RESEARCH ARTICLE

WILEY

Potential for significant precipitation cycling by forest-floor litter and deadwood

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Abstract

The forest-floor litter layer can retain substantial volumes of water, thus affecting evaporation and soil-moisture dynamics. However, litter layer wetting/drying dynamics are often overlooked when estimating forest water budgets. Here, we present field and laboratory experiments characterizing water cycling in the forest-floor litter layer and outline its implications for subcanopy microclimatic conditions and for estimates of transpiration and recharge. Storage capacities of spruce needle litter and beech broadleaf litter averaged 3.1 and 1.9 mm, respectively, with drainage/evaporation timescales exceeding 2 days. Litter-removal experiments showed that litter reduced soil water recharge, reduced soil evaporation rates, and insulated against ground heat fluxes that impacted snowmelt. Deadwood stored $\sim$0.7 mm of water, increasing with more advanced states of decomposition, and retained water for >7 days. Observed daily cycles in deadwood weight revealed decreasing water storage during daytime as evaporation progressed and increasing storage at night from condensation or absorption. Water evaporating from the forest-floor litter layer modulates the subcanopy microclimate by increasing humidity, decreasing temperature, and reducing VPD. Despite the relatively small litter storage capacity (<3.1 mm in comparison to $\sim$10^2 mm for typical forest soil rooting zones), the litter layer alone retained and cycled 18% of annual precipitation, or 1/3 of annual evapotranspiration. These results suggest that overlooking litter interception may lead to substantial overestimates of recharge and transpiration in many forest ecosystems.

KEYWORDS
deadwood, evaporation, forest, interception, litter, precipitation partitioning, storage, water cycle

1 | INTRODUCTION

Interception and retention of precipitation are important for forest ecosystems and their water budgets. While the effects of canopy interception on rates of evapotranspiration and subcanopy precipitation (throughfall) are well known, less attention has been paid to interception and retention processes in the forest-floor litter layer, including forest-floor deadwood and fruit bodies (but see Gerrits & Savenije, 2011; Klamerus-Iwan et al., 2020; Van Stan et al., 2017). Forest floors comprise organic litter at various stages of decay

(e.g. leaves, needles, bark, seeds, deadwood, fruit bodies) and short subcanopy vegetation (e.g. grasses, forbs, mosses and low shrubs) overlying the soil surface (Gerrits & Savenije, 2011). Unlike precipitation intercepted by forest canopies, which is exposed to conditions that can drive rapid evaporation (Stewart, 1977), water intercepted by the forest floor may be retained for longer periods and evaporate more slowly (Baird & Wilby, 1999). Forest-floor litter layers are mostly root-free, and thus, water fluxes are primarily controlled by gravitational forces, direct evaporation and the overall physical storage properties of the litter, rather than plant water uptake (Klamerus-Iwan et al., 2020). Although the absolute volumes that can be stored in the forest-floor litter layer are small (typically a few millimetres), the overall fraction of total annual precipitation that is temporarily retained in this layer, or potentially evaporated from this layer back to the atmosphere, can be significant (Gerrits & Savenije, 2011; Van Stan et al., 2017). This fraction could be especially large in precipitation regimes that are dominated by frequent low-intensity events separated by dry periods. Ultimately, almost all precipitation falling to the forest floor must travel through the litter layer, so storage, transport and evaporation processes taking place there can alter total evapotranspiration fluxes, plant-available water dynamics and the rates and chemical composition of soil water recharge. The key questions are: How large are litter layer storages, how long can they store, evaporate and release water, and thus how important are they for the forest water cycle?

Whereas canopy interception losses have been characterized across numerous forest sites (Yue et al., 2021), only a few previous studies have evaluated the storage and retention capacity of the forest-floor litter layer, and most of these studies have been focused on the leaf component (e.g. Gerrits & Savenije, 2011; Klamerus-Iwan et al., 2020). Laboratory experiments on forest litter samples have been conducted to quantify their water storage properties (e.g. Guevara-Escobar et al., 2007; Ilek et al., 2021; Li et al., 2013; Putuhena & Cordery, 1996; Sato et al., 2004; Walsh & Voigt, 1977). Fewer studies (to our knowledge) have measured the water retention capacity of litter in situ (e.g. Brechtel, 1969; Gerrits et al., 2007; Schaap & Bouten, 1997; Thamm & Widmoser, 1995). Likewise, only a few studies have characterized and measured water cycling through deadwood, bark or fruit bodies (e.g. Błońska et al., 2018; Harmon & Sexton, 1995; Levia et al., 2004; Van Stan et al., 2017; Woodall et al., 2020), although those studies found deadwood to be a potentially large and important storage in the forest water cycle. Deadwood has been estimated to be approximately 34 m³ per hectare (Lachat et al., 2019) or 3.5%–5.6% of total Swiss forest biomass (Hararuk et al., 2020), with substantial increases in recent decades due to changes in forest management (Lachat et al., 2019).

There is need for better estimates of how much, and for how long, water is stored in litter and deadwood of different types and decay conditions, as well as further research on how litter influences evaporation, energy balance and microclimate. In this paper, we report on a series of field and laboratory experiments to quantify forest-floor water fluxes in a temperate mixed forest, guided by two main research questions:

1. How much water is retained in the various forest-floor litter types (i.e. leaves, needles, spruce cones, deadwood), and for how long?
2. How does this litter layer storage affect the forest water cycle, that is, how does it affect rates of soil water recharge and subcanopy evaporation, and what are its implications for humidity, temperature and vapour pressure deficit in the subcanopy atmosphere?

2 | STUDY SITE AND METHODS

Our research site is located in an experimental forest in Zurich, Switzerland, recently established as part of the 'Waldlabor Zurich' initiative (www.waldlabor.ch). The Waldlabor ('forest laboratory' in German) is a 1.5-km² temperate mixed forest area at the edge of the city, with a mean annual temperature of 9.3°C and mean annual precipitation of 1134 mm. Our research site is situated in the 0.3-km² Holderbach catchment at the eastern edge of the Waldlabor, at a mean elevation of 510 m a.s.l. Since March 2020, we have measured all relevant climate variables approximately 150 m outside the forest with a compact all-in-one weather station (Meter Group: Atmos41), as well as temperature and relative humidity (using Sensirion SHT31 sensors) at different heights on two towers within the forest, all at 10-min resolution (see Figure 1). These small towers are located under spruce (Tower 1) and beech canopies (Tower 2), where we measured relative humidity and temperature at heights of 20, 95, 170, 245, 320, 395, 470 cm, and 50, 100, 200, 400 cm, respectively.

2.1 | Laboratory estimation of litter storage capacity

We estimated the storage and retention behaviour of the forest-floor litter layer both in the laboratory and in situ. In laboratory saturation experiments, we filled 63-μm-mesh laboratory sieves (area of 0.0308 m²) with a 5 cm layer of broadleaf litter or a 2.5 cm layer of needle litter (both collected from the site), dried them at 70°C for 24 h and measured the dry weight, as suggested in Carnol and Bazgir (2013). The thickness of the litter layer corresponds to the mean thickness across our field site, as estimated from collected grab samples. We then submerged the sieves with litter into water for 24 h, let the water drain gravitationally and then weighed the sieves after 30 min and again after 4 h to calculate the litter's water retention capacity (Li et al., 2013; Sato et al., 2004). During these steps, the litter was not removed from the sieves to preserve the litter structure and the water captured within it. We then removed the litter from the sieve and weighed the sieve to account for water that was captured in the sieve itself (Helvey & Patric, 1965). Afterwards, the litter was again dried at 70°C for 24 h to verify the conservation of the original dry mass of the leaf litter. This procedure was repeated for 40 samples each of broadleaf and needle litter. To evaluate the impact of litter layer thickness and structure, we also measured the retention capacity
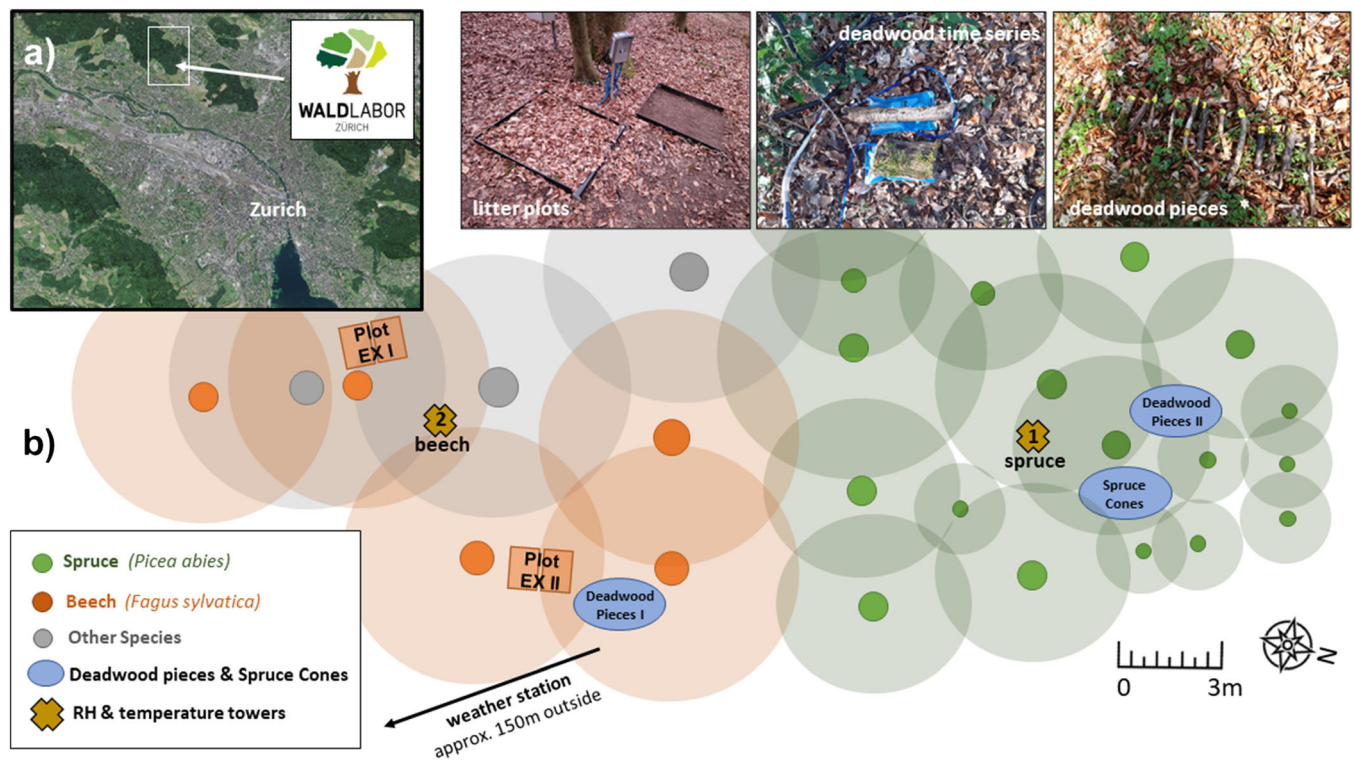
FIGURE 1 Location of the 'Waldlabor Zürich' in Zurich (a) and a schematic of our experimental site at its eastern border (b), indicating the locations of trees (spruce, beech and other species shown in green, orange and grey, respectively), two litter plots (orange squares EX I and EX II), the monitored deadwood pieces and spruce cones (blue ovals) and the small temperature/relative humidity towers (yellow crosses). The weather station is located outside the forest, approximately 150 m from our experimental site.

