Science of the Total Environment 850 (2022) 158029

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Sap flow velocities of *Acer saccharum* and *Quercus velutina* during drought: Insights and implications from a throughfall exclusion experiment in West Virginia, USA

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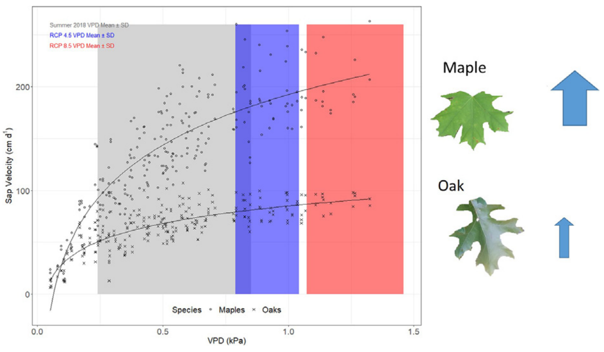
HIGHLIGHTS

- Sap velocity is affected by VPD and differ between two sugar maple and black oak.
- Sap velocity is not affected below thresholds of low soil moisture.
- Increased transpiration rates are likely in central Appalachian Mountains.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Manuel Esteban Lucas-Borja

Keywords:
Sap velocity
Transpiration
Climate change
Acer saccharum
Quercus velutina
Appalachia
Mountain water resources

ABSTRACT

Forest species composition mediates evapotranspiration and the amount of water available to human-use downstream. In the last century, the heavily forested Appalachian region has been undergoing forest mesophication which is the progressive replacement of xeric species (e.g. black oak (*Quercus velutina*)) by mesic species (e.g. sugar maple (*Acer saccharum*)). Given differences between xeric and mesic species in water use efficiency and rainfall interception losses, investigating the consequences of these species shifts on water cycles is critical to improving predictions of ecosystem responses to climate change. To meet this need, we quantified the degree to which the sap velocities of two dominant broadleaved species (sugar maple and black oak) in West Virginia, responded to ambient and experimentally altered soil moisture conditions using a throughfall exclusion experiment. We then used these data to explore how predictions of future climate under two emissions scenarios could affect forest evapotranspiration rates. Overall, we found that the maples had higher sap velocity rates than the oaks. Sap velocity in maples showed a stronger sensitivity to vapor pressure deficit (VPD), particularly at high levels of VPD, than sap velocity in oaks. Experimentally induced reductions in shallow soil moisture did not have a relevant impact on sap velocity. In response to future climate scenarios of increased vapor pressure deficits in the Central Appalachian Mountains, our results highlight the different degrees to which two important tree species will increase transpiration, and potentially reduce the water available to the heavily populated areas downstream.

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http://dx.doi.org/10.1016/j.scitotenv.2022.158029
Received 13 May 2022; Received in revised form 10 August 2022; Accepted 10 August 2022

1. Introduction

Climate change-attributed extreme hot weather in Northeastern North America is projected to be very likely to virtually certain (Seneviratne et al., 2021). In the central Appalachian Mountains, US, increases in potential evapotranspiration rates are also projected to be greater than subsequent increases in precipitation (Fernandez and Zegre, 2019), having important implications for ecosystem health and regional water security. Furthermore, the region is subject to ongoing changes in forest tree composition due to mesophication (Nowacki and Abrams, 2008), the process by which xeric species that have a higher water use efficiency are being replaced by less efficient mesic species (Caldwell et al., 2016; Ford et al., 2011a, 2011b). The higher transpiration rates of mesic forests, coupled with climate-driven changes in water availability, may lead to changes in streamflow and water resources availability during the growing season. Despite precipitation in the region being evenly distributed throughout the year, the high potential evapotranspiration of the warmest months creates the favorable conditions for high evapotranspiration (>50 % of the rainfall) (Guillén et al., 2021), most of which occur in the summer (Fernandez and Zegre, 2019). Moreover, broadleaf forests' water utilization is a key driver of evapotranspiration in the Appalachian Mountains (Guillén et al., 2021; Caldwell et al., 2016; Brown et al., 2005). To provide insight into the potential implications of change, in this study, we investigate tree-scale transpiration and controls in a temperate forest region in West Virginia (WV), a small (62,038 Km^2), heavily forested state in the eastern US.

The temperate forests of this region provide a valuable case study for determining the role of species-level hydraulic traits (e.g. xylem architecture, water-use efficiency) as well as how changes in climate can alter freshwater provisioning. West Virginia is an important "water tower" (Viviroli et al., 2007) to eastern and mid-western US, providing precipitation-driven streamflow to approximately 9 million people in the Mississippi River/Gulf of Mexico basin to the west and the Potomac River/Chesapeake Bay basin to the east (Young et al., 2019). Moreover, WV forests are emblematic of larger regional shifts in climate and species composition (Iverson et al., 2019) that are expected to alter the water cycle, likely leading to greater instances of droughts and reduced water availability downstream (Fernandez and Zegre, 2019; Kang and Sridhar, 2018).

Tree water use is determined by biotic factors such as interception (Brown et al., 2005), rooting depth (Canadell et al., 1996), and hydraulic traits that include xylem architecture (Ford et al., 2011a), water use-efficiency (Yi et al., 2019), and hydraulic safety margins (Allen et al., 2010). Abiotic factors, such as vapor pressure deficit (VPD), atmospheric water demand, and soil moisture are also important (Bovard et al., 2005; Oren and Pataki, 2001; Wullschleger et al., 1998). Furthermore, different species use different strategies to minimize the deleterious effects of water stress (Ford et al., 2011a; Wullschleger et al., 2001; Brzostek et al., 2014). Species can be classified along the isohydric-anisohydric spectrum (McDowell et al., 2008, Franks et al., 2007, Martínez-Vilalta et al., 2014; Hartmann et al., 2021) which describes their strategy. During chronic water stress, anisohydric species that include some species from the oak genera (*Quercus* spp.), (Roman et al., 2015) maintain high rates of photosynthesis and transpiration at the risk of xylem cavitation and hydraulic failure (Hartmann et al., 2021; McDowell et al., 2008). These species tend to inhabit drier, more xeric sites and can be more tolerant to chronic water stress than mesic, isohydric species (Brzostek et al., 2014). Isohydric species, such as sugar maple (*Acer saccharum*), on the other hand, reduce stomatal conductance to avoid cavitation of xylem conduits which could reduce photosynthesis and tree growth (Hartmann et al., 2021; McDowell et al., 2008). Changes in species composition are known to have effects on the water balances of mountain ecosystems (Brown et al., 2005), and importantly, shifts of dominance by xeric species towards mesophytic species have been associated to decreases in the water yield in the Appalachian Mountains (Caldwell et al., 2016). Thus, the ongoing temperate forests mesophication – partly caused by fire suppression which limits oak species (Nowacki and Abrams, 2008), coupled with the water-use strategies of the trees that will compose future forest, could play a key role in future drought resiliency (Nowacki and Abrams, 2008; Coble et al., 2017) and water availability (Caldwell et al., 2016).

This investigation's main aim was to improve the understanding of how drought influences water use dynamics of two important tree species of temperate forests in the central Appalachian Mountains. This was accomplished using a throughfall exclusion experiment, and measuring sap velocities and soil moisture in sugar maple and black oak plots. We had three specific objectives: 1) Explore how sap velocity of *A. saccharum* Marshall (sugar maple) and *Quercus velutina* Lam. (black oak), differ in their response to experimentally altered soil moisture conditions; 2) Identify which abiotic variables (i.e., soil moisture, vapor pressure deficit) are more important for determining sap velocity rates for each species; in order to, 3) Investigate the impacts of two climate change scenarios on transpiration by using ensemble climate data and a hydrologic model.

2. Material and methods

2.1. Site description and experimental design

Our research was performed at Toms Run Preserve, a 34 ha forest operated by the West Virginia Land Trust, located in Monongahela County, WV, approximately 10 km south of Morgantown, WV (39.55°N 80.00°W) (see Fig. 1). Toms Run is a second to third growth forest established during the first quarter or the beginning of 1900's and highly representative of forests throughout the region (Kutta and Hubbart, 2019). Elevation of the study site ranges from 336 m to 438 m with slopes that range from 3 to 25 % (Soil Survey Staff, 2020). Hillslopes are primarily drained by one intermittent stream, but several ephemeral streams occur during the winter or after heavy precipitation events during the growing season. Soils are classified as Alfisols order and Ultic Hapludalfs family (Soil Survey Staff, 2020). The specific soil series present are the Culleoka-Westmoreland, Dormont and Guernsey series, with silt loam and silt clay – loam textures, originated from weathered limestone, sandstone and shale. The slightly acidic (pH 4.5–6.0) soil series have a depth to lithic bedrock that ranges from 50 to 168 cm and the average water storage in the profile is low to moderate from 12.95 to 22.86 cm. (Soil Survey Staff, 2020). Mean annual temperature (1980–2010) is 11.61 °C, with monthly mean temperatures ranging from −0.39 °C (January) to 22.89 °C (July). Precipitation measured nearby (12 km) at the Morgantown Hart Field Airport (NOAA station # USW00013736) is uniformly distributed throughout the year. The mean annual precipitation is 1063 mm, with summer (June, July, and August) precipitation averaging 312 mm and winter (December, January, February) averaging 211 mm. Vegetation is mixed temperate broadleaf deciduous forests, consisting of *A. saccharum* Marshall, *A. rubrum* L. (red maple), *Q. velutina* Lam., *Q. rubra* L. (red oak), *Q. alba* L. (white oak), *Liriodendron tulipifera* L. (tulip poplar), *Carya* sp. (hickory), *Fagus grandifolia* Ehrh. (american beech), *Cornus florida* L. (flowering dogwood), *Platanus occidentalis* L. (sycamore).

