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Stem Water Storage Dynamics of Three Boreal Tree Species Under Short-Term Drought [†]

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Abstract

The predicted increase in drought frequency with climate change and its impact on boreal tree species are growing concerns. In this study, we assessed how three boreal tree species in western Quebec used stem water storage during a three-week drought. We estimated stem water deficit from radial variations using point dendrometers installed on 50 mature trees (10 trembling aspen, 20 jack pine, and 20 black spruce) located on clay (all three species) and sandy sites (only conifers). Air temperature/humidity and soil moisture measurements were used to model their effect on stem water storage. Our results reveal contrasted stem water storage use across species during drought. Before the drought, jack pine maintained higher relative stem water storage at night than both black spruce and trembling aspen (all paired $p < 0.05$) but became more water-depleted during the drought (all $p < 0.1$). Similarly, black spruce showed the same pattern as jack pine when compared to trembling aspen, both before and during the drought ($p < 0.05$). Acclimation of jack pine and black spruce to moderately dry conditions on sandy soils was evident, as relative tree water deficit remained low and stable across 20%–60% relative soil extractable water, but it increased sharply below 20%. Our research highlights that boreal trees may substantially mediate drought stress using water storage pools. Our findings emphasize the need to consider stem water storage when determining which boreal tree species will be more affected by increasingly frequent droughts.

Keywords: boreal forest; climate change; drought; dendrometer; tree water relations; *Pinus banksiana* (Lamb.); *Picea mariana* (Mill. BSP); *Populus tremuloides* (Michx.)

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1. Introduction

The increased frequency of short-term droughts associated with anthropogenic climate change exerts additional stress on many forest ecosystems worldwide [1–3]. Such droughts, which consist of abnormally dry atmospheric and soil conditions over several days to a few weeks, are triggered by low precipitation and high temperature [4]. Severe short-term droughts have been associated with declines and dieback in North American and Eurasian boreal forests [5–8]. Given that boreal forests represent a major carbon store and provide a wide spectrum of ecosystem services [9], there is an urgent need to better understand how their functioning is affected by short-term droughts.

Droughts have major impacts on tree physiological processes such as internal water balance, photosynthesis, ascent of sap, nitrogen metabolism, and overall tree growth [10]. Water travels along the soil–plant–atmosphere continuum following a water potential gradient [11–13]. During the growing season, transpiration reduces the water potential of the foliage and increases tension in the xylem vessels, which initiates water movement from the soil to the atmosphere as long as water is still available [12]. Under drought, this process may be disrupted to the point that trees can no longer compensate the amount of water lost to transpiration through root water uptake [1].

The physiological response of trees to drought depends on functional traits that may provide avoidance or resistance to the impacts of water scarcity. Stomatal regulation is one such functional trait [14,15]. Trees regulate stomatal opening to limit transpiration, maintain cell turgor, and avoid embolism [12,16,17]. Species may be classified on an isohydric (water saver) to anisohydric (water spender) spectrum, depending on how stomatal opening is coordinated with hydraulic status [15,18]. In addition to stomatal regulation, stem water storage may also be used by trees to remain hydrated during periods of drought using water reserves [19]. Stem water follows a diurnal cycle, with transpiration-induced depletion during the day and water refilling from root uptake at night. These diurnal cycles and the associated tree water deficit (the shortage of stem water storage compared to a fully hydrated stem) during drought may be tracked by high-resolution monitoring through dendrometer sensors [20–22].

Tree water relations are highly specific to the climate zone in which trees live. In boreal forests, tree water relations are shaped by the need for cold resistance mechanisms [23] and responses to heterogeneous soil properties linked to permafrost dynamics and variable glacial deposits [24]. In the boreal forest of western Quebec, some dominant tree species, including black spruce (*Picea mariana* Mill. BSP) and jack pine (*Pinus banksiana* Lamb.), can grow well on contrasted soil surficial deposits as they may acclimate to variable site conditions [25,26]. Nevertheless, tree water relations may vary across different sites for a given species because soil texture, stand density, and topography strongly influence water availability [27]. Fine-textured soils, like silt or clay, have a greater capacity to hold water than coarse-textured soils, such as the sandy eskers of the Canadian shield [28]. Because these site conditions are heterogeneous at the landscape scale, knowing how the tree water relations of dominant tree species vary at different sites is critical for management purposes [29].

The vulnerability of common boreal tree species to climate change remains uncertain [30]. In particular, tree water relations should be analyzed because they indicate how trees react to certain climatic stressors and because responses are often species- and site-specific [31,32]. In this study, we investigated how a late summer short-term drought in the Abitibi region of Quebec, Canada, influenced tree stem water storage for three common boreal tree species. We used high-frequency point dendrometers to document tree water deficits of black spruce, jack pine, and trembling aspen (*Populus tremuloides* Michx.) at four sites, including two sites on clay and two sites on sandy soil surficial deposits. Our objectives were to (1) compare the use of tree water storage evaluating its possible role to mitigate drought effects across species, (2) model the relative effects of air and soil dryness on the use of stem water storage, and (3) identify, for black spruce and jack pine, which occur on both types of surficial deposits, whether the use of stem water storage depends on the deposit type on which the trees grow.

