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Effects of phenology and meteorological disturbance on litter rainfall interception for a *Pinus elliottii* stand in the Southeastern US

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Abstract

Litter layers develop across a diverse array of vegetated ecosystems and undergo significant temporal compositional changes due to canopy phenological phases and disturbances. Past research on temporal dynamics of litter interception have focused primarily on litter thickness and leaf fall, yet forest phenophases can change many more litter attributes (e.g., woody debris, bark shedding, and release of reproductive materials). In this study, weekly changes in litter composition over 1 year were used to estimate litter water storage dynamics and model event-based litter interception. Litter interception substantially reduced throughfall (6-43%) and litter water storage capacity ranged from 1-3 mm, peaking when megastrobili release and liana leaf senescence occurred simultaneously during fall 2015. Tropical storm disturbances occurred during the sampling period, allowing evaluation of how meteorological disturbances altered litter interception. High wind speeds and intense rainfall from two tropical storms increased litter interception by introducing new woody debris which, in this study, stored more water than the pre-existing woody debris. After two extreme weather events, a third (Hurricane Hermine) did not increase woody debris (or litter interception), suggesting that the canopy pool of branches susceptible to breakage had been largely depleted. Needle and bark shedding had minor effects on litter interception. Results suggest that the release of reproductive materials and meteorological disturbances appear to be the major compositional drivers of litter interception beyond their obvious contribution to litter thickness.

KEY WORDS. Forest litter, rainfall interception, *Pinus elliottii*, phenology, tropical storm.

INTRODUCTION

The latest global inventory of hydrologic flux rates found that >60% of terrestrial precipitation is evaporated (Rodell et al., 2015). Some of the largest regional evaporative returns of terrestrial precipitation are found in vegetated landscapes – most notably in forested areas where annual precipitation reduction from the canopy, alone, can reach 50% (Carlyle-Moses and Gash, 2011). This direct feedback of moisture to the atmosphere from forests' interception and evaporation of precipitation supports continental rainfall (van der Ent et al., 2014) and regulates storm water runoff responses (McPherson et al., 2016). When interception of rainfall by the forest floor (its understory vegetation and litter layers) is added to canopy interception, total intercepted rainfall becomes substantial (Tsiko et al., 2012), even double that of the more commonly estimated canopy component (Gerrits et al., 2007; 2010). Although forest floor rainfall interception has been long-recognized (e.g., Helvey, 1964; Helvey and Patric, 1965), it has received considerably less attention than canopy rainfall interception (Gerrits and Savenije, 2011). The litter layer's contribution to forest interception, in particular, has been understudied compared to understory vegetation in recent decades (Black and Kelliher, 1989; Wedler et al., 1996; Suzuki et al., 2007; Allen et al., 2016).

Litter layers develop across a diversity of ecosystems, forming a barrier—dynamic in both thickness and composition—between the mineral soil and any meteoric water supply. Meteoric water may arrive to the forest litter (i.e. net rainfall) directly through canopy gaps, as throughfall (droplets contacting the canopy that drip or splash to the surface), or as stemflow (rain water funneled to the stem base). The degree of reduction in these "net" rainfall fluxes during their infiltration through the litter layer has been found to vary mostly in response to litter thickness and throughfall intensity (Sato et al., 2004; Guevara-Escobar et al., 2007; Gerrits and Savenije, 2011). Litter layer structures also drastically alter the timing and intensity of litter infiltration fluxes to the soil ecosystem (Dunkerley, 2015). Since measurement of litter storage, drainage and evaporation processes *in situ* is difficult, a range of laboratory (Helvey, 1964; Putuhena and Cordery, 1996; Guevara-Escobar et al., 2007) and only a few field methods (Gerrits et al., 2007; Acharya et al., 2017) have been developed for litter interception monitoring. These efforts have resulted in significant advancements in our understanding of litter interception processes, yet little research has focused on characterizing spatiotemporal variability in litter compositional influences. Few studies have, for example, measured spatial variability in litter to scale litter water storage or evaporation (Putuhena and Cordery, 1996; Wedler et al., 1996; Gerrits et al., 2010) or assessed whether temporal shifts in litter composition significantly influence interception processes (Gerrits et al., 2010; Brantley et al., 2014).

Research on seasonal variability of litter interception attributable to compositional changes has exclusively focused on leaf senescence and subsequent breakdown in deciduous hardwood stands (Gerrits et al., 2010; Brantley et al., 2014). However, there are a multitude of other processes that may alter litter composition enough to significantly influence the interception of net rainfall. No work known to the authors, for example, has focused on the impact of different biomass materials related to phenological phases in coniferous stands, like needles, megastrobili (cones), bark, or branches (Dougherty et al., 1994)—each differing in their water storage capability—on litter rainfall interception. As the only study on rainfall interception by reproductive materials (like fruiting heads) shed from forest canopies has shown them capable of storing >500% of their oven-dried weight in water (Levia et al., 2004), the dropping of cones to the litter of coniferous forests is especially likely to increase litter interception. Coniferous forest litter may also receive leaf senescence materials from deciduous vines, or liana (Leicht-Young et al., 2010). In addition to phenological phases, meteorological disturbances (like hurricanes and ice storms) can introduce significant amounts of woody and foliar debris to the litter layer (Scatena et al., 1996; Vanderwel et al., 2013), yet the authors are unaware of any work examining how these disturbance-related alterations to litter composition affect litter interception. The aim of this study is, therefore, to provide the first assessment of hypotheses regarding the influence of phenology and meteorological disturbances (tropical storms) over coniferous litter composition and related litter rainfall interception.

We hypothesized that both (1) phenologically-driven inputs of material (particularly cone production) and (2) tropical storm-related inputs of aboveground biomass will produce significant momentary increases in litter water storage, ultimately increasing total litter interception. These hypotheses were tested by analysis of weekly litter compositional elements (needles, woody debris, bark, cones, and broadleaves) and water storage measurements (per litter element) alongside hydrometeorological observations collected over one year in a *Pinus elliottii* stand with deciduous liana cover (*Berchemia scandens* and *Vitis* spp.). Lastly, a model of litter rainfall interception was generated that considered the observed water storage dynamics of each litter element over the study period.

