

Rainfall interception and redistribution by a common North American understory and pasture forb, *Eupatorium capillifolium* (Lam. dogfennel)

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Abstract. In vegetated landscapes, rain must pass through plant canopies and litter to enter soils. As a result, some rainwater is returned to the atmosphere (i.e., interception, I) and the remainder is partitioned into a canopy (and gap) drip flux (i.e., throughfall) or drained down the stem (i.e., stemflow). Current theoretical and numerical modelling frameworks for this process are near-exclusively based on data from woody overstory plants. However, herbaceous plants often populate the understory and are the primary cover for important ecosystems (e.g., grasslands and croplands). This study investigates how overstory throughfall ($P_{T,o}$) is partitioned into understory I , throughfall (P_T) and stemflow (P_S) by a dominant forb in disturbed urban forests (as well as grass- and pasturelands), *Eupatorium capillifolium* (Lam., dogfennel). Dogfennel density at the site was 56,770 stems ha⁻¹, enabling water storage capacities for leaves and stems of 0.90±0.04 mm and 0.43±0.02 mm, respectively. As direct measurement of $P_{T,o}$ (via tipping buckets or bottles, etc.) would remove $P_{T,o}$ or disturb the understory partitioning of $P_{T,o}$, overstory throughfall was modelled ($P'_{T,o}$) using on-site observations of $P_{T,o}$ from a previous field campaign. Relying on modelled $P'_{T,o}$, rather than on observations of $P_{T,o}$ directly above individual plants, leaves significant uncertainty regarding (i) small-scale relative values of P_T and P_S and (ii) factors driving P_S variability among individual dogfennels. Indeed, P_S data from individual plants were highly skewed, where mean $P_S:P'_{T,o}$ per plant was 36.8%, but the median was 7.6% (2.8%-27.2% interquartile range) and total over the study period was 7.9%. P_S variability ($n = 30$ plants) was high ($CV > 200\%$) and may hypothetically be explained by fine-scale spatiotemporal patterns in actual overstory throughfall (since no plant structural factors explained the variability). Total $P_T:P'_{T,o}$ was 71% (median $P_T:P'_{T,o}$ per gauge was 72%, 59-91% interquartile range). Occult precipitation (mixed dew/light rain events) occurred during the study period, revealing that dogfennel can capture and drain dew to their stem base as P_S . Dew-induced P_S may help explain dogfennel's improved invasion efficacy during droughts (as it tends to be one of the most problematic weeds in the southeastern US's improved grazing systems). Overall, dogfennel's precipitation partitioning differed markedly from the site's overstory trees (*Pinus palustris*), and a discussion of the limited literature suggests that these differences may exist across vegetated ecosystems. Thus, more research on herbaceous plant canopy interactions with precipitation is merited.

Key words: Rain, throughfall, stemflow, canopy water storage, stem water storage, evaporation.

37 **1. Introduction**

38 Precipitation (P_g) across most of the global land surface will interact with plant canopies. Precipitation-canopy
39 interactions during storms result in three general hydrologic processes; one which returns water to the atmosphere
40 (interception) and two others that route water to the surface (throughfall and stemflow). Interception is the evaporation
41 of droplets splashing against (Dunkerley, 2009), or stored on, canopy surfaces, like leaves (Pereira et al., 2016), bark
42 (Van Stan et al., 2017a, and epiphytes (Porada et al., 2018). Depending on the vegetation and storm conditions,
43 interception can be small per unit area (David et al., 2006) or return half the annual precipitation to the atmosphere
44 (Alavi et al., 2001). In this way, canopy interception can evaporatively cool regions (Davies-Barnard et al., 2014),
45 recycle moisture to generate nearby storms (Van der Ent et al., 2014), and reduce stormwater runoff to save millions
46 of dollars (US) in stormwater infrastructure costs (Nowak et al., 2020). Throughfall is the water that drips to the
47 surface through gaps or from canopy surfaces, while stemflow is the water that drains down plant stems. The portion
48 of precipitation that drains as throughfall versus stemflow is also highly variable depending on vegetation and storm
49 conditions: ranging annually from 10-90% for throughfall and <1-60% for stemflow (Sadeghi et al., 2020). Since
50 throughfall and stemflow reach the surface at different locations, they differentially interact with subsurface
51 hydrological and biogeochemical processes—having been implicated in fine-scale patterns in soil physicochemistry
52 (Gersper and Holowaychuk, 1971), microbial community composition (Rosier et al., 2015; 2016), N-cycling
53 functional genes (Moore et al., 2016), and metazoan community composition (Ptatscheck et al., 2018). Accurate
54 accounting for each of these precipitation partitioning fluxes is, therefore, necessary for the accurate prediction of
55 atmospheric and surface hydro-biogeochemical processes.

56 Current theoretical and numerical modeling frameworks for canopy precipitation partitioning (see review by
57 Muzylo et al. (2009)), are almost exclusively based on observations beneath woody plants, like forests and shrublands
58 (Sadeghi et al., 2020). In forests, the past 150 years of research has primarily targeted dominant overstory trees
59 (Ebermayer, 1873; Van Stan and Gordon, 2018). However, herbaceous plants commonly dominate forest understories
60 and can be abundant beneath shrublands (Jiménez-Rodríguez et al., 2020; Lajtha and Schlesinger, 1986; Specht and
61 Moll, 1983). As a result, our current understanding of “net” precipitation (as measured beneath woody overstory
62 canopies) is not representative of the actual precipitation that reaches the surface (or litter layer: Gerrits and Savenije,
63 2011) beneath the understory. Herbaceous canopies are relevant to precipitation partitioning in more than the one-
64 third of the global land surface represented by forests; they also cover 27% and 11% of the global land surface in
65 grasslands and croplands, respectively (Alexandratos and Bruinsma, 2012; Suttie et al., 2005). It is unlikely that
66 current knowledge on precipitation partitioning based on woody vegetation is applicable to herbaceous vegetation,
67 since they differ in many hydrologically-relevant morphological features: smaller height, the lack of bark structure,
68 and presence of other stem features (like trichome hairs or desiccated leaves), etc. This raises unanswered and little-
69 researched, questions that must be addressed to include herbaceous plants in precipitation partitioning theory, e.g.:
70 How do these significant morphological differences affect canopy and stem water storage capacities? Do herbaceous
71 plants also favor throughfall generation, like woody plants, or do they more efficiently drain precipitation to their stem
72 bases (and, thereafter, their shallow roots)? In fact, several long-standing (and hitherto unanswered) calls for greater
73 research on the precipitation partitioning of non-woody plants (rooted in detailed observations) have been made (Price

74 et al., 1997; Price and Watters, 1989; Verry and Timmons, 1977; Yarie, 1980). These are general questions identified
75 by the community; but, in this study we focus on: How is overstory throughfall ($P_{T,o}$: Figure 1) partitioned into
76 understory interception, throughfall (P_T : Figure 1) and stemflow (P_S : Figure 1) by a dominant forb in disturbed urban
77 forest understories (as well as grass- and pasturelands), *Eupatorium capillifolium* (Lam., dogfennel)?