of doubled and quadrupled litter thicknesses (10 and 20 cm for broadleaf litter layer and 5 and 10 cm for needle litter), with four replicates each.

2.2 | Field estimation of litter storage and retention dynamics

In a second experiment, samples of litter were collected before and after precipitation events and weighed in situ to assess the litter layer retention capacity. We used standard coffee filters to collect broadleaf and needle litter grab samples of approximately equal volume at different time steps after precipitation events (see Figure S1 for pictures of the procedure). Coffee filters are well suited for this purpose, as they retain the drip water of the litter with only minor losses, and they also can be dried in the oven with the litter inside. For three rainfall events we took 20 broadleaf and 20 needle litter samples for at least four timesteps: before the event, 2 h after the event, 24 h after the event and around 40–48 h after the event. We weighed the samples directly on site and dried them for 24 h at 70°C as suggested in Carnol and Bazgir (2013) to evaluate the water content for each sample. In a third experiment, we measured soil moisture at two pairs of 1×1 m plots at 10 and 30 cm depths to evaluate how water retention in the litter layer affects soil–water content dynamics. Each pair had one plot covered with the naturally present broadleaf-litter layer, and one plot from which we regularly removed all litter. Volumetric water content in the soil was measured with 5TE dielectric permittivity sensors and recorded using EM50 Loggers (formerly Decagon, now Meter Group). The sensors were installed in the middle of each plot to minimize boundary effects. Data were recorded at 10-min intervals.

2.3 | Field estimation of deadwood and spruce-cone storage and retention

We estimated the storage and retention behaviour of individual forest-floor deadwood pieces and spruce cones in several different ways. First, we monitored the variations in water content over time in pieces of deadwood using four self-made pressure cushions, constructed from a standard drinking-water bladder with a hose to which we attached a pressure sensor (Keller DCX-22AA). On top of each pressure cushion, we placed pieces of deadwood from 95 to 222 g dry weight at different states of decay (inferred qualitatively) and recorded the pressure at 10-min resolution. From the recorded absolute pressure, we subtracted the atmospheric pressure measured on-site and then normalized between 0 and 1 by the minimum and maximum of each sensor, respectively (since the

measurement is inherently relative rather than absolute, because the relationship between pressure and deadwood weight is determined by the contact area between the deadwood piece and the pressure cushion, which cannot be controlled). A replicate pressure cushion with no deadwood showed virtually no variations in pressure, confirming that the pressure variations observed under the deadwood pieces could be attributed to changes in deadwood weight.

In a second experiment, we selected 40 pieces of deadwood with dry weights of 6.2–88.5 g (median = 20.2 g) and 20 spruce cones with dry weights of 15.8–36.4 g (median = 24.9 g) in different states of decay. Their weights were measured daily at the same time of day (always between 2 and 3 PM) for >8 weeks from 20 March to 22 May 2020. A major difference from the samples for which weights were measured continuously is that these manually measured deadwood pieces had direct contact with the forest floor and thus could absorb water from the soil or adjacent litter particles. After the experiments, all deadwood samples from the experiments described above were fully saturated and weighed (submerged for 24 h) and then dried and weighed (multiple days at 105°, until no weight difference was measured) in the laboratory to assess the maximum storage capacity of the individual deadwood pieces. We repeated these experiments to test the reproducibility of the saturation and drying steps; results presented here are the mean values from both experiments. To assess the effect of deadwood size, we additionally repeated the evaluation of maximum water storage with 30 larger deadwood pieces that were not used in the routine measurement experiments. The state of decay of the deadwood was categorized qualitatively as high, intermediate or low, assessed by 'pocket knife testing' similar to what was described by Robin and Brang (2008): We considered decay to be low if one can superficially cut only a few millimetres into the deadwood surface, intermediate if the knife can be pushed directly into the wood easily at some locations and high if the deadwood is easily friable by the pocket knife and it readily disintegrates.

3 | RESULTS AND DISCUSSION

3.1 | Maximum water storage in the forest-floor litter layer

First, we assessed the maximum storage capacity of the two dominant litter types, collected underneath beech and spruce trees, in laboratory saturation experiments (n = 40 for each litter type). The broadleaf litter below beech trees (*Fagus sylvatica*) could store approximately 4.7 times its dry weight, and the needle litter below spruce trees of *Picea abies* species could store up to 2.4 times its dry weight (Figure 2). Sensitivity analyses with thicker litter layers (doubled and quadrupled, n = 4 for each condition) yielded similar results, implying that storage capacities scaled linearly with depth: The maximum storage, averaged over four experiments, was 3.9 and 4.2 times the dry weight, respectively, for doubled and quadrupled
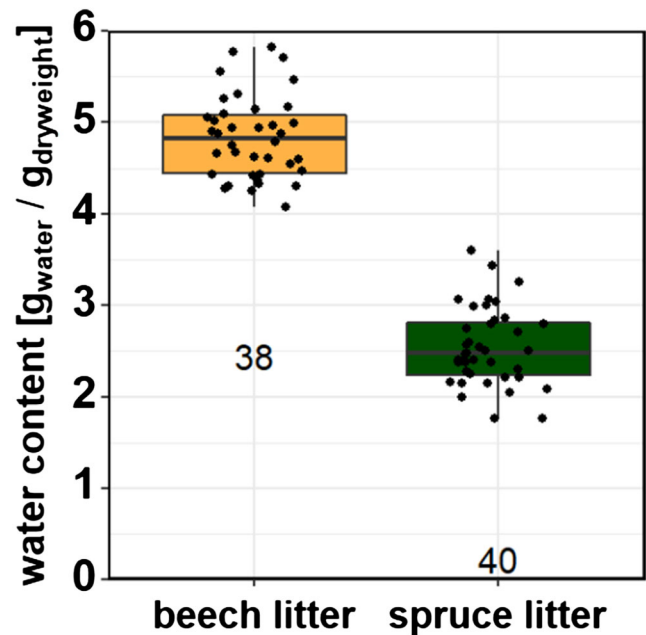
FIGURE 2 Maximum saturation of broadleaf litter (beech, *Fagus sylvatica*) and needle litter (spruce, *Picea abies*) from laboratory saturation experiments (n = 40 for each litter type). The maximum storage capacity of broadleaf litter is approximately two times higher than that of needle litter.

F. sylvatica litter and 1.8 times the dry weight for both doubled and quadrupled *P. abies* litter.

3.2 | Water retention in the forest-floor litter layer

The timescales of water retention in the litter layer reflect evaporation and drainage dynamics. We assessed the retention dynamics of broadleaf and needle litter by grab samples taken before, during and after precipitation events, as well as from litter-removal plot experiments. Grab samples taken through three moderate-intensity precipitation events (5.8, 7.5 and 8.8 mm) indicate that rainfall is retained in the forest-floor litter layer for approximately 40–48 h before the litter water content returns to pre-event levels (Figure 3). Retention timescales for saturated litter may be even longer, because in all cases except one (spruce in Figure 3a), the peak storage in our grab samples was less than half of the maximum storage capacity as estimated by the laboratory experiments (dashed lines in Figure 3).

