

Article

## Contrasting Hydraulic Strategies during Dry Soil Conditions in *Quercus rubra* and *Acer rubrum* in a Sandy Site in Michigan

Julia E. Thomsen <sup>1</sup>, Gil Bohrer <sup>2,\*</sup>, Ashley M. Matheny <sup>2</sup>, Valeriy Y. Ivanov <sup>3</sup>, Lingli He <sup>3</sup>, Heidi J. Renninger <sup>4</sup> and Karina V. R. Schäfer <sup>4</sup>

<sup>1</sup> Department of Earth and Environmental Sciences, Wesleyan University, 45 Wyllys Avenue, Middletown, CT 06459, USA; E-Mail: [jthomsen@wesleyan.edu](mailto:jthomsen@wesleyan.edu)

<sup>2</sup> Department of Civil, Environmental and Geodetic Engineering, The Ohio State University, 2070 Neil Avenue, Columbus, OH 43210, USA; E-Mail: [matheny.44@osu.edu](mailto:matheny.44@osu.edu)

<sup>3</sup> Department of Civil and Environmental Engineering, University of Michigan, 1351 Beal Avenue, 105 EWRE, Ann Arbor, MI 48109, USA; E-Mails: [ivanov@umich.edu](mailto:ivanov@umich.edu) (V.Y.I.); [linglihe@umich.edu](mailto:linglihe@umich.edu) (L.H.)

<sup>4</sup> Department of Biological Sciences, Rutgers University, 195 University Avenue, Newark, NJ 07102, USA; E-Mails: [hrenninger@gmail.com](mailto:hrenninger@gmail.com) (H.J.R.); [karinavr@andromeda.rutgers.edu](mailto:karinavr@andromeda.rutgers.edu) (K.V.R.S.)

\* Author to whom correspondence should be addressed; E-Mail: [bohrer.17@osu.edu](mailto:bohrer.17@osu.edu); Tel.: +1-614-292-4178; Fax: +1-614-292-3780.

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**Abstract:** Correlation analyses were carried out for the dynamics of leaf water potential in two broad-leaf deciduous tree species in a sandy site under a range of air vapor pressure deficits and a relatively dry range of soil conditions. During nights when the soil is dry, the diffuse-porous, isohydric and shallow-rooted *Acer rubrum* does not recharge its xylem and leaf water storage to the same capacity that is observed during nights when the soil is moist. The ring-porous, deep-rooted *Quercus rubra* displays a more anisohydric behavior and appears to be capable of recharging to capacity at night-time even when soil moisture at the top 1 m is near wilting point, probably by accessing deeper soil layers than *A. rubrum*. Compared to *A. rubrum*, *Q. rubra* displays only a minimal level of down-regulation of stomatal conductance, which leads to a reduction of leaf water potential during times when vapor pressure deficit is high and soil moisture is limiting. We determine that the two species, despite typically being categorized by ecosystem models under the same plant functional type—mid-successional, temperate broadleaf—display

different hydraulic strategies. These differences may lead to large differences between the species in water relations, transpiration and productivity under different precipitation and humidity regimes.

**Keywords:** ecohydrology; leaf water potential; plant functional type; stomatal conductance; succession; transpiration; water relations

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## 1. Introduction

In forest ecosystems, evaporative demands are projected to increase almost everywhere as a result of increasing global temperatures [1]. This will increase the tendency for plants to lose water through transpiration. However, water use strategies differ between plants, and it is necessary to understand species-specific regulation of transpiration to determine the relative contribution of species to the ecosystem water budget. This is especially true in mixed forest stands. In particular, as forest compositions change due to disturbances, climate change, succession, or land-use change, the implications for ecosystem-scale water fluxes will be highly dependent on the species-level responses.

In the forest canopy, vapor pressure deficit (VPD) and photosynthetically active radiation (PAR) are the major determinants of the maximum potential evapotranspiration at any given time [2,3]. Water is lost due to the high gradient of water vapor pressure between the interior environment of leaves and the air, which in turn drives the passive transport of water through tree's xylem [4]. To avoid cavitation, plants must maintain water potentials above a minimum threshold [5–7]. This can be achieved through a combination of root uptake of soil water and stomatal regulation of transpiration water losses [3]. Precipitation patterns, soil properties, and the structure and depth of roots all influence the amount of soil moisture available for plant uptake. One mechanism to mitigate transpiration losses is through partial or complete stomatal closure during midday periods of high evaporative demand [8–10]. This can prevent a large decrease in leaf water potential ( $\psi_L$ ) and a loss of hydraulic conductance within the xylem [11].

Quantifying water exchange at the ecosystem scale in mixed forests is complicated by the species-specific responses to the environment [12–14]. In particular, the mechanism of stomatal closure due to deficits in xylem water potential is generally not incorporated into land surface models since the variation among species is difficult to measure and generalize [9]. One proposal to characterize the differences in species water use for generalized use in modeling [9] is based on classification of xylem structure (ring-, diffuse- or non-porous).