78 Very little is known about how understory plants partition $P_{T,o}$ into understory P_T and P_S (Figure 1). Overstory
79 stemflow is currently assumed to bypass the understory and litter layers (Carlyle-Moses et al., 2018); however, this
80 assumption, particularly regarding the bypass of litter, has rarely been tested (Friesen, 2020) and overstory stemflow
81 has been observed to runoff for long distances away from the stem (Cattan et al., 2009; Keen et al., 2010). We do not
82 investigate interactions between the understory and overstory stemflow in this study, because stemflow from this study
83 site is negligible (<0.2%: Yankine et al., 2017). Most observations of precipitation partitioning beneath any plant
84 besides overstory woody plants have been done on maize (Zheng et al. (2019) and references therein) and other cash
85 crops (Drastig et al. (2019) and references therein), which leave plants of forest understories, grasslands or
86 pasturelands relatively unresearched. Even the few studies on forest understory interception, P_T , and P_S
87 overwhelmingly focus, again, on woody plants (González-Martínez et al., 2017; Price and Watters, 1989), limiting
88 net precipitation observations beneath understory herbaceous plants to ferns (Verry and Timmons, 1977) and
89 nonvascular plants (Price et al., 1997). These scant observations, however, indicate that precipitation partitioning by
90 non-woody understory plants is hydrologically relevant, as they can store as much water as woody plants (Klamerus-
91 Iwan et al., 2020), evaporate significant portions of $P_{T,o}$ (Coenders-Gerrits et al., 2020) and redistribute 7-90% of event
92 $P_{T,o}$ as P_S (Sadeghi et al., 2020). For our study on dogfennel, we hypothesized that, compared to past research on
93 woody plants, dogfennel stems and leaves (i) can store a hydrologically relevant amount of rainwater (i.e., within the
94 range of water storage capacities reported for woody plants: (Klamerus-Iwan et al., 2020), (ii) significantly reduce net
95 rainfall flux to the surface (i.e., $P_T + P_S \ll P_{T,o}$), and (iii) redistribute a substantial portion of $P_{T,o}$ to the surface via P_S
96 (i.e., P_S will often “funnel” more rainwater per storm to the soils surrounding stems than P_T , $P_{T,o}$ or P_g over the same
97 area). To test these hypotheses, $P_{T,o}$ was modelled from past on-site observations ($P'_{T,o}$) as monitoring $P_{T,o}$, P_S , and P_T
98 simultaneously were not possible without disrupting or removing $P_{T,o}$. We explicitly acknowledge that the decision to
99 rely on modelled $P'_{T,o}$ leaves a non-trivial uncertainty regarding the influence of actual overstory throughfall
100 spatiotemporal patterns on small-scale values of P_T and individual plants' P_S .

101 2. Materials and methods

102 2.1. Study site and study plant description

103 The study site, Herty Pines, is a forest fragment in Statesboro, Georgia, USA (Figure 2a), at Georgia Southern
104 University's main campus (32.430 N, -81.784 W, 65 m A.S.L.). Climate is subtropical (Köppen *Cfa*) where mean
105 monthly temperatures (1925-2014) for July range from 21-33°C and winter months are generally mild, i.e., the lowest
106 mean January temperature is 3.5°C (University of Georgia, 2019). Mean annual precipitation is 1,170 mm y^{-1} and
107 precipitation occurs almost exclusively as rain, relatively evenly spread over the year. The overstory is dominated by
108 *Pinus palustris* (longleaf pine) and overstory rainfall partitioning for this site has been reported (Mesta et al., 2017;

109 Van Stan et al., 2018; Yankine et al., 2017). Trunk diameter at breast height (DBH) was relatively consistent across
110 all trees in the study plot, 49.7 cm (mean) with an interquartile range of 36.2-55.7 cm. Mean tree height was 30.4±4.5
111 m and was derived from terrestrial lidar (terrestrial lidar methods identical to Van Stan et al., 2017a). Stand density
112 was 223 trees ha⁻¹ with 50.4 m² ha⁻¹ of basal area. Dogfennel, our study plant, was particularly dominant along the
113 forest edge. Dogfennel is a forb of the Asteraceae family, native to (and widespread across) North America (Van
114 Deelen, 1991; Wunderlin and Hansen, 2003). Although dogfennel behaves as an annual plant throughout much of its
115 North American range, it can behave as a perennial in the southern US by overwintering as a rosette, typically from
116 January to March, before re-growing from a taproot in the spring, typically in April (Macdonald et al., 1994;
117 Macdonald et al., 1992). Dogfennel can be abundant in disturbed forest understories, particularly pine forests
118 (Brockway et al., 1998) and pastures (Figure 2b). In the study pine forest, dogfennel stem density was 56,770 stems
119 ha⁻¹ along the stand edge. In pasturelands, dogfennel can reach this stem density within a single season and, if left
120 unmanaged, dogfennel densities have been measured as high as 74 stems m⁻², or ~740,000 stems ha⁻¹ (Dias et al.,
121 2018). The growth habit of dogfennel results in “clumps” of stems. Dogfennel density was estimated in ten 10x10 m
122 plots by counting the stems clump⁻¹ for 3 randomly-selected clumps in each plot. For each plot, the mean stems clump⁻¹
123 were multiplied by the number of clumps plot⁻¹. Finally, all stems plot⁻¹ were summed and scaled to 1 ha. Three
124 dogfennel clumps were randomly selected for throughfall and stemflow monitoring. Within these three clumps, 30
125 individual dogfennel stems were randomly selected for stemflow monitoring. Individual plant attributes—canopy
126 radius [cm], stem radius [cm], leaf angle at the stem [degrees from vertical] at various canopy heights (1.00, 1.25,
127 1.50, 1.75, 2.00 m), and relative location within the clump, interior (I), middle (M), or exterior (E)—were measured
128 for each stemflow-instrumented plant (Table 1). Canopy and stem radii were determined manually with a tape
129 measure, where canopy radii were the mean of measurements from eight directions (N, NE, E, SE, S, SW, W, and
130 NW) and stem radius was determined by a single manual measurement at the stem base. Leaf angle at the stem was
131 determined for two leaves at each height using the iProtactor App for iPhone (2013, Phoenix Solutions) which logs
132 an angle after the levelling of the iPhone camera (see Figure S1 for example).

133 2.2. Hydrometeorological monitoring

134 2.2.1. Rainfall measurements

135 Rainfall amount, duration and intensity for discrete rain events were automatically logged every 5 min by a weather
136 station installed above the canopy (on the rooftop of nearby Brannen Hall at ~40 m height), which is located 100 m
137 from Herty Pines. Rainfall observations were recorded by three tipping bucket gauges (TE-525MM, Texas
138 Electronics, Dallas, TX, USA) interfaced with a CR1000 datalogger (Campbell Scientific, Logan, Utah, USA). This
139 weather station logged a suite of other meteorological variables; however, since these data do not represent the
140 meteorological conditions experienced by the understory, they are not reported or examined here. A discrete event
141 was defined as any atmospheric moisture (rainfall or dew) that resulted in a measurable quantity of throughfall and
142 stemflow (more than a few mL) that occurred after a minimum interstorm dry period of 8 h. Few events consisted of
143 early morning dew contributions (visually observed during sampling and verified by air temperatures equalling dew
144 point temperatures), and these occurred after low-magnitude nighttime rainfall. When dew was present in the

145 understory, there was no response from above-canopy rain gauges; thus, a post-hoc estimate of occult dew contribution
146 to $P_{T,o}$ was made by assuming the dew contribution was equal to the understory canopy water storage capacity (1.33
147 mm – methods described later). An important limitation to this dew estimate is that it represents the maximum possible
148 dew contribution. Rain events without dewfall required at least ~4 mm of rainfall for generation of P_T or P_S from the
149 monitored dogfennel canopies.

150 2.2.2. Overstory throughfall estimation

151 As observing $P_{T,o}$ directly would prevent direct observation of P_T and P_S beneath dogfennel plants, $P_{T,o}$ was estimated
152 from previous field measurements at the site (Figure 3). Automated $P_{T,o}$ monitoring was performed from September
153 2016 to September 2017 using ten 3.048-m long and 10.16 cm diameter PVC troughs oriented at a moderate slope,
154 with a 5.08 cm slot cut lengthwise for collection and drainage of $P_{T,o}$ to a Texas Electronics (Dallas, Texas, USA) TR-
155 5251 tipping bucket gauge, resulting in 1.65 m² of collection area. Tipping bucket gauges and their associated troughs
156 were randomly placed within a 0.25 ha plot and recorded every 5 minutes by a CR1000 datalogger. All trough angles
157 were measured with a digital clinometer to correct computations of trough area receiving $P_{T,o}$. Trough and tipping
158 bucket assemblies were field tested to ensure accuracy ($\pm 5\%$) under storm conditions typical for the region (Van Stan
159 et al., 2016). These $P_{T,o}$ data were reported by Mesta et al. (2017). To estimate overstory throughfall, $P'_{T,o}$, a regression
160 model was generated from the association between $P_{T,o}$ [% of rainfall] measured on site and storm size, R [mm storm
161 ¹] using the "Aston" curve:

$$162 (2) P'_{T,o} = a (1 - e^{-bR})$$

163 where a and b are regression coefficients. This model and its fit statistics are provided in Figure 3. We assume that
164 the past observed rainfall relationship with $P_{T,o}$ at the site was similar during our study period. Although we are unable
165 to assess whether and to what degree there is a difference between these observation periods, the canopy is mature
166 and there has been no known/noticeable disturbance or change in canopy structure since the previous observation
167 period.