2. Materials and Methods

2.1. Study Sites and Experimental Design

The study area extends from 48.32° to 49.12° N and from 78.13° to 78.52° W in the fir/white birch bioclimatic domain and southern portion of the spruce/moss bioclimatic domain of western Quebec (Figure 1) [33]. Within the study area, we established four sites in spring 2021, two on fast-draining sandy soils (Authier sand, AUS; Amos sand, AMS) and two on slow-draining clay soils (Authier clay, AUC; Berry clay, BEC). Average yearly air temperature at the sites ranges from 2.51 to 2.65 °C, and average total yearly precipitation ranges from 917 to 967 mm (Table S1). The sites on sandy soils were established on eskers, which are elongated ridges of fluvio-glacial deposits with a typical sand–gravel content exceeding 60% [34]. The other two sites were located on clay deposits formed during the retreat of proglacial Lake Ojibway, characterized by a clay content greater than 30%. The four sites were established in forest stands with a mixture of common boreal tree species, namely, jack pine and black spruce at the sites with sandy soils, and jack pine, black spruce, and trembling aspen on the sites with clay soils (Table 1). While black spruce, and especially jack pine, are known to be water-saving trees with reactive stomatal responses [35,36], trembling aspen is considered anisohydric [37] and is uncommon on sandy soils. This functional behavior explains the composition of the living material used in our study. All stands are mature stands regenerated after forest fires, which, at the northern sites, occurred during the early 20th century [38].

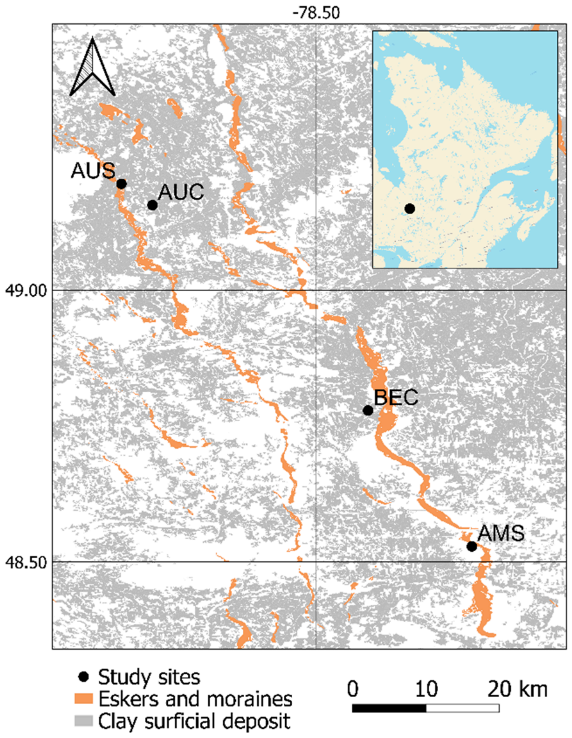

Figure 1. Location of the four study sites within Quebec, Canada, and extent of clay soil surficial deposits, eskers, and moraines. Eskers and moraines correspond to sandy soil superficial deposits [39]. Map projection: WGS84 longitude/latitude (EPSG:4326).

Table 1. Stand basal area per site and species.

Site	**Soil Surficial Deposit**	**Stand Basal Area in m^2/ha (Number of Trees)**					
		Black Spruce	**Trembling Aspen**	**Jack Pine**	**Balsam Fir**	**White Birch**	**Total**
AMS	Sand esker	9.57 (196)	0 (0)	12.4 (80)	0 (0)	0.0615 (1)	22.1 (277)
AUC	Clay	17 (156)	10.7 (35)	13.6 (63)	0.109 (6)	0 (0)	41.4 (260)
AUS	Sand esker	16.5 (313)	0 (0)	16.2 (193)	0.0655 (1)	0.141 (3)	33 (510)
BEC	Clay	22.3 (190)	8.16 (25)	5.52 (28)	0.804 (21)	0.17 (5)	36.9 (269)

2.2. Environmental and Meteorological Data

We recorded air temperature (°C) and humidity (%) at the study sites using Watchdog 1000 Series weather stations (Spectrum Technologies, Aurora, IL, USA). The stations also recorded volumetric water content (VWC) at 20 cm depth (%; SMEC 300 sensors). All records were collected at 30 min intervals. For each site, we calculated the vapor pressure deficit (VPD) using air temperature and humidity records with the R package *plantecophys* v. 1.4-6 [40]. Relative extractable water (REW) was also calculated for each study site using soil VWC records as follows:

$$\mathrm{REW_{ji}} = \frac{\mathrm{VWC_{ji}} - \mathrm{VWC_{min,j}}}{\mathrm{VWC_{max,j}} - \mathrm{VWC_{min,j}}} \tag{1}$$

where $\mathrm{VWC_{ji}}$ is volumetric soil water content (%) on a site j at a given time i and $\mathrm{VWC_{min,j}}$ and $\mathrm{VWC_{max,j}}$ are VWC values at the 5th percentile and 95th percentile over the period from 15 July to 15 September 2021 for that site, respectively. $\mathrm{VWC_{max,j}}$ corresponds to field capacity, and $\mathrm{VWC_{min,j}}$ corresponds to minimum available water at the study site [21,41]. We used REW instead of VWC observations as a measure of soil moisture to enable the comparison of soil moisture values across soil texture types.

