

RESEARCH ARTICLE

Rainfall partitioning varies across a forest age chronosequence in the southern Appalachian Mountains

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Abstract

Evaporation of precipitation from plant surfaces, or interception, is a major component of the global water budget. Interception has been measured and/or modelled across a wide variety of forest types; however, most studies have focused on mature, second-growth forests, and few studies have examined interception processes across forest age classes. We present data on two components of interception, total canopy interception (E_i) and litter interception—that is, $O_i + O_e$ horizon layers—(E_{ff}), across a forest age chronosequence, from 2 years since harvest to old growth. We used precipitation, throughfall, and stemflow collectors to measure total rainfall (P) and estimate E_i ; and collected litter biomass and modelled litter wetting and drying to estimate evaporative loss from litter. Canopy E_i , P minus throughfall, increased rapidly with forest age and then levelled off to a maximum of 21% of P in an old-growth site. Stemflow also varied across stands, with the highest stemflow (~8% of P) observed in a 12-year-old stand with high stem density. Modelled E_{ff} was 4–6% of P and did not vary across sites. Total stand-level interception losses ($E_i + E_{ff}$) were best predicted by stand age ($R^2 = 0.77$) rather than structural parameters such as basal area ($R^2 = 0.49$) or leaf area ($R^2 < 0.01$). Forest age appears to be an important driver of interception losses from forested mountain watersheds even when stand-level structural variables are similar. These results will contribute to our understanding of water budgets across the broader matrix of forest ages that characterize the modern forest landscape.

KEYWORDS

forest succession, funnelling ratios, interception, stemflow, throughfall

1 | INTRODUCTION

Evaporative return of precipitation from plant surfaces, or interception, represents approximately one fifth to one third of global terrestrial evapotranspiration making it a major, yet often undervalued, component of the terrestrial water budget (Murray, 2013; Brooks, 2015; Good, Noone, & Bowen, 2015; Porada, Van Stan, & Kleidon, 2018). Understanding how changes in vegetation cover, structure, and disturbance affect water budgets is particularly important in the south-

eastern United States. Unlike many regions, the south-eastern United States saw increases in forest cover during much of the past century due to agricultural abandonment, active forest conservation, and a vibrant forest products sector (Trimble, Weirich, & Hoag, 1987; Wear & Greis, 2012). Mean annual precipitation in this heavily forested region exceeds 1,000 mm yr⁻¹ in most areas, with some areas receiving more than twice that (Laseter, Ford, Vose, & Swift, 2012). Even in this relatively wet climate, reforestation has had a demonstrable effect on regional hydrology (Trimble et al., 1987), and once abundant water supplies and established water supply systems in this region are being challenged by rapidly growing human demands and increasing climate variability (Brantley, Vose, Band, & Wear, 2017; Caldwell et al., 2014;

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Jackson et al., 2004). Forests in the Southern Appalachians are especially critical for sustaining water supplies in the rapidly growing Piedmont region (Caldwell et al., 2014). As populations continue to grow, water yield—the difference between incoming precipitation and evapotranspiration—from forested mountain watersheds will become even more important for future water supplies.

A major, yet understudied, component of evapotranspiration is the direct evaporative loss of precipitation (P) water from living and dead plant surfaces (interception, E_i) and soils (soil evaporation, E_s), which can represent up to 50% of total precipitation in some regions (Crockford & Richardson, 2000; Gerrits, Pfister, & Savenije, 2010; Murray, 2013). The amount of precipitation intercepted by plant surfaces depends on rainfall amount and distribution, atmospheric conditions during and after rainfall, and plant structure (surface areas of leaves, branches, stems, and forest floor biomass; Rutter, Kershaw, Robins, & Morton, 1971; Gash, 1979; Muzylo et al., 2009). During small rain events (0.4 to 0.8 mm), canopies may intercept 100% of P (Hall, 2003; Helvey & Patric, 1965). Bark interception may also represent an important component of interception as bark storage capacity can be up to 80% of the surface storage capacity of a tree (Herwitz, 1985). Bark interception becomes increasingly important during larger rainfall events in which throughfall (TF) and stemflow (SF) occur. As forests age, trees increase in size, bark texture often changes, and forest structure gains complexity (e.g., shrub and vine layers form). Relationships between total forest biomass and stem/branch surface area can thus change. Interspecific variations in bark storage capacity have been measured for some southern Appalachian species, including *Betula lenta* (L.) and *Quercus rubra* (L.; Levia & Herwitz, 2005), but is unknown for many others, and a diversity in bark structure could greatly affect stand-level storage capacity. Last, interception by forest floor biomass or “litter,” defined here as the O_i + O_e horizons, may also affect water yield and depends on litter wetting and drying characteristics and litter biomass (Gerrits & Savenije, 2011; Helvey, 1964; Kuraji & Gomyo, 2015; Sharafatmandrad, Bahremand, Mesdaghi, & Barani, 2010; Van Stan, Coenders-Gerrits, Dibble, Bogeholz, & Norman, 2017).

Our knowledge base for modelling the effects of changing forest cover and structure on future forest hydrologic budgets is inadequate. Physical models used to estimate interception losses in forests often provide inconsistent results when applied to actual ecosystems and can be challenging to parameterize and validate (Muzylo et al., 2009). Empirical models that describe interception fluxes for specific ecosystems remain a viable alternative, especially in small watersheds with homogeneous land cover where interception can be scaled up to larger areas (Swank, 1968; Swank & Miner, 1968). Such empirical interception models from the south-eastern United States are relatively abundant in the literature but are often limited to mature second-growth hardwood forests, commercial *Pinus* plantations, or a limited range of ages where differences are small (Brown & Barker, 1970; Gavazzi, Sun, McNulty, Treasure, & Wightman, 2016; Helvey, 1967; Helvey & Patric, 1965; Swank, Goebel, & Helvey, 1972). Thus, existing empirical models may not adequately represent the broader range of deciduous forest age classes that characterize the current hardwood-dominated forest landscape of the region.

