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Leaf Water Storage Capacity Among Eight US Hardwood Tree Species: Differences in Seasonality and Methodology

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Abstract: Canopy hydrology and forest water inputs are directly linked to the physical properties of tree crowns (e.g., foliar and woody surfaces), which determine a tree's capacity to intercept and retain incident rainfall. The changing forest structure, notably the decline of oak's (*Quercus*) dominance and encroachment of non-oak species in much of the upland hardwood forests of the eastern United States, challenges our understanding of how species-level traits scale up to control the forest hydrologic budget. The objective of this study was to determine how the leaf water storage capacity varies across species and canopy layers, and how these relationships change throughout the growing season. We measured the leaf water storage capacity of overstory and midstory trees of native deciduous oaks (*Q. alba*, *Q. falcata*, *Q. stellata*) and non-oak species (*Carya tomentosa*, *Acer rubrum*, *Ulmus alata*, *Liquidambar styraciflua*, *Nyssa sylvatica*) using two methods (water displacement and rainfall simulation). Overstory *Q. alba* leaves retained 0.5 times less water per unit leaf area than other overstory species ($p < 0.001$) in the early growing season, while in the late growing season, *C. tomentosa* leaves had the lowest storage capacity ($p = 0.024$). *Quercus falcata* leaves displayed a minimal change in storage between seasons, while *Q. alba* and *Q. stellata* leaves had higher water storage in the late growing season. Midstory *U. alata* leaves had 3.5 times higher water storage capacity in the early growing season compared to all the other species ($p < 0.001$), but this difference diminished in the late growing season. Furthermore, the water storage capacities from the simulated rainfall experiments were up to two times higher than those in the water displacement experiments, particularly during the early growing season. These results underscore the complexity of leaf water storage dynamics, the methodology, and the implications for forest hydrology and species interactions. Broader efforts to understand species-level controls on canopy water portioning through leaf and other crown characteristics are necessary.

Keywords: mesophication; canopy interception; *Quercus*

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1. Introduction

Across central and eastern US forests, a shift in species composition is occurring from fire-tolerant, shade-intolerant upland oaks (*Quercus* spp.) to fire-sensitive, shade-tolerant species such as red maple (*Acer rubrum*) [1]. This process, termed mesophication, is driven by the hypothesized positive feedback where shade-tolerant and/or opportunistic species (i.e., mesophytes) outcompete shade-intolerant, fire-resistant species to create a shadier, moister environment that is less flammable, thereby facilitating the survival of fire-sensitive mesophytes [2]. This process promotes the continued growth and dominance of mesophytes over oaks, as mesophytes are typically more shade-tolerant than oaks and can persist in closed-canopy, low-light environments [2,3]. The growth strategies between shade-tolerant versus shade-intolerant species are manifested in the leaf characteristics [4,5] and canopy geometry of tree species [5,6]. These differences may in turn impact the partitioning of rainwater into stemflow, rainwater that flows down the branches and trunk of the tree onto the forest floor; throughfall, rainwater that flows through the canopy and onto the soil; and interception, rainwater that is collected on the leaves of the canopy and then is re-evaporated or absorbed by the leaves [7–9].

The leaf water storage capacity is the maximum amount of rainwater the foliar canopy is able to intercept during a storm event [10,11]. The leaf water storage capacity determines how much rainwater the leaves intercept and how much is shed as throughfall and stemflow [12,13]. At the tree level, the quantity of rainwater intercepted and stored is determined by the crown architecture and total leaf area. Shade-tolerant species, including mesophytes, tend to have denser, deeper crowns compared to shade-intolerant species, including many upland oaks [3]. The deeper crowns of shade-tolerant species are associated with erectophile branches, which are vertically oriented and augment the funneling of rainwater to the base of the tree as stemflow [14]. In contrast, the shallower crowns of shade-intolerant species are associated with plagiophile branches, which are horizontally oriented and create more drip points where stemflow is converted to throughfall [15]. Moreover, deciduousness may dramatically alter the partitioning of rainfall from leaf-on to leaf-off conditions, whereby throughfall and stemflow are greater when leaves are absent [16,17]. Together, these contrasting physical differences, paired with seasonality, are manifested into controls of forest water inputs [8].