Xylem anatomy imposes physical limits on the rate of water transport within a tree [8,9,15], and differences in hydraulic architecture in trees can explain some variation in water use across species [8,11]. In particular, xylem properties, such as conducting area (cross-sectional area of vessels) and hydrodynamic resistance influence the rate of xylem sap flow [15]. For example, the wide, early-season vessels in ring-porous species are advantageous during periods of high water availability as they are much more conductive than the narrow, late-season vessels [16]. However, they are also much more vulnerable to cavitation during periods of low water availability [2,17,18]. Widespread cavitation can lead to an 80%–90% reduction in conductivity [6]. Conversely, diffuse-porous trees

have narrow vessels in both early- and latewood [9,18]. Narrow vessels are less conductive overall but generally less vulnerable to cavitation. There is a continuum of hydraulic properties of stems, leaves and roots over different species with a wide spread of characteristics among both ring and diffuse porous species [19]. Nonetheless, it has been hypothesized that the two opposing xylem structures represent a tradeoff between safety and efficiency in xylem transport [18,20]. It was also recently shown using sap flow measurements that some ring-porous species, such as red oak, adopt an anisohydric strategy, characterized by increased transpiration and high stomatal conductance even when the leaf water potential is very low, whereas other diffuse porous species, such as red maple, adopt an isohydric strategy where stomatal conductance is reduced to maintain a relatively constant leaf water potential [21]. That study, however, did not provide direct observations of leaf water potential. Other components of the hydraulic system of the tree can differ in ways that will result in different hydraulic strategies. Rooting depth and the strategy with which the roots explore the soil volume for available water were shown to affect the vulnerability of different species to drought [22].

Leaf water potential is a key characteristic of the hydraulic state of the plant. Here we investigate the similarity or difference in hydraulic strategies of two co-occurring mid-late successional broadleaf species with different porosities in a mixed hardwood forest in northern Lower Michigan at the University of Michigan Biological Station (UMBS) by testing the responses in leaf water potential to VPD and soil moisture. The experimental site at the UMBS is at a successional state that is typical to large extents of forest at the Northern Midwest and Great Lakes regions. After large scale logging and fire at the turn of the twentieth century the forests in the region are currently typically 70–90 years old, dominated by early successional species such as aspen. Increased mortality rates of these short living trees marks a rapid shift in the forest composition, as part as a natural succession process [23,24]. The well-drained, sandy soils of the forest plot induce conditions of low water availability, despite the relatively abundant precipitation, and thus a certain degree of water stress for the forest [25]. *Quercus rubra*, a deeply-rooted ring-porous species (oak roots at our site were observed at nearly 3 m depth), and *Acer rubrum*, a shallow-rooted diffuse-porous species, were monitored for diurnal patterns in leaf water potential and compared against VPD and soil moisture measurements. We hypothesized that the differences in porosity between the two species would result in opposing water use strategies in response to dry soil and high evaporative demand.

## 2. Experimental Section

### 2.1. Study Site

This study was conducted within a 50 m × 50 m experimental plot of forest near the Ameriflux meteorological tower at the University of Michigan Biological Station in northern Lower Michigan, east of Pellston, MI, USA (45°33' N, 84°42' W, Elev. 235 m). The site consists of a mixed hardwood forest composed primarily of *Populus grandidentata* Michx (bigtooth aspen), *Quercus rubra* L. (red oak), *Acer rubrum* L. (red maple), *Betula papyrifera* (paper birch), *Pinus strobus* (white pine), and *Fagus grandifolia* (American beech). The forest understory is dominated by *Pteridium aquilium* (bracken fern) as well as saplings of *Q. rubra*, *A. rubrum*, *F. grandifolia*, and *P. strobus* [26]. Typical maximal leaf area index is 3.5–4.1. Stem density of trees  $\geq 8$  cm dbh is 700–800 ha<sup>-1</sup>, basal area is

$\sim 25 \text{ m}^2 \text{ ha}^{-1}$ . The area is a gently sloping outwash plain at an elevation of  $\sim 300 \text{ m}$  that varies over a range of  $\sim 20 \text{ m}$  [27]. The soils are well to excessively well drained Haplorthods (92.9% sand, 6.5% silt, 0.6% clay) of the Rubicon, Blue Lake, or Cheboygan series. Soils throughout the study area have forest floors consisting of Oe horizons 1–3 cm thick overlying bioturbated AO horizons of 1–3 cm held together by dense fine roots. The remainder of the soil profile within the predominant rooting zone includes an E horizon of 10–15 cm and a Bs horizon of sand with occasional gravel and cobble. About 53% of the fine-root mass is located within the upper 20 cm of the soil profile [23]. Average annual precipitation is 817 mm and mean annual temperature is 5.5 °C (1942–2003) [23]. Well drilling records for a location in the immediate vicinity of the AmeriFlux tower ( $\sim 50 \text{ m}$  distance) show that the water table depth is around 20 m [28]. Canopy position was defined as either canopy dominant or co-dominant canopy.