A short-term drought occurred in the study area in the late summer of 2021. To define the drought dates and climate anomalies at each site, we used meteorological data from the “Info-Climat” network of weather stations [42]. We selected the three Info-Climat network stations nearest to our sites (Val-Paradis, 49.13° N, 79.20° W, near sites AUC and AUS; Lac-Berry 48.72° N, 78.23° W, near site BEC; Manneville-2, 48.52° N, 78.33° W, near site AMS) and obtained data on daily air temperature and precipitation for 2021 and the historical reference period from 2007 to 2020. Precipitation data was used to identify the beginning and end of the drought at each site based on a series of days with no or very low (< 2 mm) precipitation. For the southern AMS and BEC sites, the drought occurred from 12 August to 4 September 2021, while for the AUS and AUC sites, it occurred from 12 to 28 August 2021. At Lac-Berry (near BEC site), two rainfall events > 2 mm occurred during the defined period (Figure S1) but were not important enough to change soil water content (Figure S2) nor to allow trees to fully recover from drought (Figure S3) according to our site records.

To assess the severity of the drought at greater spatial and temporal scales than available from nearby weather stations, we also downloaded daily air temperature and precipitation data at 0.5° resolution for the period 1981–2023 from the ERA5 reanalysis [43] through the Climate Explorer web platform [44]. Additionally, to compute the standardized precipitation–evapotranspiration index (SPEI [45]), we downloaded ERA5-derived daily potential evapotranspiration data at 0.1° resolution [46]. Because the drought occurred over approximately three weeks, we computed SPEI over a 21-day time window for the whole period from 1981 to 2023 using the SPEI R package v. 1.8.1 [47]. The SPEI provided a measure of how extreme the August 2021 drought was relative to the long-term climate of the region for time windows of comparable length.

2.3. Stem Dendrometer Measurements

At each of the four study sites, we selected five jack pine and five black spruce trees. We also selected five trembling aspen trees on clay surficial soil deposits (AUC and BEC sites) only, as this species rarely grows on sandy sites in the study region. The selected trees were dominant, of similar size within each species, and without any signs of dieback (see Table S2 for the diameter at breast height of the trees). We installed one high-frequency and precision point dendrometer (DR1W, Ecomatik, Munich, Germany) on the stem of each tree, for a total of 50 trees. Dendrometers can effectively monitor stem water variability in relation to hydric stress [20,48]. We removed dead bark using wood chisels before fitting the sensors. All dendrometers were installed at a height of one meter. Starting in spring 2021 (April–May), stem radial variations were recorded at 30 min intervals using CR1000 dataloggers (Campbell Scientific, Logan, UT, USA). From the radial variations measured by the dendrometers, tree internal water dynamics can be analyzed since radial stem shrinkage is linked to tree water deficit (TWD; measured in mm) induced by decreasing stem water potential [22,49]. In contrast, radial stem swelling may be attributed to both rehydration (reversible stem radius changes) and growth (irreversible increase in stem radius). To study water storage dynamics, irreversible stem swelling must be isolated. Different methods have been proposed to disentangle water-related stem radius variations from the irreversible stem growth patterns recorded with dendrometer data [50,51]. After manually removing outliers caused by false readings of the dendrometers using the datacleanr package v. 1.0.3 [52], we used the methodology proposed by Zweifel [22] and recently implemented in the R package Treenetproc v. 0.1.4 [51] to extract TWD time series. Based on this approach, dendrometer records that are below the maximum radius previously measured are associated with tree water deficit because shrinkage is then assumed to result from decreased water potential [22]. Thus, we can obtain TWD by subtracting the radial measurement at a given time from the previous maximum radius as follows [49]:

$$\mathrm{TWD_i} = \mathrm{radius_{max}} - \mathrm{radius_i} \tag{2}$$

TWD is, therefore, a positive value, with higher values corresponding to a greater water deficit. From TWD_i, we computed the daily minimum tree water deficit ($\mathrm{TWD_{min}}$) occurring at night for each tree. This daily timeseries allows us to assess the capacity of trees to replenish their stem water storage (rehydration) at night. The daily maximum tree water deficit ($\mathrm{TWD_{max}}$) was also extracted to provide information on peak stem water storage depletion during the day. For each day (d) during the drought, we computed the minimum and maximum tree water deficit difference relative to the two weeks preceding the drought ($\mathrm{RTWD_{min}}$ and $\mathrm{RTWD_{max}}$) as follows:

$$\mathrm{RTWDmin_d} = \mathrm{TWDmin_d} - \mathrm{TWDmin, control} \tag{3}$$
$$\mathrm{RTWDmax_d} = \mathrm{TWDmax_d} - \mathrm{TWDmax, control} \tag{4}$$

where $\mathrm{TWDmax, control}$ and $\mathrm{TWDmin, control}$ are the 95th percentile of the daily maximum and minimum TWD, respectively, for each tree two weeks before the drought (control period; from 28 July to 11 August). We chose this period as a reference because it was temporally close to the drought period while being representative of the tree water deficit values observed throughout the growing season (Figure S3). We used the 95th percentile to obtain positive values of RTWD only for days where the tree water deficit was higher than most of the reference period.

