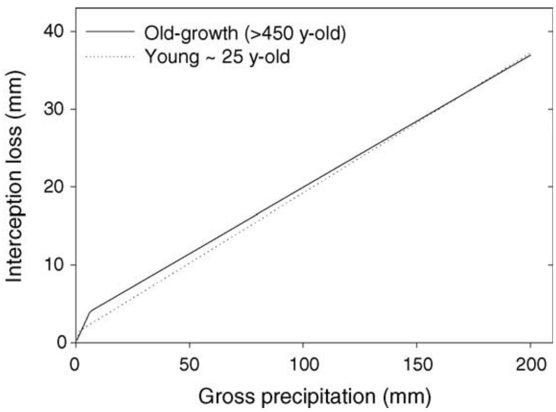

Fig. 4. The interception loss for a young (25-year-old) and old-growth (>450-year-old) Douglas-fir forests relative to gross precipitation (P_G). The interception loss for storms >10 mm did not statistically differ (p-value < 0.74).

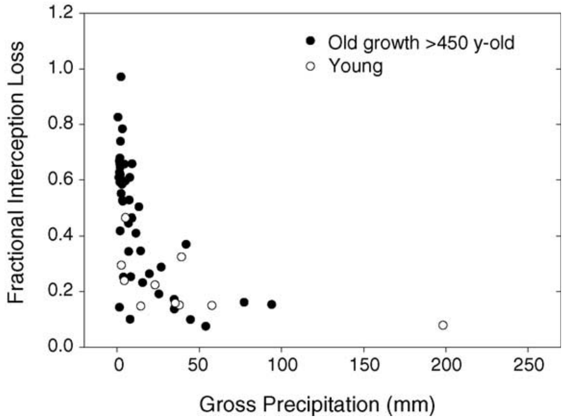

Fig. 5. The Gash model was applied to the canopy variable from the young and old-growth Douglas-fir forest (Table 2). The interception loss (I_n) is similar for the two forests after both canopies saturate.

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).

3.5. 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 $\bar{E}/\bar{R}$ determined from use of the IS Method, the errors associated with the seasonal estimates of I_n were slightly reduced from 3.3 to 2.4%. However, when seasonal variation in p, S, and $\bar{E}/\bar{R}$ were incorporated on a per storm basis, the deviation from the measured I_n decreased for all but one storm (Table 5).

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)	$\bar{E}/\bar{R}$[a]	E/P_G^2	I_n (mm)	$\bar{E}/\bar{R}$[a]	E/P_G[b]
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

[a] Calculated using the IS method.
[b] Calculated using the Subtraction method.

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

Measured variables					Gash model—average seasonal variables						Gash Model—storm variables					
Event	DOY	P_G (mm)	P_n (mm)	I_n (mm)	I_c (mm)	I_w (mm)	I_s (mm)	I_a (mm)	Total (mm)	Error (%)	I_c (mm)	I_w (mm)	I_s (mm)	I_a (mm)	Total (mm)	Error (%)
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

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. 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.

4. Discussion

4.1. 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; Fig. 2). Link et al. (2004) demonstrated that S is considerably reduced when I_w is included in the calculation of S (Eq. (4)). 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. Based on the difference between the S_w and S_{wo}, the average evaporation rate was between 0.2 and 0.3 mm h^{-1}; more than twice that commonly found for evaporation of intercepted water on 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 was 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 slightly larger in these forests even though the LAI in the study by Klaassen et al. (1998) 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, Fig. 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

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

Location	Age	Height	Density	Basal area	LAI	I_n	S	Reference
Washington, USA	25	20	2200	42	10.1	21.4[a]	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	Tiktak and Bouten (1994)
Oregon, USA	>400	N/A	N/A	33 and 47	N/A	20–30	N/A	Rothacher (1963)
Washington, USA	>450	65	441	67	9.6	25	2.71–4.17	Link et al. (2004)

[a] Assumes no stemflow.

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 square meter 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 forests may also increase because they can contain approximately 2000 kg_{dry} ha^{-1} of lichens and close to 1000 kg_{dry} ha^{-1} bryophytes (McCune, 1993). The maximum water contents of lichens and bryophytes range between 150–350% (Kershaw, 1985) and 500–1200% of their dry biomass (Proctor, 2000), respectively, implying that lichens and bryophytes in the old-growth forest may account for between 0.7 and 1.6 mm of additional water storage. Hence, it seems likely that the difference in S between these two forests may be attributed to differences 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; Fig. 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 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.

4.2. 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, Fig. 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.

4.3. 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 mean 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 170 mm (Fig. 5). The difference in I_n resulted 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 have saturated, the difference in the I_n of the young and old-growth forests remained relatively constant because $\bar{E}/\bar{R}$ was similar in the two stands; the I_n of the young forest exceeded that of the old-growth forest for storms greater than 170 mm (Table 1; Fig. 5). Initially, it is counter-intuitive that $\bar{E}/\bar{R}$ for an aerodynamically rough canopy with a greater S would be similar to that of a smoother canopy with a smaller S.