## 2.2. Meteorological Data

Above canopy meteorological measurements were taken continuously at a height of 46 m (roughly 15 m above the canopy tops) as part of the US-UMB AmeriFlux site [23,26]. Temperature and relative humidity were measured with a Temperature/Humidity probe (HMP45C, Vaisala, Helsinki, Finland) with an aspirated radiation shield at 3 m and at 47 m. Radiation was measured with a 4-channel short/long incoming/reflected radiometer (NR1, Kipp & Zonen, Delft, The Netherlands) and photosynthetic active radiation (PAR) was measured with a PAR sensor (LI-190SA, Licor-Biosciences, Lincoln, NE, USA). Measurements were taken every minute and averaged at half-hour resolution. Wind speed was measured at 10 Hz using a 3-D ultrasonic anemometer (CS CSAT3, Campbell Scientific, Logan, UT, USA) and friction velocity,  $U^*$ , was calculated at 30 min block averages. The meteorological station setup and data analysis methods at the site are described in detail by Maurer *et al.* [29].

## 2.3. Soil Moisture Measurements

Volumetric water content of the soil was measured using the time domain reflectometry (TDR) method using a MiniTrase Kit (6050X3, Soil Moisture Equipment Corp., Santa Barbara, CA, USA) fitted with 30 cm and 60 cm waveguides. Depth-integrated, volumetric soil moisture (*i.e.*, volume of water per unit volume of bulk soil) was measured around each of the 12 trees in four cardinal directions over a depth range of 0–30 cm at distances of 1, 2, and 4 m from the stem. Measurements were repeated for a depth range of 0–60 cm at 1 and 4 m from the stem. Soil moisture and leaf water potential measurements were taken near each tree on the same day. Since no significant variability due to lateral distance or direction was found among measurements (mixed linear model;  $p = 0.222$ ) the data were averaged for each depth to obtain a single soil moisture value, specific to each tree, day, and depth. Additional soil moisture data, and particularly of the soil moisture at deeper layers that 60 cm was available from our deep soil-moisture monitoring pits. Since April 2009, soil moisture was measured with a 30-min resolution at four locations in our site. At those four locations, soil moisture probes (Hydra probe SDI-12, Stevens Water Monitoring Systems, Inc., Portland, OR, USA) were permanently deployed at the depths of 5, 15, 30, 60, 100, 200, and 300 cm. For the first four depths, sensors were replicated on the opposite wall ( $\sim 1.5 \text{ m}$  apart) of each soil pit. Those sensors were calibrated using the gravimetric method. Measurements of soil moisture (in % v/v) were converted to

soil water potential using the formulation from van Genuchten 1980 [30]. The instrumentation setup and soil-moisture data analysis methods in the site are described in detail by He *et al.* [25,31].

#### 2.4. Leaf Water Potential Measurements

Leaf water potential was measured using a pressure chamber (PMS Instrument Co., Corvallis, OR, USA). Six *Q. rubra* and six *A. rubrum* were selected for leaf water potential measurements. For each species, three canopy-dominant and three co-dominant individuals were chosen. The diameters at breast height (DBH) of canopy-dominant *Q. rubra* were 36.9, 37.2, and 56.5 cm and for codominants the DBHs were 22.3, 6.3, and 4.7 cm. For canopy-dominant *A. rubrum* the DBHs were 15.6, 22.6, and 15.8 cm and for codominants the DBHs were 9.1, 9.9, and 11.9 cm. Heights were similar, and canopy dominant trees ranged between 20–31 m (in both species) and co-dominant ranged 8–11 m. Leaves were chosen from a height of roughly 5 m, which were accessible with a pruner for each tree. The choice of the height was affected by the sampling feasibility; an inherent assumption is that both the diurnal and seasonal water stress signals can still be adequately captured. Three leaf replicates were measured from each tree during the sampling period from 7 July until 9 August 2011. Leaf water potentials were measured three times throughout the day: at pre-dawn (5–6 AM), midday (11:30 AM–12:30 PM), and late day (3:30–4:30 PM), once or twice a week for each tree individual.

#### 2.5. Statistical Analysis

Mixed linear models were run in SPSS for Windows (SPSS Inc., 2001, Chicago, IL, USA) to analyze the effect of soil moisture on leaf water potential. To determine the effect of distance from the tree on soil moisture, a mixed linear model was constructed with soil moisture (averaged over the four measured directions) as the dependent variable, a unique identifier for each tree as a random subject variable, species (*A. rubrum* or *Q. rubra*) and canopy position (sub-canopy or canopy dominant) as fixed factors, distance from tree (1 m, 2 m, or 4 m) and days since rain (to account for variability due to sampling day) as fixed covariates, and an interaction term between species and distance was incorporated. This analysis was run twice: once using soil moisture measurements from the shallow layers (0–30 cm); and a second time with vertically averaged soil moisture that included deeper layers (0–60 cm).