At the individual leaf scale, characteristics such as the surface texture, surface area, age, orientation, and thickness are important factors influencing water storage [12,18,19]. The cuticle thickness, as well as the resistance to degradation, differs widely among species [20–22]. Waxy leaf coatings result in hydrophobic surfaces that shed rainwater more rapidly [23]. For example, many oaks have a resilient cuticle that slowly erodes during the growing season, resulting in seasonal differences in the leaf water storage capacity, in contrast to shade-tolerant *Fagus grandifolia* (American beech) leaves with no coating and more temporally stable canopy water storage capacities [21]. Additional textures on leaf surfaces may be created by hair-like trichomes that grow out of the leaf surface [24,25]. As the leaf ages throughout the growing season, changes in both the leaf surface texture and the area occur, leading to a decrease in the leaf water storage capacity. The leaf thickness also contributes to its ability to retain water [26]. Oaks tend to have thicker leaves than other co-occurring hardwoods in the eastern US [4,5], with thicker leaves being more rigid, creating a larger surface area for rainwater to adhere [27]. Another factor in the leaf water storage comes from the species' ability to grow in differing light environments. Leaves evolved for low light levels typically have larger, thinner leaves to capture as much light as possible [28,29], and consequently as much rainwater too. However, the tradeoff between the surface area of interception and the differences in hydrophobicity and rigidity are not well documented. As such, the degree to which the suite of these different factors contributes to creating differences in the crown storage capacity between shade-tolerant and shade-intolerant species remains unexplored. Beyond tree characteristics, ambient storm conditions also influence how much water can be retained in the canopy. Windy conditions disturb foliar surfaces, reducing interception to allow more water to fall to the forest floor as throughfall [30,31]. The water droplet size increases proportionally with the rainfall intensity, leading to higher impact velocity, breaking the water tension bonds between droplets on the leaf surface [32,33]. Taken together with the canopy and leaf-level biological characteristics, the exogenous factors controlling the canopy water storage capacity and interception are diverse.

The leaf water storage capacity is a difficult value to ascertain in the field, as any direct measurements account for the canopy water storage capacity, which includes the bark water storage capacity. Instead, destructive sampling and laboratory approaches are necessary for accurate measurements. Two common approaches are water displacement and rainfall simulation. In the water displacement method, leaves are briefly submerged in water to coat the external leaf surfaces and then slowly removed from the water to determine the mass of water detained on the leaf [11,30,34,35]. This can be done to simulate calm conditions (i.e., weighing immediately after the leaf is submerged in water) or windy conditions (i.e., shaking the leaf after submersion in water, then weighing). To elucidate more realistic storm conditions, rainfall simulators can be employed to mimic actual rainfall events, including variations in the duration and intensity [33,36,37]. Both of these approaches have merits but have not been systematically compared.

To refine our understanding of tree-level controls on canopy hydrology, the objective of this study was to determine how the leaf water storage capacity varies across species and canopy layers, and how these relationships change throughout the growing season. Furthermore, we used two methodologies (water displacement and rainfall simulation) to evaluate the leaf water storage capacity to assess their compatibility. We hypothesized that oak species would have lower leaf water storage capacity in comparison to non-oak species when standardized for the leaf surface area, due to the thicker cuticle on oak leaves [4]. We also hypothesized that early growing season (i.e., young) leaves would have lower water storage capacity compared to late growing season (i.e., mature) leaves, due to the loss of cuticle on the leaves as they age [11]. Refining our understanding of the species-level controls of the leaf water storage capacity will lead to a more holistic understanding of the hydrologic controls of the mesophication process [3].

2. Materials and Methods

2.1. Leaf Water Storage Capacity—Water Displacement Method

For our experiments on the leaf water storage capacity, we selected eight native deciduous hardwood tree species in northern Mississippi, USA. The tree species included white oak (*Q. alba* L.), southern red oak (*Q. falcata* L.), and post oak (*Q. stellata* Wangenh), as well as the co-occurring shade-tolerant species red maple, winged elm (*Ulmus alata* Michx.), mockernut hickory (*Carya tomentosa* (Poir.) Nutt), sweetgum (*Liquidambar styraciflua* L.), and black gum (*Nyssa sylvatica* Marsh.). These species are all common in the region and represent a gradient of fire-tolerant/shade-intolerant oaks species to fire-intolerant/shade tolerant mesophytic competitors [8,38,39]. To assess the water retention across species, we collected three leaves per species using a slingshot from both the midstory and overstory in the early growing season after complete leaf emergence (June) and in the late growing season prior to senescence (October). We only retained intact leaves that showed no sign of physical damage for the experiment. We collected *Acer rubrum*, *N. sylvatica*, and *U. alata* leaves only from the midstory, as no overstory trees were present on the site. Immediately after collection, the leaf samples were placed in plastic bags, sealed, and stored on ice until returned to the laboratory and stored at 4 °C. An Area Meter 3100 (LI-COR Lincoln, NE, USA) was used to determine the leaf surface area of fresh leaves (cm^2) (Table 1).