MATERIALS AND METHODS

Study site

Our study was conducted at the Oliver Bridge Wildlife Management Area (OB-WMA) located along the Ogeechee River in southeast Georgia, USA (32.4910 N, 81.5615 W; Figure 1). Monitoring equipment was installed in a stand composed of *Pinus elliottii* (Englem., slash pine) with some deciduous liana cover: *Berchemia scandens* ((Hill) K. Koch, rattan vine) and at least one *Vitis* species. These liana are common in pine stands (Shelton and Cain, 2002). Stand density was 1060 trees ha^{-1} and the stand is evenly aged. Thus, all trees were the same diameter at breast height (DBH), varying only ±5.4 cm (standard deviation) around the mean DBH of 21.8 cm. Site climate is humid subtropical with no distinct dry season (Köppen *Cfa*) and, according to the nearest long-term meteorological record (12.8 km away in Statesboro, Georgia), its mean annual (1925-2014) rainfall is 1170 mm year^{-1} (University of Georgia Weather Network, 2016). The dominant precipitation form is rainfall and it accounts for all precipitation observed during the study period. Mean minimum monthly temperatures stay above freezing all year (3.5 ºC low in January), snowfall is negligible (University of Georgia Weather Network, 2016). Mean minimum and maximum yearly temperatures are 12.4 ºC and 25.2 ºC, respectively, with the mean maximum monthly temperature reaching 33.4 ºC in July (University of Georgia Weather Network, 2016). Mean monthly rainfall is relatively even from September through May (60-100 mm month^{-1}), then increase to 110-150 mm month^{-1} for June, July, and August due to frequent convective thunderstorms (University of Georgia Weather Network, 2016). The average number of rainy days per annum over the historical record was 98 (University of Georgia Weather Network, 2016).

Hydrometeorological monitoring

Rainfall, throughfall, and in situ litter water storage measurements were taken during a 12-month study period, beginning 7 Sep 2015 and ending 12 Sep 2016. For rainfall and meteorological conditions controlling evaporation, a continuously recording meteorological station was situated in a clearing within the OB-WMA, immediately nearby the forest plot, and equipped with 3 tipping bucket gauges (TE-525MM, Texas Electronics, Dallas, TX, USA), a pyranometer (CMP6, Kipp & Zonen, Delft, The Netherlands), a 2-axis ultrasonic wind speed/direction sensor (WindSonic, Gill, Hampshire, UK), and an air temperature/relative humidity probe (HMP155, Vaisala, Vantaa, Finland). All meteorological station sensors were interfaced with a datalogger (CR1000, Campbell Scientific, Logan, UT, USA) to record observations at 5-minute intervals. Automated throughfall monitoring was performed using ten 3.048-m long and 10.16 cm diameter PVC troughs oriented at a moderate slope, with a 5.08 cm slot cut lengthwise for collection and drainage of throughfall to a Texas Electronics (Dallas, Texas, USA) TR-525I tipping bucket gauge, resulting in 1.65 m^2 of collection area. Tipping bucket gauges and their associated troughs were randomly placed within a 0.25 ha plot and recorded every 5 minutes by a CR1000 datalogger. All throughfall trough angles were measured with a digital clinometer to correct computations of trough area receiving throughfall. Trough and tipping bucket assemblies were field tested to ensure accuracy (± 5%) under storm conditions typical for the region (Van Stan et al., 2016a). 68 discrete storm events totaling 1528 mm occurred during the study period (Figure 2), where an event was defined as any rainfall >1 mm proceeded by a minimum inter-event time of 12 hours. Rarely did any storm event generate throughfall intensities that resulted in significant gauge undercatch. These few occurrences of extremely high throughfall intensity (as high as 10 mm in 5 minutes) occurred under tropical storm conditions—specifically during Tropical Storms Bonnie (29 May 2016), Colin (6 Jun 2016) and Hurricane Hermine (2 Sep 2016) (indicated in Figure 2). These meteorological disturbances not only brought substantial rainfall (195.3 mm, 69.8 mm, and 113.5 mm; Figure 2), but produced frequent 5-minute sustained wind gusts over 13 m s^{-1}, 15 m s^{-1}, and 17 m s^{-1} for Bonnie, Colin, and Hermine, respectively. Stemflow was ignored in this study as it represented <0.1% of rainfall in a nearby (28 km away) similar pine stand for 22 storms (data collection is ongoing). Stemflow so far has also never exceeded a funneling ratio of 0.8—meaning near-stem soils receive <80% of rainfall compared to the open (data not shown). Since stemflow is negligible, canopy rainfall interception was computed as the difference between rainfall and throughfall.

Litter sampling, sorting and water storage measurements

Litter samples were collected on a weekly basis with collection gaps occurring twice in the study period: (1) during the month of December 2015 and (2) for two weeks in the summer from 11-25 July 2016. A litter sampling event consisted of gathering 30 separate samples of 20 cm diameter areas to whatever depth the Oi horizon terminated (generally 5-15 cm). Sampling locations each week were chosen at random within the hectares of forest surrounding the monitoring site, and previous sampling locations were avoided. Care was taken to ensure, at least visually, that the randomly selected locations for litter sampling represented the overall litter composition that week. Because litter depth and composition varied between samplings, the oven-dried biomass of all samples collected during a single weekly sampling ranged from 230-690 g.

Immediately after sampling, the litter was manually sorted into its compositional elements (needles, woody debris, bark, cones, and broadleaves), total weight of each litter element was recorded, and then all litter elements were placed in a drying oven at 100 ºC for 72 h. Field water storage for each litter element was calculated as the difference between the oven-dried weight and the initial field weight (S_L [L]). (Conversion of volumetric water storage capacity to depth equivalent was done by dividing by the total area sampled each week (314.2 cm^2 x 30 locations = 9,426 cm^2)). After oven-dried litter elements were weighed, they were completely submerged in water for 96 h and weighed while saturated. The difference between each litter element's saturated weight and their oven-dried weight was their volumetric water storage capacity ($S_{L,max}$ [L]).

Total litter rainfall interception (I_L [L T^{-1}]) was computed as the summation of litter storage (S_L [L]) and evaporation (E_L [L T^{-1}]) as represented by the balance between throughfall (T_f [L T^{-1}]) and infiltration (F [L T^{-1}]):

$$(1)\ I_L = \frac{\partial S_L}{\partial t} + E_L = T_f - F$$

S_L of litter before a storm begins (t = 0) was determined by regression formulas relating field water storage to the days (D) since any previous storm exceeding weekly litter water storage capacity ($S_{L,max}$), with α and β being regression coefficients unique to each litter element determined from lab measurements per Bulcock and Jewitt (2012):

$$(2)\ S_L(t=0) = \alpha\,(D)^{-\beta}$$

The threshold of the litter storage "reservoir" ($S_{L,max}$) varied each week in accordance with the lab-derived water storage capacity. Water exceeding $S_{L,max}$ was assumed to enter the soil as F since the soils at the site are classified as Bladen fine sandy loam with high infiltration rates possible (National Resources Conservation Service-Web Soil Survey, 2017).