To determine the effect of VPD and soil moisture on midday leaf water potential, a mixed linear model was run with midday leaf water potential (averaged over three leaf replicates) for an individual tree (tree *i*) as the dependent variable; a unique identifier for tree *i* as a random subject variable; day of year when tree *i* was measured as a repeated measurement; species as a fixed factor; soil moisture (averaged over all measurements for tree *i*, since distance was not a significant source of variation) and VPD (during the half hour period containing the time of minimum leaf water potential of tree *i* on the sampling day) as fixed covariates; and species-soil moisture interaction term, species—VPD interaction term, and two-way interaction of soil moisture and VPD. Four of these analyses were run, with pair-wise combinations of soil moisture depth ranges (0–30 cm and 0–60 cm) and VPD measurement heights (46 m and 3 m). A similar mixed model was run to determine the significance of the effects of soil moisture on predawn leaf water potential. To investigate the nature of significant interaction terms, data were split by species and linear regressions were run with midday leaf water

potential for either oak or maple as a dependent variable and 0–30 cm soil water potential (SWP), 46 m VPD, or 3 m VPD as an independent variable. Because of the non-linear form of the soil water potential, we linearized the independent variable in the SWP regressions as:  $\Psi_L = A_1 \times \text{LOG}_{10}(-\text{SWP}) + A_2$ , where  $\Psi_L$  is leaf water potential (either pre-dawn or minimum daily), and  $A_1$  and  $A_2$  are the slope and intercept of the regression line.

### 3. Results and Discussion

#### 3.1. Leaf Water Potential

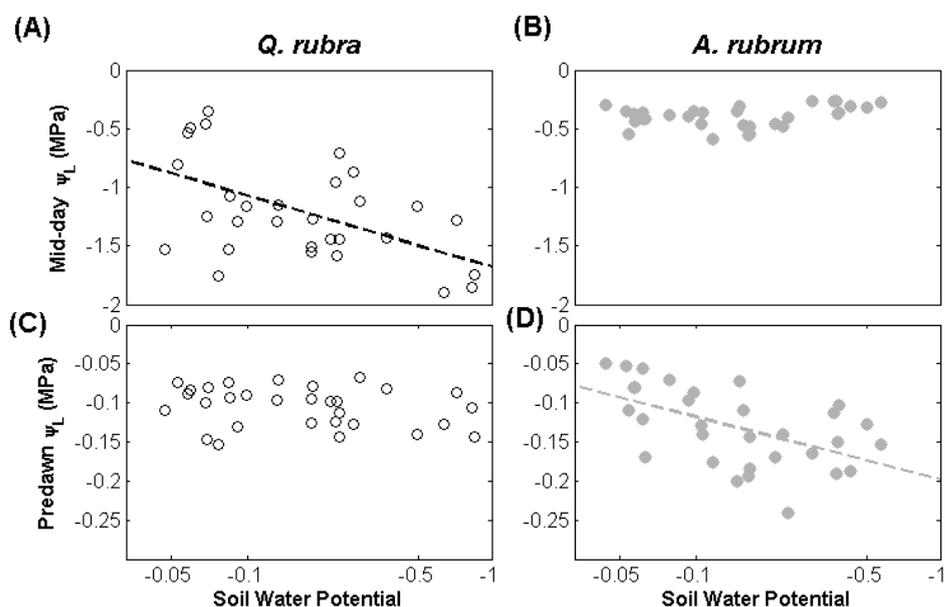
There were significant differences between species in minimum daily water potential. Overall, *Q. rubra* had lower leaf water potential during the day (Table 1, effect of Species) than *A. rubrum*. However, the overall direct effects of soil moisture or VPD on minimum leaf water potential were not significant. This was not because soil moisture or VPD had no effect, but, as indicated by the significance of the interaction terms this was driven by the fact that there were significantly different response to soil moisture and VPD between the two species (Table 1, effects of Species  $\times$  SM and Species  $\times$  VPD). These interactions are apparent in Figures 1 (upper panels, Species  $\times$  SM) and 2 (Species  $\times$  VPD), and the significance of the interaction terms in these statistical tests confirm that the regression curves that describe the response of leaf water potential to VPD and soil moisture are significantly different (Figures 1 and 2). Our hypotheses as to the differences in hydrologic strategy of the two species that drive these differences are discussed in section 3.2. The results were consistent across all four combinations of sources of environmental data—from both shallow (0–30 cm) and deeper (0–60 cm) soil and both within and above canopy atmospheric conditions indicating that the results are not sensitive to the arbitrary choice of sampling height/depth of the environmental conditions. The only exception to this was the interaction between VPD and SM that is significant only in the shallow soil and within canopy air. This interaction was driven by the fact that within canopy VPD had a consistent overall effect (in both species, combined) of decreasing leaf water potential only when the shallow soil was dry.