Our goal was to increase our understanding of how rainfall is partitioned in southern Appalachian deciduous forests across a full range of forest age classes. We used a space-for-time substitution approach in which a chronosequence of study sites had similar climate, topography, and tree species composition but varied in stand age. The chronosequence approach has worked well for tree stem area, leaf area, and plant cover (Ewers & Pendall, 2008; Letcher & Chazdon, 2009) but has not been effective in other studies in which species changes during succession occur (Johnson & Miyanishi, 2008). In southern Appalachian cove forests, species that dominate in early succession are also dominant in old-growth forests (e.g., *Liriodendron tulipifera* L.). Working in these forests, our objectives were to (a) quantify total throughfall (TF) and stemflow (SF), (b) estimate litter evaporative losses (E_{ff}) using climate data and a litter wetting and drying model, and (c) relate total canopy interception (rainfall minus throughfall and stemflow) and total forest interception losses (total canopy interception + litter interception) to forest structural parameters such as basal area, leaf area index, and stem density across forest age classes. We hypothesized that canopy interception, stemflow, and litter interception would vary across forest age classes, increasing rapidly as forest age increased due to rapid accumulation of leaf area, litter biomass, and changes in bark water storage, and reach a maximum value as basal area and leaf area neared maximum values. These data will improve our understanding of factors that drive forest interception losses and inform future research needs related to variability in water yield from forested watersheds.

2 | METHODS

2.1 | Study sites

The study was conducted in five headwater catchments in the Nantahala National Forest of western North Carolina, USA. Climate in the region is classified as marine, humid temperate, or humid subtropical depending on highly localized temperature differences due to elevation (Swift, Cunningham, & Douglass, 1988). The region is heavily forested with a mix of cove hardwood, northern hardwood, oak, and oak-pine communities (Day, Phillips, & Monk, 1988). At the initiation of the study in 2012, stands represented 2-, 12-, 35-, and 85-year-old forests (time since the last harvest) and a previously unharvested (i.e., “old-growth”) forest with many trees >200 years old. The 2- and 12-year-old stands represented shelterwood harvests, the 35-year-old stand was clear cut (Swank & Webster, 2014), and the 85-year-old stand was stump-cut removing all merchantable timber (Douglass & Hoover, 1988). Other than management history, all stands were selected based on similar climate, soils, and species composition Table 1. All stands were at elevations between 700 and 1,200 m above sea level, all were dominated by deciduous trees including *Acer rubrum* (L.), *Betula lenta*, *Carya* spp., *Liriodendron tulipifera*, and *Quercus* spp., and the furthest distance between two sites was ~30 km.

2.2 | Stand structure

To quantify stand structure two 20 m × 40 m plots were established in the 2-, 12-, 35-, and 200-year-old sites, whereas the 85-year-old site had four 25 m × 25 m plots that had been established around an eddy-covariance tower for a concurrent study. In all plots, stems >10-cm diameter at breast height (DBH) were identified to species and measured to the nearest 0.1 cm. To quantify understory structure, stems 1- to 10-cm DBH were measured in 5 m × 5 m subplots in each of the larger plots ($n = 5$ in each of the 20 m × 40 m, $n = 3$ in each of the 25 m × 25 m plots). Allometric equations from Martin, Kloeppe, Schaefer, Kimbler, and McNulty (1998) were applied to trees >10-cm DBH to determine the contribution of large trees to stand-level leaf area index (LAI), stem area, and total plant area index (leaves + stems). Equations from McGinty (1972) were applied to stems of the shrub *Rhododendron maximum*, whereas new equations were developed for other species with stems <10-cm DBH (Brantley, Schulte, Bolstad, & Miniati, 2016).

2.3 | Canopy interception

Evaporative fluxes were measured in the context of the equation:

$$ET = (E_t + E_i + E_s), \quad (1)$$

where ET is total evapotranspiration, E_t is transpiration, E_i is evaporation from rainfall interception by the forest canopy, and E_s is the combined evaporation from the forest floor (E_{ff}) and/or soil surface. Interception of rainfall by the forest canopy was determined as follows:

$$E_i = P - (TF + SF), \quad (2)$$

where P is total precipitation, TF is total canopy throughfall, and SF is stemflow. Hourly or 15 min P was determined using a recording rain gauge, a tipping bucket rain gauge, and/or a standard rain gauge as follows. All rain gauges were located within 1 km of the study sites, with four of the five located within 300 m, to minimize possible local differences in precipitation. For two sites (the 35- and 85-year-old sites) located in the Coweeta Hydrologic Lab, recording rain gauges (Belfort Instrument, Baltimore, Maryland, USA) recorded hourly rainfall and total amounts were matched weekly to nearby standard rain gauges. At the three remote sites, tipping bucket rain gauges (Campbell Scientific, Logan, Utah, USA) recorded 15 min totals. At all sites, a standard rain gauge (National Weather Service, Indianapolis, Indiana, USA) was deployed, and totals from the recording and tipping bucket gauges were calibrated against the totals. Rainfall in standard rain gauges was recorded approximately monthly.

Throughfall was measured using 12 collectors at each site. Each collector consisted of a ~20-L container with a tight-fitting lid to prevent leaks, spills, and/or evaporative loss. A 19.7-cm-diameter funnel with a ~1-cm-diameter opening was inserted through the top of the lid and sealed against leaks using a rubber stopper and waterproof silicone caulking. Poly-Fil insulation protected the funnel orifice from clogging with litter and may also reduce evaporative loss after rainfall.

Subsequent testing of these collectors in an open field with a paired rain gauge indicated 97–99% agreement with a tipping bucket rain gauge. Throughfall volume was measured approximately monthly. For volumes >500 ml, a depth measurement was taken to the nearest 5 mm and converted to volume using a polynomial equation (not shown). Volumes <500 ml were measured to the nearest 1 ml using a 1-L graduated cylinder. Throughfall was scaled to the stand by dividing the volume of water collected by the area of the funnel opening (304.34 cm²). Larger sample sizes and larger funnels were deemed impractical due to cost and the remoteness of some sampling locations. Although our sample sizes and the area of our collectors were relatively small compared with some recommendations (Zimmerman, Zimmerman, Lark, & Elsenbeer, 2009), our length of sampling (~27 months) and the number of rainfall events integrated into our monthly samples (>300) were high. Ultimately, our within-site error was small enough to meet the objectives of the study.