E_L (m s^{-1}) was the sum of within-storm and between-storm evaporation estimates. Within-storm E_L was determined per the Renner et al. (2016) formulation which stems from recent findings that, due to the thermodynamic limits of convection, vapor pressure deficit and wind speed (as is classically used to estimate potential evaporation: Brutsaert, 1982) are driven by land-atmosphere interactions with locally absorbed solar radiation (Kleidon and Renner, 2013a). This concept was successfully applied to assess hydrologic sensitivity to global climate change (Kleidon and Renner, 2013b), estimate global-scale annual average terrestrial evaporation (Kleidon et al., 2014), and estimate forest stand-scale potential evaporation (Renner et al., 2016). As rain water on the litter is stored on the same materials as in the canopy (leaves, branches, bark, etc) and wind speed is very low at the forest floor, we apply the Renner et al. (2016) formula to estimate E_L solely based on absorbed solar radiation (R_{sn}, W m^{-2}) and temperature data:

$$(3)\ \rho E_L = \frac{1}{\lambda}\frac{s}{s+\gamma}\frac{R_{sn}}{2}$$

where ρ is density of water (kg m^{-3}), λ is the latent heat of vaporization (J kg^{-1}), γ is the psychrometric constant (kPa C^{-1}), and s is the slope of the saturation vapor pressure curve (kPa C^{-1}) determined from air temperature (T in K) from Bohren and Albrecht (1998):

$$(4)\ s = 6.11 \cdot 5417 \cdot T^{-2} \cdot e^{19.83 - \frac{5417}{T}}$$

R_{sn} at the litter was computed from incident radiation (I_0, W m^{-2}) measured by the gap weather station multiplied by an estimate of albedo (a = 0.18) representative for *P. elliottii* forests (Gholz and Clark, 2002) after being reduced using a species-specific extinction coefficient (k = 0.35, Gholz et al., 1991) and site-specific Leaf Area Index (LAI = 5.7). The Beer-Lambert law was modified per Gholz et al. (1991) to include the fraction of canopy gap (F_o = 0.34) and cover (F_f = 0.66):

$$(5)\ R_{sn} = (1 - a)\, I_0(F_o + F_f e^{-k \cdot LAI})$$

Canopy gap fraction and LAI were determined using an LAI-2200TC plant canopy analyzer (LiCOR, Lincoln, NE, USA) where one of two wands was leveled in the open, logging each minute to correct manual measurements made by the second wand. Estimates of E_L between storms were determined using litter drying curves developed from field water storage measurements (as described earlier) plotted against days since rainfall.

Data analysis

Descriptive statistics were compiled for all hydrometeorological and litter compositional variables. Regressions were performed to generate drying curves for each litter element, and for testing correlation strength and significance between litter elements and water storage. All statistical work was accomplished in Statistica 12 (Statsoft, Tulsa, OK, USA).

RESULTS

Litter composition and elemental drying curves

Litter sampling resulted in the collection, sorting, and lab submersion testing of over 14.5 kg of oven-dried weight (Table 1). Total litter composition from all sampling events consisted primarily of needleleaves and cones – each representing just under a third of the total oven-dried biomass (Table 1). The remaining third of oven-dried litter biomass was composed mostly of bark flakes (18%) and woody debris (16%), leaving about 2% for broadleaves from the deciduous lianas (Table 1). Cones exhibited the greatest variation in oven-dried biomass (Table 1) since *P. elliottii* cone drop at our site was seasonally concentrated between October and March, whereafter cone biomass contributions from the canopy ceased (Figure 3). Needleaves within the litter also exhibited high variability in oven-dried biomass (Table 1), but this variability was observed throughout the study period (Figure 3). The greatest coefficient of variation (77%) in oven-dried biomass for any litter element was for broadleaves (Table 1). High variability in broadleaves' oven-dried biomass reflects leaf abscission from lianas in the fall of 2015 (exceeding 20 g), which eventually decayed to minimal proportions (<1 g) in the late summer (Figure 3). Contributions to the litter from bark flakes had the lowest variability compared to the mean oven-dried biomass (<25%; Table 1) and were the most temporally consistent, showing little-to-no seasonal trends (Figure 3). Although the range of oven-dried biomass observations for woody debris in the *P. elliottii* litter was smaller than observed for bark flakes, the standard deviation was larger (Table 1). The relatively larger standard deviation in oven-dried woody debris biomass in the litter can be, in part, explained by the large jump in woody debris in late May through June 2016 (Figure 3) after arrival of TS Bonnie and TS Colin (Figure 2).

Maximum time since saturation for all litter sampling events was 12 days, and neither the litter nor any litter element dried completely within that time (Figure 4). Nevertheless, all litter elements dried out relatively quickly within the first 3 or 4 days, then slowly thereafter depending on conditions driving evaporation (Figure 4). Equations for each regression shown in Figure 4 are provided in Table 2. Total litter water storage immediately after storms achieved just over 2 mm (Figure 4), and average $S_{L,max}$ throughout the study was 1.7 mm (Table 2). The greatest water storage immediately after rainfall was observed for broadleaves (just over 3 mL g^{-1}), but when this is converted to depth equivalent, the in situ, post-storm S_L and mean $S_{L,max}$ for broadleaves throughout the study were low (< 0.1 mm; Table 2 and Figure 4) due to its small biomass contribution (Table 1). Cones and woody debris stored 0.6 mm and 0.3 mm immediately after rainfall (Figure 4), yet accounted for more of the litter composition (Table 1) allowing for > 7 and 4 times larger average $S_{L,max}$ estimates than broadleaves, respectively (Table 2). Needleleaves and bark flakes generally stored the least water per oven-dried biomass after storms (~1 mL g^{-1}), but since needleaves composed a large proportion of the litter oven-dried biomass (Table 1), they were able to average 0.5 mm of $S_{L,max}$ (Table 2) and sometimes exceed 0.6 mm of storage immediately after a storm (Figure 4). For all litter elements, the regression α coefficients derived from field water content data (column 2 of Table 2) are smaller than the lab-derived $S_{L,max}$ (column 3 of Table 2), indicating that saturation via submersion achieved greater water storage than field conditions allowed and/or that the litter lost water within the ~24 h between field saturation and sampling.