Table 1. Average leaf surface area (±SE) for each tree species in the overstory and midstory canopy layers collected from the field site in northern Mississippi. Note that three species were only present in the midstory.

	Overstory Leaf Area (cm^2)	**Midstory Leaf Area (cm^2)**
A. rubrum (ACRU)	-	36.0 ± 4.1
C. tomentosa (CATO)	310.4 ± 53.2	589.3 ± 99.5
L. styraciflua (LIST)	54.7 ± 9.6	69.4 ± 8.6
N. sylvatica (NYSY)	-	57.0 ± 4.0
U. alata (ULAL)	-	10.0 ± 1.4
Q. alba (QUAL)	84.1 ± 14.3	88.5 ± 10.9
Q. falcata (QUFA)	99.0 ± 22.2	120.0 ± 17.8
Q. stellata (QUST)	118.1 ± 12.3	79.1 ± 15.9

To test the water displacement method, each leaf was submerged and weighed three times during calm conditions and then three times during simulated windy conditions. The mass of water detained on each leaf (M_{H2O}) was calculated by

$$M_{H2O} = M_{wet} - M_{dry} \tag{1}$$

where M_{dry} was the initial dry mass of the leaf (g) and M_{wet} was the wet mass of the leaf (g) after being submerged in water. The values were then standardized based on the leaf area.

2.2. Leaf Water Storage Capacity—Rainfall Simulator

We also measured the leaf water storage capacity using a rainfall simulator. The rainfall simulator was constructed using a hose and a standard 7-Pattern hose nozzle (Orbit Irrigation, Salt Lake City, UT, USA) set at the lowest spray setting, which had an intensity of 0.029 ± 0.001 cm s^{-1}.

The same leaves as used in the water displacement experiment were used in the rainfall simulator experiment (see Supplementary Materials Figure S1). The leaves were mounted on a 0.5 m stand attached with a clip by the petiole of the leaf. The rainfall simulator was mounted 1.5 m above the leaf sample on a second stand to maintain a consistent height and angled 90° for all the tests. We used an aluminum pan to transfer the leaf to the measuring scale without additional water loss from the leaf being unclipped from the stand. Each leaf was subject to three tests, and the volume of water detained per leaf was determined following Equation (1) above.

2.3. Data Analysis

We compared the leaf water storage capacity among the species and among the three methods for each distinct canopy layer. The amount of water detained on each leaf was standardized to leaf area by the following equation:

$$I = \frac{M_{H2O}}{A_s} \tag{2}$$

where I is the intercepted water (mL cm^{-2}), M_{H2O} is the average volume of water held per leaf over three trials per rainfall intensity (mL), and A_S is the surface area of the leaf (cm^2).

To test for species-level differences in the leaf water storage capacity, we employed linear mixed-effects models, where the species was the fixed effect and the leaf replicate was the random effect using the 'lmer' function in the lme4 package [40]. Separate analyses were conducted for each canopy layer (midstory, overstory), time of measurement (early, late growing season), and method (calm water displacement, windy water displacement, rainfall simulations). All the data analyses were performed in R version 4.4.2 [41]. All the statistical tests were performed using $\alpha = 0.05$.