The retention capacity of forest-floor litter was also assessed by monitoring changes in the water content of the underlying soils in two pairs of 1 m² plots, each pair consisting of one plot with a broadleaf litter layer and one plot where we removed the litter regularly (see Figure 4a). Qualitatively, soil sensors at 10 cm depth in the litter-covered plots detected fewer precipitation events, as indicated by fewer soil-moisture responses to rainfall in the black and grey lines (10 cm depth—with litter) in Figure 4b. Losses from evaporation and drainage, however, appeared larger in the plots without litter, as
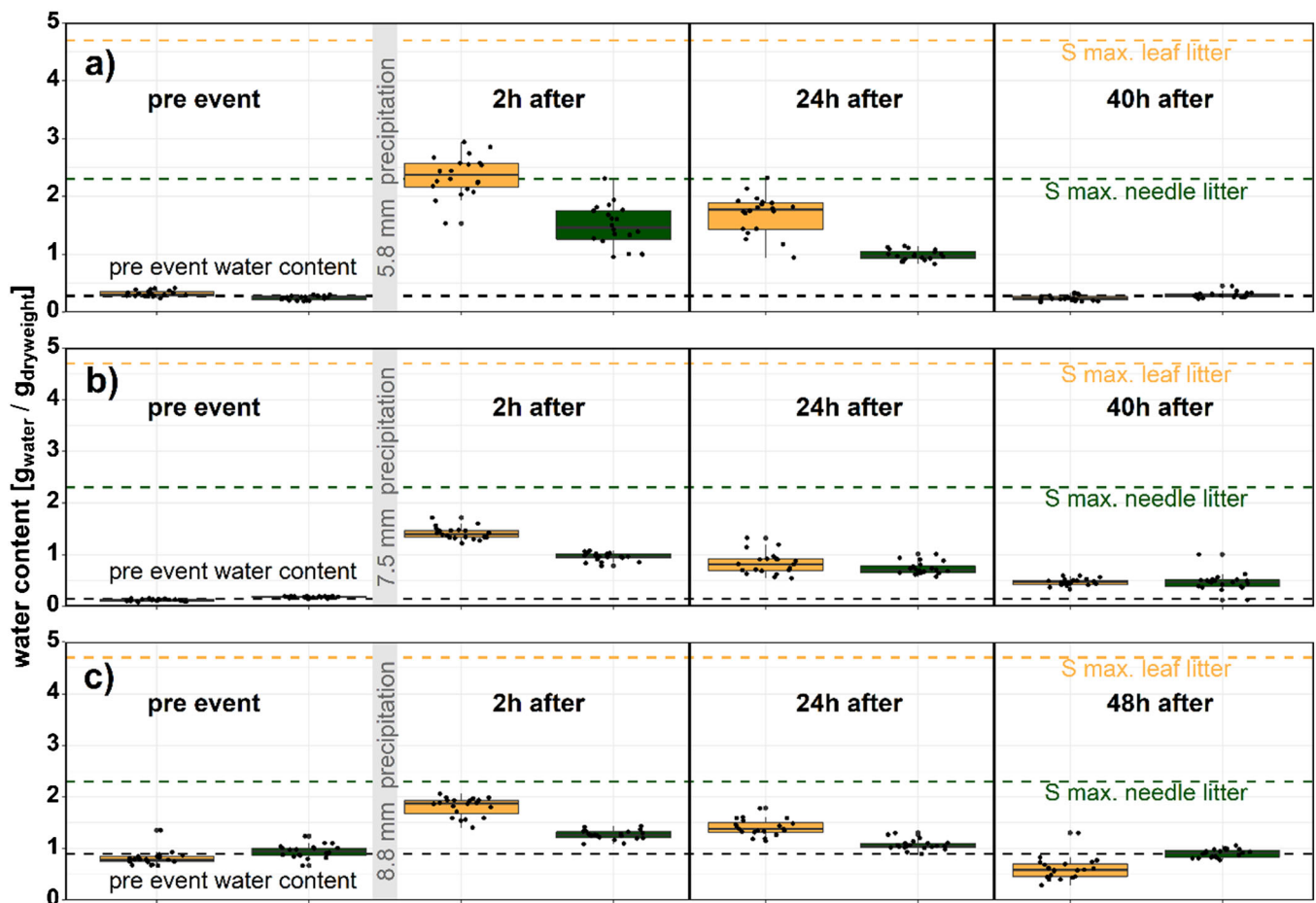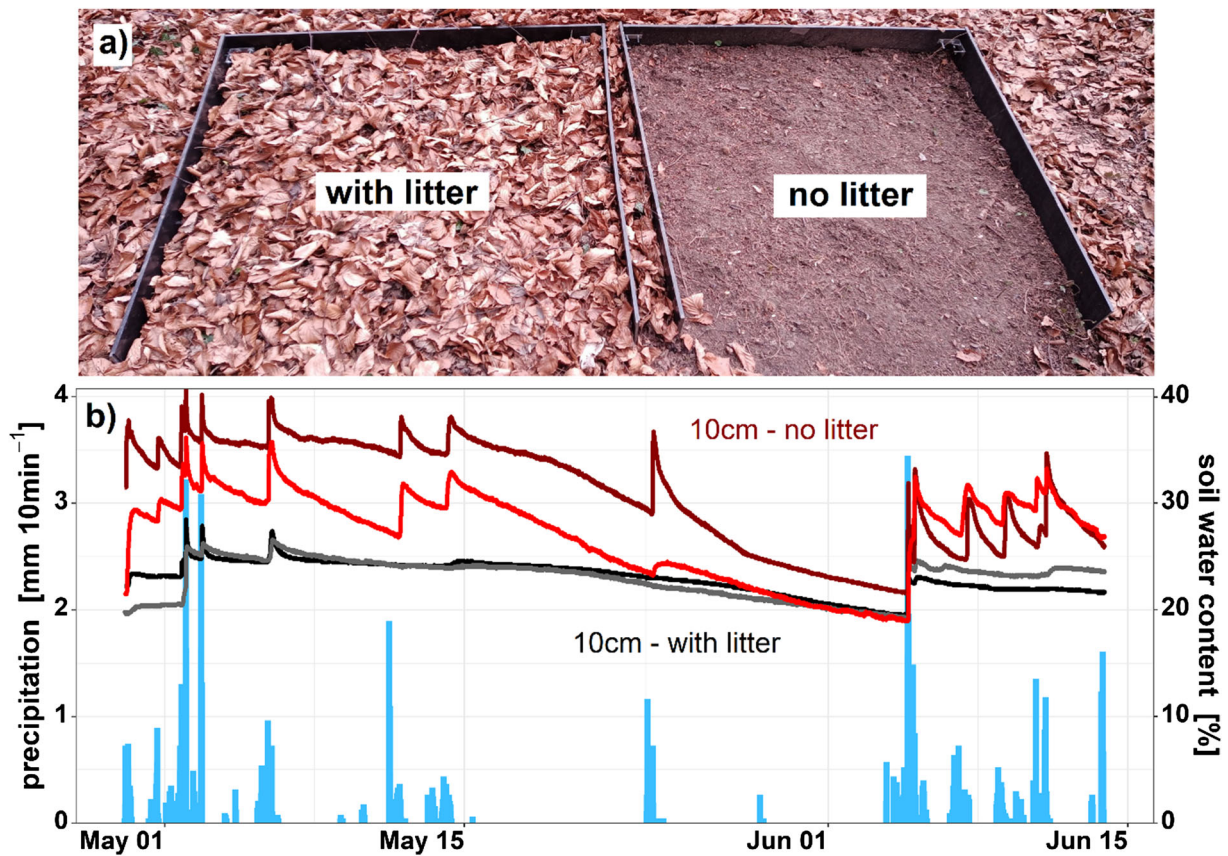
FIGURE 3 Water retention in the forest-floor litter layer after three precipitation events of 5.8 (a), 7.5 (b) and 8.8 mm (c), estimated from grab samples of broadleaf (beech) and needle (spruce) litter (orange and green, respectively) at different timesteps before and after the precipitation event ($n = 20$ for each timestep in each event). The litter retained precipitation for up to 48 h, despite starting at less than half of saturated water content (indicated by the dashed lines). Water content at 40 or 48 h can be less than the pre-event water content, because the pre-event samples were not completely dry.

suggested by the steeper soil-moisture recession (see the red line in Figure 4b) during two periods without precipitation in May 2020. The observations in Figure 4, spanning 29 April until 13 June 2020, were used to estimate the soil water balance within the plot by assuming that the water content at 10 cm depth was representative for the 0–10 cm soil layer. During the observation period, the forest received 180 mm of total precipitation (measured at a weather station outside the forest boundary). The measured fluctuations in soil water content suggest that infiltration to 10 cm depth in the litter-free and litter-covered plots totalled approximately 69 and 26 mm, respectively, implying that roughly 43 mm (or roughly 24% of ambient precipitation) was intercepted and evaporated from the litter layer (assuming that throughfall fluxes to the adjacent pairs of plots were similar). The fluctuations in soil water content also suggest that roughly 73 and 26 mm of water infiltrated or evaporated from the soil in the litter-free and litter-covered plots, respectively (not counting evaporation from the litter layer itself). These observations suggest that the litter layer inhibits both recharge to, and evaporation from, the underlying soil.