168 2.2.3. Understory throughfall and stemflow measurements.

169 Throughfall gauges consisted of 9 randomly placed funnels (506.7 cm² collection area each), three per
170 dogfennel clump (1,520.1 cm² total collection area per clump), connected to HDPE bottles that were manually
171 measured with graduated cylinders immediately after a storm ended (within 4 h). The total canopy area of dogfennel
172 plants at this site rarely exceed 2,000 cm², resulting that the total throughfall gauge area per clump generally
173 represented >75% of canopy area; which is a comparatively much larger gauge-to-canopy area than most past
174 throughfall studies on forest canopies (Van Stan et al., 2020).

175 Standard stemflow measurement methods developed for woody plants (use of flexible tubing wrapped around
176 a woody stem: Sadeghi et al., 2020) are not suitable for dogfennel; moreover, no standard stemflow collection devices
177 exist for herbaceous plants. Thus, stemflow collars were constructed from aluminum foil, 15-mm inner-diameter
178 flexible polyethylene tubing, electrical tape, and silicon (see Figure S2). Aluminum foil was folded over itself several
179 times to strengthen the collar (typically ~160 mm length of foil was folded to ~40 mm) and connected to plastic tubing

180 with stainless steel staples. The aluminum collar was then folded around the lower stem of the dog fennel and secured
181 with electrical tape. To seal the aluminum foil, staple connections, and the interstices between the foil, tubing and
182 stem, silicon was thinned with hydrotreated light (95-100%) naphtha (VM&P Naphtha, Klean-Strip, Memphis TN
183 USA), allowing for it to completely fill the aluminum cone up to the tube opening and make a water-tight seal. While
184 naphtha-thinned silicon was poured into collars, the tube opening was covered. An additional benefit of naphtha-
185 thinned silicon was that, due to the evaporation of naphtha, the silicon shrinks, thereby, pulling the collar taut and
186 stiffening/strengthening the stemflow collection device and extending the lifespan of the collar. Stemflow was
187 measured with a graduated pipette (with 1 mL graduations) from 500 mL plastic bottles connected to the tubing base.

188 **2.3. Water storage capacity estimation**

189 Maximum water storage capacity (S_u [mm]) was estimated for the dogfennel canopy and stem, both as volume [L] per
190 unit surface area [m^2]. All field leaf and stem samples were collected during an inter-storm dry period (>24 h after
191 any rainfall). For the canopy, 50 leaves representing the median size of the site dogfennel plants were sampled (broken-
192 off at the base of the leaf), taken back to the lab, their “field-dry” mass [g] determined on a bench scale, and then the
193 broken end of their leaf-stems were sealed with silicon to prevent water exchange from an area that was not previously
194 exposed in its natural state. Sampling for the stems was similar; however, since dogfennel heights reach (and can
195 exceed) 2 m, the stems were cut into 5 cm sections. Just as with the leaves, 50 representative samples of these stem
196 sections were weighed in the lab, then sealed with silicon on both ends. Next, all leaf samples and stem sections were
197 submerged in water for three days until achieving maximum saturation (per Van Stan et al., 2015), whereupon the
198 maximum saturation mass [g] was recorded. For comparison with the field-dry mass, all samples were oven-dried
199 until their mass no longer changed (mass recorded every 3 h), whereupon the oven-dried mass [g] was recorded. No
200 leaf or stem samples were oven dried longer than 15 h. The gravity convection oven (Isotemp, Fisher Scientific) was
201 set to 40 °C (confirmed with a standard thermometer). The maximum volume of all samples’ water storage capacity
202 is the difference between saturation and oven-dried mass. The oven-dried leaves and stems did not visually appear to
203 be damaged (aside from the sampling cuts, obviously) and care was taken to ensure the plant samples were not
204 damaged. It is likely that internal (not externally intercepted) water was exchanged during this process; however, this
205 is not entirely problematic as plant surfaces are known to permit interaction between externally intercepted water and
206 internal water (Berry et al., 2019). Moreover, we explicitly acknowledge that although these submersion methods are
207 commonly used, they produce the “maximum” possible water storage capacity (hence, our objective to estimate
208 maximum water storage capacity), as multiple intrinsic and extrinsic factors of plant surfaces could reduce the
209 available water storage capacity in situ (Klamerus-Iwan et al., 2020).

210 Specific water storage capacity, S_L [mL cm^{-2}], for the leaves and stems was determined by dividing the lab-
211 derived maximum volume [mL] by the samples’ surface area [cm^2]. For leaves, after sampling, levelled photos of
212 each sample were taken on a grid system (every block representing 2.5 cm x 2.5 cm for scale), then the leaf images
213 were vectorized and processed for 2-D projected surface area using the “Measure Path” extension in Inkscape (v. 0.92,
214 Inkscape.org). An example vectorized image of leaf area is provided in the supplemental materials (Figure S3). Error
215 in this vector-based leaf surface area estimate was estimated by repeating the process five times for each leaf. Stem

216 surface area for all samples was estimated from their radii and height. S_L estimates for the stem (0.436 mL cm⁻²) and
 217 leaves (0.195 mL cm⁻²) were then scaled to S_U [mm as L m⁻²] using stem and leaf surface area estimates per plant (A
 218 = 171.9 cm² plant⁻¹ and 807.5 cm² plant⁻¹, respectively), and multiplied by the site plant density ($D = 5.68$ plants m⁻²)
 219 and divided by 1000:

$$220 \quad (2) S_U = (S_{L_{stem}} \times A_{stem} \times D)/1000 + (S_{L_{leaf}} \times A_{leaf} \times D)/1000$$

221 Plant stem and leaf surface area estimates were determined from 5 representative plants that were cut from
 222 the site and separated into leaves and stems, then the sum of leaf and stem areas (determined as mentioned earlier in
 223 the paragraph) were divided by 5. Total leaf surface area compares well to values reported from ~1 m tall dogfennel
 224 plants, 212 cm² plant⁻¹ (Carlisle et al., 1980), considering our plants were much taller (~2 m).

225 2.4. Data analysis

226 Descriptive statistics were compiled for all variables presented and regression analyses were performed to relate plant
 227 canopy and hydrologic variables. All statistical analyses were done using Statistica 12 (StatSoft, Tulsa, OK, USA).
 228 Throughfall volumes [L] from all gauges were summed and converted to yields [mm] by dividing by the total gauge
 229 area [m²]. Stemflow yield [mm] for an individual plant was determined by dividing its volume [L] by the projected
 230 canopy area [m²]. To compare stemflow production across plants, two metrics were computed per plant for each storm:
 231 normalized stemflow ($\bar{P}_{S,i}$ [-]) and the funneling ratio (F [-]). $\bar{P}_{S,i}$ was computed per Keim et al. (2005):

$$232 \quad (3) \bar{P}_{S,i} = \frac{(P_{S,i} - \bar{P}_S)}{s_S}$$

233 where $P_{S,i}$ is stemflow volume [mL] from each individual plant in a single storm, \bar{P}_S is the mean stemflow for all plants
 234 in a single storm, and s_S is the standard deviation of stemflow for all plants in a single storm. F for individual plants
 235 in each storm were computed per (Herwitz, 1986):

$$236 \quad (4) F = \frac{P_{S,i}}{B_i P}$$

237 where B_i is the basal area [cm²] at the base of an individual plant and P will be either P_g or $P'_{T,o}$ (this will be explicitly
 238 indicated in the results). There are an increasing number of F metrics (Carlyle-Moses et al., 2018; Levia and Germer,
 239 2015); however, the selected method is the most common F metric applied to stemflow data to date. Moreover, in situ
 240 observations of non-collared dogfennel plants during rainfall confirmed that dogfennel P_S rates did not produce visible
 241 runoff areas.