3. Results

For the first experiment simulating calm conditions via the water displacement method, we found differences in the leaf water storage among the species in both the overstory and midstory canopy layers. In the overstory, early growing season leaves from *Q. alba* and *Q. falcata* retained half the water per unit leaf area of the other three species (72.5 ± 5.9 mL/m^2 vs. 145.0 ± 6.4 mL/m^2; $p < 0.001$) (Figure 1A). *Quercus falcata* leaves continued to have low water storage in the late growing season, along with *C. tomentosa*, both of which were 0.4 times smaller than *Q. stellata* (80.6 ± 24.4 vs. 194.2 ± 46.6 mL/m^2; $p = 0.024$) (Figure 1B). Overstory *C. tomentosa* leaves retained more water in the early growing season compared to the late growing season (133.6 ± 2.3 vs. 83.9 ± 29.6 mL/m^2), while *Q. alba* and *Q. stellata* leaves exhibited the opposite seasonal relationship (QUAL: 66.9 ± 3.9 vs. 131.3 ± 14.4 mL/m^2; QUST: 148.7 ± 12.5 vs. 194.2 ± 46.6 mL/m^2) (Figure 1C). In the midstory, *U. alata* leaves retained nearly 3.5 times more water than all the other species during the early growing season (321.9 ± 58.9 vs. 93.3 ± 9.7 mL/m^2; $p < 0.001$) (Figure 1D). During the late growing season, there were no differences observed among the species during the calm water displacement experiment ($p = 0.209$) due to the large variations in water storage, with an average leaf water storage of 128.3 ± 25.3 mL/m^2 (Figure 1E). Seasonal differences within the species were also found. All the oak species retained more water on the leaves in the late growing season compared to the early growing season (QUAL: 87.8 ± 12.6 vs. 111.2 ± 15.3 mL/m^2; QUFA: 88.6 ± 8.8 vs. 156.4 ± 22.4 mL/m^2; QUST: 84.4 ± 6.6 vs. 123.4 ± 13.8 mL/m^2), along with *A. rubrum* (85.8 ± 9.5 vs. 173.5 ± 38.7 mL/m^2) and *L. styraciflua* (113.1 ± 7.6 vs. 164.0 ± 40.4 mL/m^2). Only *U. alata* retained more water on the leaves in the early growing season compared to the late growing season (321.9 ± 58.9 vs. 95.8 ± 37.2 mL/m^2); all the other species retained more water in the late growing season compared to the early growing season (Figure 1F).

The simulated windy conditions generally led to a decrease in leaf water storage relative to the calm conditions in both canopy layers in the early growing season but not in the late growing season (Figure 1 vs. Figure 2). In the overstory, the early growing season leaf water storage was similar across the species (102.4 ± 7.6 mL/m^2), except for *Q. alba* leaves, which retained half the water per unit leaf area (55.1 ± 2.0 mL/m^2; $p < 0.001$) (Figure 2A). Similar trends were observed among the overstory species in the late growing season as in the calm conditions, where the simulated windy conditions resulted in the lowest leaf water storage by *C. tomentosa* leaves and the largest leaf water storage by *Q. stellata* leaves (96.7 ± 20.4 vs. 236.6 ± 62.8 mL/m^2; $p = 0.032$) (Figure 2B). In the midstory, early season *U. alata* leaves retained 2.5 times as much water as all the other species (174.9 ± 26.8 vs. 68.6 ± 8.1 mL/m^2; $p < 0.001$) (Figure 2D). No differences were observed among the species in late season midstory leaves, with an overall storage of 140.1 ± 29.0 mL/m^2 ($p = 0.135$) (Figure 2E).

Similar species-level seasonal trends were observed in the simulated windy conditions as the simulated calm conditions. Overstory *Q. alba* and *Q. stellata* had greater leaf water storage capacity in the late growing season compared to the early growing season under windy conditions (QUAL: 55.1 ± 2.0 vs. 121.1 ± 6.5 mL/m^2; QUST: 122.0 ± 9.7 vs. 236.6 ± 62.8 mL/m^2), similar to the trends observed during calm conditions (Figure 2C). *Liquidambar styraciflua* leaves also retained more water in the late growing season compared to the early growing season (98.3 ± 6.6 vs. 170.0 ± 45.2 mL/m^2). Midstory *Q. stellata* and *L. styraciflua* leaves retained more water in the late growing season compared to the early growing season (QUST: 64.9 ± 5.4 vs. 128.3 ± 64.3 mL/m^2;

LIST: 58.2 ± 2.6 vs. 176.5 ± 64.3 mL/m^2), in addition to *A. rubrum* (52.4 ± 4.0 vs. 191.5 ± 22.6 mL/m^2), *C. tomentosa* (68.6 ± 10.0 vs. 112.5 ± 12.5 mL/m^2), and *Q. falcata* (83.3 ± 9.0 vs. 208.4 ± 33.8 mL/m^2) (Figure 2F). There were no seasonal differences in leaf water storage in midstory *Q. alba* or *U. alata* under simulated windy conditions.