3.3 | The storage and retention capacity of forest-floor broadleaf versus needle litter

The median storage capacity (Figure 2) of broadleaf litter was roughly a factor of two higher than that of needle litter, when expressed as a multiple of dry weight (4.8 ± 0.7 g per g dry weight and 2.5 ± 0.4 g per g dry weight, respectively). Similarly, several previous studies have also found that broadleaf litter had a larger storage capacity compared to needle litter. Walsh and Voigt (1977), Sato et al. (2004) Li et al. (2013) and Ilek et al. (2021) found that the storage capacity per unit dry weight of broadleaf litter was higher than that of needle litter by factors of up to 1.6, 1.8, 2.65 and 1.4 respectively. In general, the larger storage capacity in broadleaf litter compared to needle litter can be related to structural differences between the two litter types (Klamerus-Iwan et al., 2020; Li et al., 2013). The broadleaf litter layer tends to have a higher storage capacity due to sink effects (water drops retained in depressions on the leaf surfaces) occurring on individual leaves. The broadleaf litter also has a higher surface area to weight ratio compared to the needle litter

FIGURE 4 Plot experiments with and without a broadleaf litter layer (a) showing soil-moisture measurements at 10 cm depth in two litter-covered plots (black and grey lines) and two plots without litter (red lines) (b). Water retention in the forest-floor litter layer reduces the amount of precipitation that reaches the soil at 10 cm depth, as indicated by the much smaller increases in soil moisture following precipitation events. The litter layer also appears to reduce the rate of soil evaporation, as indicated by the smaller decreases in soil moisture between precipitation events.

(Walsh & Voigt, 1977). The differences between broadleaf and needle litter storage capacity revealed by our laboratory experiments are further supported by the event-scale grab sampling (Figure 3), where for most experiments we observed more water stored in the broadleaf litter compared to the needle litter (when expressed as a multiple of dry weight). The maximum storage capacity of different litter types from several studies has been reviewed by Gerrits and Savenije (2011). It should be noted that some of these studies found no large differences between broadleaf and needle litter storage capacity or found needle storage capacity to exceed broadleaf storage capacity. For example, Putuhena and Cordery (1996) reported a broadleaf and needle litter storage capacity of 1.7 and 2.8 g per g dry weight, respectively, and Zhou et al. (2018) reported that coniferous litter storage capacity was 2.1 times larger than broadleaf litter storage capacity. However, these studies used a different experimental protocol based on sprinkling experiments instead of saturating the litter by submerging it. Zagyvai-Kiss et al. (2019) found a similar water holding capacity in beech and spruce litter (2.02 g per g dry weight and 2.09 g per g dry weight, respectively). We also speculate that there may be differences in broadleaf and needle litter storage capacity, beyond those attributable to methodology, that relate to species,

age, morphology and decay state, which all contribute to the variability observed in nature and in previous data.

The approximate timescales of water storage following the three rainfall events, ~2 days, were similar for both litter types. However, retention timescales for saturated litter may be even longer, because in all cases except one (spruce in Figure 3a), the peak storage in our grab samples was less than half of the maximum storage capacity as estimated by the laboratory experiments (dashed lines in Figure 3). Even these less-than-half-saturated grab samples retained moisture longer than the typical retention timescale of canopy interception of <2 days (Gerrits et al., 2010). The laboratory experiments for the assessment of maximum storage capacity revealed that 4 h after maximum saturation, the broadleaf litter had already lost 20% of its stored water, compared to only 9% for the needle litter.

We also tested the effect of layer thickness on the litter storage capacity and found that the thickness of the litter layer does not affect the unit storage capacity (per mass of litter), implying that storage capacity scales with litter mass independent of depth. A similar linear relation between mass of litter and storage capacity has also been reported in previous studies (Li et al., 2013; Pitman, 1989; Putuhena & Cordery, 1996; Sato et al., 2004). Sato et al. (2004) even

tested the impact of layer thickness by experimentally compacting the litter layer and found no differences in storage capacity.

Water retention in the litter layer is also reflected in our measurements of soil moisture below plots with and without litter. Fluctuations in soil moisture suggest that soils at 10 cm depth below the litter-free plots received approximately 2.7 times more infiltrated water from precipitation over a period of 6 weeks with 180 mm of precipitation. We hypothesize that this difference reflects interception and evaporation of throughfall by the litter layer. However, the overall impact on the soil water balance may be small, because the differences in recharge appear to be offset by differences in soil evaporation, with fluctuations in soil moisture suggesting 2.8 times greater losses to soil evaporation (and/or percolation) in the litter-free plots.

3.4 | Daily cycling of water in forest-floor deadwood

We used four self-made pressure cushions to observe temporal variations of water content in pieces of deadwood. Daily fluctuations in deadwood weight (Figure 5) were inversely related to vapour pressure deficit (VPD), indicating that the deadwood pieces gained moisture from the air during the night (when VPD was relatively low) by condensation or absorption and lost water to evaporation during the day (when VPD was relatively high). These daily cycles were superimposed on increases in deadwood moisture following rain events and longer-term declines in deadwood moisture during dry spells between rain events (Figure 5). The lowest relative weights were generally measured between 2 PM and 4 PM, and the highest weights (on non-rainy days) were generally measured around 6 AM. VPD varied approximately inversely to deadwood weight, reaching its maximum around 2 PM. The temporal patterns of water content were consistent across all four pieces of deadwood (Figure 5).

3.5 | Water storage and retention capacity in forest-floor deadwood (and spruce cones)