2.4. Statistical Analysis

We compared the tree water storage behavior across species and soil types under normal and drought conditions using randomization tests, given the complex structure and time dependence of the data. More specifically, we performed pairwise species comparisons of $RTWD_{max}$ and $RTWD_{min}$ for three different time periods: two weeks before the drought, during the drought, and two weeks after the drought. For each pairwise comparison, we shuffled the species associated with the time series of interest ($RTWD_{max}$ or $RTWD_{min}$) 10,000 times and computed the difference in the mean value of each species. This method provided a distribution of the differences that would be expected under a scenario where species identity has no relevance to tree water storage behavior. The differences computed from the actual observations in the dataset were compared to these random distributions to identify statistically significant differences between species.

We modeled daily responses of $RTWD_{min}$ and $RTWD_{max}$ for each species by fitting generalized additive mixed models (GAMMs) using the *bam* function from the *mgcv* R package v. 1.8-42 [53,54]. The models offered a flexible method for describing the non-linear relationship between the environmental and response variables. We were interested in evaluating the daily evolution of the response variables before, during, and after the drought. We thus included the two weeks preceding the drought and two weeks following the drought to fit the models (from 28 July to 15 September). As predictors, we used the type of soil surficial deposit (SoilType) for conifers (as we did not survey trembling aspen on sand) and, for all species, daily maximum VPD_d and daily average REW_d. The effects of site and tree identifiers (nested within sites) were added as random effects on the intercept. For conifer species, we also included the interaction between REW_d and SoilType under the assumption that the effect of soil water availability may vary based on surficial deposit. We also added an autoregressive term of order one (the $RTWD_{min}$ or $RTWD_{max}$ value on the previous day, AR1) to account for temporal autocorrelation in the data. The final model had the following form and was fitted independently for each species:

$$\mathrm{RTWD}_{\mathrm{tree}_{[d]}} = \mathrm{s}(\mathrm{REW_d}) * \mathrm{SoilType}_{\mathrm{tree}} + \mathrm{s}(\mathrm{VPD_d}) + \mathrm{AR1} + \alpha_{\mathrm{site}} + \alpha_{\mathrm{tree}} + \varepsilon \tag{5}$$

The resulting models met the required assumptions (normality and homogeneity of residuals) and did not show any residual temporal autocorrelation. Moreover, the basis dimension (parameter *k*) used for fitting smoothing parameters was large enough to enable flexible fitting of smoothing splines.

3. Results

3.1. Meteorological Conditions

The occurrence of the drought in the study area was supported by measurements made directly at the study sites, at weather stations in their vicinity, and by longer-term reanalysis data. At the study sites, measurements of air temperature (Figure S4), REW (Figures 2a and S2), and VPD (Figures 2b and S5) revealed persistently warm and dry conditions over the duration of the drought. Starting on 12 August, daily maximum VPD increased and remained high until the last week of August while peaking above 2 kPa on several days (Figures 2b and S5), a value exceptionally high for high-latitude/altitude boreal forests [55]. At all sites, REW decreased continuously from above 50% before the drought down to nearly 0% by the end of August at sites AUC and AUS and by the first week of September at sites BEC and AMS (Figures 2a and S2).

Weather data recorded over the previous decade at nearby weather stations Manneville-2 (near AMS, 2007–2021), Lac-Berry (near BEC, 2010–2021), and Val-Paradis (near AUC and AUS, 2009–2021) reported abnormally low precipitation at the end of August and beginning of September 2021. Between 12 August and 4 September, only 28 mm and 4.4 mm of precipitation fell at Lac-Berry and Manneville-2 weather stations, respectively, down from historical averages of 74.7 mm and 71.1 mm (Figure 3a,b). Similarly, the Val-Paradis weather station recorded only 4.6 mm of precipitation between August 12 and 28, down from a historical average of 57.8 (Figure 3c). Average air temperatures recorded in 2021 were also higher than the historical averages over the same time period (+1.6 °C at Lac-Berry, +2.4 °C at Manneville-2, and +2.8 °C at Val-Paradis; Figure 3). Overall, low total precipitation and high air temperature recorded by weather stations revealed the strength of the climatic anomaly during the 2021 short-term drought relative to preceding years.