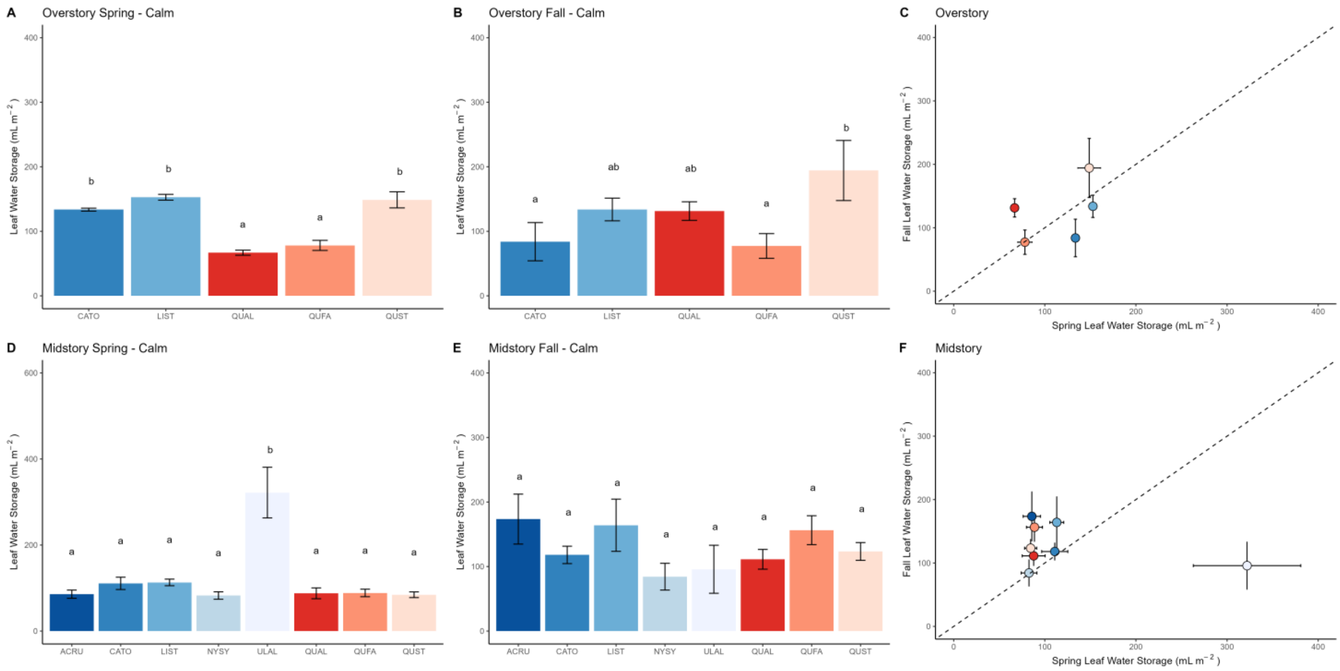

Figure 1. Mean (± SE) leaf water storage in mL cm^{-2} during the calm water displacement experiment in the (**A**) overstory during spring, (**B**) overstory during fall, (**C**) overstory comparison between spring and fall, (**D**) midstory during spring, (**E**) midstory during fall, and (**F**) midstory comparison between spring and fall. In panels (**C**,**F**), deviations from the 1:1 dotted line indicate seasonal differences in leaf water storage. Significant differences ($p < 0.05$) between species are denoted with different lowercase letters.

In the final experiment, we used a rainfall simulator to assess the leaf water storage capacity under prolonged wetting conditions. *Liquidambar styraciflua* overstory leaves from the early growing season held 3.2 times more water than all the other species (502.5 ± 102.0 vs. 157.2 ± 16.5 mL/m^2; $p < 0.001$) (Figure 3A). The late growing season leaves were similar in their water retention across the species, with *Q. stellata* leaves holding 1.3 times more water than *C. tomentosa* and *Q. alba* (135.7 ± 6.4 vs. 101.8 ± 6.2 mL/m^2; $p = 0.016$) (Figure 3B). In the midstory, *U. alata* leaves retained 4.0 times more water than all the other species (772.1 ± 127.0 vs. 183.3 ± 24.8 mL/m^2; $p < 0.001$) (Figure 3D). During the late growing season, only differences among the non-oak species were present, with *L. styraciflua* holding twice the water on the leaves than *C. tomentosa* (151.4 ± 42.7 vs. 75.8 ± 6.5 mL/m^2; $p = 0.037$) (Figure 3E).