Effects of phenology and meteorological disturbance on litter water storage capacity

The percentage representation of $S_{L,max}$ by different litter elements (Figure 5a) and the magnitude of $S_{L,max}$ (Figure 5b) varied markedly throughout the study period. Values of $S_{L,max}$

ranged from 0.8 mm in early April to a maximum that was 4 times greater than the minimum (3.2 mm) in mid-October (Figure 5b). Maximum $S_{L,max}$ closely corresponded to a maximum in cone biomass (Figure 3) and the cones' proportion of $S_{L,max}$ (Figure 5a). Broadleaf inputs to the litter from the deciduous lianas also briefly, but measurably, contributed to the elevated $S_{L,max}$ values from September through November 2015—during the same time as cone drop (Figures 3 and 5a). Although small magnitudes were measured in some weeks, $S_{L,max}$ rarely fell below 1 mm (Figure 5b). In fact, 1 mm marks the 10 percentile boundary and the interquartile range of $S_{L,max}$ is 1.2 – 2.1 mm. The early April minimum in $S_{L,max}$ occurred when overall litter biomass was low (Figure 3) and the dominant contribution to $S_{L,max}$ (~40%) was from needleaves (Figure 5a).

Soon after the measurement of minimum $S_{L,max}$ in April, meteorological disturbances (TS Colin and Bonnie) supplied the litter with fresh woody debris. This woody debris increased woody debris contributions to $S_{L,max}$ by 10% compared to all weeks previous (~25% versus 15%: Figure 5a). The highest woody debris contribution to $S_{L,max}$ was measured at nearly 30% shortly after TS Colin during the month of June (Figures 2 and 5a). The result of this supply of fresh woody debris to the litter was that $S_{L,max}$ increased by 40-50% of its magnitude during the preceding weeks (Figure 5). However, it is interesting to note that trends in $S_{L,max}$ for woody debris (Figure 5b) corresponds well with trends in its oven-dried biomass (Figure 3) for the entire study period.

Univariate regressions were performed to assess the strength of relationships between individual litter elements' oven-dried biomass and $S_{L,max}$ during times where these litter elements appeared to drive $S_{L,max}$. A significant correlation was only found for oven-dried cone biomass during the cone drop period: about 12 weeks after the start of the study on 7-Sep-2015 (Figure 6). Oven-dried cone biomass exerted a strong positive linear influence over $S_{L,max}$ until the spring of 2016 (Figure 6). After March 2016 no significant correlation could be found between any individual litter element and $S_{L,max}$.

Total canopy rainfall partitioning and litter rainfall interception

The majority of rainfall events during the study period ranged in magnitude between 4 and 40 mm (Table 3), with only eight storms exceeding 50 mm (Figure 2). Four of these eight storms exceeded 100 mm (02-Feb-2016, TS Bonnie, TS Colin, and Hurricane Hermine; Figure

2), with TS Bonnie producing the greatest storm magnitude measured during the study year (195.3 mm; Table 3). Although significant 5-minute rainfall intensities were observed (as mentioned in Section 2.2), hourly rainfall intensity rarely exceeded 1 mm h^{-1}, maximizing around 8 mm h^{-1} (Table 3). Throughfall represented 64.5% of rainfall per storm on average, with an interquartile range between 40-81% of rainfall (Table 3). These relative throughfall proportions corresponded to an average throughfall receipt at the litter of 23 mm $storm^{-1}$ (Table 3). The litter intercepted a significant quantity of throughfall, reducing throughfall amounts to the soil surface by 23% on average (Table 3). Modelled litter interception exceeding 1/3 of throughfall was relatively common, being within the interquartile range of 68 measured storms (Table 3). During large magnitude storms with high rainfall intensity and low radiation receipt (due to dense cloud cover), litter interception was minimized—i.e., the minimum 0.6% reduction in throughfall was observed during TS Bonnie (Table 3). Smaller magnitude, low intensity storms resulted in the litter being able to store and evaporate all throughfall (Table 3). The largest storm magnitude where 100% of throughfall was intercepted by the *P. elliottii* litter at this site was 3.6 mm at an intensity of 0.72 mm h^{-1}.

DISCUSSION

Litter interception is generally neglected by past forest ecohydrological research (Gerrits and Savenije. 2011), yet our findings align well with past work showing large litter water storage capacities ($S_{L,max}$ = 0.8–3.2 mm) that can consistently and significantly reduce throughfall (9–46%) reaching the soil surface (Table 3). Throughfall reductions of this magnitude have been reported in other forests: 22% for temperate *Fagus sylvatica* (L., European beech) in Luxembourg (Gerrits et al., 2010), 20% for *Brachystegia spiciformis* (Benth., Msasa) savannah in Zimbabwe (Tsiko et al., 2012), 16-18% for maritime *Picea abies* (L., Norway spruce) forests in Scotland (Miller et al., 1990), and 8-12% in Himilayan forests (Pathak et al., 1985). The annual range in $S_{L,max}$ observed for *P. elliottii* litter in this study (Table 2; Figure 5) spans the range of observations from past research. For instance, litter $S_{L,max}$ from the broadleaved *Lithocarpus edulis* (Makino, Japanese stone oak) and *Asperulo-Fagetum* forests maximized around 3 mm (Thamm and Widmoser, 1995; Sato et al., 2004), yet needleleaf litter from *Pinus sylvestris* (L., Scots pine) and *Cryptomeria japonica* (L.f., Japanese cedar) typically stored less than 1.7 mm (Walsh and Voigt, 1977; Sato et al., 2004). Diminished water storage for needleleaves compared to broadleaves was also observed between *Cedrus atlantica* (Endl., blue cedar) and European beech, with cedar litter storing half as much water as beech (Gerrits, 2010). Our results agree with these findings as water storage per oven-dried mass was greater for broadleaves than for needleleaves (3 mL g^{-1} versus 1 mL g^{-1}). Despite this difference in water storage per dry mass needleleaves stored more total water (Table 2 and Figure 4) as a result of needleleaf contributions from the *P. elliottii* canopy exceeding the liana broadleaf contributions (Table 1; Figure 3).

