

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

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

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8  
9 **Abstract**

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

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

## 30 INTRODUCTION

31 The latest global inventory of hydrologic flux rates found that >60% of terrestrial  
32 precipitation is evaporated (Rodell et al., 2015). Some of the largest regional evaporative returns  
33 of terrestrial precipitation are found in vegetated landscapes – most notably in forested areas  
34 where annual precipitation reduction from the canopy, alone, can reach 50% (Carlyle-Moses and  
35 Gash, 2011). This direct feedback of moisture to the atmosphere from forests' interception and  
36 evaporation of precipitation supports continental rainfall (van der Ent et al., 2014) and regulates  
37 storm water runoff responses (McPherson et al., 2016). When interception of rainfall by the  
38 forest floor (its understory vegetation and litter layers) is added to canopy interception, total  
39 intercepted rainfall becomes substantial (Tsiko et al., 2012), even double that of the more  
40 commonly estimated canopy component (Gerrits et al., 2007; 2010). Although forest floor  
41 rainfall interception has been long-recognized (e.g., Helvey, 1964; Helvey and Patric, 1965), it  
42 has received considerably less attention than canopy rainfall interception (Gerrits and Savenije,  
43 2011). The litter layer's contribution to forest interception, in particular, has been understudied  
44 compared to understory vegetation in recent decades (Black and Kelliher, 1989; Wedler et al.,  
45 1996; Suzuki et al., 2007; Allen et al., 2016).

46 Litter layers develop across a diversity of ecosystems, forming a barrier—dynamic in  
47 both thickness and composition—between the mineral soil and any meteoric water supply.  
48 Meteoric water may arrive to the forest litter (i.e. net rainfall) directly through canopy gaps, as  
49 throughfall (droplets contacting the canopy that drip or splash to the surface), or as stemflow  
50 (rain water funneled to the stem base). The degree of reduction in these “net” rainfall fluxes  
51 during their infiltration through the litter layer has been found to vary mostly in response to litter  
52 thickness and throughfall intensity (Sato et al., 2004; Guevara-Escobar et al., 2007; Gerrits and  
53 Savenije, 2011). Litter layer structures also drastically alter the timing and intensity of litter  
54 infiltration fluxes to the soil ecosystem (Dunkerley, 2015). Since measurement of litter storage,  
55 drainage and evaporation processes *in situ* is difficult, a range of laboratory (Helvey, 1964;  
56 Putuhena and Cordery, 1996; Guevara-Escobar et al., 2007) and only a few field methods  
57 (Gerrits et al., 2007; Acharya et al., 2017) have been developed for litter interception monitoring.  
58 These efforts have resulted in significant advancements in our understanding of litter interception  
59 processes, yet little research has focused on characterizing spatiotemporal variability in litter

60 compositional influences. Few studies have, for example, measured spatial variability in litter to  
61 scale litter water storage or evaporation (Putuhena and Cordery, 1996; Wedler et al., 1996;  
62 Gerrits et al., 2010) or assessed whether temporal shifts in litter composition significantly  
63 influence interception processes (Gerrits et al., 2010; Brantley et al., 2014).

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

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

90 rainfall interception was generated that considered the observed water storage dynamics of each  
91 litter element over the study period.

## 92 **MATERIALS AND METHODS**

### 93 *Study site*

94 Our study was conducted at the Oliver Bridge Wildlife Management Area (OB-WMA)  
95 located along the Ogeechee River in southeast Georgia, USA (32.4910 N, 81.5615 W; Figure 1).  
96 Monitoring equipment was installed in a stand composed of *Pinus elliottii* (Englem., slash pine)  
97 with some deciduous liana cover: *Berchemia scandens* ((Hill) K. Koch, rattan vine) and at least  
98 one *Vitis* species. These liana are common in pine stands (Shelton and Cain, 2002). Stand density  
99 was 1060 trees ha<sup>-1</sup> and the stand is evenly aged. Thus, all trees were the same diameter at breast  
100 height (DBH), varying only  $\pm 5.4$  cm (standard deviation) around the mean DBH of 21.8 cm. Site  
101 climate is humid subtropical with no distinct dry season (Köppen *Cfa*) and, according to the  
102 nearest long-term meteorological record (12.8 km away in Statesboro, Georgia), its mean annual  
103 (1925-2014) rainfall is 1170 mm year<sup>-1</sup> (University of Georgia Weather Network, 2016). The  
104 dominant precipitation form is rainfall and it accounts for all precipitation observed during the  
105 study period. Mean minimum monthly temperatures stay above freezing all year (3.5 °C low in  
106 January), snowfall is negligible (University of Georgia Weather Network, 2016). Mean  
107 minimum and maximum yearly temperatures are 12.4 °C and 25.2 °C, respectively, with the  
108 mean maximum monthly temperature reaching 33.4 °C in July (University of Georgia Weather  
109 Network, 2016). Mean monthly rainfall is relatively even from September through May (60-100  
110 mm month<sup>-1</sup>), then increase to 110-150 mm month<sup>-1</sup> for June, July, and August due to frequent  
111 convective thunderstorms (University of Georgia Weather Network, 2016). The average number  
112 of rainy days per annum over the historical record was 98 (University of Georgia Weather  
113 Network, 2016).