Interestingly, when subjected to prolonged wetting conditions, the leaves of all the overstory species had greater leaf water storage in the early growing season compared to the late growing season, except for *Q. stellata* (Figure 3C). This seasonal difference was most pronounced in *L. styraciflua* leaves, which retained 4.6 times as much water in the early growing season. Similarly, the leaves from all the midstory species retained more water in the early growing season (Figure 3F). The most pronounced difference was observed in *U. alata* leaves, which retained 4.8 times as much water in the early growing season.

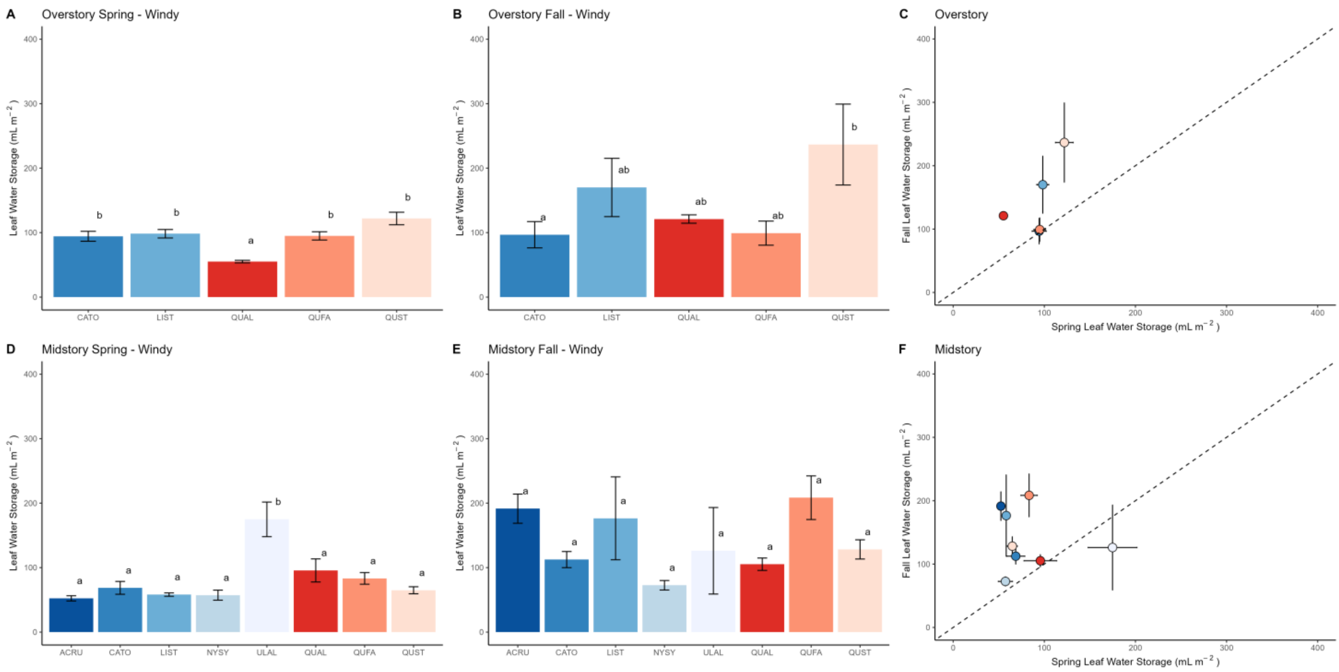

Figure 2. Mean (± SE) leaf water storage in mL cm^{-2} during the windy water displacement experiment in the (**A**) overstory during spring, (**B**) overstory during fall, (**C**) overstory comparison between spring and fall, (**D**) midstory during spring, (**E**) midstory during fall, and (**F**) midstory comparison between spring and fall. In panels (**C**,**F**), deviations from the 1:1 dotted line indicate seasonal differences in leaf water storage. Significant differences (p < 0.05) between species are denoted with different lowercase letters.