2.1.1. Throughfall exclusion experiment

Precipitation manipulation experiments are important efforts to study the effects of changing climate regimes on forest ecosystems (Asbjornsen et al., 2018; Hanson and Wullschleger, 2003). These experiments have been less frequent on forest ecosystems than in other drier and low vegetation ecosystems (Asbjornsen et al., 2018). Precipitation manipulation experiments are particularly crucial to study the implications that sustained rainfall reductions could have on tree hydraulic dynamics (see e.g. Moreno et al., 2021; Grossiord et al., 2018; Wullschleger and Hanson, 2006). Information on how long-term reductions decrease sap velocity is still limited (Grossiord et al., 2018) and further efforts to implement long-term studies are needed (Grossiord et al., 2018). On the other hand, balancing costs and logistical complexity of such studies can limit its implementation and continuation (Asbjornsen et al., 2018). Yet, important information on atmosphere-soil-plant relationships could still be obtained, despite their variety in design and length (Asbjornsen et al., 2018). In 2017, we established, to our knowledge, the first throughfall exclusion experiment in

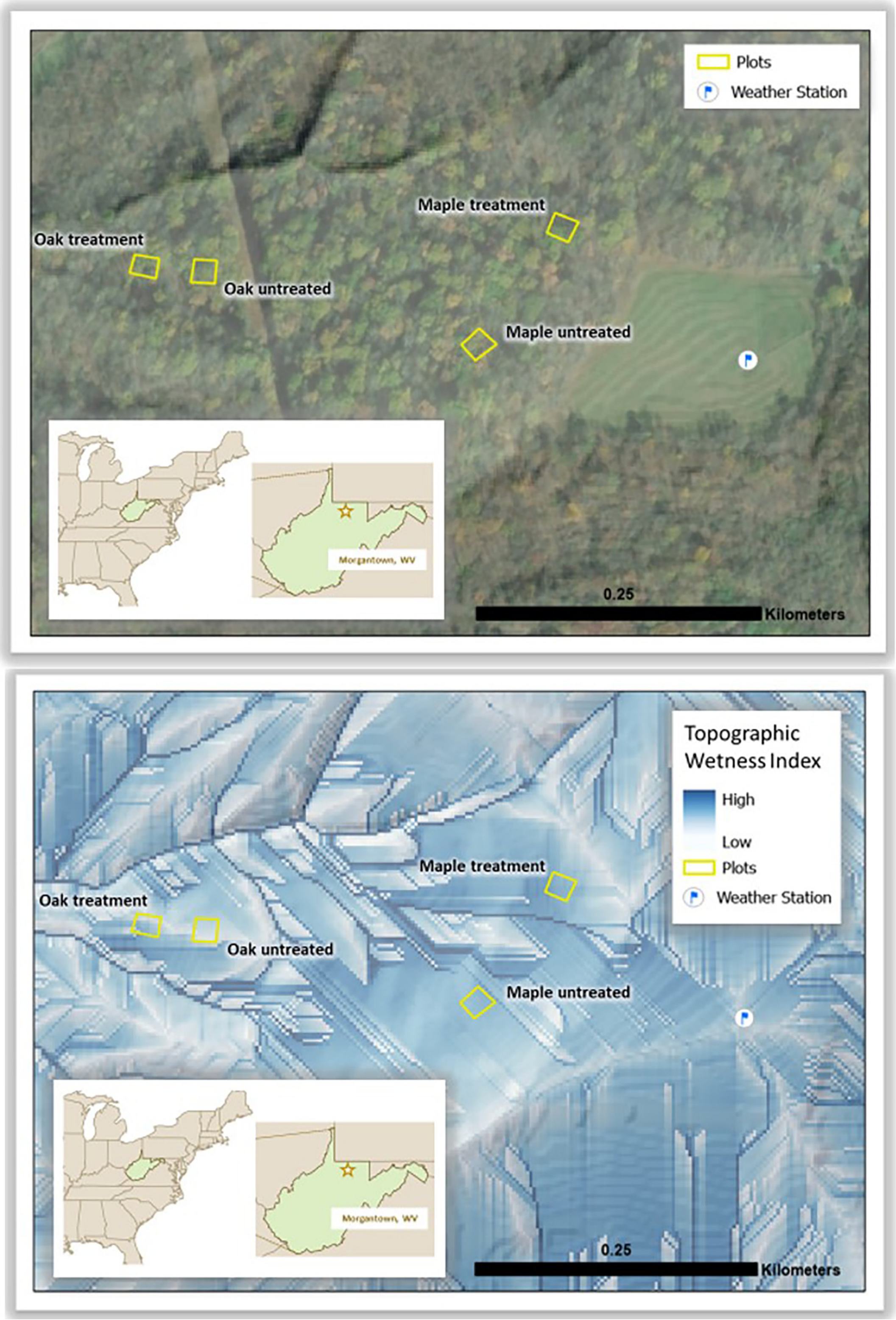

Fig. 1. Location of the throughfall exclusion study, experimental plots, and weather station at Toms Run Preserve, including experimental plots and weather station location. Background is composed by an overlay of an air photo with the site-based Topographic Wetness Index (Beven and Kirkby, 1979), which is used to explain the spatial variation of soil moisture based on slope and upstream contributing area. The darker areas represent higher potential for groundwater saturation.

West Virginia, USA, to study the effects of water stress on these temperate forest ecosystems. Using the natural species distribution of study site, four experimental plots were established in either *Q. velutina* or *A. saccharum* forest stands. *A. saccharum* dominated in the Maple plots with 79 % (treatment plot) and 59 % (untreated plot) of basal area; in the oak plots, *Q. velutina* had 75 % (treatment) and 76 % (untreated plot) of the basal area (see Table S1 for basal areas of all species at each plot). For each species, one 20 m × 20 m untreated plot and one 20 m × 20 m treatment plot where throughfall was experimentally reduced were co-located within a 100 m of each other on similar aspects and slopes resulting in a 2 species ×

2 treatments = 4 plots total study design. Project expenses and logistics limited further plot replication; hence, individual trees were considered as our experimental level of replication. However, we note that many large-scale ecosystem experiments where replication is limited due to logistical constraints use a similar design where plots are sub-divided into replicated sub-plots on which statistical inferences are made (Melillo et al., 2011; Frey et al., 2014). In addition, plots were selected based on as similar as possible basal areas, leaf area indices and tree diameter at breast height (Tables S1, S2, and S3) and encompassing at least six dominant overstory canopy trees where sap velocity was measured. Sap velocities were measured in trees that were farthest away from the edges of the plot (>5 m) to minimize edge effect. In the treatment plots, throughfall was excluded using a wood structure to support plastic panels at a height of 1.2 m–2.5 m that converged into gutters that transported and discharged precipitation downslope of experimental plot areas (Fig. S1a). Outside of the growing season (e.g. winter), the plastic panels were removed to limit snow and ice damage, allow natural litterfall, and to only exclude throughfall and manipulate soil moisture during the time of peak forest water use (Fig. S1b). Dormant season precipitation was sufficient to refill soil water storage and soil field capacity prior to the start of the next growing season, an important feature of eastern forests (Hanson and Weltzin, 2000). Throughfall exclusion during 2018 had three configurations: a) 0 % throughfall exclusion from 2018-01-01 to 2018-03-10 or day-of-year (DOY) 1–69; b) 50 % throughfall exclusion from 2018-03-10 to 2018-05-31 (DOY 70–151) and 2018-07-19 to 2018-11-08 (DOY 200–312); and c) 90 % throughfall exclusion from 2018-06-01 to 2018-07-18 (DOY 152–199). Overall, in 2018, the 50 % exclusion totaled 195 days and the 90 % exclusion totaled 48 days. These two configurations provided a larger range of conditions on which to investigate the sap velocity dynamics.