Because the mid-day leaf water potentials of tree individuals were significantly influenced by species but not by canopy dominance, data were split according to species and linear regressions were performed to determine the influence of soil water potential and VPD on minimum (mid-day) and maximum (predawn) leaf water potentials (Figures 1 and 2). Predawn leaf water potential of *Q. rubra* was not significantly influenced by soil moisture (linear regression:  $p = 0.213$ ,  $R^2 = 0.050$ ; Figure 1C). For *A. rubrum*, however, there was a positive correlation between predawn leaf water potential values and soil moisture (linear regression:  $p = 0.0015$ ,  $R^2 = 0.298$ ; Figure 1D). Midday leaf water potentials for *Q. rubra* were positively correlated with volumetric soil water content (regression:  $p = 0.0003$ ,  $R^2 = 0.348$ ; Figure 1A), while for *A. rubrum* this relationship was non-significant (linear regression:  $p = 0.09$ ,  $R^2 = 0.097$ ; Figure 1B).

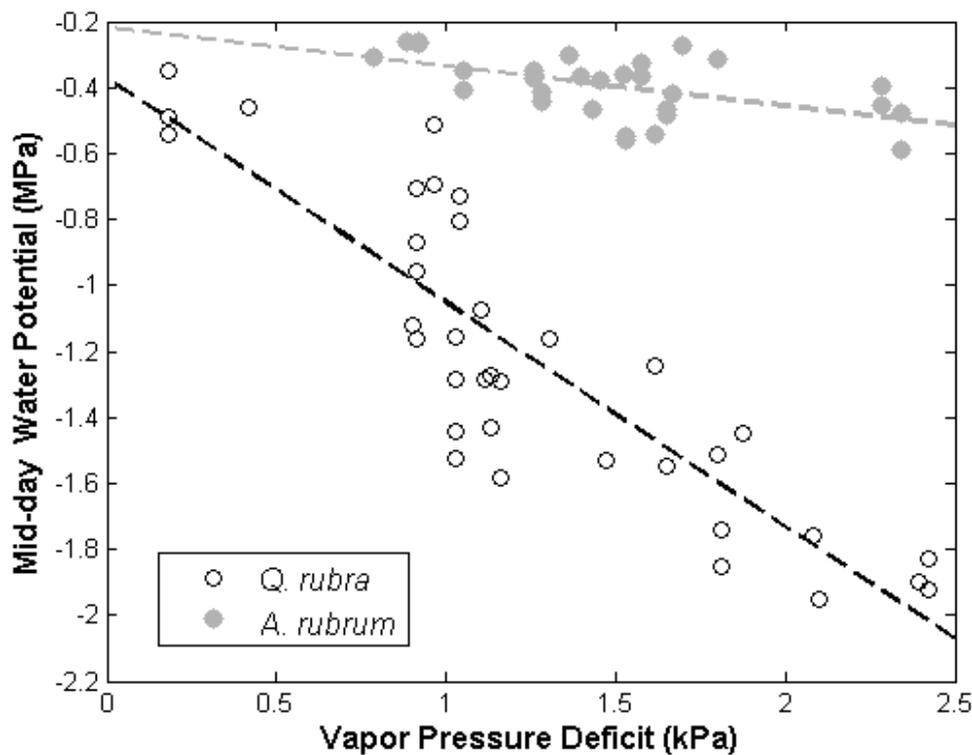
**Table 1.** The results of mixed linear models testing the significance of different variables and interactions affecting minimal leaf water potential in twelve trees of two species (*Q. rubra* and *A. rubrum*). Vapor pressure deficit (VPD), soil moisture (SM) and species were included as effective variables. Sample size in each test is  $n = 67$ . Soil moisture was measured over two depth intervals: 0–30 cm and 0–60 cm. VPD was measured at two heights: at 46 m above ground (above canopy) and at 3 m above ground (sub-canopy). For both soil moisture and VPD, data at different levels were highly correlated. Four models were run using pair-wise combinations of the two depths and heights. The p-values for each output are listed. Statistical significance was assumed at  $p < 0.05$ . (NS) means not significant. The product sign denotes the interaction term of the variables tested for in the mixed linear model.