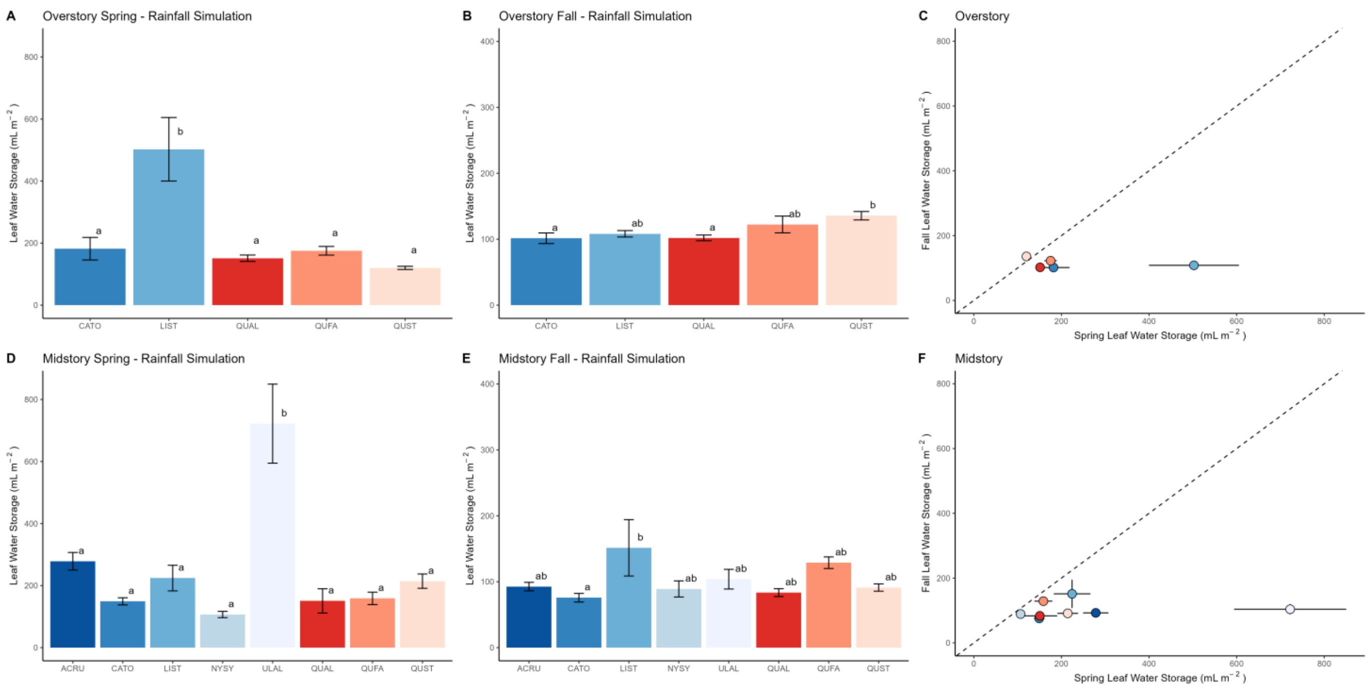

Figure 3. Mean (± SE) leaf water storage in mL cm^{-2} during the rainfall simulation experiment in the (**A**) overstory during spring, (**B**) overstory during fall, (**C**) overstory comparison between spring and fall, (**D**) midstory during spring, (**E**) midstory during fall, and (**F**) midstory comparison between spring and fall. In panels (**C**,**F**), deviations from the 1:1 dotted line indicate seasonal differences in leaf water storage. Significant differences (p < 0.05) between species are denoted with different lowercase letters.

4. Discussion

In this study, we evaluated the leaf water storage capacity in midstory and overstory trees across a variety of oak and non-oak species to understand the crown controls on canopy water partitioning. We conducted experimental wetting tests using a variety of methodologies (submersion and simulated rainfall) at the beginning and end of the growing season to assess the effect of seasonal changes in the leaf surface properties on water storage. Our first hypothesis, that oak species would have lower leaf water storage capacity than non-oak species, was partially confirmed but was not consistent across all the oak species. Our second hypothesis, that early growing season leaves would have lower leaf water storage capacity, was only supported under the simulated rainfall experiments.