242 3. Results

243 3.1. Storm and plant structural conditions

244 Discrete rain events, as measured above the forest canopy, ranged in magnitude from 0.1 mm (during dewfall) to 101.3
 245 mm (Table 1). The distribution of storm magnitudes was skewed, such that the mean, 16.5 mm, was many times
 246 greater than the median, 6.6 mm (Table 1). Estimated overstory throughfall ($P'_{T,o}$), per Figure 3, ranged from 0 (again,
 247 during dewfall) to 72.2 mm, with a median of 3.5 mm (Table 1). Thirty of the plants in the selected dogfennel clusters

248 - those being monitored for stemflow - had an average canopy radius of 18.3 cm (± 4.5 cm standard deviation), which
249 was nearly identical to the median canopy radius (Table 1). The stem radii of all measured dogfennel plants ranged
250 from 0.1 - 0.7 cm, with a mean radius of 0.6 cm (Table 1). The resulting ratio of canopy:stem radii was also normally
251 distributed, with a mean and median of ~ 36 (dimensionless), but ranging from 24 to 50 (Table 1). For all plants, the
252 mean leaf angle decreased from 54° to 32° from vertical with increasing canopy height; i.e., the higher in the dogfennel
253 canopy, the closer the leaf angle approaches vertical (Table 1). This trend appears consistent across each individual
254 study plant regardless of which clump the plants' resided, as the standard deviation across all elevations are low, 1.8-
255 3.1° from vertical, and do not overlap (Table 1).

256 3.2. Partitioning into water storage, throughfall and stemflow

257 Note that $P'_{T,o}$ is an event-scale estimate derived from past observations, limiting its utility in examining fine-scale P_T
258 and individual-plant scale P_S . The sum of data from all storms throughout the study period resulted in P_T , P_S and I of
259 71%, 8%, and 21% as a portion of $P'_{T,o}$, respectively, beneath dogfennels at our site. Water storage capacity achieved
260 by dogfennel leaves in the lab was 0.90 ± 0.04 mm, while dogfennel stems stored a capacity of 0.43 ± 0.02 mm (Figure
261 4). This resulted in the total S_U of dogfennel plants in the understory of this study site being approximately 1.3 mm.
262 This S_U estimate agrees with the reductions of $P'_{T,o}$ below dogfennels: for example, mean $P_T:P'_{T,o}$ was 76.6% for rain-
263 only storms (Table 2), or a mean yield of $P_T = 12.9$ mm which exceeds a 1.3 mm reduction (due to S_U and evaporation)
264 in the estimated mean $P'_{T,o}$ yield, 16.5 mm (from Table 1). A large portion of the rainwater captured on dogfennel
265 canopies was able to overcome stem water storage capacity and generate P_S . Dogfennel P_S data were highly skewed,
266 producing a mean relative P_S ($P_S:P'_{T,o}$) of 36.8%, but a median of 7.6% within a narrow interquartile range, 2.8%-
267 27.2% (Table 2). For events including occult precipitation, both maximum $P_S:P'_{T,o}$ and $P_T:P'_{T,o}$ exceeded 100%:
268 $P_T:P'_{T,o}$ during mixed storms maximized at 192%; whereas, the maximum for $P_S:P'_{T,o}$ was just over 900% (Table 2).
269 Note that dew in the understory was not measured by the above-canopy rainfall gauges and $P'_{T,o}$ was only increased
270 by an assumed maximum dew contribution equal to S_U (1.33 mm), thus dew accumulation allows P_T and P_S to exceed
271 100% of P_g and $P'_{T,o}$ (Table 2). When compared to rainfall above the overstory (P_g), the medians are much smaller:
272 $P_T:P_g$ being 45% and 58% for rain-only storms and mixed storms, respectively, and $P_S:P_g$ being 4.1% and 14.7%,
273 respectively (Table 2).

274 Yield [mm] were estimated for dogfennel P_T and P_S across storms, and both event-level P_T and P_S yields
275 linearly correlated with estimated event-level $P'_{T,o}$ (Figure 5a-b). Since, for P_T , the catchment area (canopy area above
276 the gauge) is equal to the input area (soil area below the gauge), P_T yield from the canopy and P_T supply to the surface
277 are equal and the term "yield" will be applied for both. Median P_T yield beneath dogfennel for the measured storms
278 was 4.4 mm with an interquartile range of 1.1 mm to 11.3 mm (Figure 5c). Maximum P_T yield approached 50 mm
279 during a large-magnitude rain storm (where $P_g = 101.3$ mm). Since the canopy area that generates stemflow is many
280 times greater than the surface area around plant stems that receive stemflow (see Table 1), P_S yield and F will differ.
281 F are typically used to represent P_S supply to soils, and is done so in the proceeding section. Yields of P_S from
282 dogfennel were as high as 24 mm, but the median was 0.4 mm and the interquartile range was narrow, 0.1-1.3 mm
283 (Figure 5c).

284 3.3. Stemflow and throughfall variability

285 Coefficients of variability (CV) and quartile variability (CQV) were computed for both P_S and P_T , relative to P_g and
286 $P'_{T,o}$ (Table 2), and storm-normalized temporal stability plots were generated for P_S yield only (Figure 6). Storm-
287 normalized temporal stability plots were not generated for P_T yields because the experimental design accounts for its
288 spatial variability through deployment of large gauge areas (compared to dogfennel canopy area); which permit
289 estimates of variability across a few large-area gauges (Table 2), but limits the observable variability. CV and CQV
290 for relative P_T ranged from 22-90% and were generally lower for rain-only storms, <40%, than for mixed storms,
291 >60% (Table 2). Variability in relative P_S across study plants, ranging from 77-257%, was always greater than
292 observed for relative P_T for the monitored storms (Table 2). Due to the greater skew in the relative P_S data compared
293 to relative P_T , CV was many times greater than CQV for relative P_S (Table 2). CV and CQV for $P_S:P'_{T,o}$ was similar
294 for rain and the mixed storms; however, the CV for $P_S:P_g$ was greater for rain-only storms compared to mixed storms.

295 Temporal stability of normalized stemflow, $\bar{P}_{S,i}$ (Figure 6) indicates that there were only a few plants that
296 captured most of the $P_{T,o}$ drained as stemflow (three plants' mean $\bar{P}_{S,i} \gg 1$). Thus, most of the studied dogfennel
297 plants captured similar amounts of $P'_{T,o}$ as stemflow—having $\bar{P}_{S,i}$ between -1 and 1 ($y = 0$ represents the central
298 tendency of $\bar{P}_{S,i}$ data). Funneling ratios (F based on $P'_{T,o}$) show that all plants concentrated P_S yields to the surface
299 around their stem bases (Figure 6). Mean F across all plants was 87, and for the 27 plants whose mean $\bar{P}_{S,i}$ fell between
300 -1 and 1, median F ranged 18-200 (Figure 6). However, for the three plants with the highest $\bar{P}_{S,i}$, their mean F values
301 were 287, 476 and 484 (Figure 6). These voluminous stemflow-generating plants, alone, account for one-third of total
302 P_S volume (8,734 mL / 27,870 mL). To evaluate possible canopy structural influences over P_S variability, various
303 directly-measured structural metrics were compared: radii of canopies and stems and the vertical variability in leaf
304 angle (see supplemental Figure S4). No clear visible or statistical correlations or correspondences were found between
305 these structural variables and $\bar{P}_{S,i}$ across plants (Figure S4). In fact, variability in the measured canopy structural
306 variables was low (Table 1) compared to the variability observed for dogfennel P_S and $\bar{P}_{S,i}$ (Figure 6).