### 114 *Hydrometeorological monitoring*

115 Rainfall, throughfall, and in situ litter water storage measurements were taken during a  
116 12-month study period, beginning 7 Sep 2015 and ending 12 Sep 2016. For rainfall and  
117 meteorological conditions controlling evaporation, a continuously recording meteorological  
118 station was situated in a clearing within the OB-WMA, immediately nearby the forest plot, and

119 equipped with 3 tipping bucket gauges (TE-525MM, Texas Electronics, Dallas, TX, USA), a  
120 pyranometer (CMP6, Kipp & Zonen, Delft, The Netherlands), a 2-axis ultrasonic wind  
121 speed/direction sensor (WindSonic, Gill, Hampshire, UK), and an air temperature/relative  
122 humidity probe (HMP155, Vaisala, Vantaa, Finland). All meteorological station sensors were  
123 interfaced with a datalogger (CR1000, Campbell Scientific, Logan, UT, USA) to record  
124 observations at 5-minute intervals. Automated throughfall monitoring was performed using ten  
125 3.048-m long and 10.16 cm diameter PVC troughs oriented at a moderate slope, with a 5.08 cm  
126 slot cut lengthwise for collection and drainage of throughfall to a Texas Electronics (Dallas,  
127 Texas, USA) TR-525I tipping bucket gauge, resulting in 1.65 m<sup>2</sup> of collection area. Tipping  
128 bucket gauges and their associated troughs were randomly placed within a 0.25 ha plot and  
129 recorded every 5 minutes by a CR1000 datalogger. All throughfall trough angles were measured  
130 with a digital clinometer to correct computations of trough area receiving throughfall. Trough  
131 and tipping bucket assemblies were field tested to ensure accuracy ( $\pm 5\%$ ) under storm  
132 conditions typical for the region (Van Stan et al., 2016a). 68 discrete storm events totaling 1528  
133 mm occurred during the study period (Figure 2), where an event was defined as any rainfall >1  
134 mm preceded by a minimum inter-event time of 12 hours. Rarely did any storm event generate  
135 throughfall intensities that resulted in significant gauge undercatch. These few occurrences of  
136 extremely high throughfall intensity (as high as 10 mm in 5 minutes) occurred under tropical  
137 storm conditions—specifically during Tropical Storms Bonnie (29 May 2016), Colin (6 Jun  
138 2016) and Hurricane Hermine (2 Sep 2016) (indicated in Figure 2). These meteorological  
139 disturbances not only brought substantial rainfall (195.3 mm, 69.8 mm, and 113.5 mm; Figure 2),  
140 but produced frequent 5-minute sustained wind gusts over 13 m s<sup>-1</sup>, 15 m s<sup>-1</sup>, and 17 m s<sup>-1</sup> for  
141 Bonnie, Colin, and Hermine, respectively. Stemflow was ignored in this study as it represented  
142 <0.1% of rainfall in a nearby (28 km away) similar pine stand for 22 storms (data collection is  
143 ongoing). Stemflow so far has also never exceeded a funneling ratio of 0.8—meaning near-stem  
144 soils receive <80% of rainfall compared to the open (data not shown). Since stemflow is  
145 negligible, canopy rainfall interception was computed as the difference between rainfall and  
146 throughfall.

147 *Litter sampling, sorting and water storage measurements*

148 Litter samples were collected on a weekly basis with collection gaps occurring twice in  
149 the study period: (1) during the month of December 2015 and (2) for two weeks in the summer  
150 from 11-25 July 2016. A litter sampling event consisted of gathering 30 separate samples of 20  
151 cm diameter areas to whatever depth the Oi horizon terminated (generally 5-15 cm). Sampling  
152 locations each week were chosen at random within the hectares of forest surrounding the  
153 monitoring site, and previous sampling locations were avoided. Care was taken to ensure, at least  
154 visually, that the randomly selected locations for litter sampling represented the overall litter  
155 composition that week. Because litter depth and composition varied between samplings, the  
156 oven-dried biomass of all samples collected during a single weekly sampling ranged from 230-  
157 690 g.

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

168 Total litter rainfall interception ( $I_L$  [L T<sup>-1</sup>]) was computed as the summation of litter  
169 storage ( $S_L$  [L]) and evaporation ( $E_L$  [L T<sup>-1</sup>]) as represented by the balance between throughfall  
170 ( $T_f$  [L T<sup>-1</sup>]) and infiltration ( $F$  [L T<sup>-1</sup>):

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

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

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

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

179  $E_L$  ( $\text{m s}^{-1}$ ) was the sum of within-storm and between-storm evaporation estimates.  
 180 Within-storm  $E_L$  was determined per the Renner et al. (2016) formulation which stems from  
 181 recent findings that, due to the thermodynamic limits of convection, vapor pressure deficit and  
 182 wind speed (as is classically used to estimate potential evaporation: Brutsaert, 1982) are driven  
 183 by land-atmosphere interactions with locally absorbed solar radiation (Kleidon and Renner,  
 184 2013a). This concept was successfully applied to assess hydrologic sensitivity to global climate  
 185 change (Kleidon and Renner, 2013b), estimate global-scale annual average terrestrial  
 186 evaporation (Kleidon et al., 2014), and estimate forest stand-scale potential evaporation (Renner  
 187 et al., 2016). As rain water on the litter is stored on the same materials as in the canopy (leaves,  
 188 branches, bark, etc) and wind speed is very low at the forest floor, we apply the Renner et al.  
 189 (2016) formula to estimate  $E_L$  solely based on absorbed solar radiation ( $R_{sn}$ ,  $\text{W m}^{-2}$ ) and  
 190 temperature data:

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

191 where  $\rho$  is density of water ( $\text{kg m}^{-3}$ ),  $\lambda$  is the latent heat of vaporization ( $\text{J kg}^{-1}$ ),  $\gamma$  is the  
 192 psychrometric constant ( $\text{kPa C}^{-1}$ ), and  $s$  is the slope of the saturation vapor pressure curve ( $\text{kPa}$   
 193  $\text{C}^{-1}$ ) determined from air temperature ( $T$  in K) from Bohren and Albrecht (1998):