		VPD, SM combinations			
VPD measurements height		46 m	46 m	3 m	3 m
SM integration depth		0–30 cm	0–60 cm	0–30 cm	0–60 cm
Effects on minimum daily leaf water potential	Species	<0.001	0.009	<0.001	0.012
	SM	0.638 (NS)	0.461 (NS)	0.128 (NS)	0.180 (NS)
	VPD	0.873 (NS)	0.448 (NS)	0.157 (NS)	0.129 (NS)
	Species × SM	0.001	0.027	0.003	0.041
	Species × VPD	<0.001	<0.001	<0.001	<0.001
	SM × VPD	0.434 (NS)	0.244 (NS)	0.037	0.052 (NS)

**Figure 1.** Responses of leaf water potential values ( $\psi_L$ ) to soil water potential at the top 30 cm for 6 *Q. rubra* and 6 *A. rubrum* individuals. Significant regressions are shown in dashed lines. Soil water potential is in (MPa) and listed on reversed logarithmic scale with highly negative values (dry soil) on the right hand side of the scale. Mid-day leaf water potentials for: (A) *Q. rubra*; and (B) *A. rubrum*. Predawn leaf water potentials for: (C) *Q. rubra*; and (D) *A. rubrum*.



**Figure 2.** Relationship between mid-day leaf water potentials of *Q. rubra* and *A. rubrum* and sub-canopy vapor pressure deficit. *A. rubrum* shows very mild response to VPD while *Q. rubra*'s response slope to VPD is significantly steeper.



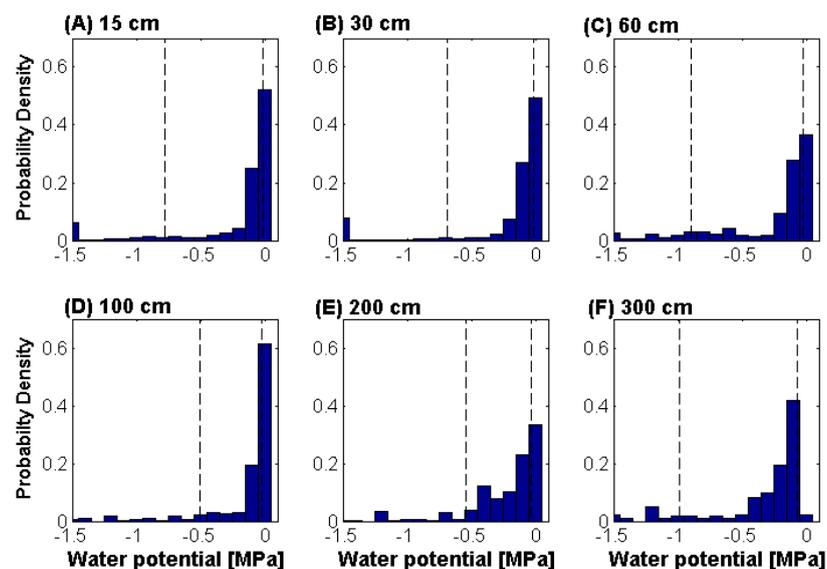
Mid-day (minimum) leaf water potential values were positively correlated with both above-canopy VPD (measured at 46 m) and inside-canopy VPD (measured at 3 m above ground) for both *Q. rubra* (linear regression; 46 m VPD:  $p < 0.0001$ ,  $R^2 = 0.74$ ; 3 m VPD:  $p < 0.0001$ ,  $R^2 = 0.76$ ) and *A. rubrum* (linear regression; 46 m VPD:  $p < 0.0001$ ,  $R^2 = 0.35$ ; 3 m VPD:  $p < 0.001$ ,  $R^2 = 0.30$ ) (Figure 2). In general, *Q. rubra* exhibited a much larger range of minimum leaf water potentials ( $-2.06$  to  $-0.275$  MPa) during day-time hours, as compared to *A. rubrum* ( $-0.6$  to  $-0.14$  MPa). While both species are significantly affected by VPD, regression slope between mid-day leaf water potentials and VPD in *Q. rubra* was significantly steeper than *A. rubrum*.

### 3.2. Discussion

The results indicate contrasting water use strategies for *Q. rubra* and *A. rubrum*. Changing soil moisture conditions did not induce a significant response in the pre-dawn leaf water potential values of *Q. rubra*. This suggests that *Q. rubra* may be able to access a sustained soil water source in deeper soil layers and recharge its stem storage overnight, so that its water potential remains stable even when the top soil layers are very dry. Observations of soil water potential in our site confirm that possibility (Figures 3 and 4). The variation in soil moisture and the fraction of time that the soil was drier than  $-0.5$  MPa ( $-5$  bar) are far smaller in the soil at depth between 1–2 m (Figure 3D,E) than in the shallower soil layers ( $\leq 60$  cm) (Figure 3A–C). By correlating pre-dawn water potentials with the soil moisture in each layer separately (rather than the mean for the top 30 cm), we found that pre-dawn leaf water potential in *A. rubrum* were correlated with soil water potential in each depth up to 60 cm

(15, 30 and 60 cm) while those of *Q. rubra* were not correlated with soil water potential at any depth, including the shallow layers. Similar observations were reported by Bréda *et al.* [32], which found that predawn water potentials were not sensitive to soil moisture for members of the *Quercus* genus. However, that finding was limited above a 40% threshold of plant extractable water, much higher than in our site. Thus, *Q. rubra* may be above the threshold necessary to induce a response to soil moisture deficits. *Q. rubra* and *Quercus* species in general have been found to be deeply rooted tree species [33,34] and thus should have access to a larger reservoir of soil water within the profile than shallow rooted species. It has been shown that water is increasingly taken up from deeper soil horizons during periods of drought in the *Quercus* genus [32,35].