307 4. Discussion

308 4.1. Overstory throughfall partitioning by dogfennel

309 Partitioning of overstory throughfall by this example dominant understory and pasture forb resulted in hydrologically
310 relevant losses of rainwater to the surface at our site (Table 2). As maximum water storage capacity is a major driver
311 of rainfall interception (Klaassen et al., 1998), the magnitude of dogfennel's overstory throughfall interception may
312 be attributed to its canopy being able to store a sizeable magnitude of rainwater per unit area, 1.33 mm (Figure 4).
313 Although mass changes of dried-and-submerged vegetation samples are discrepant from the processes and temporal
314 scales of natural rainfall interception, it is a common method with well-known and long-discussed limitations selected
315 to estimate water storage capacity since more direct water storage capacity estimation methods are still under
316 development to date—see discussions in reviews by Friesen et al. (2015) and Klamerus-Iwan et al. (2020).
317 Methodological limitations withstanding, the S_U estimates in this study fit within the range of water storage capacities

318 of other herbaceous plants synthesized by Breuer et al. (2003). This synthesis is focuses on the leaves of herbaceous
319 plants (alongside other plant types) (Breuer et al., 2003), but less research has estimated the stem component (or a
320 reported a total including the stem component) of water storage capacity for short vegetation (Bradley et al., 2003;
321 Wang et al., 2016; Wohlfahrt et al., 2006; Yu et al., 2012). The stems of herbaceous plants, even thick smooth stems
322 (>1 cm in diameter) can store nearly 0.5 mm: e.g., *Taraxacum officinale* (dandelion) (Wohlfahrt et al., 2006). Even
323 thin (<1 cm radius) herbaceous stems with epidermal outgrowths, like hairs, can store large amounts of rainwater:
324 e.g., 0.25 mm for *Achillea millefolium* (yarrow) and 0.20 mm for *Trifolium pretense* (red clover) (Wohlfahrt et al.,
325 2006). In the case of dogfennel stem water storage capacity at our site, the 0.43 mm estimate is within this range and
326 its magnitude is likely a result of two principal factors: (1) dense stem coverage by desiccated leaves (photo in Figure
327 4); and (2) this species can achieve large densities, up to 700,000 stems ha⁻¹ (Dias et al., 2018) – 56,770 stems ha⁻¹ at
328 our study site. We note that, to our knowledge, stem water storage capacities for herbaceous plants with spines, thorns,
329 etc. have not been evaluated.

330 Overstory throughfall was also redistributed into a highly spatially variable (Table 2), but temporally
331 persistent pattern beneath dogfennel canopies (where CV or CQV was approximately 20-40% for P_T and 80-250% for
332 P_S ; Table 2), despite all measured canopy structures—like branch angle, stem size, canopy size, etc—being similar
333 (Table 1). Since our sampling plan measured P_T over a large area of the dogfennel canopy (rather than at numerous
334 localized points), this discussion point will focus on the intraspecific P_S observations. The high spatial variability and
335 temporal persistence of P_S across plants despite canopy structural similarity, raises the question: What caused the
336 intraspecific P_S patterns observed in this study? A likely explanation may be that, in this case, access to precipitation
337 for stemflow production is related to overstory throughfall patterns (which, we reiterate, were not able to measure
338 without removing or disrupting P_T and P_S). Overstory throughfall patterns are well-known to be spatially variable,
339 but temporally persistent across forest types (Van Stan et al., 2020). Specifically, individual dogfennel plants that
340 persistently generated greater P_S than other plants may have just received greater overstory throughfall from persistent
341 overstory drip points. If the overstory throughfall pattern is a major driver of intraspecific variability in P_S in this
342 study, then the funneling ratios computed from mean overstory throughfall (per Figure 3) would be incorrect (in Figure
343 6). In this case, funneling ratios (computed from the localized overstory throughfall above each plant) could be similar
344 across the monitored dogfennels. Testing this hypothesized relationship between dogfennel P_S patterns and overstory
345 throughfall patterns was not possible in the field, since sampling overstory throughfall would prevent P_S from being
346 generated by the plant. Future work to test this hypothesis could, however, make use of rainfall simulators.

347 The large diversion of rainwater and dew to their stem base may be partially responsible for dogfennel
348 survival during extended periods of drought (or improved invasion efficacy during droughts: Loveless, 1959;
349 Forthman, 1973), and may also explain why this species tends to be one of the most problematic in improved grazing
350 systems located in Florida (Sellers et al., 2009). Rainfall patterns in central and south Florida may also intersect with
351 dogfennel's canopy water balance to “tip the scales” in its favor. Specifically, rainfall in our study region is often
352 limited from January through May, with the bulk of rainfall occurring from June through October, and the water
353 storage capacity of burgeoning dogfennel plants during early spring may enhance chances of individual plant survival
354 (resulting in large infestations as referenced previously).

355 **4.2. Overstory (woody) and understory (herbaceous) canopies may partition rainfall differently**

356 The dominant understory plant at our study site, dogfennel, intercepted similar amounts of modelled overstory
357 throughfall, interquartile range 11-59% storm⁻¹ (Table 2), as compared to the gross rainfall interception by their
358 overstory pine canopy, interquartile range 19-60% storm⁻¹ (Van Stan et al., 2017b). Similar rainwater interception
359 between dogfennel and the pine overstory may be due to dogfennel's maximum water storage capacity comparing
360 favorably to that of overstory tree species, 0.07-4.30 mm (Klamerus-Iwan et al., 2020). Even the maximum stem water
361 storage capacity is of similar magnitude to values reported by past work on woody plants, 0.2-5.9 mm (Klamerus-
362 Iwan et al., 2020), albeit on the lower end of the range. Most current research on stem water storage has focused on
363 intrinsic factors of woody plant stems, like bark thickness, porosity, microrelief, or roughness (Ilek et al., 2017; Levia
364 and Herwitz, 2005; Levia and Wubbena, 2006; Sioma et al., 2018; Van Stan et al., 2016; Van Stan and Levia, 2010);
365 however, other stem structures besides bark may be capable of storing substantial water: e.g., the desiccated leaves of
366 our study plant.

367 There were differences in how gross rainfall was redistributed by the overstory canopy compared to how
368 modelled overstory throughfall was redistributed by the dogfennel understory. Stemflow from the overstory, *P.*
369 *palustris*, was negligible at this site, 0.2% of gross rainfall (Yankine et al., 2017), but median dogfennel P_S was 7.6%
370 of modelled overstory throughfall (with an interquartile range of 2.8-27.2%) (Table 2). Annual relative P_S (and P_T)
371 estimates from trees and herbaceous plants reported by previous work indicates that herbaceous plants are generally
372 greater stemflow producers than woody plants (Sadeghi et al., 2020). Although relative P_T beneath dogfennel was
373 similar to observations of relative overstory throughfall beneath *P. palustris* at this site (Mesta et al., 2017), throughfall
374 has been found to be generally lower beneath herbaceous plant canopies than for woody ones (Sadeghi et al., 2020).
375 This seems reasonable, because, if interception is similar between herbaceous plants and woody plants, then an
376 increase in relative stemflow would necessitate a decrease in relative throughfall. The results of this study support
377 statements by several past studies suggesting that plants in the understory and overstory interact differently with
378 rainfall. Thus, we repeat the long-standing calls for greater research on understory precipitation partitioning,
379 particularly stemflow, research (Price et al., 1997; Price and Watters, 1989; Verry and Timmons, 1977; Yarie, 1980).