The timing of leaf senescence from broadleaved lianas hosted by *P. elliottii* coincides with the tree canopies' cone drop (Figure 5). Since liana broadleaves can store double the amount of water per dry mass compared to most other litter elements (~3 mL g^{-1} for broadleaves versus 1 mL g^{-1} for needleaves or bark flakes), they likely enhance the elevated $S_{L,max}$ effect produced by the contribution of new cones (Figure 6). This intersection of liana and *P. elliottii* phenophases resulting in both significant broadleaf and cone biomass contributions is not unusual. The phenophase where *P. elliottii* drops cones typically occurs every 3-4 years (after nearly a year of cone development) for mature stands (Dougherty et al., 1994), typically beginning in October and ending as late as March or April for the southeastern US (Moore and Wilson, 2006). Meanwhile, the lianas (*B. scandens* and *Vitis* spp.) senesce their leaves each year, beginning in late October to early November (per observations at site). Many previous studies have discussed reasons undergirding the significant water storage of broadleaves (e.g., Walsh and Voigt, 1977; Sato et al., 2004; Gerrits, 2010; Gerrits and Savenije, 2011), but to the knowledge of the authors, only two studies have examined the role of any type of reproductive materials in enhancing $S_{L,max}$ (Levia et al., 2004) and litter interception (Levia et al., 2005)—and these studies focus on one species, *Liquidambar styraciflua* L. (sweetgum). These two studies found that empty fruiting heads with complex morphological structures (numerous openings, ledges, and roughly-textured surfaces) and a large surface area are not only capable of storing nearly 5 mm of rainfall (Levia et al., 2004), but can evaporate that storage at rates similar to those found for saturated canopies under favorable meteorological conditions (Levia et al., 2005). Storage by *P. elliottii* cones in this study was not as high as observed for *L. styraciflua* fruiting heads, but both were capable of storing as much water as all the leaf litter elements (Figure 5; Levia et al., 2004). As such, we echo the call from Levia et al. (2004; 2005) that future work is needed on throughfall interception from reproductive materials in other forest systems with morphologically complex reproductive materials. This includes a vast array of tree species around the globe: *Magnolia*, *Platanus*, *Liriodendron*, *Picea*, etc. Perhaps the historical neglect of litter rainfall interception by forest ecohydrological studies is, in part, a result of past litter interception studies' focusing on the more temporally consistent (but lower water storage) elements (like leaves).

Average $S_{L,max}$ for *P. elliottii* bark flakes was low (0.27 mm; Table 2) compared to bark water storage capacities measured in the lab using intact bark sampled from the stems of rough, thick-barked tree species, being 1-2.7 mm (Levia and Herwitz, 2005; Van Stan et al., 2016b). Water storage experiments performed on the bark of in situ *P. elliottii* trunks by others in nearby North-Central Florida (USA) were closer to our estimate (0.5 mm), but still nearly double the magnitude of bark flakes sampled from the litter at our study site (Liu, 1998). It may be that the flakes from bark shedding are much thinner than the bark on tree stems, with bark flakes collected from the litter being only 2-10 mm thick compared to the 15-25 mm bark thicknesses measured on tree stems by a Haglöf Barktax (Stockholm, Sweden) bark thickness gauge. As the lowest $S_{L,max}$ estimate for stem bark is double that of bark flakes in the litter at our site, the difference in thickness does not entirely reconcile the two values. Recent work indicates that significant inter- and intraspecies variability in "interception surface" morphology can alter the ability of bark surfaces to retain water (Ilek and Kucza, 2014). *Pinus* species shed "flakes" of bark during trunk growth (in a process called periderm shedding) which produces thin, flat bark flakes. It is likely that the flatter interception surface morphology of these bark flakes compared to the rougher trunk bark reduces $S_{L,max}$ by preventing water retention on the surface of this litter element.

Few studies examine the role of woody debris in the storage and evaporation of water (Unsworth et al., 2004; Sexton and Harmon, 2009), and only one quantifies the reduction of throughfall by woody debris—specifically logs (Sexton and Harmon, 2009). The absorption and evaporation of throughfall by logs was 47-70% for Oregon forests (Sexton and Harmon, 2009). This finding indicates that litter interception by woody debris at our site was likely greater as we did not measure water dynamics for whole logs, and these are observable at the site. However, woody debris in our *P. elliottii* stand after meteorological disturbances appear to more markedly affect contributions to $S_{L,max}$ than previous pulses of woody debris inputs (Figure 5). This may be a result of a change in the quality of the woody debris. Winds and heavy rainfall from TS Bonnie and TS Colin resulted in a sudden increase in fresh branches to the litter layer. It is likely that the relatively intact bark on fresh branches stores more water compared to shed bark flakes (see discussion point above). In addition, the clumps of fresh needles attached to these branches were not separated from the freshly deposited woody debris to keep litter elements as intact as possible, and these have been shown to efficiently intercept and store rainfall in the canopy by others (Keim et al., 2006). It is probable that needles attached to fresh branches similarly store significant water at the forest floor. A third quality of the freshly deposited branch materials that may increase water storage include the broken ends of the branches, which may permit significant water absorbance into internal structures. No significant woody debris drop after Hurricane Hermine (Figure 5) suggests that the "pool" of canopy materials to be contributed to the litter layer was depleted by the previous two storms.

Although $S_{L,max}$ varied weekly with litter composition in our litter rainfall interception estimates, some parameters in the litter interception process did not. Specifically, infiltration processes are expected to change with litter composition, as was found by sprinkler experiments (Guevara-Escobar et al., 2007). This could have allowed the litter to retain more water in some instances (perhaps due to water pooling in the proximal area of pine cones' ovuliferous scales) and less water in other cases (perhaps water drains more rapidly along the hydrophobic cutin layers of a needleaf-dominated litter: Dufrenoy, 1918; Hansel et al., 2008). Canopy traits controlling receipt of radiation were also held constant, yet the LAI and fraction of canopy gap (F_o) will change with phenological shifts in *P. elliottii* stands (Gholz et al., 1991; Gholz and Clark, 2002) and, likely, after meteorological disturbance due to downed branches. LAI variability also affects throughfall (Dietz et al., 2006), yet the throughfall was measured directly over time (i.e., across LAI conditions) in this study.

CONCLUSIONS

Our findings from a *Pinus elliottii* stand in the southeastern US not only show substantial rainfall interception by the litter layer (2-32%), but indicate that the effects of different biomass materials related to phenological activity and meteorological disturbances on the temporal variability of litter composition can significantly alter litter interception processes. The magnitude of litter rainfall interception observed in this study was similar to the few previous estimates in other forests, but exceeded those that solely considered the water storage and evaporation of individual litter elements. Pine cones (and likely reproductive materials from other tree species as well) were capable of storing significant quantities of water compared to other litter elements. In forests where multiple phenophases from different canopy plants coincide, the substantial biomass contributions may result in a seasonal spike of litter rainfall interception. A spike in litter interception at our site occurred during the concurrent pine cone release and liana leaf senescence that tripled litter water storage (from ~1 mm to 3 mm). Per these findings and the current underrepresentation of litter rainfall interception, we recommend future forest ecohydrological research measure its magnitude, underlying processes and temporal dynamics, as failure to do so may introduce significant uncertainties into soil hydrological (and related biogeochemical) processes.

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Figure captions

Figure 1. Site location within the Oliver Bridge Wildlife Management Area (WMA) in southeastern Georgia (USA) and orientation of the 10 trough-based automated throughfall gauges.

Figure 2. Daily rainfall amount throughout the study period with the tropical storms (TS) and hurricane disturbances highlighted.