**Figure 3.** Distribution of soil water potential at different depths at our site during the experiment (summer 2011). The normalized histogram (probability density function, PDF) of half-hourly measurements of soil water potentials (in MPa) is plotted. Each depth is a result from 8 (A–D) or 4 (E,F) soil moisture probes at different locations. Dashed lines illustrate the 10th and 90th percentiles of the soil moisture distribution.

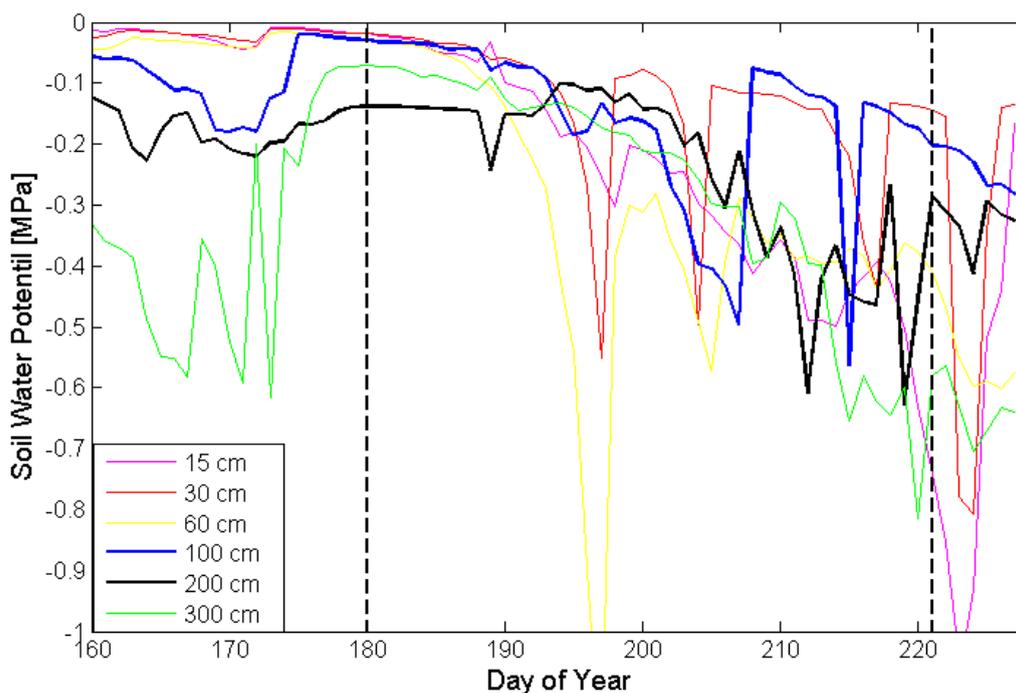


In contrast, *A. rubrum* shows a significant positive correlation between pre-dawn leaf water potential values and soil moisture levels. This indicates that the amount of water recharge *A. rubrum* can accomplish is linked to the amount of water in the shallow soil layers, and that members of this species do not fully recharge overnight unless soil water is sufficiently high [36]. *A. rubrum* was found to be a shallow rooted species with most root biomass concentrated in upper soil layers [34].

Both *Q. rubra* and *A. rubrum* show a positive correlation between mid-day leaf water potential and vapor pressure deficit (Figure 1). This is consistent with many studies, including Turner *et al.* [37] in which it was found that increasing VPD leads to decreases in leaf water potential and gas exchange, but also leads to an increase in transpiration rate in woody species. However, the specific response to VPD was different between the two species. Leaf water potentials of *Q. rubra* showed a more pronounced response to VPD than those of *A. rubrum*, as seen in the steeper slope of the regression line. As explained by McDowell *et al.* [38] anisohydric plants allow leaf water potential to drop when the soil or the air are dryer, while isohydric plants maintain a relatively constant leaf water potential by

reducing stomatal conductance as soil and air conditions dry. Our leaf water potential observations confirm that *Q. rubra* presents an anisohydric strategy with larger diurnal variation and overall lower mean values of leaf water potential. Our observations that mid-day water potential in *A. rubrum* was not correlated with soil moisture confirm the predictions of Meinzer *et al.* [21], which used sap-flow observations to analyze the hydraulic strategies of trees in a forest plot in the Eastern US. *A. rubrum* in our site presented a characteristic isohydric strategy by maintaining relatively constant and high leaf water potential even when soil moisture and VPD conditions were stressing.