The $\bar{E}/\bar{R}$ is larger 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, $\bar{E}/\bar{R}$ in the young forest ranged between 0.01 and 0.30 and averaged 0.18. It is not uncommon for forests with low rainfall intensities to have $\bar{E}/\bar{R}$ ranging between 0.20 and 0.40 (e.g Gash et al., 1980; Zinke, 1967). The rate of evaporation partially 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 $\bar{E}/\bar{R}$.

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; Teklehaimanot et al., 1991). The above-canopy windspeeds for the forests in this study were 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). But despite the greater above-canopy windspeeds, the $\bar{E}/\bar{R}$ ratio in the old-growth forest was not greater than in the young forest. The $\bar{E}/\bar{R}$ may be similar in these two forests because r_a depends not only on windspeed, but on the canopy structure (Monteith, 1965). For a canopy in neutral stability, r_a is frequently calculated by:

$$r_a = \frac{1}{k^2 u}\left[\ln\left(\frac{z-d}{z_0}\right)\right]^2 \qquad (11)$$

where k is the von Karman's constant (0.41), u the windspeed (m s^{-1}), z the height of windspeed measurement, d the zero plane displacement and z_0 is the roughness length (where z_0 for momentum and sensible heat are assumed equal) (Monteith and Unsworth, 1990). For uniform canopies, values of d and z_0 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 $\bar{E}/\bar{R}$, 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 and increased gaps size may influence the r_a for the old-growth forest. Western hemlocks 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 $\bar{E}/\bar{R}$ is similar in the young and old-growth forests because the greater gap fraction in the old-growth forest causes $\bar{E}/\bar{R}$ 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 effective area for evaporation (Gash et al., 1995, 1999) and/or increased resistance to evaporation (Asdak et al., 1998; Teklehaimanot et al., 1991). However, an increase in gap size may not always decrease evaporation. Aboal et al. (2000) reported that throughfall in a *Pinus canariensis* forest was smaller in thinned stands relative to unthinned stands because of reduced fog entrapment in the thinned forests. However, fog entrapment has not been observed at this site and is assumed to be negligible. Thus, 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).

$$E = E_p c \tag{12}$$

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 Eq. (11), and c is assumed to be 0.77 for the old-growth forest, the following shows that calculated estimates of $\bar{E}/\bar{R}$ for these two forests are similar. If one assumes that: (1) the windspeeds at the top of the young forest are 1/3 of the windspeeds above the old-growth forest; (2) the young forest has a canopy height of 20 m; (3) the old-growth forest has an effective height between the average height of the Douglas-fir and the Western hemlock (39 m), and (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 $E_{p(\text{old-growth})}/E_{p(\text{young})} = 1/0.7 = 1.4$. Applying a gap-fraction correction $c = 0.77$ to the old-growth estimate would make $E_{p(\text{old-growth})}/E_{p(\text{young})} = 1.4 \times 0.77 = 1.1$, providing support for the similarity of $\bar{E}/\bar{R}$ 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.

4.4. The Gash model

When applied to each rainfall event, the Gash model predicted the I_n 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., 1992). However, the model has been unsuccessful when assumptions have not been fulfilled. For example, I_n is overestimated if there is insufficient time between storms for the canopy to dry (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 $\bar{E}/\bar{R}$ 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). After monitoring the I_n for individual storms in a *Pinus sylvestris* forest, Llorens (1997) reports a similar discrepancy between observed (throughfall collectors) and predicted (Gash model) estimates of I_n. He reported that the Gash model had difficulty estimating I_n on a per storm basis, but when applied annually, the estimates were within 3–12% of the observed values. 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 estimates of I_n for individual storms may cancel each other out, thereby, improving the estimate. The larger errors associated with individual storms highlight the inter-storm variability of S, p and $\bar{E}/\bar{R}$. If the inter-storm variation in S, p and $\bar{E}/\bar{R}$ were incorporated in the model, the individual storm estimates would improve.

When the Gash model incorporates the values of S, p and $\bar{E}/\bar{R}$ 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 $\bar{E}/\bar{R}$ 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 (Fig. 2), so incorporating seasonal change in S may improve Gash model estimates for individual storms (van Dijk and Bruijnzeel, 2001a,b). In future work, it would be desirable to have a larger dataset of storm events to confirm the affect that seasonal changes in S, p and $\bar{E}/\bar{R}$ have on estimates of I_n. This dataset was limited in size and we were required to use all the storm events to provide a seasonal estimate of S, p and $\bar{E}/\bar{R}$. With a larger dataset, a portion of the data could be withheld from the seasonal estimate of S, p and $\bar{E}/\bar{R}$. The withheld storm events could then provide more independent confirmation of the seasonal effect of these variables on the estimates of I_n.

5. Conclusions

The IS method worked well on the young Douglas-fir forest. The canopy of the young forest is uniform, closed, and the spatial variability of canopy water storage capacity (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 resulted from the presence of epiphytes, differences in canopy species and increased surface area of boles and branches. The value of p was greater in the old-growth forest due to the increased gap fraction. Lastly, even though the values of p and S were very different between the two forest ages, the ratio of evaporation to rainfall intensity ($\bar{E}/\bar{R}$) was not. As Douglas-fir forests develop, changes in the p, S and gap fraction may act to mitigate changes in $\bar{E}/\bar{R}$, 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 variations in S, p and $\bar{E}/\bar{R}$ 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.

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