2.2. Data

2.2.1. Sap velocity

Sap velocity measurements were made on six dominant trees in each plot using the heat pulse method developed by Marshall (1958) and improved by Swanson and Whitfield (1981) by accounting for wounding effects on the xylem (Green, 1998). The rate of water flowing through the xylem of a tree is estimated based on the thermal dissipation of a heat pulse applied to a tree's sapwood (McJannet and Fitch, 2004). Three probes were used - one as heater in the center and the other two as thermocouples parallel to each other in vertical orientation. The probes were inserted into the tree at breast height (130 cm) with a fixed spacing: the thermocouple upstream was distanced 5 mm from the heat probe and 10 mm from the downstream (or higher) thermocouple (for a detailed methodology see McJannet and Fitch (2004)). Heat pulse velocity Hv (cm h^{-1}) (Eq. (1)) was calculated using the distance D (cm) from the heater probe to the center of the thermocouples, divided by the time T (h) from the application of the heat pulse until the two thermocouples reached the same temperature (McJannet and Fitch, 2004):

$$Hv = \frac{D}{T} \tag{1}$$

Heat pulse velocity (Hv) was corrected using coefficients from Swanson and Whitfield (1981) that account for the wounding effects of the installation of the probes in the trees (McJannet and Fitch, 2004) (see supporting information for correction equations). The corrected heat pulse velocity (Hc (cm h^{-1})) was then transformed into sap velocity (Sv (cm h^{-1})) (Eq. (2)) by considering the specific properties of the woody matrix (Becker and Edwards, 1999):

$$Sv = Hc(0.441 * Fwood + Fwater) \tag{2}$$

where, 0.441 (unitless) is the coefficient to convert heat pulse velocity to sap velocity which is given by the wood's heat capacity at 20 °C (Becker and Edwards, 1999), Fwood (m^3m^{-3}) is the volume fraction of wood, and Fwater (m^3m^{-3}) is the volume fraction of water (see supporting information). Stand level transpiration (T [mm h^{-1}]) was calculated by multiplying the average sap velocity of the plot (cm h^{-1}) by the plot's sapwood area (cm^2ha^{-1}). Because forest health is a primary conservation objective at the Toms Run Preserve, coring of the trees for sapwood area determination was not possible. Hence, sapwood area was estimated using species-specific allometric equations developed by Wullschleger et al. (2001) for Appalachian tree species (Eq. (3)):

$$Swa = B_0 DBH^{B_1} \tag{3}$$

where, Swa (cm^2) is the sapwood area at diameter at breast height (DBH) in cm, and B_0 (maple: 1.036; oak: 1.122) and B_1 (maple: 1.859; oak: 1.44) are species-specific parameters obtained from Wullschleger et al. (2001).

While sap velocity can be measured using probes inserted around a tree's trunk diameter and at multiple depths, we only measured sap velocity at one depth and with one probe set per tree since our focus was to understand plant - soil- atmosphere interactions, and carry out more relative than absolute comparisons. Moreover, to account for the uncertainty of using sapwood areas and volume fractions of water and wood estimated using allometric equations, we assumed a relative error of 20 % and performed a Gaussian error propagation analysis following Bevington and Robinson (1992) (see supplementary information). Transpiration rates obtained from heat pulse methods are practical, but have inherent uncertainty (Forster, 2017). Thus, we focused the analysis on sap velocities instead of focusing on transpiration. Transpiration results served as indicative values and aided in the contextualization of our findings, and are not considered a quantification of exact whole tree water use. The measurement period started on 2018-06-01 (DOY 152) and ended on 2018-10-04 (DOY 277). Sap velocity was recorded using CR1000 Dataloggers located in each plot (Campbell Scientific, Logan UT, USA). The heat pulse was fired every 30 min for 2 s and subsequent heat dissipation was recorded for 5 min following the pulse. The system was powered by deep cycle batteries that were changed approximately every fortnight. Sap velocity was calculated from the measured temperatures using R (R Core Team, 2019). Time series of daily sap velocity and meteorological variables were constructed using the R package hydroTSM (Zambrano-Bigiarini, 2017). Mean daily sap velocity for each tree and plot was calculated only for daytime periods since nighttime transpiration was expected to be minimal and cannot be measured correctly with the type heat pulse velocity system used (Forster, 2017).

2.2.2. Meteorological and soil moisture data

A weather station was installed in an open field adjacent to the study site (Fig. 1) to measure precipitation, air temperature, air humidity and net solar radiation. Precipitation was measured using a tipping-bucket rain gauge (TR525, Texas Electronics, Dallas TX, USA) and supplemented with data from Hartfield Airport National Weather Service (NWS) station (12 Km away) during 8 days of instrument malfunction (missing days). Linear regression between the study and NWS stations were used to reconstruct missing data ($R^2 = 0.67, p < 0.01, n = 110$ days). Air temperature and relative humidity were measured using a HMP60 probe (Campbell Scientific, Logan UT, USA) and net solar radiation was measured using a CMP6 sensor (Campbell Scientific, Logan UT, USA). Data were logged every 60 min (except precipitation which was logged every 10 min) using a CR6 Datalogger (Campbell Scientific, Logan UT, USA).

Within each plot, volumetric soil water content (VWC) (m^3m^{-3}) of the top 30 cm was measured using four time domain reflectometry (TDR) probes installed in random locations (CR616, Campbell Scientific Logan UT, USA), and recorded every 30 min during the duration of the experiment. Soil samples were collected weekly from May until September and biweekly from October until April near TDR probes to calculate gravimetric soil moisture. Standard gravimetric methods were used to calculate actual water content, which was compared to the soil moisture probes to assure the probes reflected the changes in the soil moisture. VPD was calculated following the equation by Monteith and Unsworth (2007) (Eq. (4)):

$$VPD = \left(1 - \frac{RH}{100}\right) \times 610.7 \times 10^{\frac{7.5Ta}{(237.3+Ta)}} \tag{4}$$

where VPD (Pa) is vapor pressure deficit, RH (%) is relative humidity and Ta (C°) is air temperature recorded at the weather station.

2.3. Future climate projections and sap velocity

We used the MACAv2-METDATA dataset (Abatzoglou, 2013) to assess the sensitivity of sap velocity to future climate projections. The MACAv2-METDATA dataset consists of downscaled biased corrected outputs from 19 different General Circulation Models (GCMs) for the continental US. The MACAv2-METDATA includes two emission scenarios: a low emissions scenario (RCP 4.5) and a high emissions scenario (RCP 8.5). The MACAv2-METDATA includes the atmospheric variables important for transpiration, including daily VPD and incoming solar radiation. Since MACAv2-METDATA does not include soil moisture data, soil moisture from 0 to 1 m deep was simulated using the Variable Infiltration Capacity (VIC) model (Hamman et al., 2018; Liang et al., 1994). VIC model is a semi-distributed hydrologic model widely used in climate change studies (Hamman et al., 2018). A daily time series for the atmospheric variables from the MACAv2-METDATA was used to run the VIC model for the watershed containing the study site for a period of 94 years (2006–2099). Trends in future climatic variables for summer months (June, July, August, September [JJAS]) were assessed using the ranked, non-parametric Mann Kendal tests with the help of the ‘trend’ package (Pohlert, 2018) in R.

Using JJAS data from 2018, a stepwise linear regression was carried out to find the most parsimonious model of sap velocity based on the Akaike Information Criteria (AIC), utilizing R package MASS (Venables and Ripley, 2002). The model selection included interactions between the variables as well as their logarithmic transformation, based on initial model fitting that found increased correlations after logarithmic transformations. Future sap velocity was projected using the models shown in Table S4.

In addition to the future climate, we also explored hypothetical changes in tree species composition of future forest to provide insight into how a shift from oaks to maples expected with mesophication and continuous fire suppression could potentially affect water use under climate change. The experiment consisted of increasing 10 % (from 60 % to 70 %) of basal area of maples and decreasing 10 % (from 40 % to 30 %) of basal area of oaks, then new transpiration values were calculated for each future climate scenario. Given that forest composition changes entail a migration of species to new habitats or sites that might not be as suitable under drought conditions, we decided to also include conditions of 50 % reduction in soil moisture in our simulations. This extra step aimed at mimicking a situation in which mesic species would occupy xeric sites in the future.