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

194  $R_{sn}$  at the litter was computed from incident radiation ( $I_0$ ,  $\text{W m}^{-2}$ ) measured by the gap  
 195 weather station multiplied by an estimate of albedo ( $a = 0.18$ ) representative for *P. elliotii*  
 196 forests (Gholz and Clark, 2002) after being reduced using a species-specific extinction  
 197 coefficient ( $k = 0.35$ , Gholz et al., 1991) and site-specific Leaf Area Index ( $\text{LAI} = 5.7$ ). The  
 198 Beer-Lambert law was modified per Gholz et al. (1991) to include the fraction of canopy gap ( $F_o$   
 199  $= 0.34$ ) and cover ( $F_f = 0.66$ ):



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

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

#### 205 *Data analysis*

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

210

## 211 **RESULTS**

#### 212 *Litter composition and elemental drying curves*

213 Litter sampling resulted in the collection, sorting, and lab submersion testing of over 14.5  
214 kg of oven-dried weight (Table 1). Total litter composition from all sampling events consisted  
215 primarily of needleleaves and cones – each representing just under a third of the total oven-dried  
216 biomass (Table 1). The remaining third of oven-dried litter biomass was composed mostly of  
217 bark flakes (18%) and woody debris (16%), leaving about 2% for broadleaves from the  
218 deciduous lianas (Table 1). Cones exhibited the greatest variation in oven-dried biomass (Table  
219 1) since *P. elliotii* cone drop at our site was seasonally concentrated between October and  
220 March, whereafter cone biomass contributions from the canopy ceased (Figure 3). Needleleaves  
221 within the litter also exhibited high variability in oven-dried biomass (Table 1), but this  
222 variability was observed throughout the study period (Figure 3). The greatest coefficient of  
223 variation (77%) in oven-dried biomass for any litter element was for broadleaves (Table 1). High  
224 variability in broadleaves' oven-dried biomass reflects leaf abscission from lianas in the fall of  
225 2015 (exceeding 20 g), which eventually decayed to minimal proportions (<1 g) in the late  
226 summer (Figure 3). Contributions to the litter from bark flakes had the lowest variability

227 compared to the mean oven-dried biomass (<25%; Table 1) and were the most temporally  
228 consistent, showing little-to-no seasonal trends (Figure 3). Although the range of oven-dried  
229 biomass observations for woody debris in the *P. elliotii* litter was smaller than observed for bark  
230 flakes, the standard deviation was larger (Table 1). The relatively larger standard deviation in  
231 oven-dried woody debris biomass in the litter can be, in part, explained by the large jump in  
232 woody debris in late May through June 2016 (Figure 3) after arrival of TS Bonnie and TS Colin  
233 (Figure 2).

234 Maximum time since saturation for all litter sampling events was 12 days, and neither  
235 the litter nor any litter element dried completely within that time (Figure 4). Nevertheless, all  
236 litter elements dried out relatively quickly within the first 3 or 4 days, then slowly thereafter  
237 depending on conditions driving evaporation (Figure 4). Equations for each regression shown in  
238 Figure 4 are provided in Table 2. Total litter water storage immediately after storms achieved  
239 just over 2 mm (Figure 4), and average  $S_{L,max}$  throughout the study was 1.7 mm (Table 2). The  
240 greatest water storage immediately after rainfall was observed for broadleaves (just over 3 mL g<sup>-1</sup>  
241 <sup>1</sup>), but when this is converted to depth equivalent, the in situ, post-storm  $S_L$  and mean  $S_{L,max}$  for  
242 broadleaves throughout the study were low (< 0.1 mm; Table 2 and Figure 4) due to its small  
243 biomass contribution (Table 1). Cones and woody debris stored 0.6 mm and 0.3 mm immediately  
244 after rainfall (Figure 4), yet accounted for more of the litter composition (Table 1) allowing for >  
245 7 and 4 times larger average  $S_{L,max}$  estimates than broadleaves, respectively (Table 2).  
246 Needleleaves and bark flakes generally stored the least water per oven-dried biomass after  
247 storms (~1 mL g<sup>-1</sup>), but since needleleaves composed a large proportion of the litter oven-dried  
248 biomass (Table 1), they were able to average 0.5 mm of  $S_{L,max}$  (Table 2) and sometimes exceed  
249 0.6 mm of storage immediately after a storm (Figure 4). For all litter elements, the regression  $\alpha$   
250 coefficients derived from field water content data (column 2 of Table 2) are smaller than the lab-  
251 derived  $S_{L,max}$  (column 3 of Table 2), indicating that saturation via submersion achieved greater  
252 water storage than field conditions allowed and/or that the litter lost water within the ~24 h  
253 between field saturation and sampling.

#### 254 *Effects of phenology and meteorological disturbance on litter water storage capacity*

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

257 ranged from 0.8 mm in early April to a maximum that was 4 times greater than the minimum  
258 (3.2 mm) in mid-October (Figure 5b). Maximum  $S_{L,max}$  closely corresponded to a maximum in  
259 cone biomass (Figure 3) and the cones' proportion of  $S_{L,max}$  (Figure 5a). Broadleaf inputs to the  
260 litter from the deciduous lianas also briefly, but measurably, contributed to the elevated  $S_{L,max}$   
261 values from September through November 2015—during the same time as cone drop (Figures 3  
262 and 5a). Although small magnitudes were measured in some weeks,  $S_{L,max}$  rarely fell below 1 mm  
263 (Figure 5b). In fact, 1 mm marks the 10 percentile boundary and the interquartile range of  $S_{L,max}$   
264 is 1.2 – 2.1 mm. The early April minimum in  $S_{L,max}$  occurred when overall litter biomass was low  
265 (Figure 3) and the dominant contribution to  $S_{L,max}$  (~40%) was from needleleaves (Figure 5a).