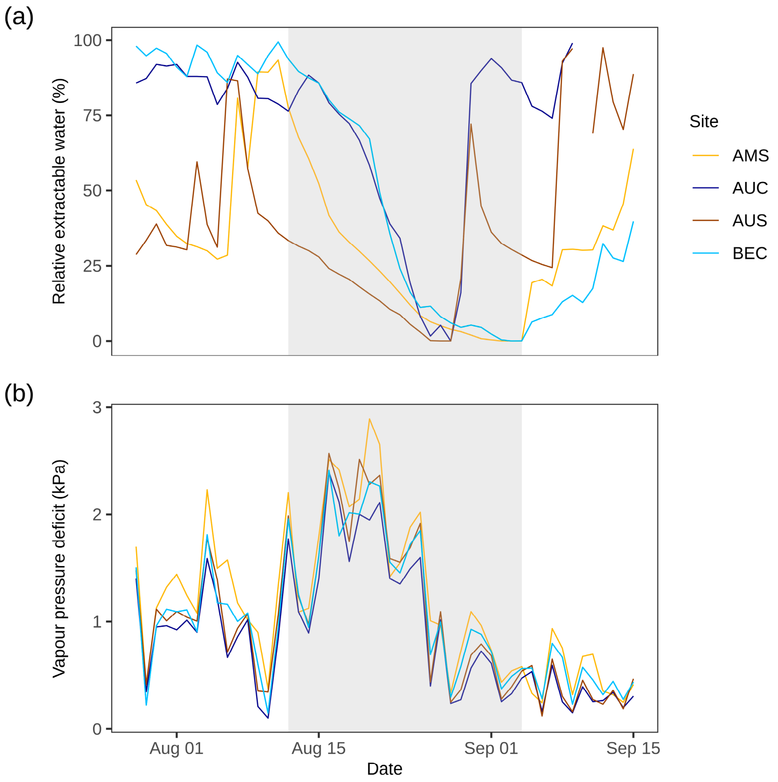

Figure 2. Daily (**a**) average relative extractable water and (**b**) maximum vapor pressure deficit at the four sites from 28 July to 15 September 2021. The gray area represents the drought period at AMS and BEC from 12 August to 4 September 2021. The drought instead terminated on 28 August at AUC and AUS, as evidenced by their earlier increase in relative extractable water.

At a broader spatial and temporal scale, climate reanalysis data supported the occurrence of a severe short-term drought in western Quebec at the end of August 2021. The SPEI time series computed over 21-day time windows reached a minimum (from −2.47 to −2.34, depending on the site) on 31 August (Figure S6), with the period from August 11 to 31 being the driest one of 2021. More generally, based on SPEI values, this period was drier than 99.6% of all three-week periods between 1981 and 2023. Anomaly maps computed over the same time of the year (11 to 31 August) revealed warmer air temperatures (Figure 4a) and scarcer precipitation (Figure 4b) for the August 2021 drought in western Quebec (including the study area) than for the broader 1981–2023 (excluding 2021) period. The map of SPEI from 11 to 31 August 2021 showed that the drought was prevalent throughout southern Quebec, but it was especially strong in our study area (Figure 4c).

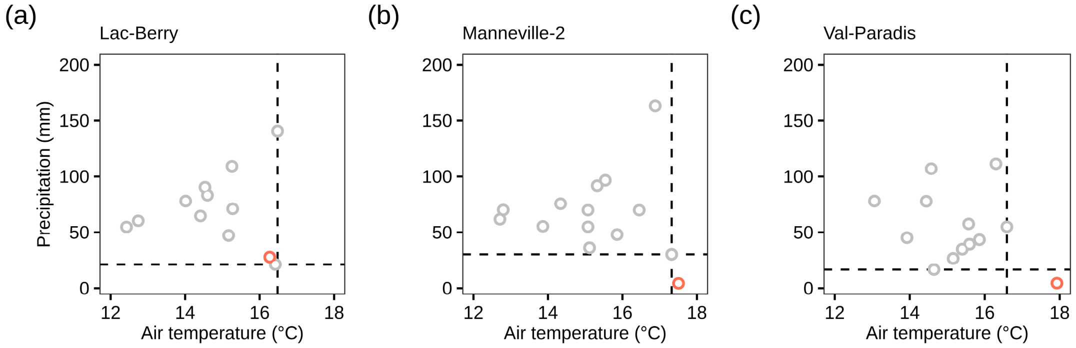

Figure 3. Historical (gray points) and 2021 (red points) average daily air temperature and total precipitation recorded from 12 August to 4 September at Lac-Berry (near BEC, (**a**)) and Manneville-2 (near AMS, (**b**)) and from August 12 to 28 at Val-Paradis (near AUS and AUC, (**c**)). Historical records are available starting in 2010, 2007, and 2009 at Lac-Berry, Manneville-2, and Val-Paradis, respectively. Dotted lines are the maximum average air temperature and minimum precipitation historically recorded for the same interval, excluding 2021.