We assessed the water storage dynamics of 40 pieces of deadwood (divided between two sites, one under beech and the other under spruce canopies; see Figure 1b) and 20 spruce cones (only under spruce canopy) by weighing them daily for 8 weeks. The temporal patterns of water retention capacity and the timescale of water storage recession were broadly similar for deadwood (at both sites) and for the spruce cones, as indicated by the boxplots in Figure 6. The median storage capacity of deadwood pieces is 1.7 times their dry weight, and for spruce cones is 1.3 times their dry weight. Overall, deadwood—even when not fully saturated—retains moisture for more
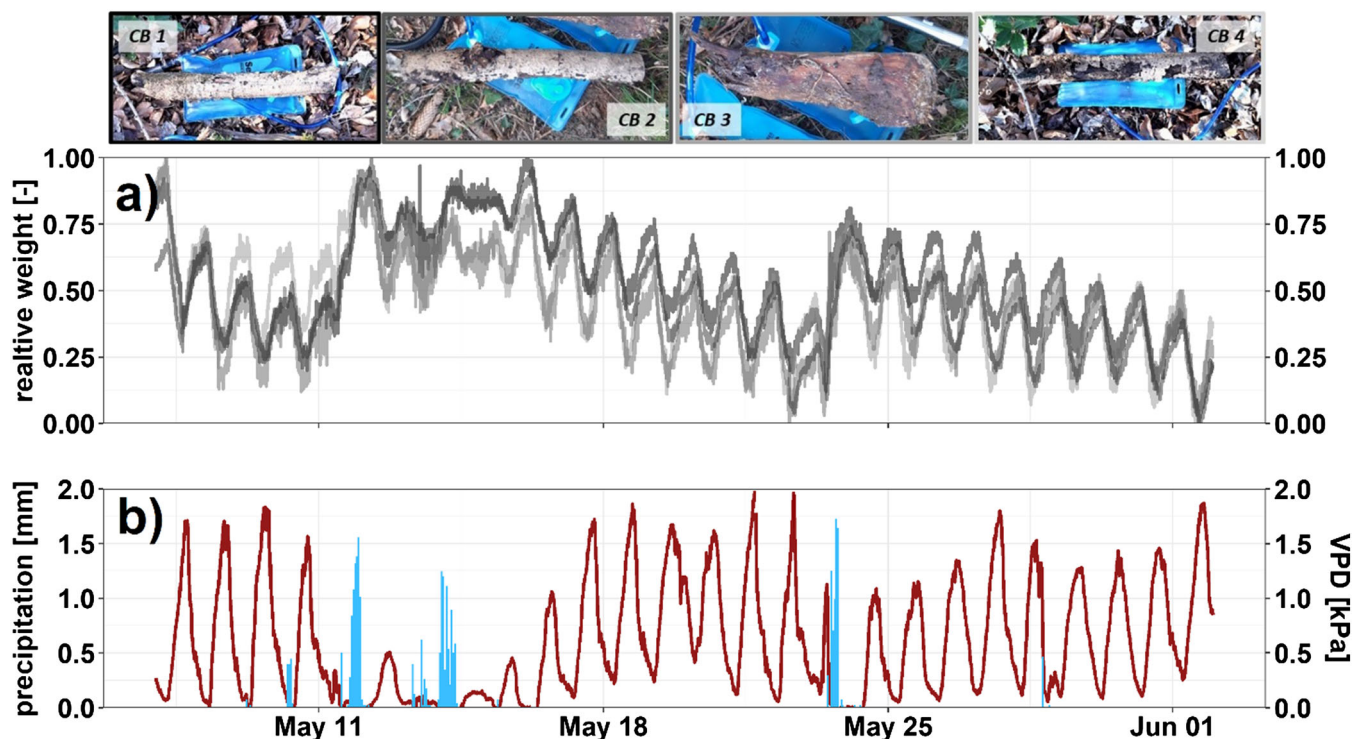
FIGURE 5 Daily fluctuations in deadwood moisture content (grey lines), measured by pressure cushions for four deadwood pieces (CB1–CB4), normalized between 0 and 1 (a), compared to precipitation events (blue bars) and daily variations in vapour pressure deficit (VPD; red line) (b). Deadwood absorbed moisture from the air during the night, when VPD was low, and evaporated moisture to the subcanopy atmosphere during the day, when VPD was high.
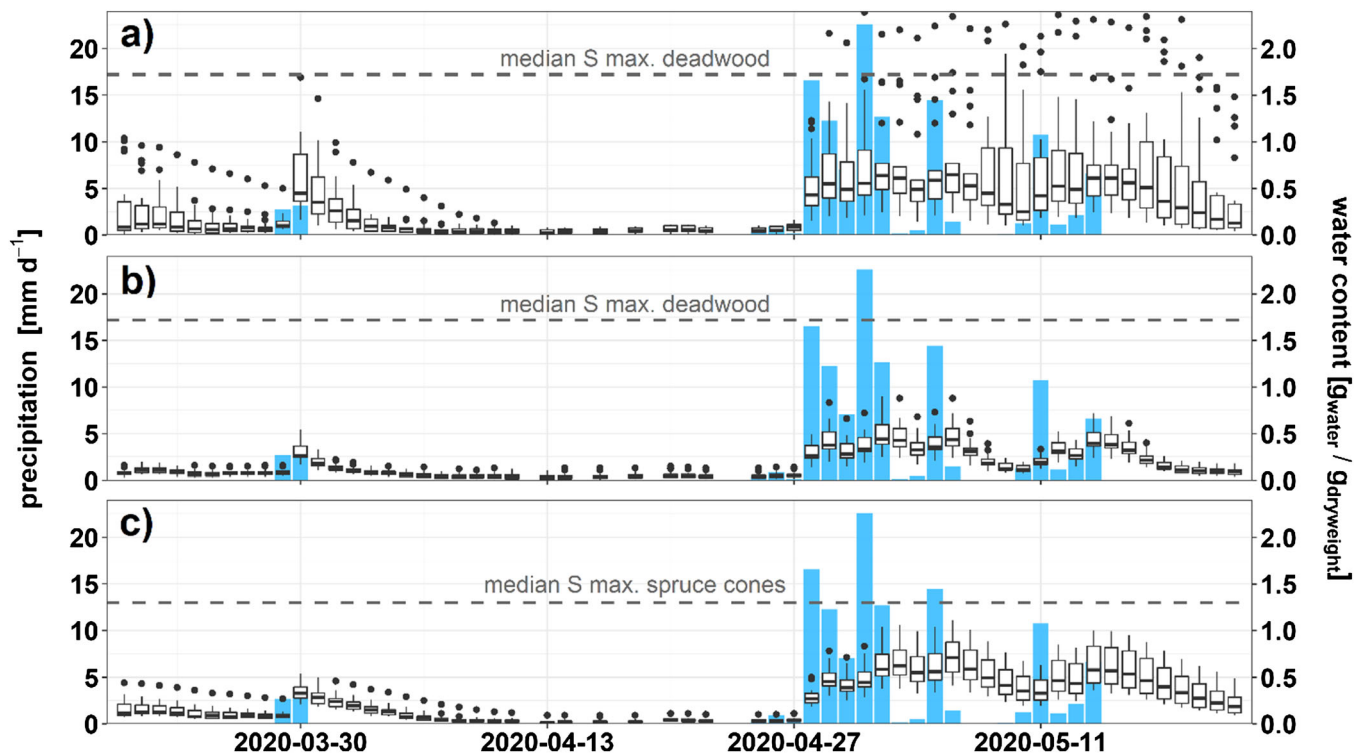
FIGURE 6 Ten weeks of daily measurements of deadwood weights (at two sites) and of spruce cone weights. Each boxplot shows the statistics of 20 measurements. In the background, we show the daily precipitation sums (light blue columns).

than 7 days, and spruce cones retain moisture over even longer time periods, as indicated by the duration of declining water content values in Figure 6. The mean time between the highest saturation following each precipitation event, and the time when 50% of the moisture was lost, was approximately 2.5–3.5 days for deadwood and 3.5–4.5 days for the spruce cones.

We assessed the relationship between deadwood weight and maximum storage capacity in laboratory measurements with 76 deadwood pieces at different levels of decay (low–intermediate–high; Figure 7). The median storage capacity of deadwood was around 1.7 times the dry weight, but storage capacities were markedly higher at more advanced states of decay (1.5 ± 0.1, 2.5 ± 0.4 and 4.4 ± 0.6 g per g dry weight for low, intermediate and high decay, respectively; $n = 36$, 30 and 10). Similar values were reported in the HJ Andrews forest by Harmon and Sexton (1995), with maximum storage capacities of 3.5 times the dry weight. The influence of deadwood decay on water storage was expected because decay separates wood fibres, decreases wood density and consequently increases the porosity (Błońska et al., 2018; Paletto & Tosi, 2010; Pichler et al., 2012; Sexton & Harmon, 2009). The specific water storage capacity (g water/g dry wood) was not related to the thickness of the deadwood pieces, but only to their state of decay. We did not account for differences in wood type, or bark and moss water storage, which might also affect deadwood storage capacity (e.g. Błońska et al., 2018; Thielen et al., 2021; Van Stan et al., 2016). We also assessed the storage capacity of spruce cones (Figure 6c) and found that their median storage capacity (1.30 g water/g dry weight) was
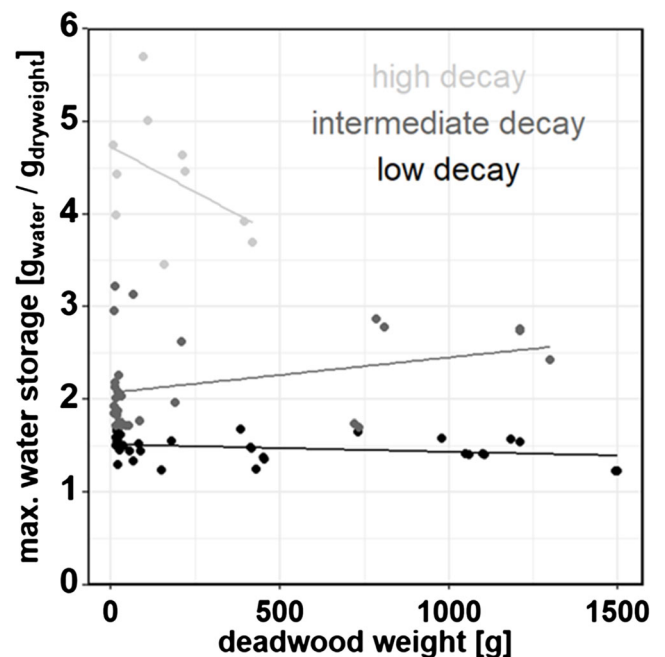
FIGURE 7 The relation of deadwood weight and maximum water storage for 76 deadwood pieces with different levels of decay (low–intermediate–high). Note that the regression lines indicate the general direction of the relationship and not its statistical significance.

lower than that of deadwood. This result contrasts with previous studies for other forest fruiting bodies (sweetgum, pine cones) that stored more water (Levia et al., 2004; Van Stan et al., 2017).

The overall timescale over which water was stored in the deadwood can only be roughly estimated from our experiments. From the daily measurements of relatively small pieces of deadwood that never were close to their potential maximum saturation, we found a water retention timescale of at least 7 days (Figure 6). However, the time series from the longer-term experiments suggest that larger pieces may store water for much longer timescales (Figure 5).

Forest-floor deadwood may be important in water cycling beyond its obvious role in directly retaining precipitation. Deadwood pieces lying on the forest floor may actively contribute to water cycling from the underlying soil and litter layer to the atmosphere, if the capillary forces of the deadwood structures are larger than those of the forest top soil layer or compounds of the litter layer, such that these deadwood pieces will take up water from the underlying soil and litter. In this scenario, deadwood may increase soil and litter evaporation rates by wicking water from soil and litter upwards to the atmospheric interface.

We observed daily fluctuations in deadwood water content with the pressure-cushion experiments (Figure 5), consistent with deadwood taking up atmospheric water (i.e. dew, fog, humidity) whenever the VPD is smaller than the capillary forces of the deadwood (i.e. during nighttime) and evaporating water when VPD is higher (i.e. during daytime). It should be noted that in these measurements, the wood was not lying directly on the forest-floor litter or soil, but on the pressure cushions. Given the water storages and flux modulation introduced by the litter layer, we hypothesize that the litter layer may function as a moisture battery, buffering (and generally increasing) subcanopy microclimatic humidity.