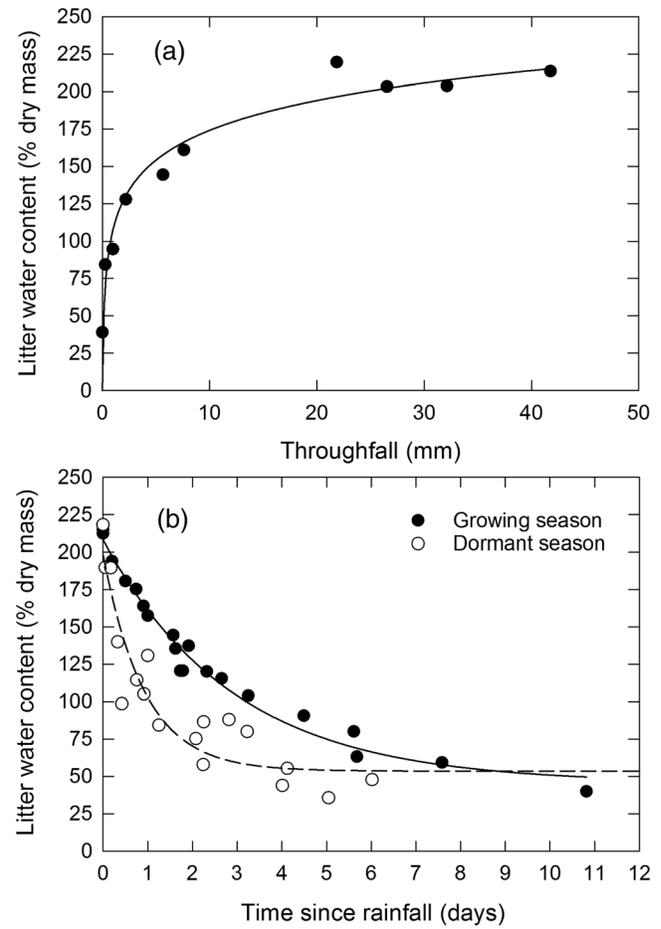
Stemflow volume was collected by sealing aluminium collars with silicone caulk around smoothed tree boles at an angle and funnelling the water running down the bole into plastic tubing that led to large (either 20 or 121 L) plastic containers with water-tight, removable lids (Hoover, 1953). Water that collected in the containers during rain events was then measured by volume in the same manner as TF. Four to 10 collars were installed at each site to represent the dominant size class and dominant species in the stand, with more collars installed in stands with higher stem density (i.e., the 2- and 12-year-old site). For each tree, projected crown area (A) was determined as $A = \pi r^2$, where r is the average of four crown radius measurements taken by measuring from the base of each tree bole to the outer edge of the crown. For each tree and storm, stemflow volume was converted to linear units by dividing by A of each tree canopy. Stemflow ratio (S_r) was calculated as the fraction of total rainfall during a given event that reached collectors as SF and converted to a percent. We tested for significant effects of DBH, season, site, total precipitation, and species on log-transformed S_r using multiple linear regression and used the resulting equation to scale stemflow from tree to stand level. We used scaled stand-level stem flow and gross precipitation to calculate SF as a percentage of P and as a depth and calculated stand-level funnelling ratios ($F_{P,BS}$) using SF and stand basal area (Carlyle-Moses et al., 2018; Table 1).

2.4 | Litter interception

Daily litter interception was modelled based on daily P measured at each site, estimated TF from the precipitation-throughfall relationships described above, and the potential of standing forest floor biomass (litter) to absorb new moisture from TF or lose moisture to evaporation after rainfall. Moisture absorbance and subsequent drying of forest floor were estimated from equations derived for litter wetting and drying in a previous study at the Coweeta Hydrologic Lab (Helvey, 1964). Data in Figures 3 and 4 in Helvey (1964) were digitized and used to derive new equations (Figure 1, Table 2) for predicting declines in litter moisture content based on number of days since rain (i.e., “drying curves”) and increases in litter moisture content based on throughfall (i.e., “wetting curves”). Separate drying curves for dormant

TABLE 1 Site locations and stand structural and tree community characteristics for five sites across a forest age chronosequence in the southern Appalachian Mountains in North Carolina, USA

Stand age (years) at initiation of the study	Location	Basal area (cm ² /m ²)		Leaf area index (m ² m ⁻²)		Stem density (ha ⁻¹)		Dominant species (% basal area)		Evergreen
2	35.10 N, 83.64 W	10.6	1.6	1,120	106	A. rubrum (53%), Carya spp. (33%)		Tsuga canadensis (2%)		Deciduous
12	35.18 N, 83.50 W	15.7	6.5	10,080	75	L. tulipifera (33%), Quercus spp. (32%)		NA (<1%)		Deciduous
35	35.07 N, 83.44 W	32.5	5.1	1,400	1,093	L. tulipifera (64%), Quercus spp. (10%)		NA (<1%)		Deciduous
85	35.06 N, 83.43 W	29.1	4.7	3,467	404	L. tulipifera (24%), Quercus spp. (20%)		R. maximum (15%)		Deciduous
>200	35.27 N, 83.55 W	30.5	4.5	3,200	284	Quercus spp. (58%), A. rubrum (21%)		R. maximum (15%)		Deciduous

**FIGURE 1** Equations for hardwood litter moisture content as a function of throughfall (a) and days since the last rain event (b), during wetting-up and drying-down cycles in the dormant and growing seasons. Data were digitized from Helvey (1964) and fitted with non-linear equations (see Table 2)

and growing seasons accounted for differences in potential evaporation at the forest floor during those two periods. All curve fit analyses were performed in SigmaStat version 13.0 (Systat Software, Inc., San Jose, California, USA).