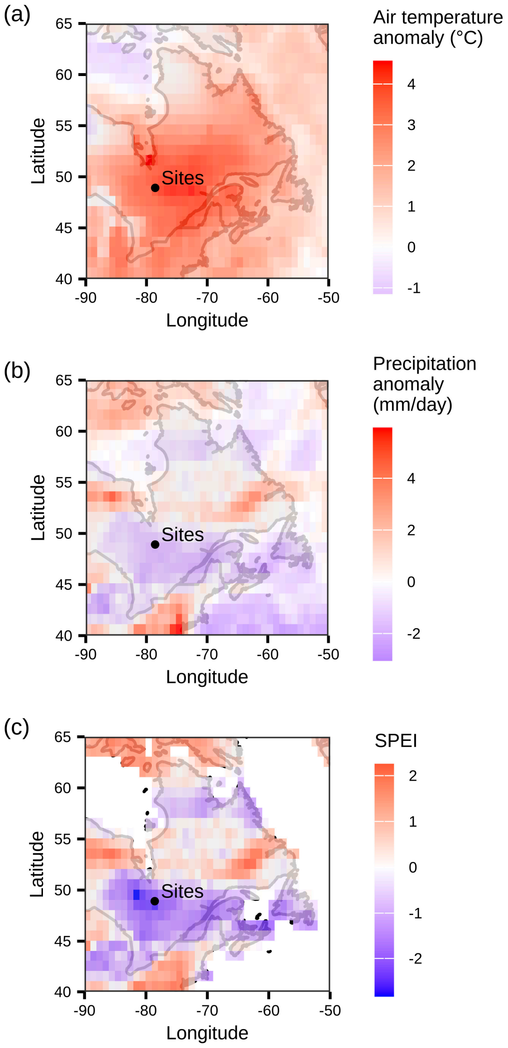

Figure 4. (**a**) Air temperature anomalies, (**b**) precipitation anomalies, and (**c**) standardized precipitation–evapotranspiration index (SPEI) in Quebec from 11 August to 31 August 2021. Anomalies in (**a**,**b**) were computed using August data from the 1981–2023 period, excluding 2021, as the reference baseline. Climate data were derived from the ERA5 reanalysis, as described in the main text. The location of the study sites is indicated on the maps.

3.2. Drought Impact on Tree Water Deficit

Dendrometer measurements (Figure S7) and derived tree water deficit records (Figure S3) showed that tree growth did not occur during the drought and that variations in tree radius were then entirely determined by tree water status, as tree water deficit was above 0 for the whole drought. Dendrometer-derived measurements showed an increase in water deficit ($RTWD_{min}$, Figure S8, and $RTWD_{max}$, Figure S9) for all study trees during the short-term drought, with marked differences among species and slight differences across the examined soil types (Figure 5). Changes in relative stem water deficit occurred in several phases during the drought, prior to recovery (deficit < 0). Across all sites and species, deficits increased after 12 August (Figure 5), concurrent with rising VPD and declining soil water content (Figure 2). Deficits decreased around 28 August, when a localized rain shower partially affected the study area and was recorded at only one nearby weather station (Figure S1). This event reduced VPD at all sites but increased VWC only at AUS and AUC, where rainfall occurred (Figure 2). Accordingly, in Figure 5, $RTWD_{min}$ of trees at AUS and AUC dropped on 28 August, whereas the decrease at AMS and BEC was less pronounced. At AMS in particular, trees showed a sharp, complete recovery of stem water status only after September 4, without distinct intermediate phases. Finally, trees at AUS consistently exhibited lower relative stem water deficits compared to the other sites, suggesting that the use of internal water storage is not necessarily greater on sandy soils with faster drainage.