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

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

### 282 *Total canopy rainfall partitioning and litter rainfall interception*

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

286 2), with TS Bonnie producing the greatest storm magnitude measured during the study year  
287 (195.3 mm; Table 3). Although significant 5-minute rainfall intensities were observed (as  
288 mentioned in Section 2.2), hourly rainfall intensity rarely exceeded  $1 \text{ mm h}^{-1}$ , maximizing around  
289  $8 \text{ mm h}^{-1}$  (Table 3). Throughfall represented 64.5% of rainfall per storm on average, with an  
290 interquartile range between 40-81% of rainfall (Table 3). These relative throughfall proportions  
291 corresponded to an average throughfall receipt at the litter of  $23 \text{ mm storm}^{-1}$  (Table 3). The litter  
292 intercepted a significant quantity of throughfall, reducing throughfall amounts to the soil surface  
293 by 23% on average (Table 3). Modelled litter interception exceeding 1/3 of throughfall was  
294 relatively common, being within the interquartile range of 68 measured storms (Table 3). During  
295 large magnitude storms with high rainfall intensity and low radiation receipt (due to dense cloud  
296 cover), litter interception was minimized—i.e., the minimum 0.6% reduction in throughfall was  
297 observed during TS Bonnie (Table 3). Smaller magnitude, low intensity storms resulted in the  
298 litter being able to store and evaporate all throughfall (Table 3). The largest storm magnitude  
299 where 100% of throughfall was intercepted by the *P. elliotii* litter at this site was 3.6 mm at an  
300 intensity of  $0.72 \text{ mm h}^{-1}$ .

301

## 302 **DISCUSSION**

303 Litter interception is generally neglected by past forest ecohydrological research (Gerrits  
304 and Savenije. 2011), yet our findings align well with past work showing large litter water storage  
305 capacities ( $S_{L,max} = 0.8\text{--}3.2 \text{ mm}$ ) that can consistently and significantly reduce throughfall (9–  
306 46%) reaching the soil surface (Table 3). Throughfall reductions of this magnitude have been  
307 reported in other forests: 22% for temperate *Fagus sylvatica* (L., European beech) in  
308 Luxembourg (Gerrits et al., 2010), 20% for *Brachystegia spiciformis* (Benth., Msasa) savannah  
309 in Zimbabwe (Tsiko et al., 2012), 16-18% for maritime *Picea abies* (L., Norway spruce) forests  
310 in Scotland (Miller et al., 1990), and 8-12% in Himalayan forests (Pathak et al., 1985). The  
311 annual range in  $S_{L,max}$  observed for *P. elliotii* litter in this study (Table 2; Figure 5) spans the  
312 range of observations from past research. For instance, litter  $S_{L,max}$  from the broadleaved  
313 *Lithocarpus edulis* (Makino, Japanese stone oak) and *Asperulo-Fagetum* forests maximized  
314 around 3 mm (Thamm and Widmoser, 1995; Sato et al., 2004), yet needleleaf litter from *Pinus*  
315 *sylvestris* (L., Scots pine) and *Cryptomeria japonica* (L.f., Japanese cedar) typically stored less

316 than 1.7 mm (Walsh and Voigt, 1977; Sato et al., 2004). Diminished water storage for  
317 needleleaves compared to broadleaves was also observed between *Cedrus atlantica* (Endl., blue  
318 cedar) and European beech, with cedar litter storing half as much water as beech (Gerrits, 2010).  
319 Our results agree with these findings as water storage per oven-dried mass was greater for  
320 broadleaves than for needleleaves (3 mL g<sup>-1</sup> versus 1 mL g<sup>-1</sup>). Despite this difference in water  
321 storage per dry mass needleleaves stored more total water (Table 2 and Figure 4) as a result of  
322 needleleaf contributions from the *P. elliotii* canopy exceeding the liana broadleaf contributions  
323 (Table 1; Figure 3).

324         The timing of leaf senescence from broadleaved lianas hosted by *P. elliotii* coincides  
325 with the tree canopies' cone drop (Figure 5). Since liana broadleaves can store double the  
326 amount of water per dry mass compared to most other litter elements (~3 mL g<sup>-1</sup> for broadleaves  
327 versus 1 mL g<sup>-1</sup> for needleleaves or bark flakes), they likely enhance the elevated  $S_{L,max}$  effect  
328 produced by the contribution of new cones (Figure 6). This intersection of liana and *P. elliotii*  
329 phenophases resulting in both significant broadleaf and cone biomass contributions is not  
330 unusual. The phenophase where *P. elliotii* drops cones typically occurs every 3-4 years (after  
331 nearly a year of cone development) for mature stands (Dougherty et al., 1994), typically  
332 beginning in October and ending as late as March or April for the southeastern US (Moore and  
333 Wilson, 2006). Meanwhile, the lianas (*B. scandens* and *Vitis* spp.) senesce their leaves each year,  
334 beginning in late October to early November (per observations at site). Many previous studies  
335 have discussed reasons undergirding the significant water storage of broadleaves (e.g., Walsh  
336 and Voigt, 1977; Sato et al., 2004; Gerrits, 2010; Gerrits and Savenije, 2011), but to the  
337 knowledge of the authors, only two studies have examined the role of any type of reproductive  
338 materials in enhancing  $S_{L,max}$  (Levia et al., 2004) and litter interception (Levia et al., 2005)—and  
339 these studies focus on one species, *Liquidambar styraciflua* L. (sweetgum). These two studies  
340 found that empty fruiting heads with complex morphological structures (numerous openings,  
341 ledges, and roughly-textured surfaces) and a large surface area are not only capable of storing  
342 nearly 5 mm of rainfall (Levia et al., 2004), but can evaporate that storage at rates similar to  
343 those found for saturated canopies under favorable meteorological conditions (Levia et al.,  
344 2005). Storage by *P. elliotii* cones in this study was not as high as observed for *L. styraciflua*  
345 fruiting heads, but both were capable of storing as much water as all the leaf litter elements  
346 (Figure 5; Levia et al., 2004). As such, we echo the call from Levia et al. (2004; 2005) that future