2.4. Statistical analysis

We used a two-way ANOVA with species (maple, oak) and treatments (untreated, treatment) as factors to test for differences of growing season mean daily values of soil moisture and sap velocity between the plots. Because replications of treatment and the controls plots were not possible and we focused on replicate trees within each plot, we are cautious to claim statistical inference about the effect of experimental drought treatments by not focusing specifically on them in the discussion. Notwithstanding, our analyses still provide important insights into the site's ecohydrology. Post hoc comparison between plots was carried out using the Tukey-HSD test. Tree-to-tree variability caused by technical factors (probe insertion misalignment, differences in probe depth with respect to conducting tissue), and biological differences (xylem anatomy, tree specific rooting depth), likely added random noise to the signal of how environmental conditions influence sap velocity. To enhance this signal, sap velocity was mean centered and scaled within each individual tree. The resulting tree level z-scores were averaged by species, treatment, and day. The new data set of z-scores reduced the large variability between the treatments and permitted better comparisons of sap velocity sensitivity and controlling variables. A linear mixed effects model was then developed using the ‘nlme’ (Pinheiro et al., 2019) and ‘MuMin’ (Barton, 2019) packages to examine the influence of the environmental controls and their interactions on sap velocity. From 113 candidate models, the most parsimonious model was selected using Akaike Information Criteria (AIC), a common approach for LME (Zuur, 2009). The best model differed by >4 AICc to the second-best model, information that permitted identification of the nature of the relationship between the best explanatory variables and sap velocity (Mathias and Thomas, 2018). The four measured explanatory variables (VPD, radiation, soil moisture, precipitation) and their interactions were initially included as fixed effects to the models, while species, treatment, and tree were included as random effects. Furthermore, an autocorrelation structure AR (1,0) (e.g., 1-day lag in the covariance structure) was included in the model to account for temporal autocorrelation (Mathias and Thomas, 2018). Nonlinearity between the variables was accounted for using logarithmic transformation of the variables to improve the linear fit. The two-way ANOVA and the linear mixed effect model each had a robust sample size of $n = 2775$, obtained from 23 individual trees and 126 daily values measured from 2018-06-01 to 2018-10-04 (123 data points had to be omitted due to missing or erroneous values at individual trees across the growing season). All statistical analysis was carried with a significance level of $\alpha = 0.05$.

3. Results

3.1. Differences in sap velocity

3.1.1. Sugar maple had higher sap velocity rates than black oak

Sap velocities during the study period were almost twice as high in sugar maple trees than in the black oak trees (Fig. 2b and Table 1). The sap velocity was not only significantly different among the species but also between treatments and between the species and treatment interaction (Table 2). Due to the lack of treatment replication and potential issues due to pseudoreplication (Hurlbert, 1984; Heffner et al., 1996), we cautiously interpret these results as an indication of differences between the plots and not as treatment effects. Mean daily sap velocity was highest in the maple treatment plot with 147 ± 22 cm d^{-1} (SD = 58), followed by sap velocity at the maple untreated plot with 126 ± 19 cm d^{-1} (SD = 50). Daily sap velocity in the oak treatment plot averaged 67.80 ± 10 cm d^{-1} (SD = 22) and 64 ± 9 cm d^{-1} (SD = 19) in the oak untreated plot, which was the lowest sap velocity across plots. Sap velocity differed between species during most days of the season, except for rainy days where sap velocities were low for both species (Fig. 2c).

Transpiration in the maples was approximately five times higher than in the oaks – daily transpiration averaged 3.22 ± 0.6 mm (SD = 1.29) in the maple treatment plot, 1.67 ± 0.3 mm (SD = 0.66) in the maple untreated plot, 0.49 ± 0.1 mm (SD = 0.17) in the oak treatment plot, and 0.38 ± 0.06 mm (SD = 0.11) in the oak untreated plot. The total transpiration over the four-month growing period (2018-06-01 to 2018-10-04) was 308 ± 54 mm for maples and 55 ± 12 mm for the oaks. Precipitation during that same period totaled 574 mm, higher than the average summer precipitation.

Overall, transpiration was highly uneven between species, which is caused by the large differences in sapwood areas, in which maples had more than twice as large sapwood areas than oaks (Table S3).

3.1.2. Tree size unimportance on sap velocity and its sensitivity to VPD

Sap velocity was highly variable between trees within each plot (Fig. 3a). The maple treatment plot only included data from five trees due to the malfunction of one sensor during most of the study period. The maple treatment plot had three trees with median values near 200 ± 30 cm d^{-1} and the remaining with medians of approximately 60 cm d^{-1}. The maple untreated plot had one tree with median above 200 ± 30 cm

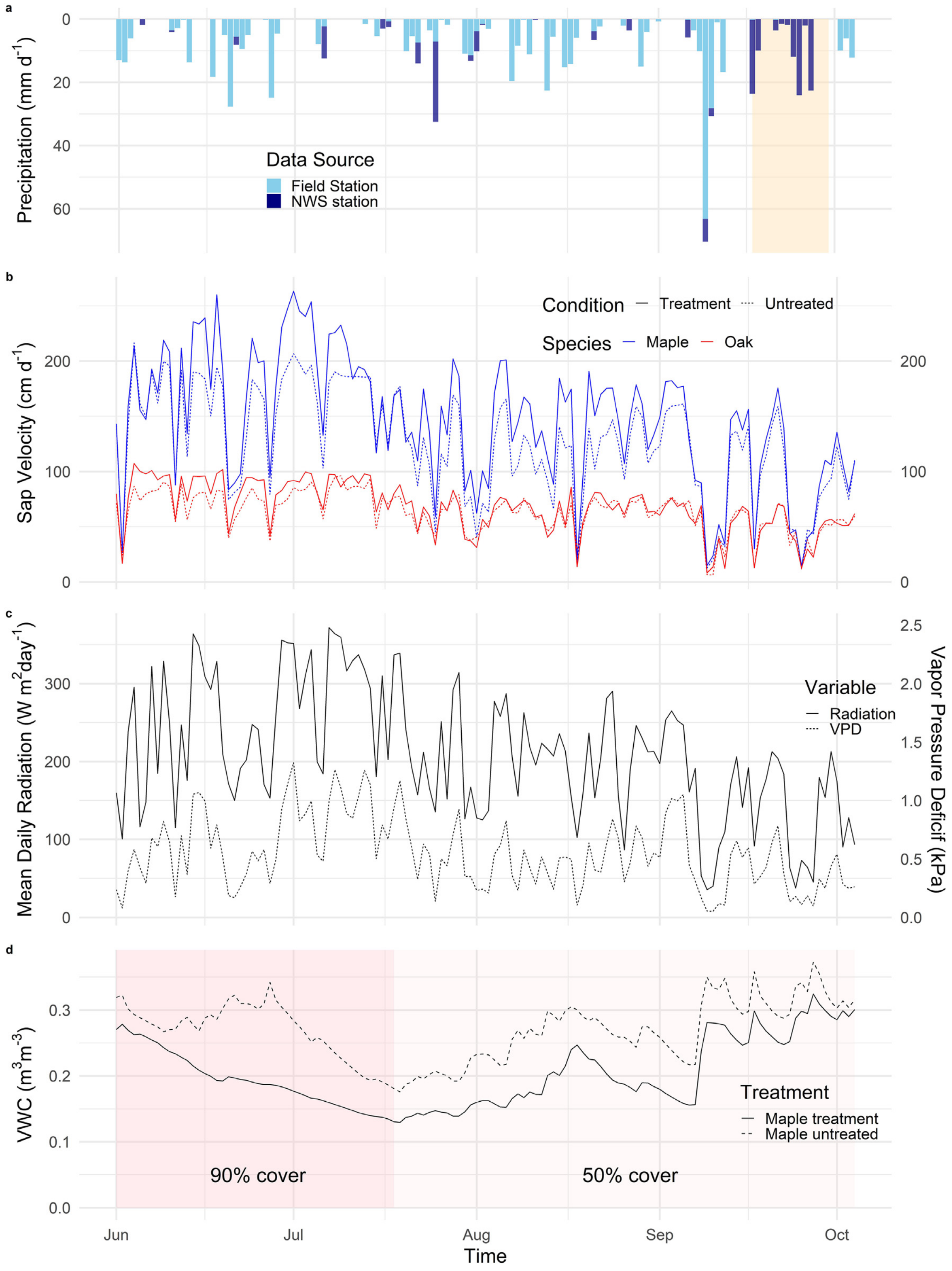

Fig. 2. Daily Time Series for a) Precipitation from field station and Hartfield Airport National Weather Service (NWS) station; b) Sap velocity; c) VPD and radiation and d) 0–30 cm soil moisture from maple plots expressed as volumetric water content (m^3m^{-3}) from 2018 to 06-01 until 2018-10-04 (Daily soil moisture in Oak plots not shown, as they follow similar trends), colored backgrounds represents the percentage of throughfall exclusion at the treatment plots. Note that precipitation events have important influences on the other variables and was used to identify missing data due to rain gauge malfunction at the field station during the third week of September (shaded area in yellow). When data from the NWS is used to fill in the gap, the rain events match the increasing soil moisture and the lower sap velocity, VPD and radiation magnitudes.

d^{-1}, two trees between 100 ± 15 and 150 ± 22 cm d^{-1} and the remaining below 100 ± 15 cm d^{-1}. All the oak trees had median and mean values lower than 100 ± 14 cm d^{-1}. The oak treatment plot had two trees with very low medians of 25 ± 4 cm d^{-1} and 35 ± 5 cm d^{-1}, while the remaining trees had a median around 60 ± 9 cm d^{-1}. The oak untreated plot had the lowest variability in sap velocity with most trees having medians of

Table 1
Summary of variables used, units and range.