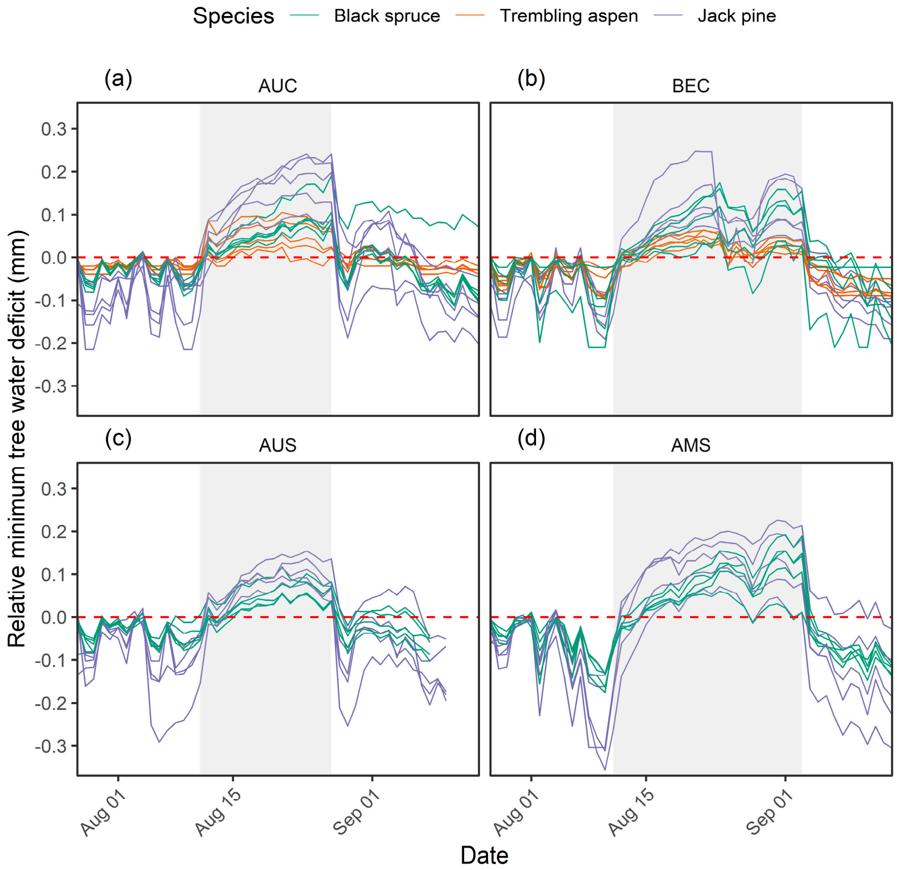

Figure 5. Time series of daily relative minimum tree water deficit ($RTWD_{min}$) of all surveyed trees at four sites (**a**–**d**) over the period considered for statistical modeling (28 July–15 September). The shaded gray region delineates the drought period at each site.

Randomization tests on $RTWD_{min}$ and $RTWD_{max}$ showed that jack pine maintained more stem water storage than both black spruce and trembling aspen before the drought (Figures S10 and S11; all one-tailed $p < 0.05$, except for the $RTWD_{max}$ pine–spruce comparison on clay). This behavior shifted completely under drought conditions, with jack pine being clearly more water-depleted than trembling aspen (all one-tailed $p < 0.001$) and having a tendency to be more water-depleted than black spruce (Figures S10 and S11; all one-tailed $p < 0.1$). There was no clear effect of the type of soil on the relative behavior of jack pine and black spruce. Black spruce displayed the same behavior as jack pine (greater water storage under normal conditions and lower water storage under drought conditions) compared to trembling aspen (Figures S10 and S11; all one-tailed $p < 0.05$). After the drought, trees tended to revert to their pre-drought behavior, although the differences between species were not as marked as before the drought, suggesting that trees may take a few weeks to fully recover from the effects of the drought (Figures S10 and S11; all one-tailed $p > 0.05$).

3.3. Effect of Air and Soil Dryness on Tree Water Deficit

The variance explained by the models evaluating daily responses of $RTWD_{min}$ and $RTWD_{max}$ as a function of VPD, REW, and soil type was high (R^2 values between 0.818 and 0.871; Tables S3–S8), consistent with the similarity between model predictions and observed data (Figures 6, S12 and S13). The models revealed a stronger response (steeper slope) of $RTWD_{min}$ for jack pine to increasing VPD during the study period (Figure 6a). Daily maximum stem contractions ($RTWD_{max}$) exceeded 0 (i.e., higher than control period) at maximum daily VPD values of approximately 1 kPa for black spruce and jack pine and 1.2 kPa for trembling aspen, showing that the conifer species surpassed $TWDmax, control$ earlier during the drought (Figure S12a).

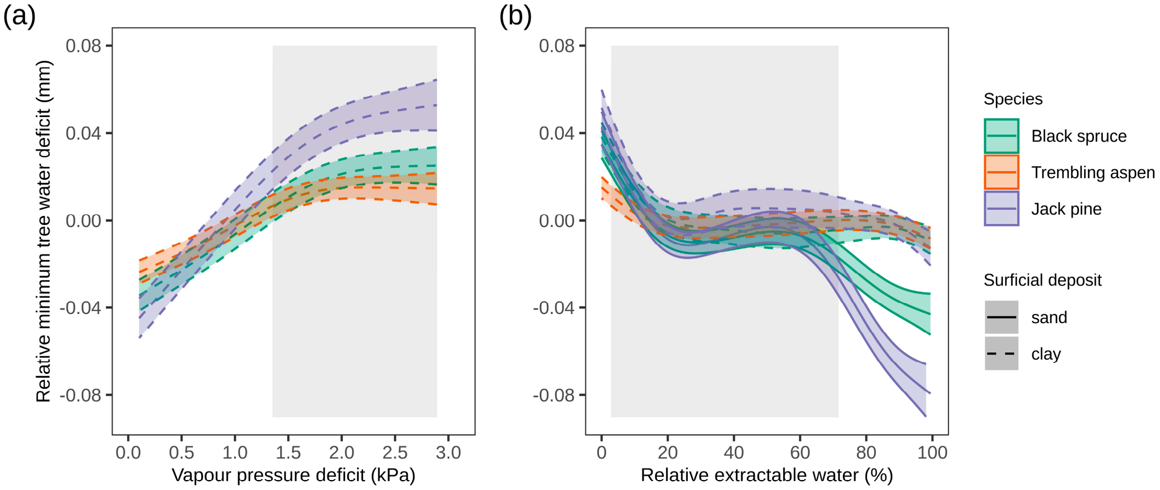

Figure 6. Predicted responses (±standard error) of relative minimum tree water deficit ($RTWD_{min}$) to varying (**a**) vapor pressure deficit (VPD) and (**b**) relative extractable water (REW) according to the fitted generalized additive mixed models (Equation (5)). Results are presented for each species and soil surficial deposit. The gray shaded areas indicate the range of daily average VPD and REW values observed at the height of the drought, from 19 to 25 August.