347 work is needed on throughfall interception from reproductive materials in other forest systems  
348 with morphologically complex reproductive materials. This includes a vast array of tree species  
349 around the globe: *Magnolia*, *Platanus*, *Liriodendron*, *Picea*, etc. Perhaps the historical neglect of  
350 litter rainfall interception by forest ecohydrological studies is, in part, a result of past litter  
351 interception studies' focusing on the more temporally consistent (but lower water storage)  
352 elements (like leaves).

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

370 Few studies examine the role of woody debris in the storage and evaporation of water  
371 (Unsworth et al., 2004; Sexton and Harmon, 2009), and only one quantifies the reduction of  
372 throughfall by woody debris—specifically logs (Sexton and Harmon, 2009). The absorption and  
373 evaporation of throughfall by logs was 47-70% for Oregon forests (Sexton and Harmon, 2009).  
374 This finding indicates that litter interception by woody debris at our site was likely greater as we  
375 did not measure water dynamics for whole logs, and these are observable at the site. However,  
376 woody debris in our *P. elliotii* stand after meteorological disturbances appear to more markedly  
377 affect contributions to  $S_{L,max}$  than previous pulses of woody debris inputs (Figure 5). This may be

378 a result of a change in the quality of the woody debris. Winds and heavy rainfall from TS Bonnie  
379 and TS Colin resulted in a sudden increase in fresh branches to the litter layer. It is likely that the  
380 relatively intact bark on fresh branches stores more water compared to shed bark flakes (see  
381 discussion point above). In addition, the clumps of fresh needles attached to these branches were  
382 not separated from the freshly deposited woody debris to keep litter elements as intact as  
383 possible, and these have been shown to efficiently intercept and store rainfall in the canopy by  
384 others (Keim et al., 2006). It is probable that needles attached to fresh branches similarly store  
385 significant water at the forest floor. A third quality of the freshly deposited branch materials that  
386 may increase water storage include the broken ends of the branches, which may permit  
387 significant water absorbance into internal structures. No significant woody debris drop after  
388 Hurricane Hermine (Figure 5) suggests that the “pool” of canopy materials to be contributed to  
389 the litter layer was depleted by the previous two storms.

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

402

## 403 CONCLUSIONS

404 Our findings from a *Pinus elliotii* stand in the southeastern US not only show substantial  
405 rainfall interception by the litter layer (2-32%), but indicate that the effects of different biomass  
406 materials related to phenological activity and meteorological disturbances on the temporal  
407 variability of litter composition can significantly alter litter interception processes. The

408 magnitude of litter rainfall interception observed in this study was similar to the few previous  
409 estimates in other forests, but exceeded those that solely considered the water storage and  
410 evaporation of individual litter elements. Pine cones (and likely reproductive materials from  
411 other tree species as well) were capable of storing significant quantities of water compared to  
412 other litter elements. In forests where multiple phenophases from different canopy plants  
413 coincide, the substantial biomass contributions may result in a seasonal spike of litter rainfall  
414 interception. A spike in litter interception at our site occurred during the concurrent pine cone  
415 release and liana leaf senescence that tripled litter water storage (from ~1 mm to 3 mm). Per  
416 these findings and the current underrepresentation of litter rainfall interception, we recommend  
417 future forest ecohydrological research measure its magnitude, underlying processes and temporal  
418 dynamics, as failure to do so may introduce significant uncertainties into soil hydrological (and  
419 related biogeochemical) processes.

420

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428

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578 **Figure captions**

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

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

584 Figure 3. Weekly oven-dried biomass for all litter compositional elements during the 2015-  
585 2016 study period. Lines with asterisks indicate when TS Bonnie and then TS Colin  
586 occurred.

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

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

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

596 **Tables**

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

Element	Mean	CV	Percentile		Min	Max
			25%	75%		
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