Variable	Symbol	Mean (SD)	Range	Unit
Precipitation	P	4.13 (8.16)	0, 63	mm d^{-1}
Radiation	Rad	209.13 (83.55)	36, 372	W m^{2}d^{-1}
Soil volumetric water content	VWC	0.21 (0.06)	0.12, 0.37	m^{3}m^{-3}
Vapor pressure deficit	VPD	0.55 (0.31)	0.05, 1.32	kPa
Sap velocity	Sv			cm d^{-1}
Acer saccharum		136.27 (55.37)	12.33, 263.24	
Quercus velutina		65.63 (21.04)	6.27, 107.25	
Transpiration	T			mm d^{-1}
Acer saccharum		2.44(1.28)	0.16, 5.78	
Quercus velutina		0.43(0.15)	0.04, 0.78	

between 40 ± 6 and 60 ± 9 cm d^{-1}. Sap velocity of the trees within each plot showed similar behavior despite large variations in magnitude (Fig. 2b).

Variation in tree-to-tree sap velocity was likely due to small differences in probe insertion depth and the inherent characteristics of the xylem around each sap flow probe. The influence of tree size on sap velocity was not clearly recognizable due to the large variance of sap velocity between trees, as both large and small trees presented a wide range of sap velocities for all the species and treatments (Fig. 3a). On the other hand, after we checked the relationship between the slope of the linear regression of sap velocity vs VPD and the size of each tree we found that sap velocity sensitivity to VPD was not influenced by differences in DBH (Fig. 3b). This could mean that DBH is not an important factor to determine sap velocity in our site.

3.2. Environmental controls on sap velocity

3.2.1. VPD, radiation and precipitation:VPD interaction are the most important controls on sap velocity

Total daily precipitation, mean daily VPD, radiation, soil moisture and four interactions (precipitation:radiation, precipitation:VPD, radiation: VPD and soil moisture:VPD) were significant predictors of sap velocity, after controlling for the effects of species, treatments, and individual trees (Table 3). According to the linear mixed effects model obtained from 113 models based on the combinations from 16 variables, VPD was the most important control, followed by radiation, the precipitation:VPD interaction, and the soil moisture:VPD interaction, which was more important than soil moisture by itself. All the interactions had positive effects on sap velocity, except for the precipitation:radiation interaction and radiation:VPD interaction that had negative effects on sap velocity (Table 3).

3.2.2. Maple exhibited higher plasticity to changes in VPD

Effects of VPD on sap velocity were similar between the untreated and treatment plots for each species but were different between the two species (Fig. 4). In particular, sugar maple had a more sensitive response to both high and low VPD values (Fig. 4). The response of sap velocity to changes in VPD decreased as the VPD reached higher magnitudes (Fig. 4).

3.2.3. Shallow soil moisture needs to be very low to affect the tree sap velocity

Significant differences in soil moisture were found (ANOVA, F = 665.1, $p < 0.0001$) between the sugar maple and black oak plots. Soil moisture varied during the summer, increasing after precipitation events which had larger effects on the untreated plots (Fig. 2d). Generally, shallow soil moisture was higher in the sugar maple plots than in the black oak plots, and higher in the maple untreated plot compared to the rest of the plots (Fig. 5a). Daily VWC averaged 0.27m^{3}m^{-3} (SD = 0.05) in the maple untreated plot and 0.2 m^{3}m^{-3} (SD = 0.05) in the maple treatment plot. Moreover, daily VWC were lower in the respective oak plots, averaging 0.2 m^{3}m^{-3} (SD = 0.03) in the oak untreated plot, and 0.18 m^{3}m^{-3} (SD = 0.04) in the oak treatment plot. Interestingly, dry conditions of shallow soil moisture below a VWC of 0.15 m^{3}m^{-3} lowered sap velocity for the same VPD magnitudes for all the plots (Fig. 5b).

Table 2
Analysis of variance results. Response variable was sap velocity and the listed explanatory variables were the categorical factors.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Species	1	3,748,743.11	3,748,743.11	1083.55	0.000
Treatment	1	219,640.10	219,640.10	63.49	0.000
Species:Treatment	1	33,809.82	33,809.82	9.77	0.002
Residuals	2771	9,586,831.03	3459.70	NA	NA

3.3. Future VPD, soil moisture and sap velocities

Average VPD and radiation are projected to significantly increase (Mann-Kendal, $p < 0.001$) during future growing seasons. The greatest increases in VPD were in the RCP 8.5 by 0.078 kPa/decade, which is more than twofold of the projected increases in the RCP 4.5 by 0.0305 kPa/decade (Fig. 6b). Radiation increased by 0.797 Wm^{2}day^{-1}/decade for the RCP 4.5 and by 0.996 Wm^{2}day^{-1}/decade for the RCP 8.5 (Fig. 6c). In contrast, shallow soil moisture was projected to significantly decrease (Mann-Kendal, $p < 0.001$), with a larger decrease in the RCP 8.5 by −0.004 m^{3}m^{-3}/decade, than for RCP 4.5 VWC that decreased by −0.002 m^{3}m^{-3}/decade (Fig. 6d). Despite its projected decrease, average summer soil moisture would be higher than VWC 0.20 m^{3}m^{-3} for both climate scenarios, meaning that it would not be much lower than the soil moisture we measured, and possibly would not cause major limitations to VPD.

Future summer VPD for the last quarter of the century had an average of 0.92 kPa (SD = 0.13) for the RCP 4.5 and 1.27 kPa (SD = 0.19) for the RCP 8.5. These values are much higher than the mean values of the first 25 years (2006–2030) of model output (RCP4.5: 0.70 kPa (SD = 0.09) and RCP 8.5: 0.74 kPa (SD = 0.1)), and higher than the average values in the summer of 2018 (0.55 kPa (SD = 0.3)). Fig. 6a shows how future VPD would be in relation to 2018 values. Average future VPD correspond to VPD values that are currently seldom (RCP 4.5) or extreme (RCP 8.5); and that created the appropriate conditions for the highest magnitudes of sap velocity, especially for the maples (Fig. 6a). Summer transpiration predictions for 2075–2099 based on the two climate change scenarios showed important increases: future stand transpiration in the maples would increase by 32 ± 5 % (RCP 4.5) and by 39 ± 6 % (RCP8.5). Similarly, the black oak stand would increase transpiration by +21 ± 9 % (RCP4.5) and + 29 ± 10 % (RCP 8.5) (see Table S5).

Climate change scenarios combined with our simplified changes in forest composition showed that tree water use would largely increase. Hence, a forest composed of 60 % maples and 40 % oaks, would increase transpiration by +31 ± 5 % (RCP 4.5) and + 38 ± 6 % (RCP8.5). If forest species composition shifts to 70 % maple and 30 % oak, transpiration could increase by +47 ± 6 % (RCP 4.5) and + 56 ± 7 % (RCP 8.5) (Table 4). Inclusion of speculative soil moisture reductions (50 % lower soil moisture), to mimic xeric microsite conditions, showed that trees in xeric sites had circa 20 % lower transpiration than those in mesic sites in each of the climate and forest composition scenarios (Table 4).

4. Discussion

4.1. Differences in species sap velocity and responses to environmental controls

Our study provides important insights on the higher sap velocity and water use of maples in comparison to oaks, the importance of sapwood areas, and the influence of environmental controls on sap velocity.