To populate the litter interception model, litter biomass was collected approximately monthly from December 2012 to November 2014. Five forest floor biomass samples were collected in a 0.1-m² square at each site. Samples were collected in plastic bags to prevent evaporation, and a field weight was taken immediately after returning from the site (within 4 hr of collection). Samples were subsequently dried at 60°C for 3–5 days, sifted to remove mineral soil and fine organic matter (O_a layer), and a dry weight was taken to determine dry biomass. Dry weights were used as model inputs to estimate stand-level E_{ff} as a function of litter biomass, throughfall wetting and drying relationships above, and daily TF estimates for each site. The model provided a daily estimate of litter moisture content, and daily differences, either from wetting due to additional TF or drying, were interpreted as evaporative losses. Wet litter weights were used to test model outputs by comparing observed and predicted daily moisture content.

TABLE 2 Equations predicting litter moisture content (MC, % of dry mass) either as a function of throughfall (TF, mm) or days since rainfall (D , days), depending on whether the litter was in a wetting-up or a drying-down cycle in the growing or dormant season

Function	Equation	Fit to original data (R^2)
Litter wetting	$MC = 28.7338 * \ln(TF) + 200.9245$	0.914
Litter drying (growing season)	$MC = 162.6766 * e^{(-0.3418 * D)} + 45.5698$	0.977
Litter drying (dormant season)	$MC = 144.9547 * e^{(-1.0785 * D)} + 53.5308$	0.860

Note. All equations describe litter moisture for hardwood deciduous forests in the southern Appalachian Mountains. Raw data were manually extracted from Helvey (1964; see Figure 1) and fitted with non-linear equations.

2.5 | Statistics

We tested for differences in canopy interception ($E_{i, \text{canopy}} = P - TF$) and SF using a one-way repeated measures analysis of variance with age as the primary factor and a fixed effect and collection period as the repeated effect. We tested for differences in litter biomass using a one-way repeated measures analysis of variance, with age as the fixed-effect and month as a repeated effect. If significant differences were detected among main effects, we used a post hoc mean separation (Tukey's adjusted t) on LS means. To determine how $E_{i, \text{canopy}}$ related to stand age, basal area, and leaf area index, we used linear and nonlinear regression analyses on cumulative interception values (% total P) using individual throughfall collectors as samples. To determine how total canopy interception losses (E_i) and total stand

interception losses ($E_i + E_{\text{ff}}$) related to stand age, basal area, and leaf area index, we used linear and nonlinear regression analyses using stand-level estimates. All analyses were conducted in SigmaStat 14.0.

3 | RESULTS

3.1 | Canopy interception

Canopy interception ($P - TF$) varied significantly across forest age classes ($F(4, 26) = 27.97, p < 0.001$) from $3.9 \pm 2.2\%$ for the youngest stand to $20.7 \pm 3.4\%$ in the oldest stand (Figure 2 and Table 3). Canopy interception was essentially zero in the youngest stand in the first year of the study, increased rapidly during the first ~35 years of

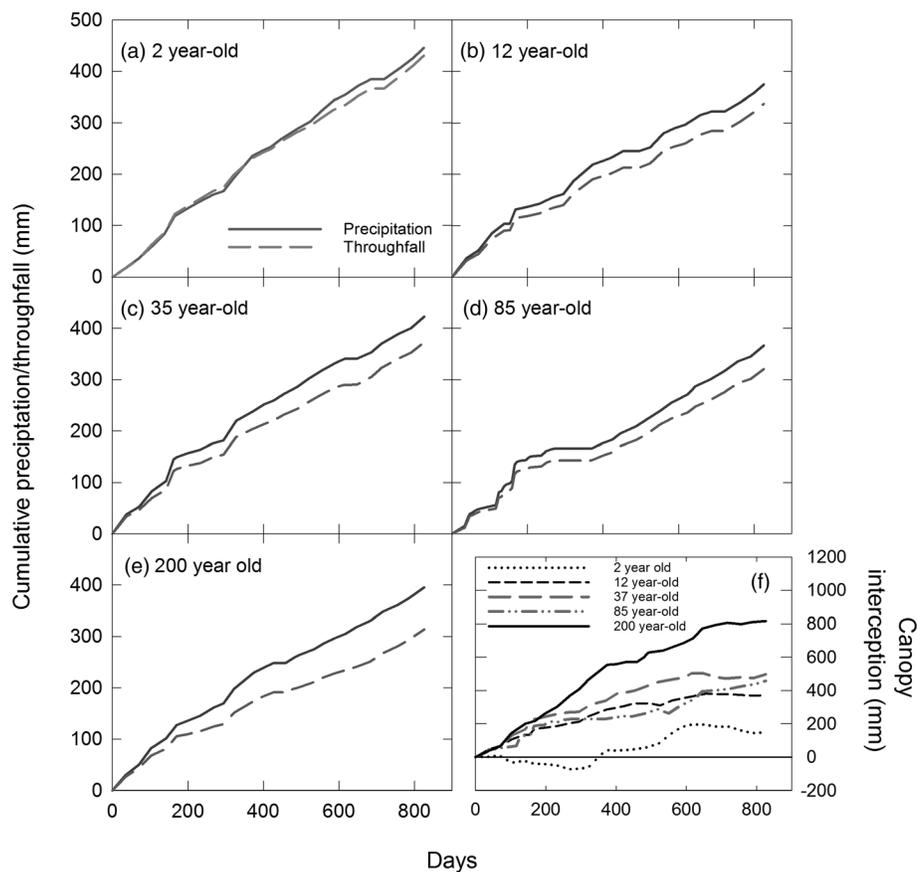


FIGURE 2 Cumulative precipitation (solid line) and throughfall (dashed line, a–e) and canopy interception (f) measured as the difference between precipitation and throughfall over time for the five sites across a forest chronosequence

TABLE 3 Precipitation (P , mm) partitioning and total interception loss across five age classes of hardwood forest in the southern Appalachian Mountains