3.6 | Effect of litter layer evaporation on subcanopy microclimate

Forest canopies modulate the spatial and temporal input of precipitation (Levia & Frost, 2006; Staelens et al., 2006); they also create a within-forest microclimate by inhibiting exchange between subcanopy air masses and the above-canopy atmosphere. To monitor vapour transport to and from the forest floor, we recorded relative humidity and temperature with two small towers, one surrounded by spruce trees (Tower 1, up to 4.7 m) and the other surrounded by beech trees (Tower 2, up to 4 m). Figure 8a shows the temporal variations in absolute humidity at ~2 m height, relative to the humidity at the lowest monitored level (0.2 and 0.5 m at Towers 1 and 2, respectively). The scale is inverted so that negative humidity gradients (i.e. lower absolute humidity at ~2 m height than at the near surface, consistent with evaporation from the surface into the subcanopy atmosphere) are plotted as upward fluxes. From Figure 8a, one can see that, unsurprisingly, humidity gradients above the forest floor are stronger during daytime, synchronized with the daily cycle in subcanopy air temperature. This pattern is also consistent with the daily variations in deadwood weight shown in Figure 5; humidity gradients above the forest floor are stronger during daytime, when VPD is relatively high and

deadwood weights are declining, consistent with water loss to evaporation. The height profiles in Figure 8b–e show average daytime (8 AM to 7 PM) absolute humidity and VPD for April through July, expressed relative to the near-surface values for each tower. Consistent with turbulent exchange of water vapour fluxes originating from the litter layer (and potentially also the underlying soil), humidity decreases, and VPD increases, non-linearly with height above the forest floor.

3.7 | Thermal heat shielding of the forest-floor litter layer

The forest-floor litter not only modulates water fluxes but also affects energy fluxes, with potential effects on snow cover and melt dynamics. During winter 2020–2021, we observed that snow melted more quickly on the litter-free plots compared to the litter-covered plots (Figure 9b). The following winter, we used infrared thermometry to compare the surface temperatures of a litter-covered and adjacent litter-free plot on a snow-free December day with overcast skies and temperatures below freezing (thus minimizing the effects of radiative heating and evaporative cooling). Surface temperatures in the litter-free plot were approximately 1–2°C higher than in the litter-covered plot (Figure 9c). This could reflect the insulating effects of the litter layer; however, the differences could also result from other measurement effects, for example, the difference in infrared diffusivity between the two plots.

Our observations suggest that the litter layer affects forest-floor temperature dynamics and associated heat fluxes. In previous research (Floriancic et al., 2018), we showed that snowmelt from geothermal heat fluxes might account for up to 2% of winter baseflow, but the winter heat fluxes from energy stored during warmer seasons are potentially much larger. The porous matrix of the litter layer should reduce energy exchange in both directions. That is, it should shield the snow cover from the ground heat flux in winter and reduce heat fluxes to the underlying soil during summer, with the net result that during winter, there should be less subsurface heat available to melt snow where the litter layer is thicker. We acknowledge that these are qualitative interpretations that require more empirical support and theoretical exploration, but they suggest that these thermal effects could be important enough to deserve further study.

3.8 | Limitations and uncertainties in our single-site set-up

Our study has obvious limitations. The findings presented above are derived from plot-scale observations within a single small forest site. Most of our measurements span only a single growing season (or less), and the degree of replication (e.g. among plots and precipitation events) is limited. Many of our experiments were labour intensive and thus could only be carried out for short time spans and for
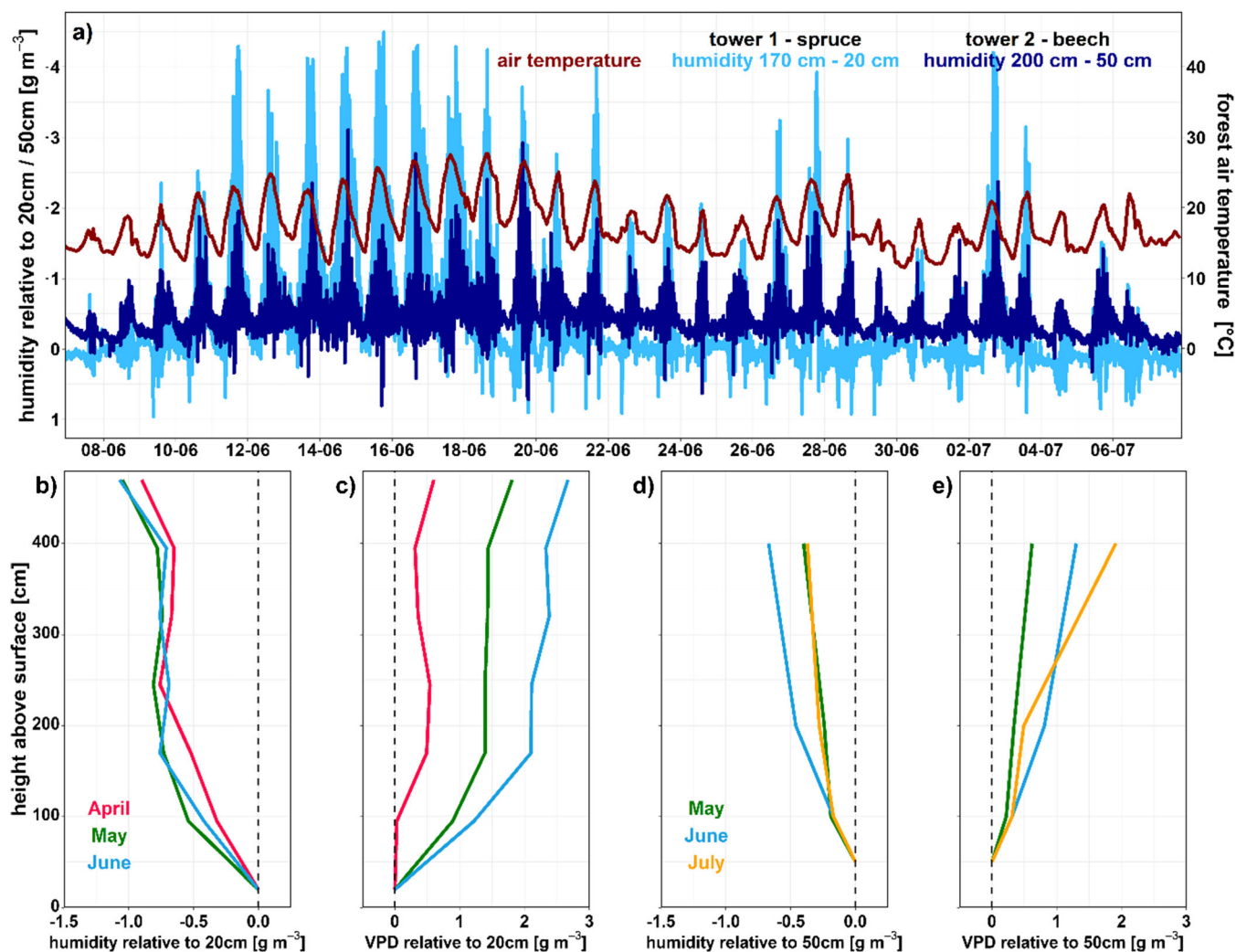
FIGURE 8 Time series of the difference in absolute humidity measured at two small towers within the forest, below spruce (Tower 1; difference between 20 and 170 cm; light blue line) and beech (Tower 2; difference between 50 and 200 cm; dark blue line) as well as forest air temperature (red line) (a). Daytime height profiles of absolute humidity and VPD, relative to values measured at the lowermost sensors at Tower 1 (spruce, b and c) and Tower 2 (beech, d and e), respectively. The profiles show monthly averages at the respective height for daytime hours (8 AM to 7 PM).

few replications. For example, the sampling campaign for litter grab samples occurred during a rather dry period with only three (rather low-intensity) rain events. Because the major purpose of that experiment was to confirm the maximum storage capacity of the litter, rather than to estimate litter retention timescales, the data here are limited and so are the potential conclusions we can draw from them. Many of our time series were also cut short due to technical issues. For example, the time series of soil moisture in Figure 4 show the only 6 weeks where all four sensors at both plots were working reliably. Similar sensor problems limited the pressure-cushion data in Figure 5 to only 1 month. Nevertheless, these limited observations reveal processes that are potentially important but widely neglected in studies of the forest water cycle. Thus, although many of our results are suggestive rather than definitive, they point to the need for further work to more rigorously quantify the water dynamics of the forest-floor litter layer.

3.9 | Upscaling the impact of litter on water fluxes to the overall forest water cycle

Using the procedures described below, we quantified how interception by, and evaporation from, the forest-floor litter layer may contribute to the overall forest water cycle.