We found that maple plots used about five times more water than the oaks plots, commensurate with other studies in the midwestern and the eastern USA (Yi et al., 2017; Bovard et al., 2005; Wullschleger et al., 2001; Ford et al., 2011a) and despite of differences in site (e.g. elevation, topography, latitude) and forest characteristics (e.g. types, ages, size, species). Specifically, Yi et al. (2017) reported six-fold differences in sap

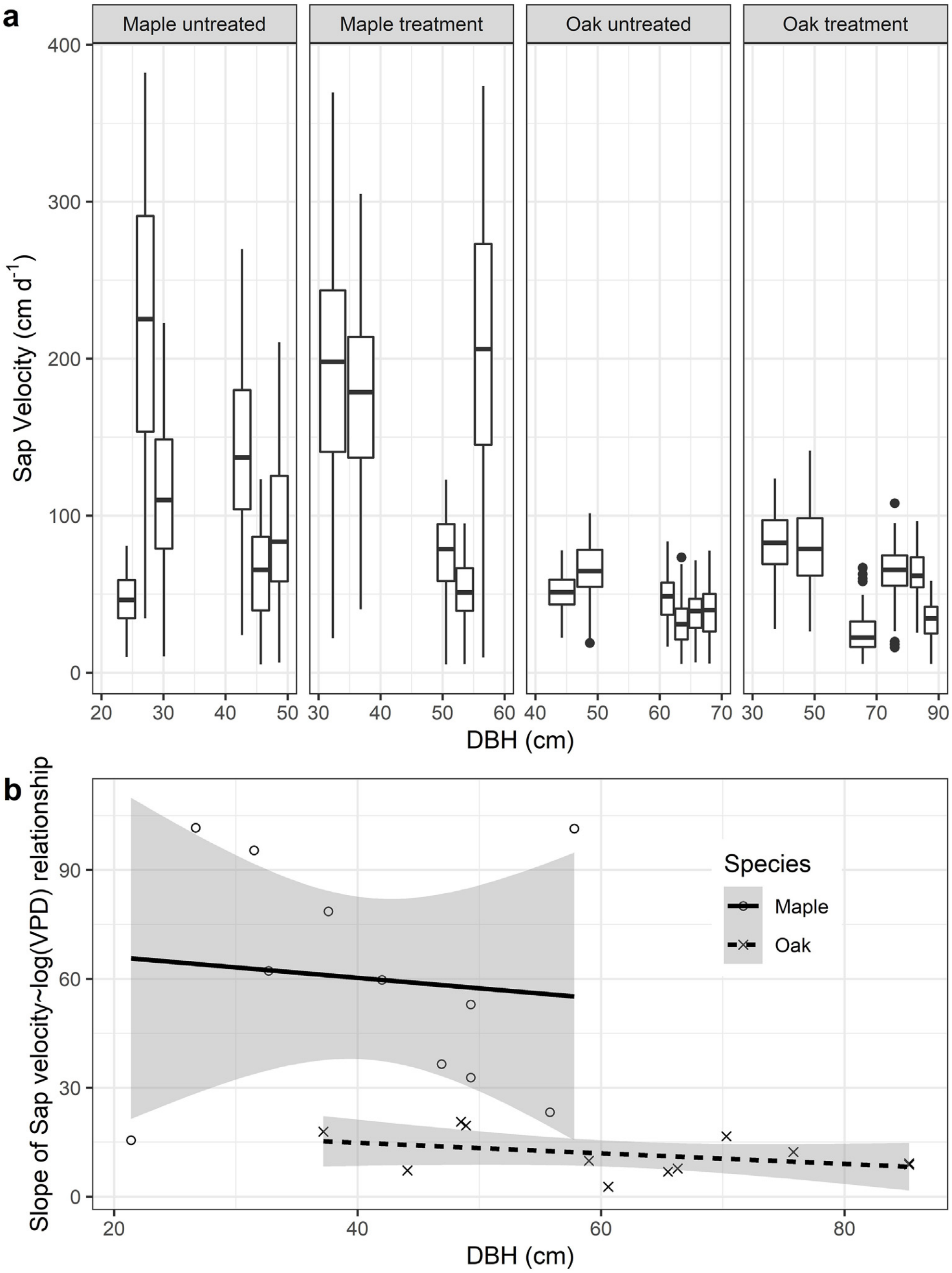

Fig. 3. DBH and Sap Velocity relationships. Panel a) Boxplots of sap velocity against tree DBH. b) Scatterplot of the slope of the regression between sap velocity and log(VPD) against DBH for maples ($R^2 = 0.012$, *p*-value = 0.64, *n* = 11) and oaks ($R^2 = 0.16$, *p*-value = 0.75, *n* = 12).

flux mid-day rates during certain periods of the growing season in Indiana, USA, and Wullschleger et al. (2001) reported maples species using 2–3 times more water than oak species in Tennessee, USA. One reason for the diverse water use, may be the difference in water conducting capacities between species (Ford et al., 2011a; Gebauer et al., 2008; Oren and Pataki, 2001). Generally, diffuse porous species (e.g. sugar maple) transport more water than ring porous species (e.g. black oak) (Pallardy and Kozlowski, 2008). Hence, the higher sap velocity of sugar maples in comparison to the black oak is a confirmation of the species-specific xylem anatomy characteristics of their genera (Ford et al., 2011a; Gebauer et al., 2008; Wullschleger et al., 1998; Benson et al., 2018; Cermak et al., 2004).

Moreover, different sap velocity rates between the species is likely attributable to their distinct sensitivity to environmental controls (Yi et al., 2017; Dragoni et al., 2009; Oren and Pataki, 2001). In that respect, the strong influence of VPD on sap velocity helps to confirm its role as a first-order control on transpiration (Grossiord et al., 2020; Novick et al., 2016; Sulman et al., 2016; Tang et al., 2006; Bovard et al., 2005; Oren et al., 1999). Our results show relationships between sap velocity and VPD (Figs. 4 and 6a) that are similar to findings in forests in eastern North America (Bovard et al., 2005; Oren and Pataki, 2001). Specifically, we found that the rate of change of sap velocity decreased at higher VPD, yet, the slope did not completely flatten. Based on previous literature (e.g. Yi et al., 2017), we expected that sugar maple would show a stronger response to changes in VPD, and stopped increasing sap velocity during high VPD. Hence, our results suggest a deviation from the isohydric behavior reported by Roman et al. (2015) and Yi et al. (2017). Instead, the behavior we observed is closer to the anisohydric classification in Loewenstein and Pallardy (1998). Since drought severity can influence

Table 3
Estimate results (standard error) for Linear Mixed Effects Model.

Scaled dependent variable	Estimate
Precipitation	0.113*** (0.029)
Radiation	0.274*** (0.031)
Soil moisture	0.081*** (0.024)
VPD	0.460*** (0.035)
Precipitation:Radiation	−0.138*** (0.031)
Precipitation:VPD	0.265*** (0.048)
Radiation:VPD	−0.059*** (0.017)
Soil moisture:VPD	0.133*** (0.018)
Constant	0.158*** (0.032)
Model information	
Observations	2775
Log Likelihood	−2987.494
Akaike inf. crit.	6002.988
Bayesian inf. crit.	6085.941
Significance levels: *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$	

the evaluation of isohydric-anisohydric behavior (Coble et al., 2017), we presume that the sugar maples might had enough access to water, allowing them to keep increasing sap velocity even at periods of high VPD. Oaks did not present contrasting results to the anisohydric behavior reported in previous literature (Yi et al., 2017).

4.2. Sap velocity had limited sensitivity to soil moisture reductions

Trees in our study showed little sensitivity to reductions in soil moisture from the throughfall exclusion. Generally, soil moisture limitations are known to control sap velocity and tree water use (Yi et al., 2017). We believe this can be attributed to two primary reasons: water limitation was not sufficient to affect sap velocity, and access to deep water by the trees root system.

First, sap velocity can be insensitive to changes in soil moisture when water is not a limiting factor (Bovard et al., 2005; Oren and Pataki, 2001; Yi et al., 2017). The absolute minimum VWC recorded in our study was 0.12 m^3m^{-3} (DOY 152–153) and averaged 0.21 m^3m^{-3} during the growing season, values that are higher than the 0.10 m^3m^{-3} threshold for soil moisture's influence on sap velocity determined by Bovard et al. (2005) in a mixed hardwood forest in Michigan, US. The high precipitation magnitudes received during 2018 might have reduced the effectiveness of the treatment to reach the point at which water becomes a limiting factor. Future studies that investigate more varied and extreme conditions could aid in disentangling these results. Moreover, longer studies could allow to evaluate acclimation effects of hydraulic behavior (Grossiord et al., 2018), instead of extrapolating seasonal to inter-annual behavior. The treatment plot structure was established in 2017, with the plastic panels set only during the summer months at a maximum of 50 % cover. Yet, given such short-lived manipulation, we could expect our results from 2018 to have minimal acclimation effects (e.g. Moreno et al., 2021 reports effects after 3–5 month; Limousin et al., 2009 reports transpiration adjustments starting from the second year).