380 **4.3. A brief discussion on dew-generated throughfall and stemflow**

381 For a few storms ($n = 5$), dew contributed significantly to P_T and P_S by the studied dogfennel plants. The median P_T
382 generated from dew beneath dogfennels at our site was 0.74 mm plant⁻¹ with an interquartile range of 0.47-0.99 mm
383 plant⁻¹, resulting in a total dew-related contribution to T of 17.1 mm over the study period. Volumes of stemflow under
384 dewfall totaled 558 mL for all study plants, with individuals supplementing the dew-related P_T with up to 61 mL plant⁻¹
385 (yielding an additional ~0.6 mm). Dew contributions to net precipitation below plant canopies have rarely been
386 studied. The earliest quantity for dew drainage was 0.08 mm from a single event on a single tree in Johanniskreuz,
387 Germany (Ney, 1893). Since then, to our knowledge, only one other study has examined dew-related drainage from
388 plants, focusing on stemflow from the herbaceous *Ambrosia artemisiifolia* (common ragweed) (Shure and Lewis,
389 1973). They estimated that the drainage of dew via P_S resulted in an additional input of 1.1 L month⁻¹ during the
390 growing season, and hypothesized that this process may “play a vital role in governing the density, diversity, and

391 distribution of plant species within field ecosystems” (Shure and Lewis, 1973). Dew drainage from plant canopies and
392 down stems may, in addition to being a valuable water source, influence plant-soil interactions by transporting leached
393 or dry deposited materials to the soils—something also discussed by Shure and Lewis (1973). Globally, dew
394 contributes a small percentage to the annual precipitation (Baier, 1966), however, in semiarid and arid (Baier, 1966;
395 Hao et al., 2012), as well as summer-dry climates (Tuller and Chilton, 1973), dew can form a significant water input.
396 It is reasonable to suppose, then, that in such ecologic settings as these any factor which doubles the frequency of
397 plant-moisture availability, even though the amounts be small, must materially affect the plant growing condition.
398 Therefore, further research is needed to assess dew (and mixed storms) drainage in arid and semiarid climates, with
399 days on which dew occurs being $\geq 70\%$ per year (Hao et al., 2012). The global importance of occult precipitation and
400 resulting wet canopy conditions has recently been reviewed and described as a critical future research direction for
401 plant sciences (Dawson and Goldsmith, 2018). Given these scant but ecologically relevant findings, further research
402 on the influence of condensation events on plant-soil interactions via throughfall and stemflow may be merited.

403 **5. Conclusions**

404 *Eupatorium capillifolium* (Lam., dogfennel) in the understory of an urban forest fragment intercepted 20.4% of
405 modelled overstory throughfall from *Pinus palustris* (Mill.). The remaining 71.0% and 7.9% of modelled overstory
406 throughfall reached the surface beneath dogfennels as understory throughfall and stemflow, respectively. At the stand
407 scale, the partitioning of modelled overstory throughfall by this understory forb differs considerably from the rainfall
408 partitioning of the woody overstory, especially regarding stemflow (7.9% versus $<0.2\%$). During a few storms that
409 occurred in tandem with dewfall, dogfennels were able to augment stemflow (and throughfall) production through
410 capturing dew. These processes may help explain how dogfennels survive extended droughts, and even show improved
411 invasion efficacy during droughts, making it one of the most problematic weeds in southeastern US grazing systems.
412 Stemflow variability among individual plants was very high (CV $\sim 250\%$), but no dogfennel canopy structures
413 measured in this study provided statistically significant insights into this stemflow variability. Future work will assess
414 to what extent actual overstory throughfall variability drives understory stemflow variability for plants, like dogfennel,
415 of similar intraspecific canopy structure. The inability to measure fine-scale overstory throughfall patterns without
416 disturbing understory rainfall partitioning in the field is a non-trivial limitation of this study—a limitation that future
417 work may overcome with rainfall simulations. Still, in forests, overstory throughfall is not the final frontier for
418 determining net rainfall, and investigations on how it is intercepted and redistributed by herbaceous plants is needed
419 to improve our understanding of exactly how much (and in what pattern) rainfall reaches the surface. For other
420 vegetated ecosystems where herbaceous plants are the overstory (grasslands and croplands), precipitation partitioning
421 research is also needed.

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425 **Code/Data availability**

426 Data is permanently archived at <https://digitalcommons.georgiasouthern.edu/> and freely available.

427 **Author contribution**

428 DARG conceived and designed the study in consultation with JTVS and AMJCG. DARG designed field collection
429 devices in consultation with JTVS and AMJCG, then deployed devices, collected data, performed the data analysis,
430 and drafted the initial manuscript with input from all authors. BAS contributed expertise regarding relevant range-
431 and pastureland topics, assisting with data analysis/interpretation. SMMS performed a literature synthesis for
432 discussions comparing herbaceous and woody plants' rainfall partitioning and used this synthesis to assist in
433 manuscript writing. JTVS was the principal undergraduate research supervisor for DARG. All authors contributed to
434 manuscript revisions.

435 **Competing interests**

436 The authors have no competing interests.

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600 **Table 1:** Descriptive event statistics for rainfall (observed), overstory throughfall (estimated per Figure N) and
 601 measured individual plant traits. When minimum overstory throughfall was zero, dew occurred – as verified by air
 602 temperatures equalling dew point temperatures.
 603

Parameter (units)	Mean	Median	±SD	Min.	Max.
Rainfall (mm)	16.5	6.6	25.8	0.1	101.3
Overstory throughfall (mm)	11.0	3.5	18.7	0.0	72.2
Canopy radius (cm)	18.3	18.4	4.5	12.2	26.2
Stem radius (cm)	0.5	0.6	0.1	0.3	0.7
Canopy:stem radii	36.3	36.1	7.4	24.1	50.0
Leaf angle at the stem (degrees from vertical)					
1.00 m height	54.0	54.0	2.0	50.5	59.0
1.25 m height	45.9	46.5	3.1	40.5	50.5
1.50 m height	39.6	39.5	1.8	36.0	43.0
1.75 m height	34.0	34.5	2.3	30.0	39.0
2.00 m height	31.9	32.0	2.8	25.0	36.5

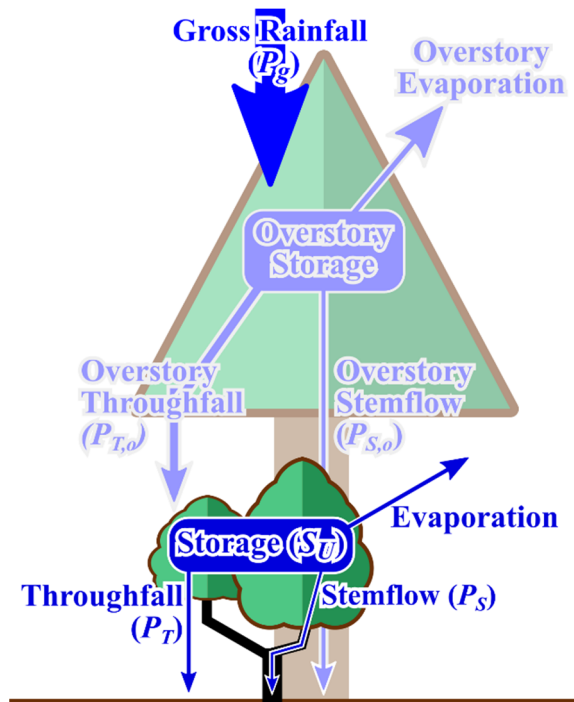
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605 **Table 2:** Descriptive statistics of relative throughfall (P_T) and stemflow (P_S) yield from dogfennel plants expressed
606 as a proportion of gross rainfall (P_g) and estimated overstory throughfall ($P_{T,o}$). Coefficients of variation (CV) and
607 quartile variation (CQV) are also provided. For storms where dew occurred in the understory, dew was not measured
608 by above-canopy P_g gauges, but was included in the estimated $P_{T,o}$ estimate by assuming dew represented at least
609 additional 1.33 mm (i.e., S_u).
610