Figure 3. Weekly oven-dried biomass for all litter compositional elements during the 2015-2016 study period. Lines with asterisks indicate when TS Bonnie and then TS Colin occurred.

Figure 4. Scatterplots showing field water content of litter elements with increasing days (*D*) since the last storm that exceeded weekly litter water storage capacity. Regression equations in Table 2.

Figure 5. Total weekly litter water storage capacity ($S_{L,max}$) plotted atop (a) the proportion (%) each litter element contributed as percentage and (b) the actual depth equivalent of each litter element.

Figure 6. During the ~3 months long period of cone drop from *Pinus elliottii* canopies, total weekly litter water storage capacity ($S_{L,max}$) significantly and positively correlated with oven-dried cone biomass.

Tables

Table 1. Total oven-dried biomass (g m^{-2} ground area) for all compositional elements and full litter samples across the study period alongside descriptive statistics (where CV indicates coefficient of variation).

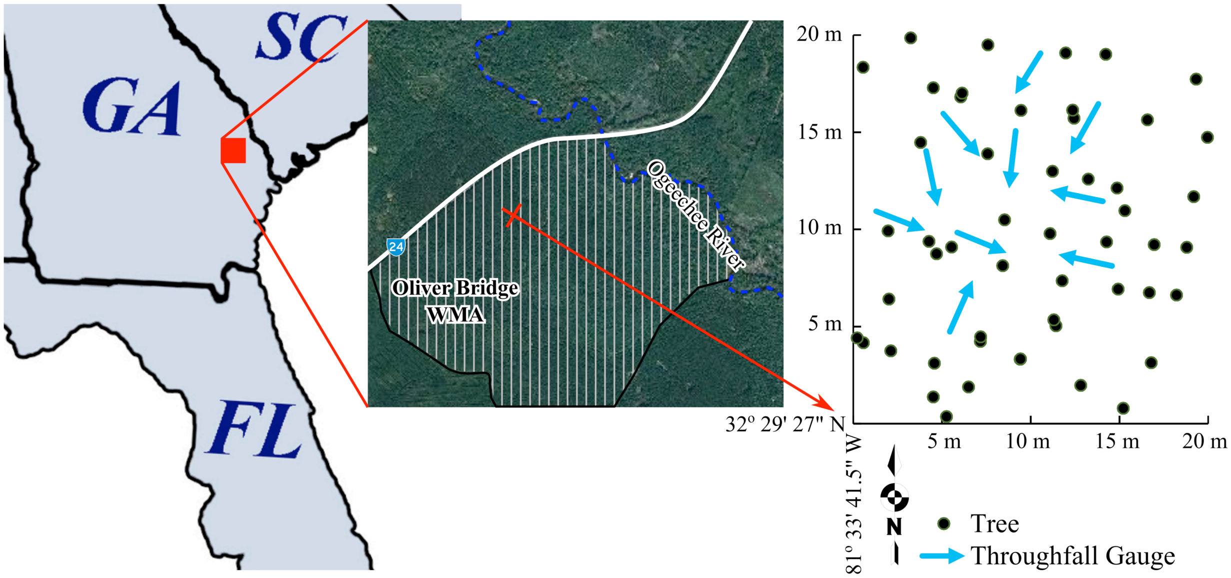
			Percentile			
Element	Mean	CV	25%	75%	Min	Max
Cones	116.9	0.50	80.3	148.2	20.4	288.8
Needleleaves	115.0	0.37	88.1	143.2	42.3	251.5
Broadleaves	6.6	0.81	3.5	8.1	0.8	21.6
Wood	56.9	0.33	42.5	73.3	24.2	88.7
Bark	64.8	0.25	55.6	75.5	20.3	96.1
Litter (all)	360.1	0.27	291.7	404.2	242.2	729.9

Table 2. Drying curve regression equations for determination of pre-storm field water storage (S_L [mm]) from days (D) since the last storm exceeding weekly litter water storage capacity ($S_{L,max}$) and mean $S_{L,max}$ for all litter compositional elements derived from laboratory experiments. Data plotted in Figure 4.

Element	Drying curve equation	Mean (SD) $S_{L,max}$ (mm)
Cones	$S_L = 0.512\ (D)^{-0.7362}$	0.57 (0.44)
Needleleaves	$S_L = 0.420\ (D)^{-0.5449}$	0.51 (0.16)
Broadleaves	$S_L = 0.061\ (D)^{-1.0103}$	0.07 (0.05)
Wood	$S_L = 0.229\ (D)^{-0.6844}$	0.30 (0.13)
Bark	$S_L = 0.190\ (D)^{-0.6128}$	0.27 (0.06)
Litter (all)	$S_L = 1.607\ (D)^{-0.7362}$	1.73 (0.65)

Table 3. Descriptive statistical summary of event-based rainfall, throughfall, and litter interception (sum of storage and evaporation components) during the 2015-2016 study period.

			Percentile			
Variable	Mean	SD	25%	75%	Min	Max
Rainfall (R)						
Amount (mm)	28.8	37.7	4.6	36.9	1.0	195.3
Intensity (mm h^{-1})	0.82	0.95	0.27	1.02	0.05	8.14
Throughfall (T_f)						
Amount (mm)	23.1	32.8	1.8	30.0	0.4	168.2
T_f:R (%)	64.5	17.9	40.2	81.3	13.1	87.7
Canopy interception (I_c)						
Amount (mm)	5.6	5.0	2.7	6.9	0.6	27.0
I_c:R (%)	35.5	18.0	18.7	59.8	12.3	86.9
Litter interception (I_L)						
Amount (mm)	5.3	6.5	0.2	9.8	0.1	16.7
I_L:T_f (%)	23.3	24.0	6.4	43.2	0.6	100.0
I_L: R (%)	17.8	17.2	1.9	31.8	0.1	56.6