600



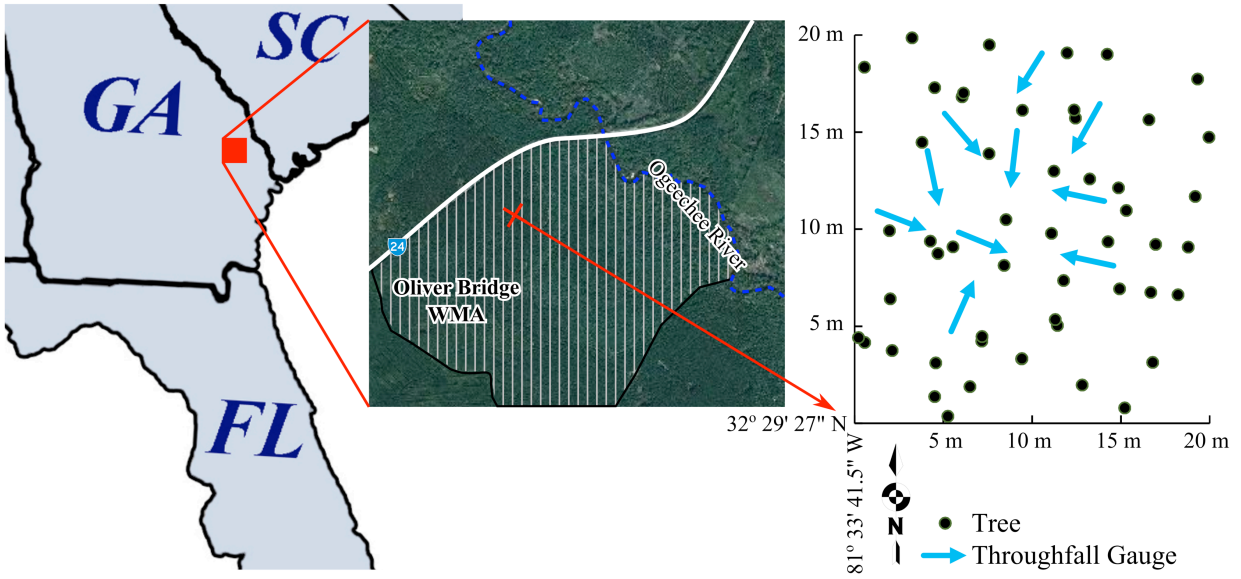
601 **Table 2.** Drying curve regression equations for determination of pre-storm field water storage  
 602 ( $S_L$  [mm]) from days ( $D$ ) since the last storm exceeding weekly litter water storage capacity  
 603 ( $S_{L,max}$ ) and mean  $S_{L,max}$  for all litter compositional elements derived from laboratory  
 604 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)

605

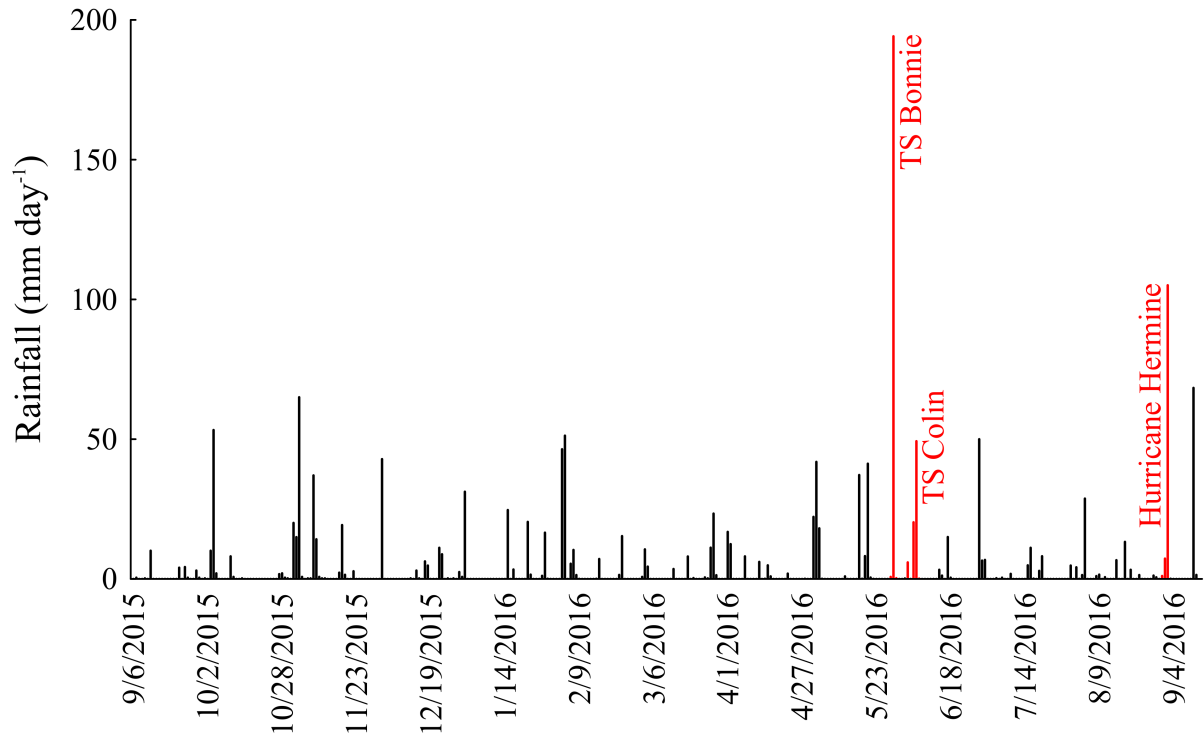
606 **Table 3.** Descriptive statistical summary of event-based rainfall, throughfall, and litter  
 607 interception (sum of storage and evaporation components) during the 2015-2016 study period.

Variable	Mean	SD	Percentile		Min	Max
			25%	75%		
Rainfall ( $R$ )						
Amount (mm)	28.8	37.7	4.6	36.9	1.0	195.3
Intensity ( $\text{mm h}^{-1}$ )	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