3.9.1 | Litter interception and water storage

To upscale the effect of litter interception across our study site, we sampled three randomly selected 1 m^2 plots of broadleaf and needle litter, obtaining oven-dried litter weights of about 400 +/− 120 g m^{-2} for broadleaf litter and 1230 +/− 152 g m^{-2} for needle litter. Previous studies have reported litter weights of 785 (Li et al., 2013) and 1090 g m^{-2} (Zagyvai-Kiss et al., 2019) for broadleaf

FIGURE 9 Plots with and without litter (a) transmit different amounts of ground heat flux to the forest-floor surface from the underlying soil. Snowmelt was quicker (b), and surface temperatures on a cold day without snow cover were higher (c) in the litter-free plot.
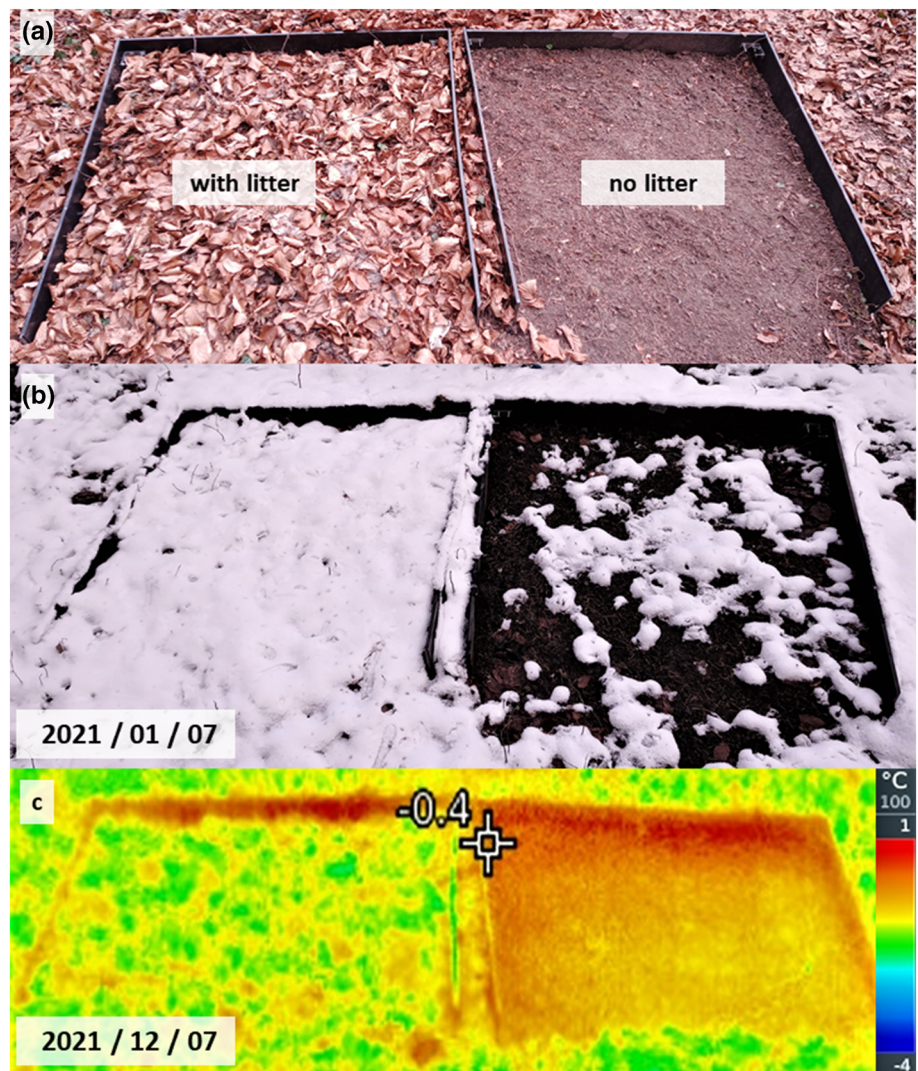
TABLE 1 To estimate the mean storage potential of the forest-floor litter layer at our field site, we combine laboratory and field measurements (in bold) with assumptions on the typical saturation reached during precipitation events (in italics) as summarized below

Litter type	Median max. saturation (lab experiments) $g_{water}/g_{dryweight}$	Mean litter weight at the site [g m^{-2}]	mm	Estimated mean saturation [%]	$g_{water}/g_{dryweight}$	Resulting mean storage potential [mm]
Broadleaf litter	**4.8**	**400**	1.9	70	3.4	1.3
Needle litter	**2.5**	**1230**	3.1	70	1.8	2.2
Deadwood	**1.7**	**412**	0.7	50	0.85	0.4
Total	-	-		-	-	2.2

litter and 115 (Van Stan et al., 2017) to 1890 g m^{-2} (Zagyvai-Kiss et al., 2019) for needle litter in temperate mixed forests. Scaling our litter weights by the median specific storage capacities (g water per g dry weight) reported in Section 3.1 yields a potential total water storage of 1.9 mm for beech litter and 3.1 mm for spruce litter. However, these figures are derived from laboratory experiments in which the litter was fully saturated by being submerged in water. Assuming that the litter layer actual storage capacities are 70% of these laboratory

values (resulting in specific storage capacities of 3.4 and 1.8 times the dry weight for broadleaf and needle litter, respectively), we estimate the storage capacity of the broadleaf and needle litter layers to be 1.3 and 2.2 mm, respectively (Table 1).

The amount of deadwood water storage was estimated similarly, from randomly selecting three 4 m^2 plots and weighing the (oven-dried) deadwood. These measurements yielded a deadwood volume of about 32 m^3 ha^{-1}. This is consistent with values reported

across Switzerland of 34 m^3 ha^{-1} (Lachat et al., 2019) and from other temperate mixed forests in previous studies including 47 m^3 ha^{-1} in Romania (Öder et al., 2021) and up to 50.5 m^3 ha^{-1} in Poland (Bujoczek et al., 2021). We estimated the overall storage capacity of deadwood at our site by using a mean dry deadwood density of 240 kg m^{-3} (Přívětivý & Šamonil, 2021) and assuming that deadwood pieces usually can take up at least 50% of the median saturation estimated during our laboratory saturation experiments (0.85 times the dry weight), resulting in a storage potential of 0.4 mm for our forest site.

Assuming that our mixed beech/spruce forest is underlain by half beech litter and half spruce litter, and adding 0.4 mm for deadwood storage, yields a total value of 2.2 mm of water storage in the forest-floor litter layer, including deadwood. This is consistent with previous estimates of 1.8–2.8 mm reported by Gerrits et al. (2010) for a beech forest in Luxembourg, where they also reported that forest-floor interception was nearly constant throughout the year, with no significant seasonal variation. Zagyvai-Kiss et al. (2019) estimated an average water holding capacity of forest-floor litter in an oak, beech and spruce mixed forest site in Hungary of around 2.6 mm, and Sato et al. (2004) found litter storage capacities between 1.7 and 3.0 mm for pine and oak plots, respectively. Van Stan et al. (2017) reported 5.3 mm of total storage in all litter components of a pine forest in the Southeastern United States. Although the absolute magnitudes of water storage of the forest-floor broadleaf litter, needle litter, and deadwood seem to be rather small, they rapidly fill and empty (either by drainage or by evaporation). Thus, fluxes from litter storages can be a significant fraction of the total annual precipitation, because they can retain this small absolute amount of water following many individual precipitation events.

We can estimate the cumulative effect of interception by forest-floor litter (including deadwood) as follows. For each precipitation event during our study period (15 March 2020 to 8 August 2022), we assume that 20% of incoming precipitation is lost to canopy interception, and the remaining 80% reaches the forest floor as throughfall. Literature values for canopy interception range from 9% to 29% for beech forests (Minďaš et al., 2018; Rowe, 1983) and from 23% to 37% for spruce forests (Dohnal et al., 2014; Holko et al., 2009; Kofroňová et al., 2021; Ringgaard et al., 2014; Xiao et al., 2000). For each precipitation event, we assume that interception by the litter layer equals the total throughfall amount, or the available litter layer water storage (the storage capacity of 1.75 mm for litter and 0.4 for deadwood, minus the actual storage in litter and deadwood), whichever is smaller. Between precipitation events, the actual litter storage is assumed to decline linearly to zero over 48 h (consistent with Figure 3), and deadwood storage is assumed to decrease exponentially with a characteristic time constant of 4 days (corresponding to a half-life of 2.8 days), consistent with the observations shown in Figure 6. In this way, we account for the litter layer storage that is already filled at the onset of each precipitation event. Summing the water taken up by the litter layer across all precipitation events yields a total of about 23% of annual throughfall or 18% of total annual precipitation (Table 2 and Figure 10). This is not an unrealistic estimate,

TABLE 2 Storage in leaf litter, deadwood and the sum of all forest-floor litter components and the resulting soil water recharge as annual totals and fractions of annual precipitation and throughfall, respectively

	Annual total [mm y^{-1}]	Fraction of annual total precipitation [%]	Fraction of annual throughfall [%]
Precipitation	1046	-	-
Throughfall	837	80.0	-
Leaf litter storage	163	15.6	19.4
Deadwood storage	29	2.7	3.4
Total storage	**192**	**18.3**	**22.9**
Soil water recharge	**645**	**61.7**	**77.1**

as previous studies found that interception by leaf litter alone accounts for up to 18% of total annual precipitation in a spruce forest in Scotland (Miller et al., 1990) and up to 22% in a beech forest in Luxembourg (Gerrits et al., 2010). When all forest-floor litter components are included, forest-floor interception has been calculated at up to 47% of precipitation in a pine catchment in Australia (Putuhena & Cordery, 1996) and up to 32% in a pine catchment in the Southwestern United States (Van Stan et al., 2017).