Stand age (years)	Total P (mm yr ⁻¹)	Canopy interception, $E_{i, \text{canopy}}$ (% P)	Stemflow, SF (% P)	Total canopy interception, E_i (% P)	Litter interception (% P)	Total interception loss (% P)	Annualized interception loss (mm yr ⁻¹)
2	2060	3.9 ± 2.2 ^a	0.3 ± 0.1 ^a	3.6	4.1 ± 0.7	7.7	159
12	1858	9.9 ± 3.1 ^b	8.3 ± 2.3 ^d	1.6	5.1 ± 0.4	6.7	124
35	1849	12.2 ± 2.2 ^b	2.4 ± 0.7 ^c	9.8	4.8 ± 0.6	14.6	270
85	1795	14.1 ± 3.0 ^b	1.2 ± 0.4 ^b	12.9	4.4 ± 0.4	17.3	311
>200	1817	20.7 ± 3.4 ^c	0.5 ± 0.2 ^a	20.2	6.2 ± 0.7	26.4	480

Note. Canopy interception was the difference between P and throughfall. Total canopy interception was calculated by subtracting stemflow and throughfall from P . Litter interception was modelled according to equations in Figure 1. Superscript letters denote significant differences among sites.

regeneration, and then continued to increase more slowly as stands aged (Figure 2 and Table 3). For these stands, the best model to predict canopy interception used the logarithmic growth function:

$$E_{i, \text{canopy}} = 3.3650 * \ln(\text{stand age}) + 1.0607, \quad (3)$$

where $E_{i, \text{canopy}}$ is % canopy interception and stand age is in years since the last harvest ($R^2 = 0.217$, $p < 0.001$). A non-linear relationship between $E_{i, \text{canopy}}$ and basal area explained less variation than the forest age model ($R^2 = 0.150$, $p = 0.004$). There was no significant relationship between $E_{i, \text{canopy}}$ and LAI across these stands ($p = 0.0871$, $R^2 = 0.04$).

The percentage of precipitation that was stemflow (S_R) for individual trees was related to DBH ($t = -19.985$, $p < 0.001$, $r^2 = 0.560$), season ($t = -7.349$, $p < 0.001$, $r^2 = 0.100$), and whether the tree was *B. lenta* ($t = 3.457$, $p < 0.001$, $r^2 = 0.066$) or *Carya* spp. ($t = 4.293$, $p = 0.001$, $r^2 = 0.030$). Site and total precipitation were not significant predictors of S_R or $\log S_R$ ($p \geq 0.05$). Thus, the final multiple linear model for $\log S_r$ used a combination of DBH, season, and the presence/absence of *B. lenta* (BELE) and *Carya* spp. (CASP; $F = 149.218$, $p < 0.001$, $R^2 = 0.642$). The final equation for predicting S_R was the following:

$$S_R = 10^{(1.303 - (0.0307 * \text{DBH}) - (0.413 * \text{Season}) + (0.313 * \text{BELE}) + (0.350 * \text{CASP}))}, \quad (4)$$

where DBH is in centimetre, season has a value of either 1 (leaf-off) or 2 (leaf-on), and the other two terms in Equation 4 represent the presence (1) or absence (0) of either *B. lenta* or *Carya* spp.

Scaled stemflow comprised a relatively small amount of total precipitation (<3%) in four of the five age classes, was a much larger proportion (~8% of P) in the 12-year-old stand, and was largely driven by density of small stems (Figure 3 and Table 1). The percent of total precipitation that was stemflow was lowest in the youngest age class stand (0.3%), highest in the 12-year-old stand (8.3%), and then declined across the chronosequence as stem density declined and stand structure shifted towards dominance by larger trees (Table 3). Funnelling ratio was also highest in the 12-year-old stand (52.9), with other stands at 2.8, 7.4, 4.1, and 1.6 for the 2, 35, 85, and 200-year-old sites, respectively. Stand-level stemflow was not well predicted by either basal area ($R^2 = 0.079$, $p = 0.648$) or leaf area index ($R^2 = 0.0163$, $p = 0.275$) but was best predicted by a linear model using total stem density ($R^2 = 0.879$, $p < 0.019$).

Subtracting stemflow (SF) from canopy interception ($P - \text{TF}$) to calculate total interception (E_i) reduced the variation in $E_{i, \text{canopy}}$ across sites. Total canopy interception (E_i , Equation 2) in the 12- and 35-year-old stands was 8.3% and 2.6% lower than canopy interception, respectively, but <2% lower than canopy interception at other sites (Table 3 and Figure 5). Total canopy interception losses varied greater than tenfold across sites, from 1.6% of P for the second youngest stand to 20.2% in the oldest stand. The relationship between E_i and stand age resembled the relationship between canopy interception and stand age but was more muted due to the countering effects of $E_{i, \text{canopy}}$ and stemflow. There was no significant relationship between mean stand-level E_i and basal area ($R^2 = 0.505$, $p = 0.110$), or between mean stand-level E_i and leaf area index across stands ($R^2 < 0.001$, $p = 0.971$; Figure 4). For these stands, mean stand-level E_i was best predicted by a non-linear relationship with stand age ($R^2 = 0.703$, $p = 0.048$; Figure 4) where

$$E_i = 3.678 * \ln(\text{stand age}) - 2.4984. \quad (5)$$

3.2 | Litter interception

The model to predict litter moisture content explained 31% of the variation in the measured daily litter moisture content ($p < 0.001$). The model tended to overpredict litter moisture at low moisture values and underpredict litter moisture at high values, but the absolute percent bias was fairly low at -3%. Modelled litter interception varied across sites over the study period (Table 3); however, most of the variation in litter interception did not come from differences in litter biomass which did not vary significantly across sites ($F(4, 23) = 0.931$, $p = 0.609$; Figure 5). Rather, variation in modelled litter interception among sites was due to differences in precipitation timing across sites during the study period, and sites with a larger proportion of small rain events (specifically the oldest site) had higher overall litter interception.