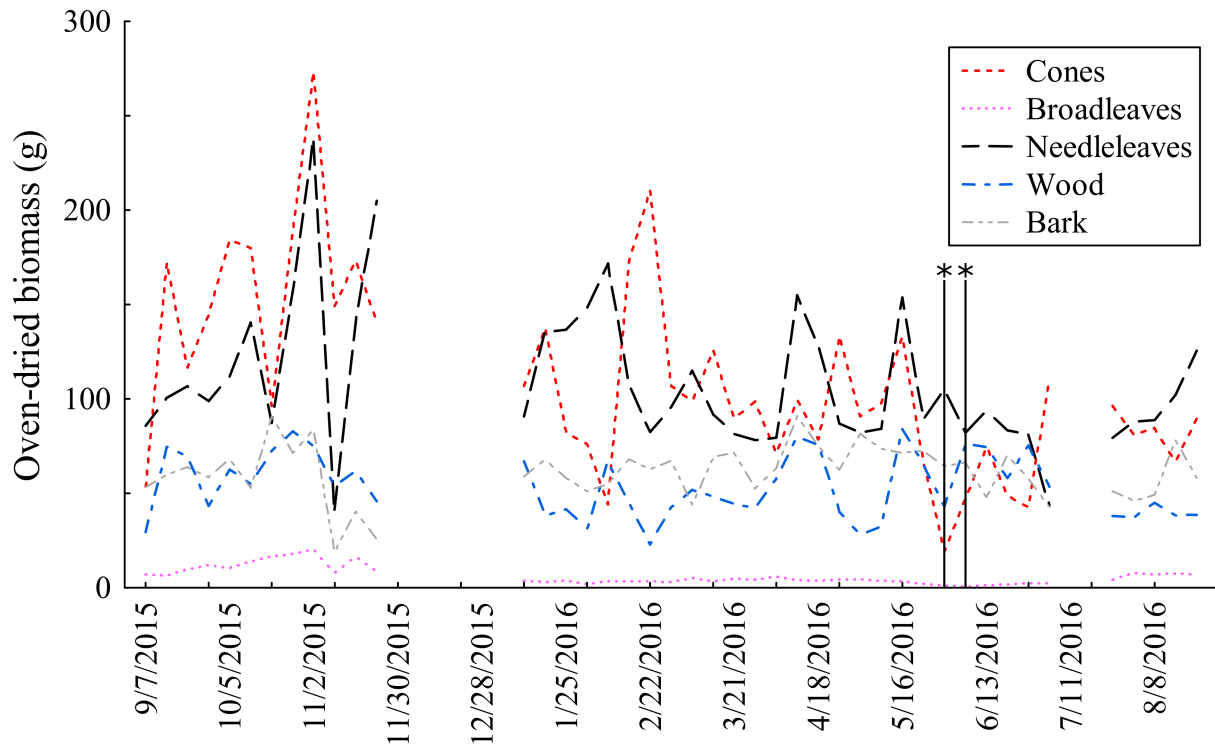
609

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



613

614 Figure 2. Daily rainfall amount throughout the 2015-2016 study period with the tropical storms  
 615 (TS) and hurricane disturbances highlighted.