3.9.2 | Litter evaporation

Water stored in the forest-floor litter layer will be evaporated back to the atmosphere or drained by gravity. Height profiles of absolute humidity and VPD suggest that the litter layer contributes significantly to evaporation in our forest stand (Figure 8). Water vapour evaporated from the forest-floor litter layer significantly reduces VPD below the forest canopy by exchanging latent for sensible heat and thus increasing absolute humidity and lowering temperature. If we assume that all litter layer storage evaporates (or, equivalently, we assume that drainage occurs only during precipitation events when the maximum storage capacity is reached), Table 2 yields an estimate of 191 mm y^{-1} for annual litter evaporation. Together with evaporation from the forest canopy (assumed to be 20% of precipitation), this sums to a total of 38% of annual precipitation or a total of ~400 mm y^{-1}, with some seasonal variation. This is consistent with previous studies. For example, Gerrits et al. (2010) reported that around 22% of annual evaporation at a beech forest site originated from water retained in the litter layer; combined with canopy interception, this sums to a total of 26% and 36% of precipitation in winter and summer, respectively.

3.9.3 | Implications for forest water balances

Together, the forest canopy and the forest-floor litter layer modulate a large fraction of the incoming precipitation at our site, as they likely
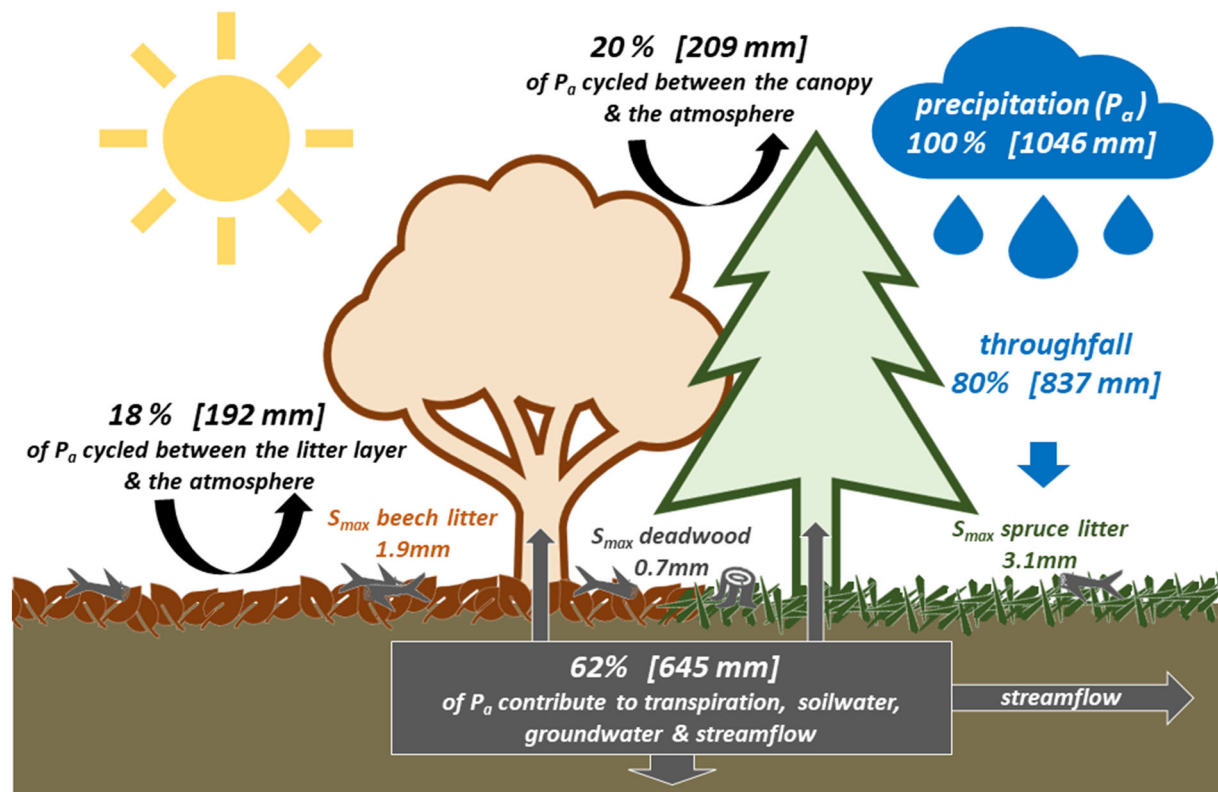
FIGURE 10 Conceptual scheme of the 'Waldlabor' forest water cycle, accounting for the storage in the forest litter layer estimated from field and laboratory experiments and their implications for the larger forest water cycle. Roughly 38% of annual precipitation are intercepted in the forest-floor litter layer and canopies; therefore, only 62% of annual precipitation reaches the subsurface soil and groundwater storages and is available for plant transpiration, groundwater recharge and streamflow.

also do in many other forests around the world. Significant fractions of annual precipitation are exchanged between the atmosphere, the canopy and the forest-floor litter layer, without contributing to soil moisture recharge, groundwater recharge or runoff production (Figure 10). This also limits the water that is available to plants for transpiration. This is important because these interception losses are not well represented in many conventional water balances, or their magnitudes are greatly underestimated. At our site, forest-floor interception losses are similar to rates of canopy interception. Together, they reduce the available recharge by approximately 38% on an annual basis (and by a substantially higher percentage during summer when VPD is high, and a lower percentage during winter when VPD is low). Thus at our site, and in similar forests and similar climates, the fraction of summer precipitation that actually infiltrates through the forest floor may be very small. This could help to explain why during the summer months, forest trees across Switzerland have been observed to transpire precipitation from the previous winter (as shown in Allen et al., 2019).

Overlooking forest-floor interception losses can lead to substantial overestimates of forest transpiration rates (Coenders-Gerrits et al., 2014). A simple thought experiment illustrates the potential magnitudes. In many humid temperate forests, total evaporation and transpiration from all sources (as estimated from long-term mass balances of precipitation and stream discharge) is very roughly 60% of

precipitation (Oki & Kanae, 2006; Schlesinger & Jasechko, 2014; Zhang et al., 2016). If canopy interception and evaporation account for 20% of precipitation (Allen et al., 2017; Miralles et al., 2010; van Dijk et al., 2015; Wang et al., 2007; Zheng & Jia, 2020), the remaining $60 - 20 = 40\%$ of precipitation would be attributed to transpiration if forest floor evaporation is ignored. But if interception and evaporation from the forest floor account for an additional ~20% of precipitation, as suggested by our analysis and previous studies (Gerrits et al., 2010; Miller et al., 1990; Putuhena & Cordery, 1996; Van Stan et al., 2017), then transpiration accounts for only $60 - 40 = 20\%$ of precipitation, or only half of the transpiration flux that would be inferred if forest-floor evaporation is ignored. If these magnitudes are even approximately correct, many transpiration fluxes may be overestimated by factors of roughly 2, with potential implications for other fluxes linked to transpiration, that is, underestimates of plant water use efficiency.

4 | CONCLUSION

Our measurements at a mixed beech–spruce forest site indicate that the forest-floor litter layer intercepts and temporarily stores significant amounts of total annual precipitation and that this is an important (yet often overlooked) component of the forest water cycle.

Field observations and laboratory measurements show that storage capacities of spruce needle litter, beech broadleaf litter and deadwood average 3.1, 1.9 and 0.7 mm, respectively (Figure 2), with the storage capacity of deadwood varying with its degree of decay (Figure 7). Fluctuations in soil moisture suggest that the fraction of precipitation reaching the forest soil at 10 cm depth was a factor of 2.7 smaller in litter-covered plots than at plots without litter (Figure 4). Similarly, the litter layer shields the underlying soil from evaporation (2.8 times less evaporation at the plot with litter) and potentially also insulates against ground heat fluxes from the subsurface, thus decreasing snowmelt rates (Figure 10). Measurement time series following rain events show that beech broadleaf and spruce needle litter can retain water for 2 days or longer (Figure 3) and deadwood can retain water for more than 7 days (Figure 6). Water storage in deadwood fluctuated diurnally, suggesting water uptake from the nighttime atmosphere (from dew and fog) when VPD was low and evaporation of water during daytime when VPD was high (Figure 5). Evaporation from forest-floor litter is likely to significantly increase the humidity, lower the temperature and reduce the VPD in the subcanopy environment (Figure 8). Overall, interception by the canopy and forest-floor litter layer amounted to approximately 38% of annual precipitation, thereby significantly reducing the water available for recharge and transpiration. Forest water balances that overlook forest-floor interception and evaporation are likely to overestimate recharge and transpiration rates, potentially by large factors.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Floriancic, M. G., Allen, S. T., Meier, R., Truniger, L., Kirchner, J. W., & Molnar, P. (2022). Potential for significant precipitation cycling by forest-floor litter and deadwood. *Ecohydrology*, e2493. https://doi.org/10.1002/eco.2493