3.3 | Total interception loss and forest age

Total stand-level interception losses, the combination of E_i and E_{ff} , was strongly related ($p = 0.009$) to forest age (Figure 5) and was best predicted by a linear relationship with stand age where

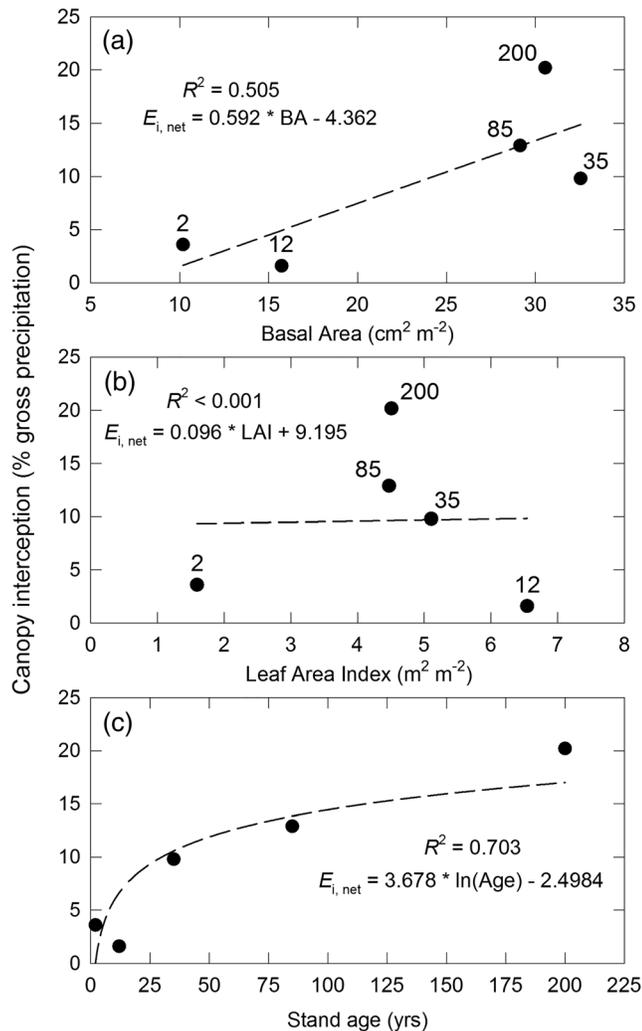


FIGURE 3 Total canopy interception, or precipitation minus throughfall and stemflow, versus basal area (a), leaf area index (b), and stand age (c) for five sites across a hardwood forest chronosequence in the southern Appalachians. Numbers in top two panels adjacent to symbols denote stand age

$$E_{i+ff} = 0.095 * \text{stand age} + 8.185. \quad (6)$$

Basal area explained less of the variation in total interception, whereas the relationship between total interception and leaf area index was not significant (Figure 5). Total interception loss accounted for 6.7–28% of precipitation, which equates to an annual water loss of 124–480 mm yr^{-1} in this relatively wet region (Table 3).

4 | DISCUSSION

Our hypothesis of interception increases as forests age was supported overall; however, partitioning of incoming rainfall did not change uniformly with age and was relatively poorly predicted by stand structural parameters such as basal area and LAI. Canopy interception increased with age but not with leaf area or stem basal area. Stemflow rerouted

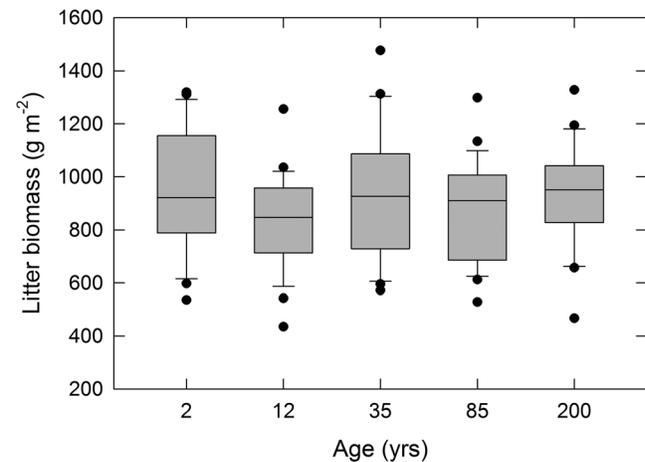


FIGURE 4 Monthly variations in forest floor biomass for five sites across a hardwood forest chronosequence in the southern Appalachian Mountains. Median value (line) with 25th and 75th percentiles (box ends), 10th and 90th percentiles (whiskers), and outliers (symbols) shown

a substantial proportion of precipitation to the forest floor in the 12-year-old stand (~8%), due to the high density of small stems. Litter interception was relatively low (4–6% of precipitation) and consistent across stand ages, varying more with precipitation distribution than structural or age characteristics.

Variations in interception among stands of different ages were substantial and were not solely explained by physical variables such as basal area or leaf area. As expected, interception increased rapidly in the first decade after harvesting as regeneration of small trees increased basal area and leaf area and closed the tree canopy. However, once the canopy closed, the relationship between throughfall and leaf area was highly variable among sites. Allometrically derived leaf area peaked in the 12-year-old stand, but interception continued to increase with age. For example, LAI was 8% higher in the 12-year-old stand than the 35-year-old stand, but interception was 19% lower. Although the structure of the 12-year-old stand in this study may seem anomalous, this pattern of high woody recruitment and rapid leaf area recovery during the first two decades of regeneration after disturbance is common in the southern Appalachians (Elliott & Swank, 1994; Elliott & Swank, 2008) and was previously observed in the 35-year-old stand in the current study (Elliott, Boring, Swank, & Haines, 1997). Ultimately, stand age was a better predictor of interception than variables such as basal area or leaf area index.