Second, the high soil moisture and the insensitivity of soil moisture to the throughfall exclusion was likely attributed to the experimental design that did not explicitly consider access to deep water from subsurface flows or runoff from upslope contributing areas. In our study site, the micro topography and soil characteristics contributed to greater water accumulation in the maple stands, that had a higher topographic wetness index (Fig. 1) and higher VWC (Fig. 5a). Hence, we believe that water

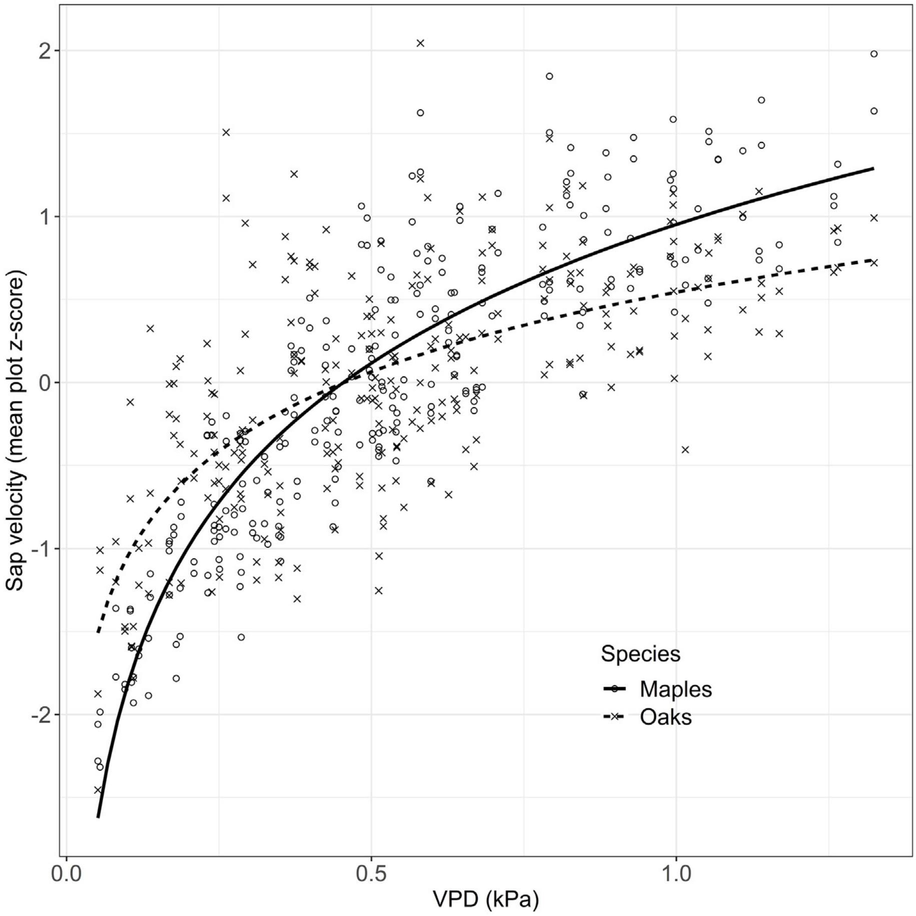

Fig. 4. Sap velocity and VPD relationships. Daily sap velocity *Z*-scores vs VPD for maples and oaks during the 2018 growing season.

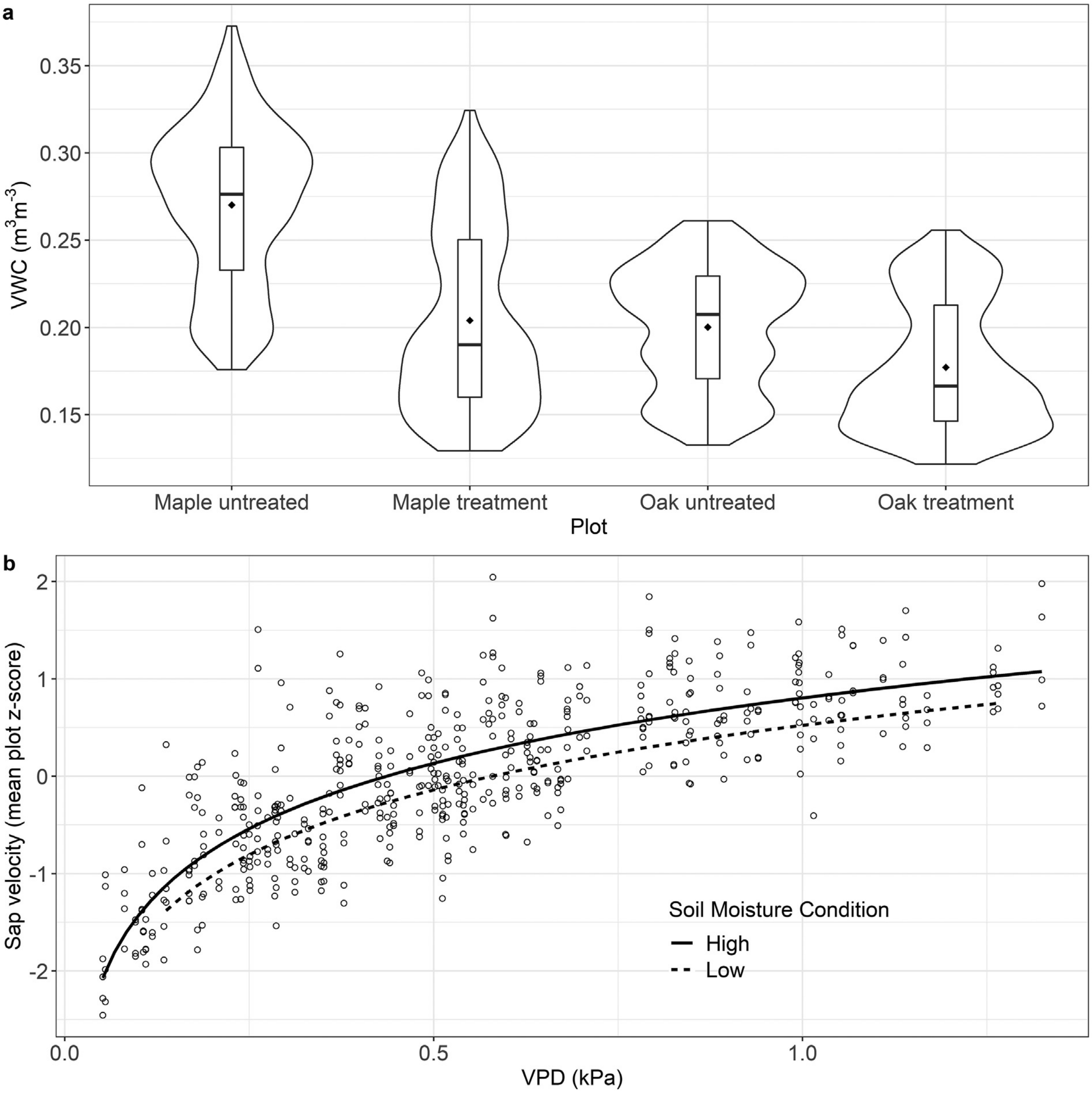

Fig. 5. Soil moisture results. a) Violin plot of soil moisture for four different plots during the study period. b) Scatterplot of Z scores of sap velocity vs VPD, with regression lines for low and high soil moisture for both species.

from upslope contributing areas overshadowed the strong effects of throughfall exclusion on sap velocity. However, the importance of soil moisture on transpiration cannot be completely ruled out since periods of low soil moisture <0.15 m^{3}m^{-3}, obtained thanks to the conditions created by our experimental design, did show a slight decrease in sap velocity (Fig. 5b). Additional research during periods with less precipitation would be helpful to better elucidate soil moisture and sap velocity dynamics in our study site. Furthermore, in the case that trees access deep soil water, subsurface water movement could be avoided with larger plot sizes (Asbjornsen et al., 2018). Yet, for our study, logistic and financial constrains limited the plot size and replication efforts.

4.3. Potential implications of climate change and forest species composition change on forest transpiration

Model predictions of future climate indicated increases in VPD and modest reductions in soil moisture (Fig. 6), meaning that the high atmospheric water demand concurrently with sustained water supply will enhance transpiration. When differing climate scenarios were coupled with change in forest composition, in line with mesophication of eastern forests (Nowacki and Abrams, 2008; Nowacki and Abrams, 2015), transpiration was even greater than changes solely due to climate change (Table 4). This supports the findings of Hernandez-Santana et al. (2015) who report that scenarios of 100 % sugar maple dominance could lead to substantial increases (+74 %) in transpiration compared to forest with a mix of ring and diffuse porous species. However, as species migrate, their new habitats might not be as suitable compared to their historical ones, creating a mismatch between species traits and site conditions, e.g. mesic species occupying xeric sites. In that case, microsite conditions will likely have important implications for transpiration. Including microsite conditions in our experiment resulted in less extreme transpiration, even if transpiration was still 29 % (RCP 4.5) – 38 % (RCP 8.5) higher than the estimated summer transpiration for 2018. Our experiment is speculative and does not account for possible feedbacks (e.g. higher transpiration reducing soil moisture, higher transpiration dampening VPD by increasing water vapor in the atmosphere, higher atmospheric CO_2 decreasing