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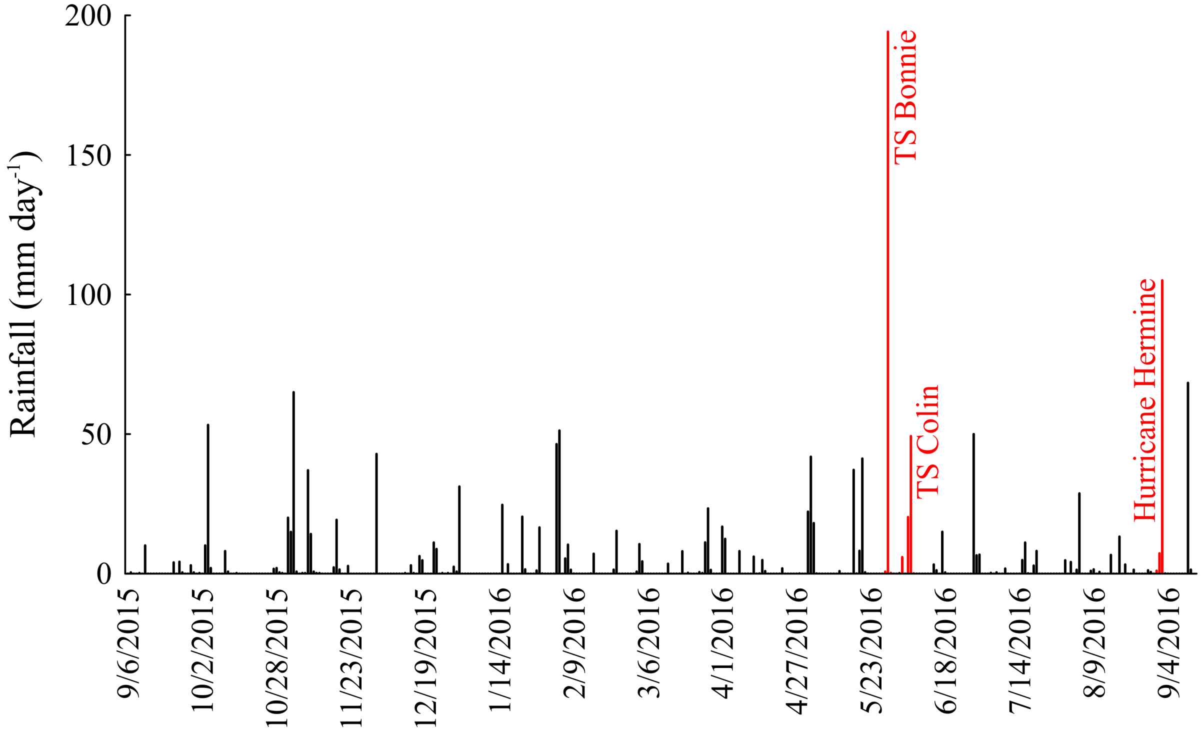

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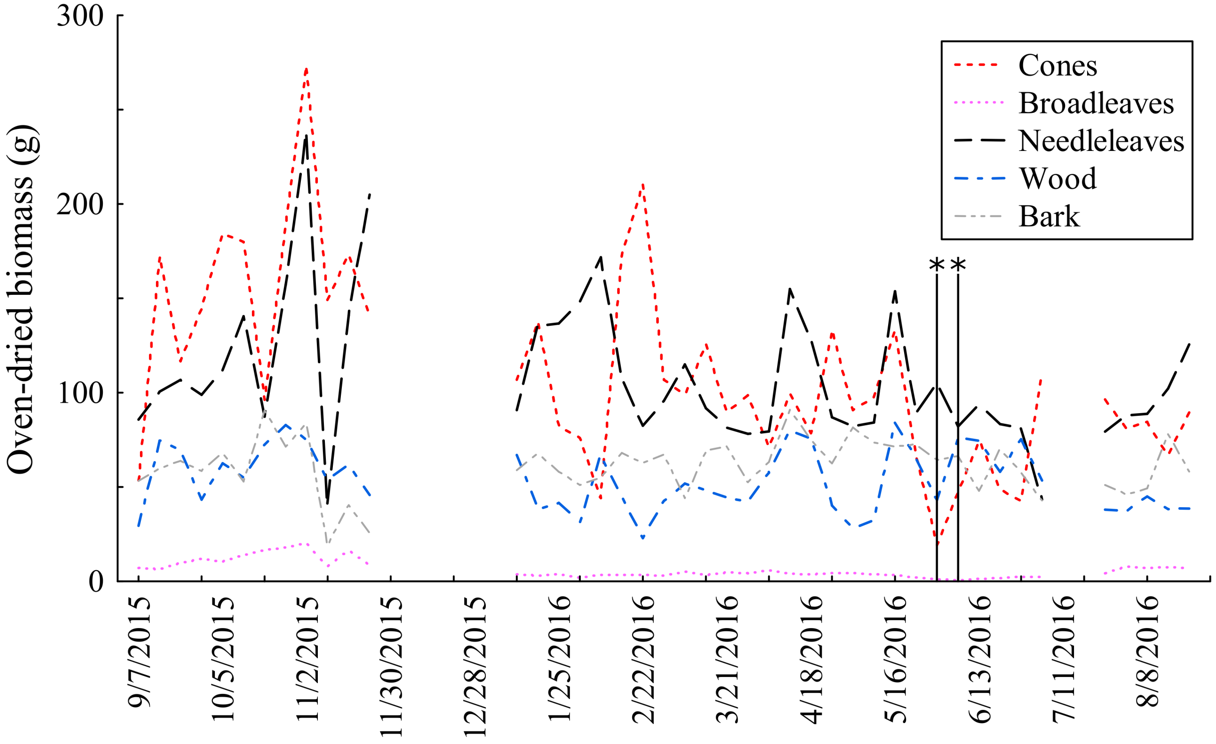