The finding of a weak relationship between leaf area index and interception is not without caveats. Although we report significant differences in LAI among age classes, it should be noted that allometric equations used to derive LAI can be prone to error, especially for large trees. For the 12-year-old site, we used allometric equations developed concurrently with this study (Brantley et al., 2016). We also used allometric equations to estimate leaf area for large trees (Martin et al., 1998), and potential error in allometric equations tends to increase as tree size increases. Thus, it is possible that variation in LAI among these sites is somewhat less than reported. Second, some of the

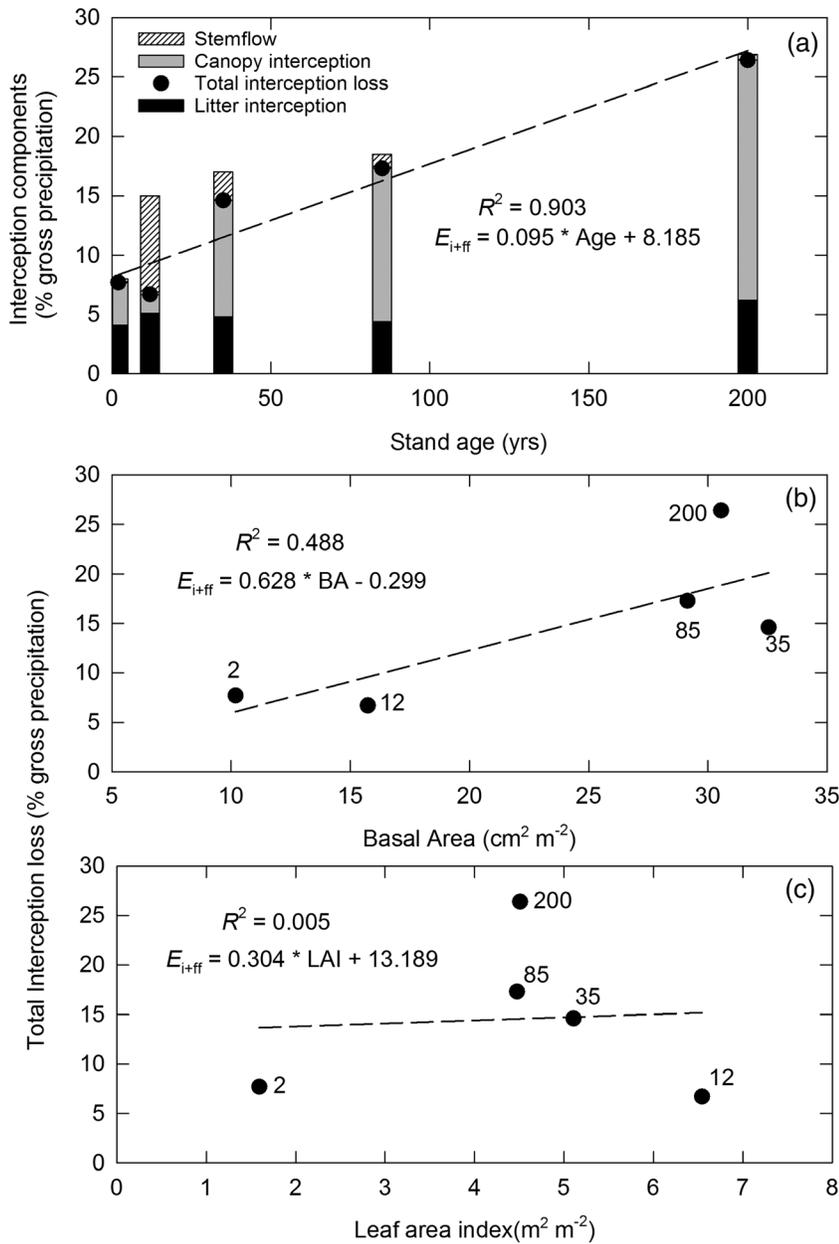


FIGURE 5 Precipitation partitioning versus stand age (a) and total stand-level interception loss versus stand age (a), basal area (b), and leaf area index (c) for five sites across a hardwood forest chronosequence in the southern Appalachians. Numbers in b and c adjacent to symbols denote stand age

variations in this study could have been related to the effects of rainfall distribution (i.e., frequent small storms versus fewer large one) on interception. However, that effect was likely small and limited to the older stand that experienced a higher proportion of small rain events in which no throughfall was generated. Third, our results in no way imply that LAI is not an important variable affecting interception in stands of similar age, as a rather large body of literature supports the use of LAI as a key parameter in interception modelling (Muzyllo et al., 2009). Still, this finding has important implications for the many models that use stand structure and vegetation cover to predict throughfall across large areas of forest where multiple age classes may occur and suggests that other factors related to forest age are driving increases in canopy interception. Possible factors may include changes in bark storage capacity as forests age and/or an increase in epiphyte cover in older forests, both of which have been shown to

affect various components of interception (Herwitz, 1985; Levia & Herwitz, 2005; Porada et al., 2018).

Variability in stemflow was also high among age classes and was poorly related to either leaf area or basal area. Tree-level stemflow generation is known to vary strongly with differences in bark water storage, tree branching structure, and weather conditions (Levia & Frost, 2003; Levia & Germer, 2015; Levia & Herwitz, 2005). In our study, tree-level stemflow ratio was highest on small trees and generally declined as tree size increased. Stemflow ratio varied among species and age classes, with young, smooth-barked trees such as *B. lenta* and *Carya* species, having relatively higher stemflow and rough-barked species such as mature *Quercus* species and mature *L. tulipifera* generating relatively less stemflow. At the stand level, total stemflow and funnelling ratios varied significantly with age, peaked in the 12-year-old stand, and were largely driven by stem density. Funnelling ratios

>1 in all stands suggest a more important role for stemflow in precipitation partitioning than would be indicated by its proportion relative to total precipitation (Carlyle-Moses et al., 2018). The exceptionally high funnelling ratio in the 12-year-old stand suggests that small trees in these young stands may be facilitating their own hydrological and biogeochemical hotspots and possibly enhancing their own growth during this stage of regeneration, but further work is needed to demonstrate this conclusively.

These results agree well with expectations of stemflow generation from previous research that showed wide variations in stemflow and bark water storage among a similar suite of species (Levia & Herwitz, 2005; Van Stan & Gordon, 2018). Although we did not quantify it specifically, we also observed that younger trees generally had smoother bark than older trees, especially in *A. rubrum*, *B. lenta*, and *Carya* spp. Species with smoother bark have been shown to have higher stemflow and funnelling ratios compared with trees with rougher bark (Alexander & Arthur, 2010; Carlyle-Moses & Price, 2006). Thus, the high density of young trees, the species composition of young forests, and the smoother bark of young trees may all contribute to increased stemflow in young, regenerating stands, and this flux helped mitigate the effect of rapid increases in leaf area during regeneration on overall interception.