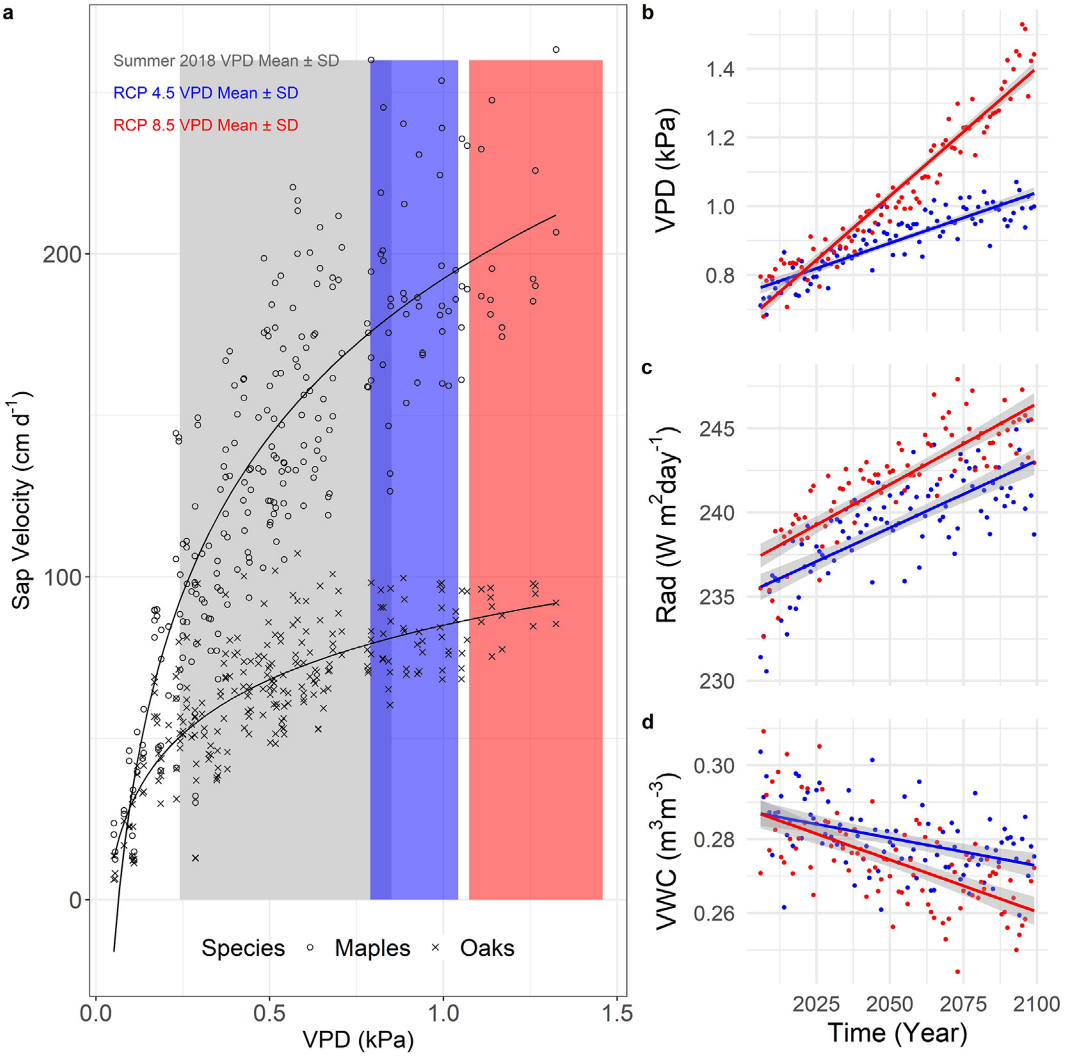

Fig. 6. Projections of future sap velocity and its drivers. a) Sap velocity as a function of VPD for maples and oaks (background colors represent mean (± standard deviation) for the summers of 2018 and between 2075 and 2099); and future projections of summer (June, July, August and September [JJAS]) averages based on 19 MACAv Model Ensemble and emission scenario RCP 4.5 (blue) and RCP 8.5 (red) for b) VPD; c) Radiation; and d) Soil moisture as volumetric water content (VWC).

stomatal conductance and therefore transpiration). Nevertheless, this theoretical experiment sheds light on some of the challenges of predicting future transpiration rates (Fisher et al., 2017), and highlights the importance of coupling the information on future climate (e.g. projections of VPD, soil moisture), shifts in tree species composition (with different water-use strategies), and specific site conditions (e.g. xeric vs mesic sites).

Forests throughout the central Appalachian Mountains are already changing (Morin et al., 2016), resulting in potential alterations in the energy balance through increased evapotranspiration (Budyko, 1974), reducing sensible heat and leading to wetter and more temperate regional climate (Kutta and Hubbart, 2019). These increasingly mesic conditions could limit more drought tolerant species (e.g. *Quercus sp*, *Carya sp*) (Nowacki and Abrams, 2008). Greater water use by mesic species in a warmer future can change the regional water balance and, ultimately, decrease streamflow to downstream urban areas that rely on water from headwater catchments (Caldwell et al., 2016). Moreover, reductions in long-term streamflow have been attributed to increased evapotranspiration due to vegetation changes in the Appalachian Mountains, the northeastern USA and in other continents (Caldwell et al., 2016; Hornbeck et al., 1993; Brown et al., 2005). Yet, the effects of climate and forest composition change on transpiration should be contextualized within the complexity and uncertainty around future dynamics between forests and the water

Table 4
Future transpiration for two representative concentration pathways, different forest composition scenarios and mesic and xeric soil moisture conditions.

2018 T (mm) 60 % maple: 40 % oak	Scenario	Soil moisture site conditions	Future T (mm) 60 % maple 40 % oak	% Δ	Future T (mm) 70 % maple 30 % oak	% Δ
206.4 mm	RCP 4.5	Mesic	270 ± 11	+31 ± 5	304 ± 12	+47 ± 6
		Xeric	236 ± 14	+14 ± 7	265 ± 16	+28 ± 8
	RCP 8.5	Mesic	286 ± 12	+38 ± 6	322 ± 14	+56 ± 7
		Xeric	253 ± 16	+23 ± 8	283 ± 18	37 ± 9

cycle (Sheil, 2018). Other factors such as scale, forest type and climatic regimes can determine forest cover effects on streamflow (Zhang et al., 2017) and should be also considered to inform land use policies and their impacts on water supply (Ellison et al., 2012). Our results, although specific to the central Appalachian Mountains, serve to reflect on how other forested mountain regions in the world that also serve as “water towers” will be affected by climate change (Viviroli et al., 2011).

5. Conclusion

In conclusion, our research reaffirms that sap velocity rates are strongly affected by VPD and differ between two species of varying water transport regulation strategies. We found that soil moisture did not modulate sap velocity despite our throughfall exclusion experiment, underscoring the need for further investigation on possible thresholds of low soil moisture. Additionally, using GCM downscaled information to model future VPD and soil moisture revealed the possible interplay between future climate, the transpiration rates of forest species, and microsite conditions, showing that increased transpiration rates are likely in WV. This original effort seeks to initiate the discussion of coupling forest transpiration and climate change in order to understand the effects of future regional water balance. The modeled increases in transpiration by mesic species could result in streamflow deficits during summer months, yet it is unknown if forest water use efficiency adaptations could dampen the effects of higher atmospheric demands on transpiration. Further investigations could look into these questions, given the importance of transpiration in the water cycle, and the role that forested regions around the world have as water towers to downstream populations.

CRediT authorship contribution statement

Guillén: Conceptualization, Methodology, Investigation, Formal analysis, Data curation, Writing original draft Preparation, Writing - review & editing. **Brzostek:** Conceptualization, Methodology, Writing - review & editing, Project administration, Resources. **Brenden McNeil:** Conceptualization, Methodology, Writing - review & editing, Resources. **Raczka:** Investigation, Data curation. **Casey:** Investigation, Visualization. **Zegre:** Conceptualization, Methodology, Writing - review & editing, Supervision, Resources.

Data availability statement

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

Data availability

Data will be made available on request.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This research was funded by the National Science Foundation, grant number OIA-148952 and the USDA National Institute of Food and Agriculture Hatch project, grant number 1004360, both to Zegre; the BOLD award to Brzostek and “Bring Out Lasting Discoveries” grant from Eberly College to McNeil. We would like to profusely thank the WV Land Trust and, in particular, Dr. Rick Landenberger, for their continuous support of research activities at Tom Run's Natural Area and the preservation of natural areas in West Virginia. We thank Barnes Nugent and the field landowners for allowing the installation of the weather station on their property. We would like to express our gratitude to researchers for their scientific support: Michael Chitwood for the aid in the experimental drought design; Tyler Roman, Yi Koong and Kim Novick for giving the tools and advice to initiate sap flow studies; Christopher Oishi, Chelcy Miniat and Chris Sobek for facilitating field, lab and analysis training in sap flow methods; Mark Vadeboncoeur and Heidi Asbjornsen for insights on analysis; Justin Mathias for his advice in the use of statistical models.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.158029.

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