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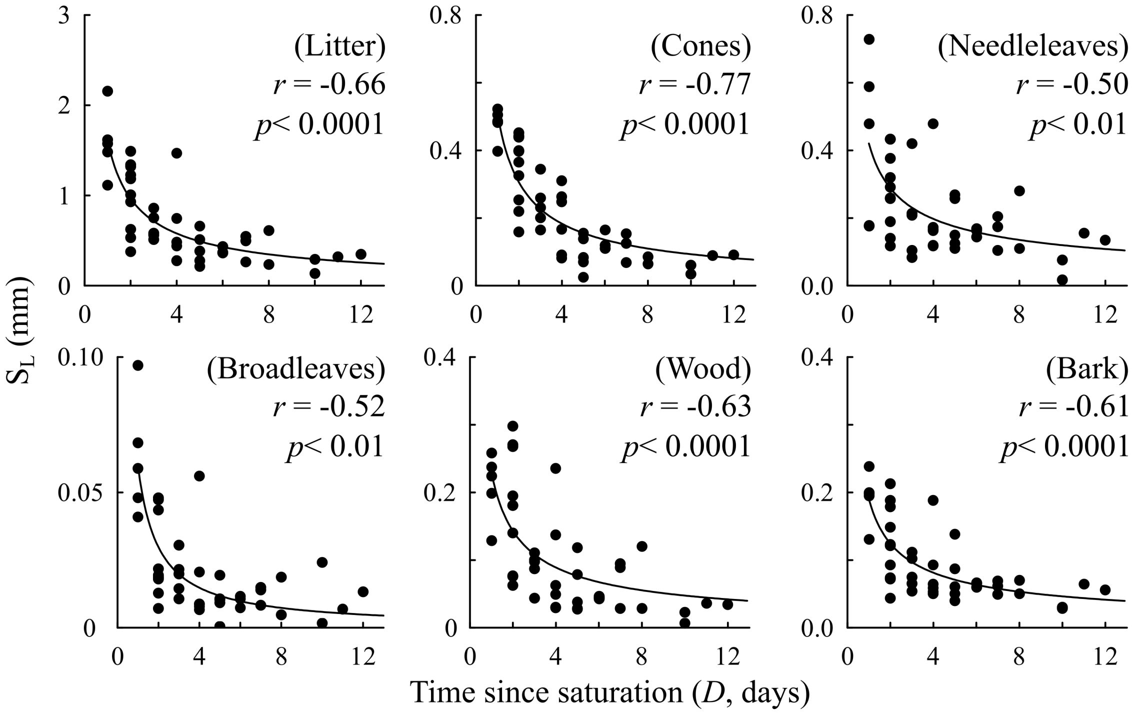
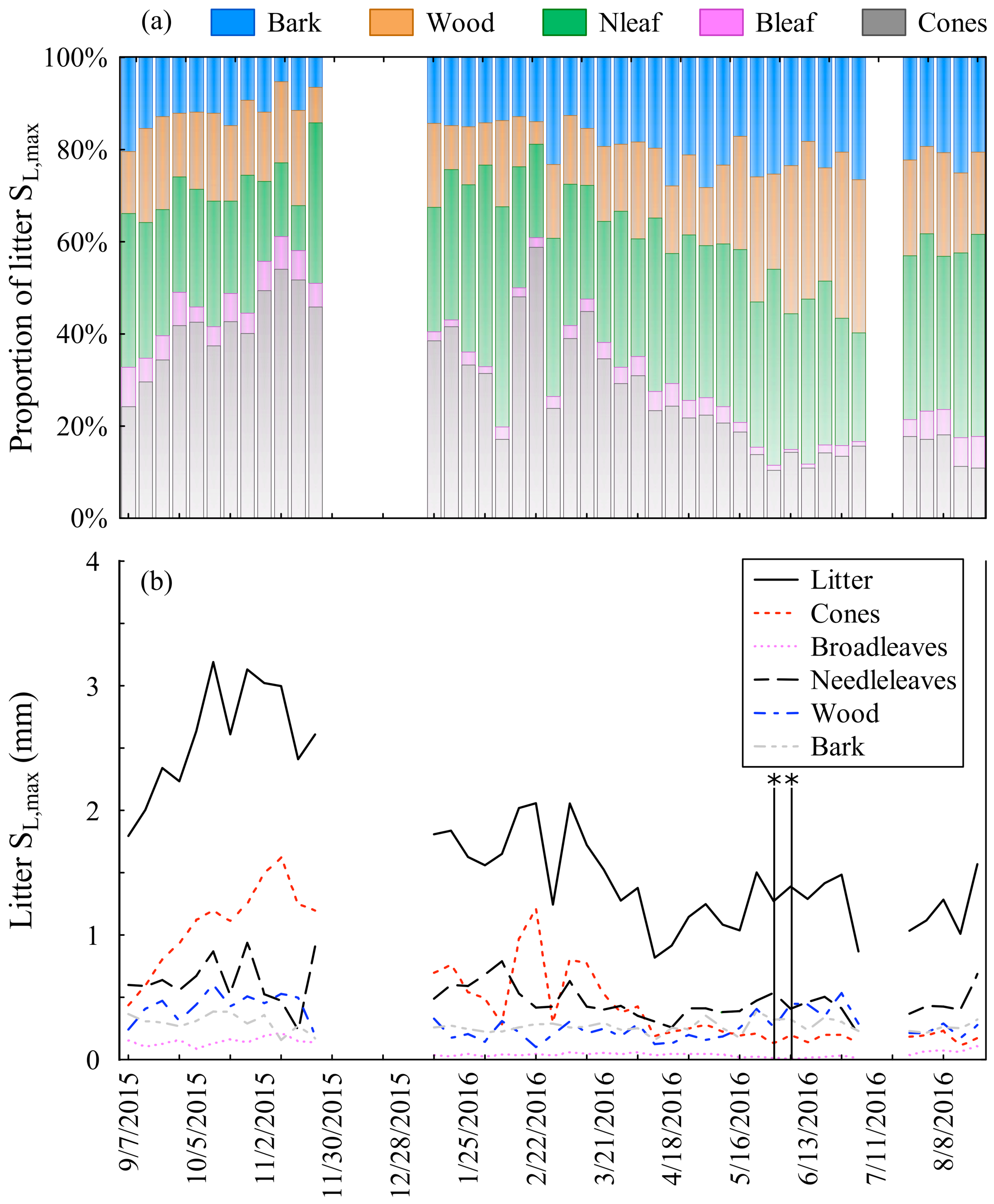


Figure 4. Scatterplots showing field water content (S_L) of litter elements with increasing days (D) since saturation (i.e., the last storm that exceeded weekly litter water storage capacity). Regression equations in Table 2.



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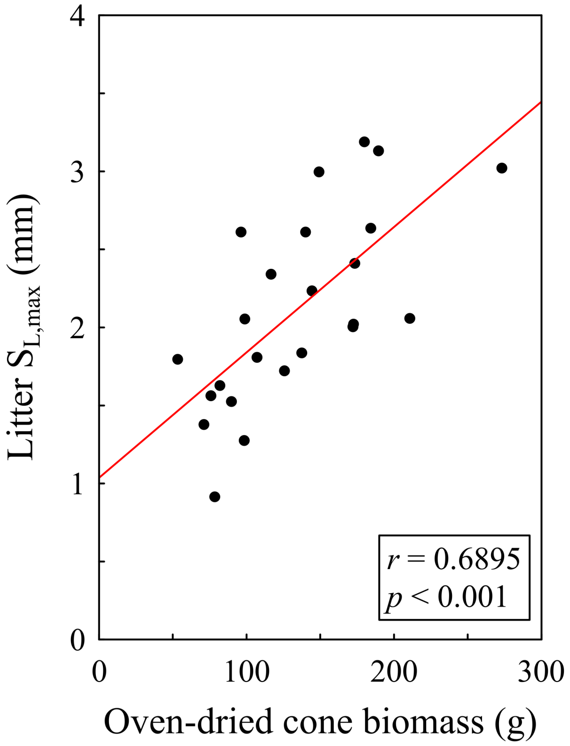

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