Last, we showed relatively little variation in litter interception. Although the effects of litter interception on forest water yield have received relatively scant attention in the literature, a few studies have shown small (<5% of total P) but significant effects of litter interception on water yield at the catchment level (Kuraji & Gomyo, 2015; Li, Xiao, Niu, Yu, & Xie, 2015). Our estimates of E_{ff} agree well with litter interception losses reported in these studies in terms of proportion of total rainfall lost to litter interception but are lower than some other values reported in stand-level studies (Gerrits et al., 2010; Van Stan et al., 2017). Litter interception showed relatively little variation across age classes compared with canopy interception and stemflow because litter biomass ($O_i + O_e$) did not vary across sites as we had hypothesized. This lack of variation in litter biomass likely resulted from a combination of factors. Although it was not measured specifically, O_i was likely highest immediately after harvest and then gradually declined with age as O_e simultaneously increased (Yanai, Arthur, Siccama, & Federer, 2000). In these sites, we observed rapid growth of herbaceous groundcover in the youngest stand, likely due to increased light availability. The subsequent closure of the canopy in the other stands likely contributed to similar leaf area index values, which contributed to similar litter inputs, and thus a lack of variation in litter biomass across age classes. These litter inputs do not lead to a long-term build-up of litter because of rapid cycling and high litter turnover from the warm, moist climate (Knoepp, See, Vose, Miniati, & Clark, 2018). Because litter biomass did not vary among sites, forest age did not affect litter interception losses in this study.

Modelled litter interception was slightly higher in the oldest stand; however, this difference was a result of rainfall distribution rather than litter biomass. The many small rain events recorded at this station rarely saturated the litter; thus, water from these small events was intercepted at a relatively higher rate than in sites with less frequent, but larger, rain events that did saturate litter. Although our results

show that evaporation from litter typically makes up a smaller fraction of total water fluxes, we also suggest that litter interception may be relatively more important in some circumstances, such as in sites with more small rain events or during periods of drought when litter dryness could contribute to increased litter moisture absorption rates which would increase evaporative losses. These issues are important to consider as climate change has already had a significant impact on temporal patterns of rainfall in this region (Burt, Miniati, Laseter, & Swank, 2018), and these changes could promote additional litter interception losses.

Quantifying variations in litter interception losses remains challenging. Our model is one of only a few methods that can estimate how variations in litter biomass and climate affect litter interception in forests (Guiditta, Coenders-Gerrits, Wenninger, Greco, & Rutigliano, 2018; Van Stan & Gordon, 2018). Other methods used to quantify total understory water fluxes (e.g., understory eddy covariance towers, weighing lysimeters) may not discriminate between litter interception losses, soil evaporation, and transpiration from understory vegetation. This lack of discrimination limits the ability of these indiscriminate methods to inform how forest structure, and potentially forest management activities, affect litter biomass (e.g., prescribed fire), can drive variations in litter interception, and ultimately affect water yield. Interactions and trade-offs between litter interception and soil evaporation add further to the complexity of understanding the importance of litter interception losses to watershed hydrology (Naeth, Baily, Chanasyk, & Pluth, 1991; Sharafatmandrad et al., 2010). We found our method reasonably effective at predicting litter moisture content, and thus, the model may also be useful for other systems if litter wetting and drying dynamics are known.

In summary, variations in total interception losses among stands of different ages were substantial, from 6.7% in the second youngest stand to 26.4% in the oldest stand. This variation was best related to stand age, somewhat related to basal area, and poorly related to leaf area for these stands. Total interception losses represented a complex combination of trends that either changed with forest age, for example, canopy closure and stem density, or did not, for example, litter biomass. As with E_i , the poor correlation between total interception losses and leaf area index suggests that other factors related to forest age, such as bark water storage and epiphyte abundance (Levia & Herwitz, 2005; Porada et al., 2018), are important at driving stand-level interception. These data shed light on some of those complexities, such as the relationship between stem density and stemflow, and also suggest additional areas for study, especially the relationship between E_i and forest age.

Episodes of water scarcity with negative impacts for both human well-being and ecological function of aquatic and semi-aquatic ecosystems are increasing in the south-eastern United States (Brantley et al., 2017; Lockaby et al., 2011; Petes, Brown, & Knight, 2012; Sun, McNulty, Myers, & Cohen, 2008). Many of the fastest growing metropolitan areas in the region, including cities such as Atlanta, GA, and Charlotte, NC, draw on water from the southern Appalachian Mountains, which supply water to more than 18 million people (Caldwell et al., 2014). These mountain watersheds also serve as headwaters for a number of river basins that are ecologically vulnerable due to either

past or predicted flow alterations (Brantley et al., 2017; Martin et al., 2017; Petes et al., 2012; Suttles et al., 2018). Although many of the fluxes reported here are small relative to transpiration, the aggregate effect of variations in interception should not be ignored. Drivers of interception have been studied extensively using both physical and empirical models (Gash, 1979; Muzylo et al., 2009; Rutter et al., 1971), but variations in interception are often not adequately represented in regional water budgets (Murray, 2013; Savenije, 2004). Interception is a highly variable and dynamic process, and changes in interception over time can have significant effects on forest water budgets and impact regional hydrology (Crockford & Richardson, 2000; Murray, 2013; Swank, 1968; Swank & Miner, 1968). For example, increases in interception by vegetation in the 20th century have had a significant negative effect on global run-off generation and may contribute to water scarcity in some regions (Murray, 2013).

Changes in forest structure and species composition, overlain with climate change, may alter future water yield from forested watershed and ultimately affect water supplies for humans and sustainable flow for aquatic ecosystems. If the variations we attribute to forest age were the result of climate change, forest disturbance, changes in species composition, land-use conversion, or human extraction of water, they would be considered significant and would likely provide justification for management action to mitigate water losses (Caldwell et al., 2016; Caldwell, Sun, McNulty, Cohen, & Myers, 2012). Although we do not suggest that management actions need to be taken against old-growth forest to increase water yield, we do advise considering stand age in predictions of forest water yield. We believe that these results will be useful for parameterizing future hydrologic models and will ultimately contribute to a better understanding of how age-related forest heterogeneity affects regional water budgets.

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