**Figure 4.** Time series of soil water potential at different depths. The period of the experiment, characterized by a 2-week sequence of low precipitation and consequent drying of the soil column is marked by vertical dashed lines. The soil layers between 100 and 200 cm deep show the lowest variation and never reached below  $-0.5$  MPa during the experiment period.



We hypothesize that by reducing stomatal conductance *A. rubrum* is able to keep leaf water potentials high, even when VPD and soil moisture are restrictive. This is despite the fact that *A. rubrum* is not fully recharged with water in most mornings. This is consistent with the results of Oren & Pataki [13], who found that *A. rubrum* had higher stomatal sensitivity to VPD than co-occurring *Q. Alba* and attributed the difference to the differences in xylem properties between diffuse- and ring-porous species. In contrast, the ring-porous *Q. rubra* exhibits a risk-prone strategy. Its larger ring-porous vessels are more conductive and therefore can continue providing water at adequate rates even when VPD is high. As leaf water potential data suggest, this is done without down-regulating of the stomatal conductance, which implies a higher risk of hydraulic failure. The hypothesis of strong stomatal regulation as a mechanism of maintaining isohydric leaf water potential in *A. rubrum* is in contrast with those of Bush *et al.* [9]. They found that diffuse porous species (including *Acer platanoides*) showed increased transpiration with increasing VPD, indicating that

down regulation of stomatal conductance did not take effect at high VPD values. However, their experiment was set in an irrigated site with soil water content between 20%–30% (of garden top-soil) while our experiment site was set in deep sandy soil and soil water content was between 4%–9%. It is highly possible that for the range of soil moisture conditions tested by Bush *et al.* [9] the trees did not reach the level of stress that demanded down regulation of stomatal conductance. Consistent with our results, Ni *et al.* [39] showed that saplings of different Oak species maintain non-negligible transpiration rates in soil water potentials below  $-0.5$  MPa while the stomatal conductance of *Acer saccharum* at such low water potential approaches zero.

Deep roots can provide sufficient night-time recharge to full capacity and, possibly, additional water supply during the day. By allowing transpiration at maximal rates, *Q. rubra* leaf water potential is reduced to low levels and may potentially lead to increased risk of widespread cavitation. *A. rubrum*, which as a diffuse porous species is potentially more sensitive to xylem cavitation than ring porous species, may however reduce cavitation risk by closing stomata at less negative leaf water potentials [40]. Our results indicate that *Q. rubra* and *A. rubrum* take different ends of the safety-efficiency tradeoff [41] with the ring porous species optimizing at the efficiency end of the scale. Taneda & Sperry [18] showed that although the ring-porous species *Quercus gambelii* was highly vulnerable to cavitation during the day, it was able to refill embolized vessels overnight. That study also indicated that *Q. gambelii* accessed a much deeper pool of soil water compared to the co-occurring *Acer grandidentatum*.

#### 4. Conclusions

We showed that two different broad-leaf deciduous tree species have different hydraulic strategies. The diffuse-porous and shallow-rooted *A. rubrum* insufficiently recharges during the nights to refill day-time loss of water storage, and compensates by reducing stomatal conductance to reduce water loss when conditions are limiting. The ring-porous, deep-rooted *Q. rubra* appears to be capable of recharging to capacity at night-time even when soil moisture at the upper 30 cm near the wilting point. Our observations at the site show that the intermediate soil layers, between 1–2 m deep, have low variability of soil water potential and only very rarely dry below  $-0.5$  MPa. These layers could be used as a reservoir for *Q. rubra* when the top layers, above 60 cm are dry. While the deepest observed soil moisture contents at our site is only 3 m deep and a much deeper water table, further research may address what soil reservoir precisely *Q. rubra* and *A. rubrum* are capable of accessing.

The pronounced differences between the two species point to a need for more hydrodynamic detail when modeling the function of a mixed broadleaf forest. The different hydraulic strategies of these isohydric vs. anisohydric species may lead to different growth trajectories for each of the species, though further studies of the stomata-conductance, sap flow, water use efficiency and drought sensitivity of the two species are needed to accurately quantify the consequences of their hydraulic strategies at our and similar sites. These may be further compounded with potential changes to climate and particularly drought and precipitation regimes. In almost every ecosystem model, these two species are a part of the same plant functional type, often representing the same “big-leaf”. However, because their strategies are so different, we predict that the transpiration of a forest patch will change if the species composition will shift between one of these species to the other. Current land-surface and ecosystem models will, therefore, not be able to predict such interactions between hydraulic strategy,

forest composition and climate change. Species-specific stomatal conductance parameterizations (e.g., [42,43]) and/or tree-level hydrodynamic models using mechanistic water transport principles or parameterization for tree-level water storage and multiple resistance levels, such as the Finite-Elements Tree-Crown Hydrodynamics (FETCH) [44], SPA [45] and Expert-N [46] may be able to fulfill this need.

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## Conflicts of Interest

The authors declare no conflict of interest.

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