In general, we found that overstory *Q. alba* leaves had the lowest water storage capacity in the early growing season, while in the late growing season, *C. tomentosa* leaves had the lowest storage capacity and *Q. stellata* leaves had the greatest. *Quercus falcata* leaves displayed a minimal change in storage between seasons, while *Q. alba* and *Q. stellata* leaves had higher water storage in the late growing season versus earlier. These upload oak species have leaves with a thick waxy coating that slowly degrades over time [24]. Leaves collected late in the growing season, yet prior to senescence, likely experienced a degradation of their waxy coating that resulted in a reduction of leaf hydrophobicity and therefore a greater capacity to retain water [23]. The tomentose leaves characteristic of *Q. stellata* [42] may offset the early growing season hydrophobicity by providing increased roughness and adhesive surfaces for water [43], which could explain why *Q. stellata* had high leaf water storage in the early growing season when the other oak species did not. As a consequence, species with lower leaf water storage capacity (e.g., *Q. alba*) shed intercepted rainwater more efficiently and generate greater throughfall fluxes [8].

In the midstory, *U. alata* leaves had significantly higher water storage capacity in the early growing season compared to all the other species, but this capacity diminished in the late growing season. *Ulmus alata* leaves are also covered with a fine layer of pubescence on the underside and have doubly serrated margins [42], with both characteristics enhancing the surface roughness and water retention [43]. Interestingly, *U. alata* was the only midstory species to exhibit a decrease in leaf water storage throughout the growing season in all three wetting experiments. This may be due to the loss of pubescence via rainwater abrasion as leaves age, but further observation is necessary to confirm this mechanism. Fungal pathogens may also reduce leaf hydrophobicity and increase leaf wettability [44]. While care was taken to obtain healthy leaves from both sampling dates, late season disease is common when trees become more drought stressed [45,46].

The water storage capacities from the simulated rainfall experiment were much higher than those generated in the submersion experiments, particularly during the early growing season. These higher values observed in the rainfall simulator experiments may be because early season leaves are more capable of foliar water uptake [47], as thinner leaves have been demonstrated to have greater uptake [48]. This absorption may not have been observed in the submersion experiments, during which the leaves were exposed to water for shorter durations and therefore experienced a shorter period to absorb water. Evidence of foliar water uptake in the simulated rainfall experiments was observed, with some leaves increasing mass with each simulation (Supplementary Materials Table S1). Leaf maturation throughout the growing season increases the leaf thickness [49], which reduces the foliar water uptake. As such, it is likely that the results observed in the simulated rainfall experiment are most representative of real-world conditions where leaves are exposed to continuous wetting during rainfall events. However, the specific mechanisms underlying our observations have not been tested and deserve further attention.

The results of this study suggest that oak and non-oak species have different leaf water storage capacities that will lead to differences in the canopy interception and partitioning of water resources to the forest floor. We acknowledge that broader efforts are needed to quantify these differences across upland oak forests in the eastern US to capture the impact of shifting forest composition on forest hydrology. Furthermore, we stress that scaling from tree to leaf to catchment scales must consider measurement uncertainties in the two methods of leaf water storage capacity determination.

5. Conclusions

Throughout the eastern United States, upland oak forests are undergoing a compositional shift wherein oak dominance is being displaced by more mesic species. Recent work has shown that mesophytic species have functionally different morphological characteristics than upland oaks. The canopy hydrology and forest water inputs are directly linked to these observed species and seasonal differences. While prior research has emphasized the differences between broad functional groups (e.g., conifers vs. broadleaves), this study considered species frequent across the forested landscape of the southeastern US and found pronounced differences in water storage within these closely related species. Changes in the species composition away from oak-dominance will likely have an impact on forest hydrology, but the magnitude of this compositional shift on each component of the hydrologic budget (e.g., throughfall, stemflow, interception) is still largely unknown [3]. Clear trends have been observed in stemflow, with non-oak species having smoother, thinner bark that is more conducive to stemflow generation than thicker and more porous bark oaks [8,50]. However, the response of throughfall and canopy interception are more complex and inconsistent, as further supported by our findings. It is assumed that the greater leaf water storage capacity of some oak species observed in this study infers greater throughfall flux. However, greater throughfall input has not consistently led to greater moisture availability on the forest floor; the opposite has been observed, wherein non-oak species that partition less throughfall still have wetter soils [8,51]. These results underscore the complexity of leaf water storage dynamics and their implications for forest hydrology and species interactions. As such, broader efforts to understand the species-level controls on canopy water partitioning through leaf and other crown characteristics are necessary.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/hydrology12020040/s1, Table S1: Wetting experiment results in mL per m^2 leaf area for individual leaves in each of the three water storage capacity methodologies. Figure S1: Rainfall simulator setup.

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Data Availability Statement: The raw data supporting the conclusions of this article are available in the Supplemental Information.

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