Parameter	Mean (SD)	Median	Q1	Q3	Max	CV	CQV
Rain storms							
$P_T:P_g$ (%)	43.6 (15.2)	44.9	34.3	52.4	101.7	34.9	20.9
$P_S:P_g$ (%)	18.8 (47.3)	4.1	1.7	13.8	434.3	251.6	78.1
$P_T:P_{T,o}$ (%)	76.6 (29.3)	72.0	58.5	91.1	190.6	38.3	21.8
$P_S:P_{T,o}$ (%)	36.8 (93.5)	7.6	2.8	27.2	900.3	254.1	81.3
Mixed storms*							
$P_T:P_g$ (%)	70.3 (43.7)	58.0	39.5	102.9	149.4	62.2	44.5
$P_S:P_g$ (%)	32.7 (45.2)	14.7	5.2	39.7	198.0	138.2	76.8
$P_T:P_{T,o}$ (%)	72.0 (30.2)	69.1	53.2	86.9	191.6	41.9	24.1
$P_S:P_{T,o}$ (%)	33.4 (86.2)	8.1	3.0	24.3	900.3	257.4	78.0

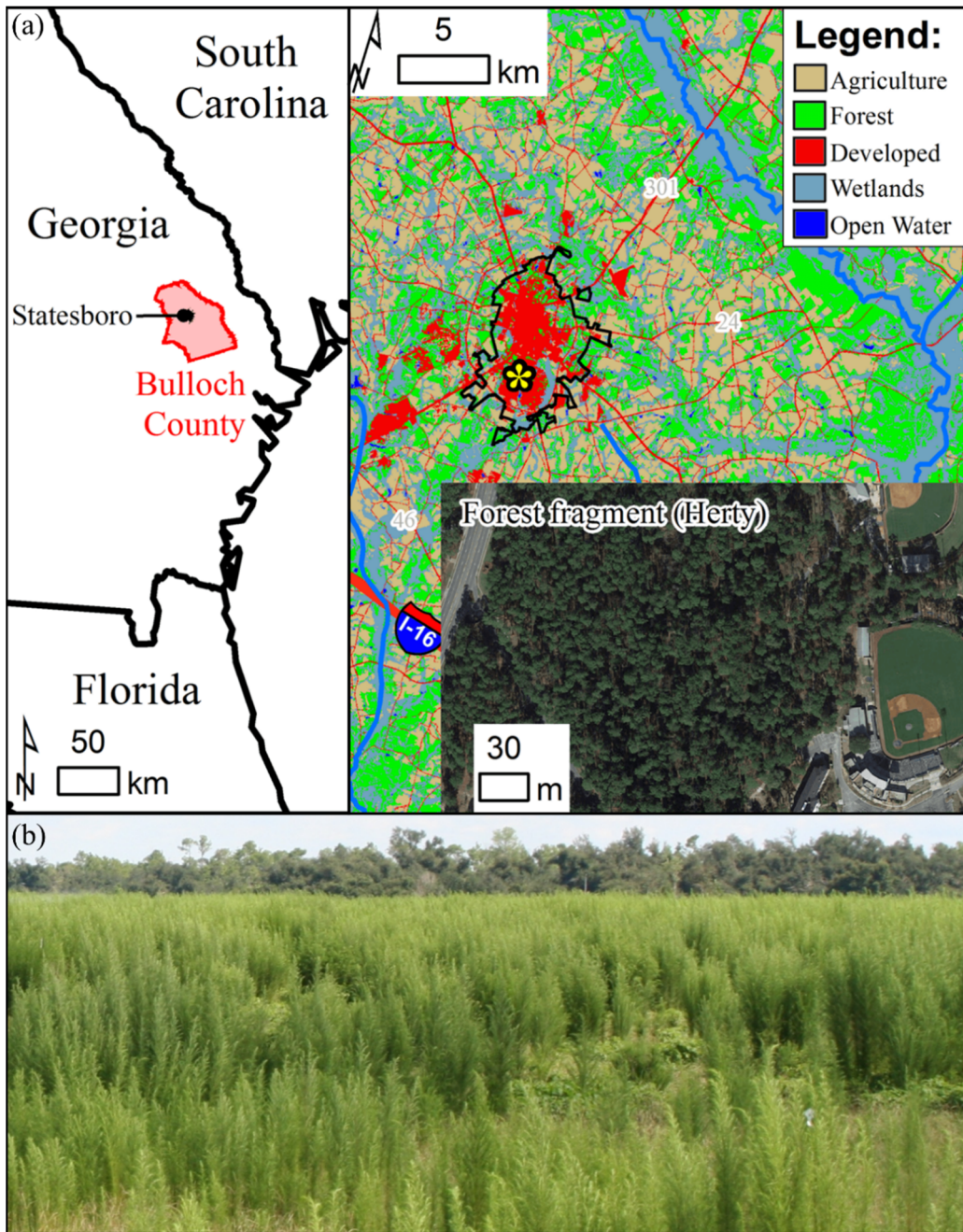
*Storms with occult precipitation.

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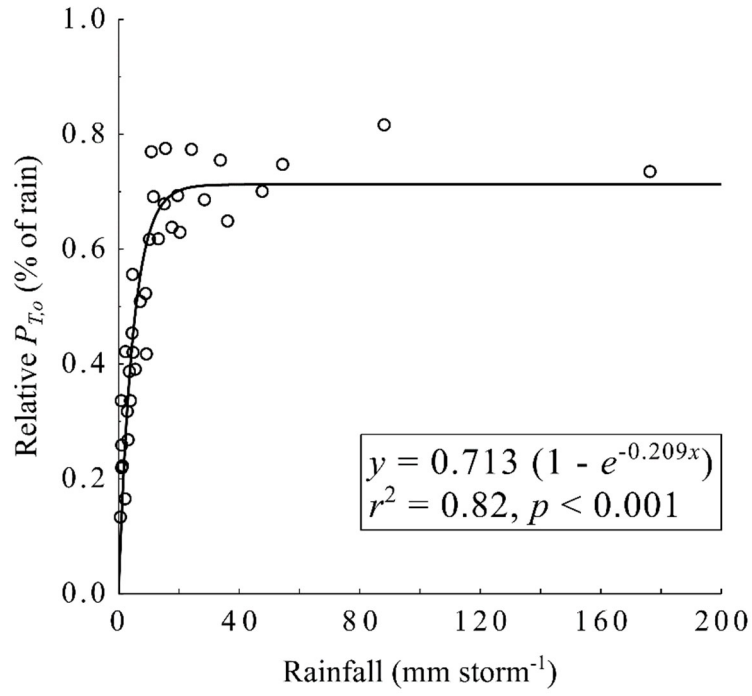


612

613 **Figure 1:** Partitioning of gross rainfall by the overstory (light blue) and by the understory (dark blue). Overstory
 614 throughfall ($P_{T,o}$), the input to the understory canopy, was estimated from past work at the site (see supplemental
 615 materials). In this study, overstory throughfall was modelled ($P'_{T,o}$ per Methods Section 2.2.2.) and maximum
 616 understory water storage capacity (S_U), throughfall (P_T), and stemflow (P_S) were measured.