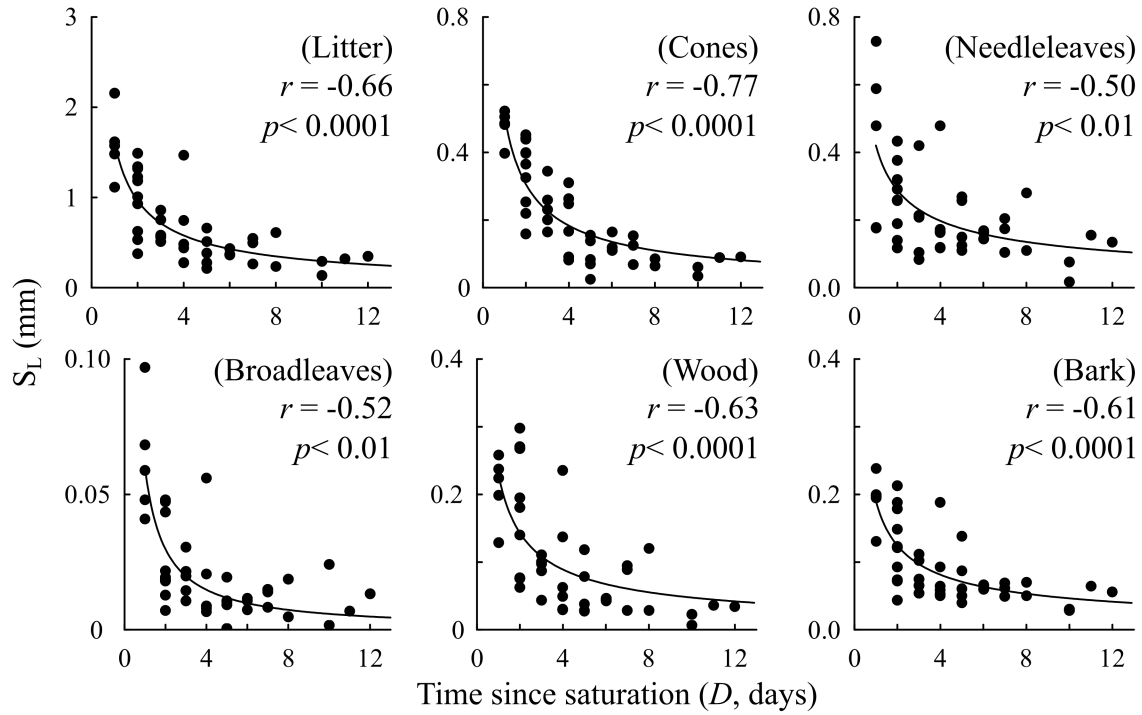
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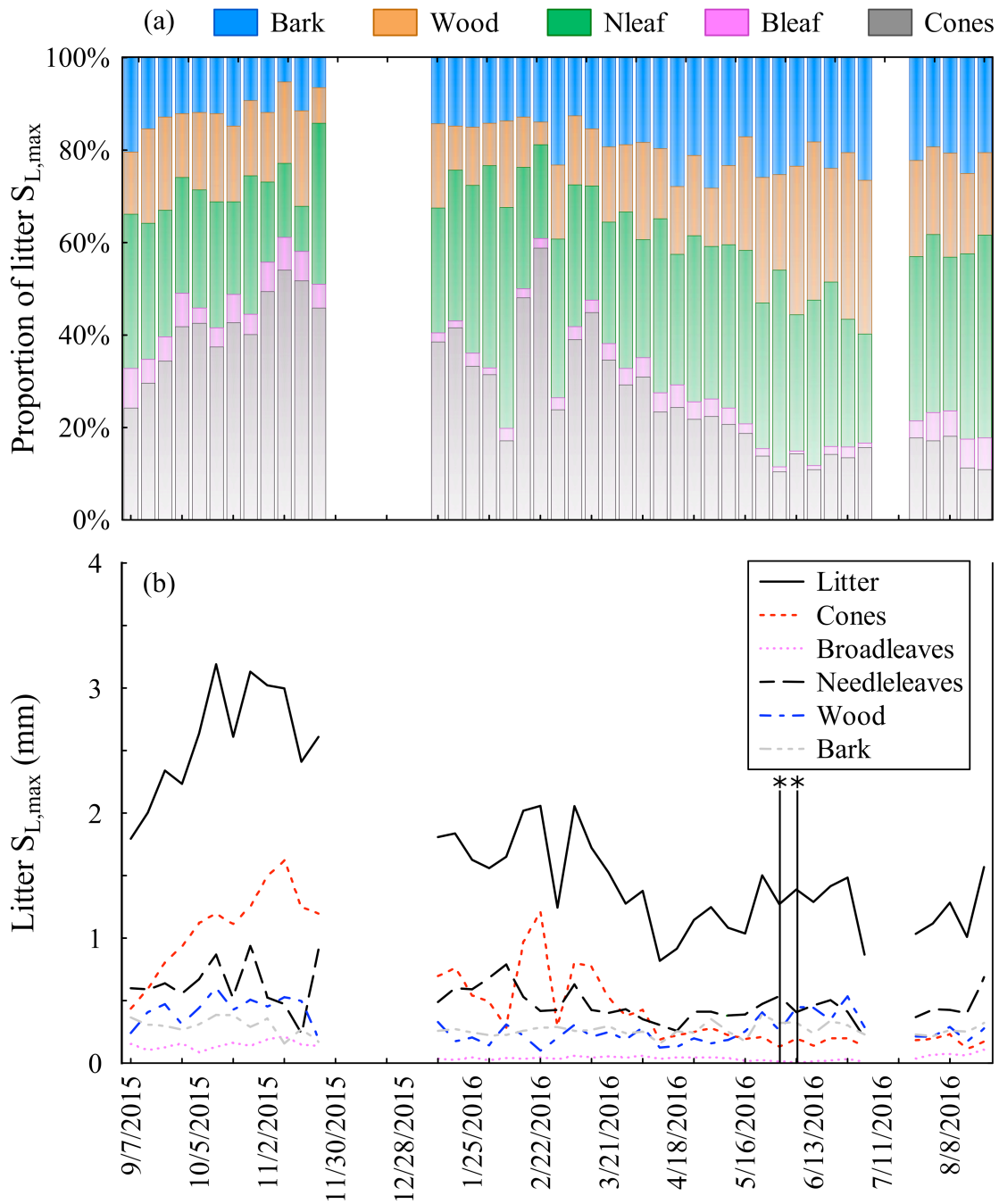
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Figure 3. Weekly oven-dried biomass for all litter compositional elements during the 2015-2016 study period. Lines with asterisks indicate when TS Bonnie and then TS Colin occurred.



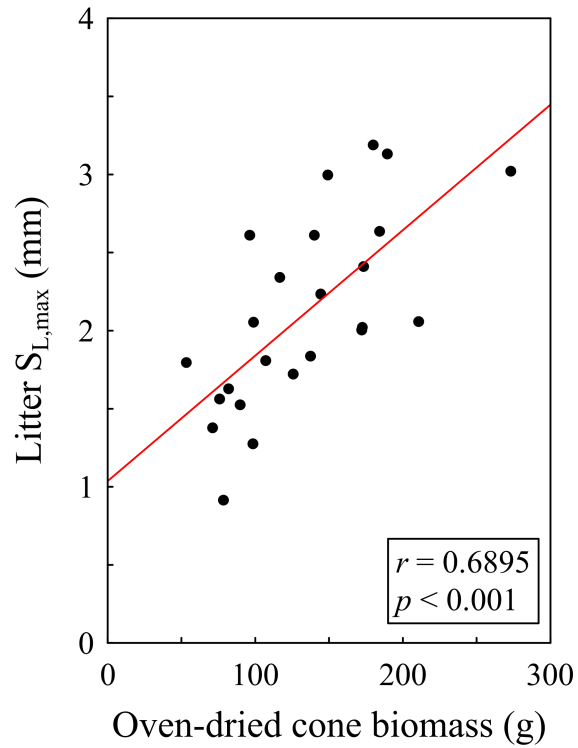
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621 Figure 4. Scatterplots showing field water content ( $S_L$ ) of litter elements with increasing days  
 622 ( $D$ ) since saturation (i.e., the last storm that exceeded weekly litter water storage  
 623 capacity). Regression equations in Table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



624

625 Figure 5. Total weekly litter water storage capacity ( $S_{L,max}$ ) plotted as (a) the proportion (%)  
 626 each litter element contributed as percentage and (b) the actual depth equivalent of  
 627 each litter element. Lines with asterisks indicate when TS Bonnie and then TS Colin  
 628 occurred.



629

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