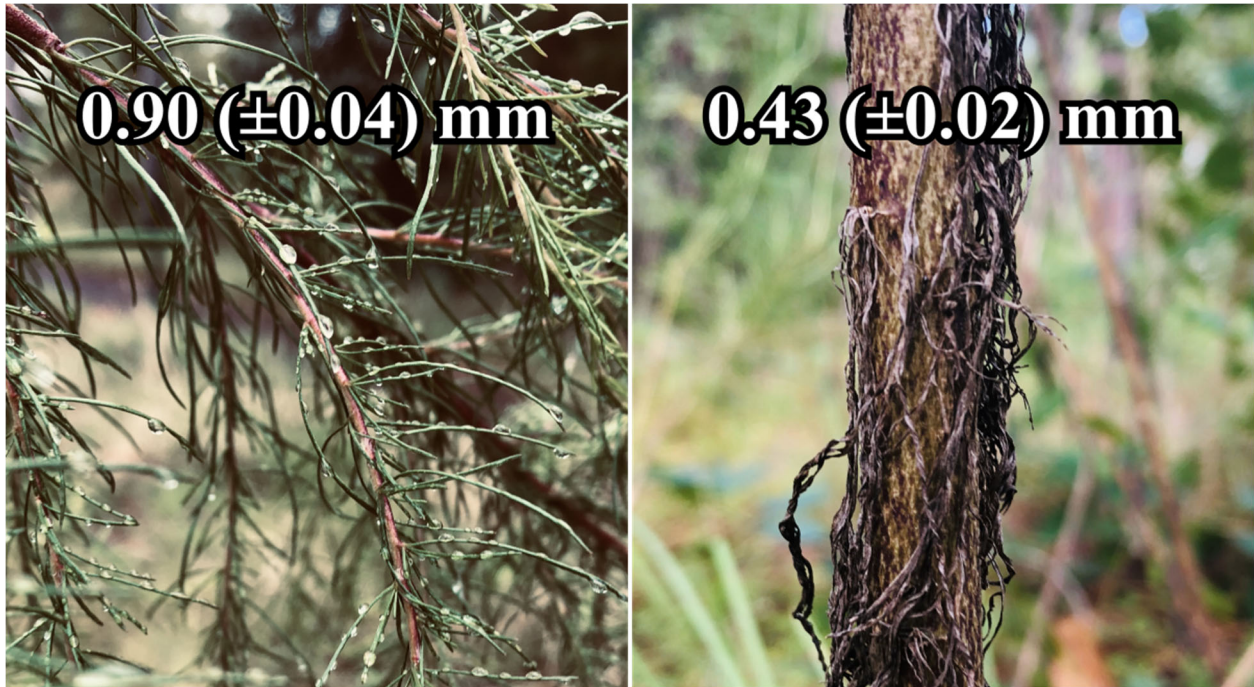


617
 618 **Figure 2:** (a) Location of the studied *Pinus palustris* (longleaf pine) forest fragment, Charles H. Herty Pines Nature
 619 Preserve, on the Statesboro, Georgia (USA) campus of Georgia Southern University, where *Eupatorium capillifolium*
 620 (dogfennel) is a dominant understory plant. (b) Dogfennel can dominate pastures as well, as shown by the photograph
 621 (credit: Brent A. Sellers). Map layer sources: State and county boundaries, and aerial imagery ©ESRI, TomTom North
 622 America, Inc. The land use layer was derived from the National Land Cover Database 2011 (full metadata and data
 623 access link: <https://gdg.sc.egov.usda.gov/Catalog/ProductDescription/NLCD.html>).



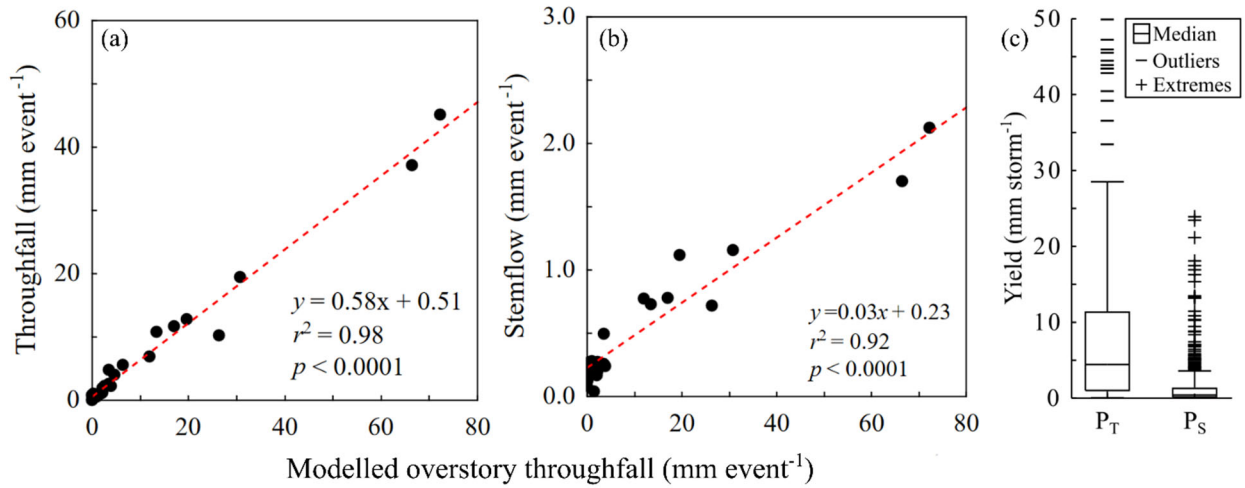
624

625 **Figure 3:** Observed relative overstory throughfall ($P_{T,o}$) in relation to above-canopy rainfall at the study site.



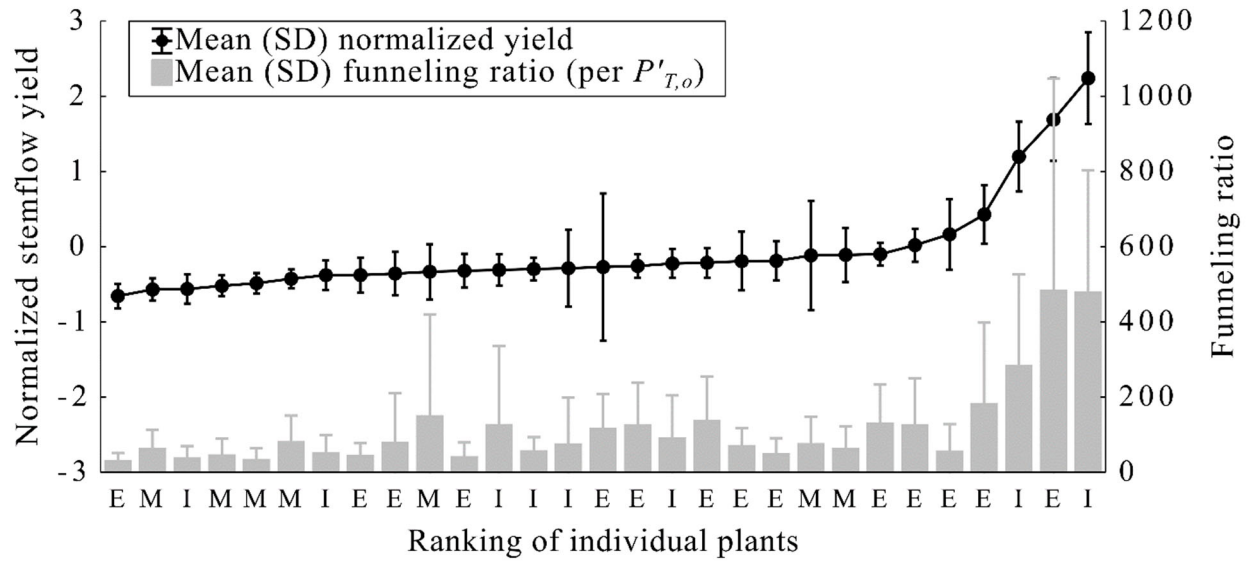
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627 **Figure 4:** Water storage capacity (standard error) for the (left) canopy and (right) stem of *Eupatorium capillifolium*
628 (dogfennel) per lab-based submersion tests on samples collected from the Herty Pines understory.



629

630 **Figure 5:** Scatter plots showing the response of *Eupatorium capillifolium* (dogfennel) (a) throughfall (P_T) and (b)
 631 stemflow (P_S) yields across all rainfall events (without occult precipitation). (c) Boxplot showing yields from
 632 individual P_T gauges and plants' P_S (Line and box: median and interquartile range; whiskers: non-outlier range; other
 633 symbols represent outliers and extreme values).



634

635 **Figure 6:** Mean and standard deviation (SD) of normalized stemflow yield plant⁻¹ and associated funnelling ratio per
 636 Herwitz (1986) and using modelled overstorey throughfall ($P'_{T,o}$) in order of rank per mean normalized stemflow yield.
 637 Plant locations within clusters are indicated (E = external, M = middle, between the interior and exterior, and I =
 638 interior).