Decreasing REW during the short-term drought was generally associated with increasing $RTWD_{min}$ (Figure 6b) and $RTWD_{max}$ (Figure S12b), but sensitivity to soil dryness varied, depending on species and soil type. Trembling aspen showed the weakest response and did not appear sensitive to depletion in REW during the drought, even under very low water availability. Conifers growing on clay soils appeared to start using their stored water during the day ($RTWD_{max}$) under 50% REW (Figure S12b) but were still able to replenish their reserves overnight ($RTWD_{min}$) until under 20% REW (Figure 6b). Under high (>60%) water availability, conifers growing on sand maintained a large amount of stem water storage, as evidenced by strongly negative $RTWD_{min}$ and $RTWD_{max}$ values

(Figures 6b and S12b). This was especially the case for jack pines, suggesting that jack pines growing on sand take up large amounts of water for storage in their stem when water indeed becomes available (e.g., on rainy days). Under moderate (20 to 60%) REW conditions, conifers appear to be able to maintain higher stem water storage on sand than on clay (Figures 6b and S12b), which suggests acclimation as trees growing on sand operate under such moisture conditions most of the time. Below 20% of field capacity, however, their stem water storage decreased rapidly and became similar to those growing on clay (Figures 6b and S12b). In the case of trees growing on sand, the level of water availability at which the trees suffer from dryness during daytime seems to occur simultaneously with the time when they can no longer replenish their storage overnight, as evidenced from the 20% threshold observed for both $\mathrm{RTWD_{min}}$ (Figure 6b) and $\mathrm{RTWD_{max}}$ (Figure S12b).

4. Discussion

4.1. Species-Specific Stem Water Use Strategies and Effects of Drought

Here, we analyzed drought-induced tree water deficit (TWD) in three boreal tree species using point dendrometer data, applying the technique described by Zweifel [22] and implemented in analytical tools [50], as it is considered simple and robust. However, analyzing hydration-related fluctuations from dendrometer data can be challenging. Zweifel's method [22] is based on the Zero Growth (ZG) assumption, which posits that growth occurs only when the stem radius exceeds its previous maximum, indicating complete cell turgor; otherwise, the tree is considered to be in a state of water deficit. This approach may underestimate growth patterns when small increments are masked by hydration-related fluctuations [56]. Alternative approaches, using more detailed stem-cycle analysis [49], can potentially extract additional parameters. However, because we did not analyze growth in this study, we did not apply these methods. The following interpretations should, therefore, be considered in light of this limitation.

Drought is increasingly causing reduced growth and decline in many tree species worldwide [57]. The impacts on forest carbon dynamics, soil properties, and the ecosystem services provided by forests are substantial and require further investigation [58]. For example, it is important to disentangle species-specific drought resistance from other sources of variability, such as resistance associated with stand structure or diversity [59]. In this study, we compared the use of stem water as a means to mitigate drought effects across three boreal tree species with contrasting functional traits. From our results, it is clear that jack pine and, to a lesser extent, black spruce, use stem water storage more extensively than trembling aspen under drought conditions. Based on their isohydric behavior [35,36], we expected that jack pine and black spruce would use stem water more conservatively than the anisohydric trembling aspen [37], which turned out not to be the case. Consequently, our results indicate that water storage dynamics may be more complex than expected in the studied tree species.

The observed low stem rehydration at night, especially for jack pine, suggests that this species did not access additional water pools through its root system at the selected sites, despite being known for developing taproots [60]. In contrast, black spruce usually has a surficial root system [61,62], which may explain its use of stem water under drought conditions. Trembling aspen, on the other hand, showed little change in tree water deficit and low variations of the stem water storage during the drought. These findings suggest that trembling aspen maintained adequate access to soil water during the drought. This is likely attributable to its deeper root system, enabling access to water in deeper soil layers, and to the higher hydraulic conductivity of its xylem [62]. This is consistent with the fact that trembling aspen displayed little sensitivity to soil water availability according to GAMM models. Although aspen did not seem to experience negative effects from the 2021 observed drought, this species is known for its vulnerability to hydraulic failure, and aspen stands in western Canada have already significantly suffered from drought impacts in the last decade [63,64]. This vulnerability is also shown by the fact that this species, contrary to pine and spruce, is not often found on sandy soils in our study region. The drought sensitivity of trembling aspen in the study region remains an open question for future research. To explain our results, it is possible that trembling aspen has limited internal water reserves to buffer the impacts of drought once connectivity with soil water is lost. This is especially important because our results demonstrate the sensitivity of trembling aspen to high vapor pressure deficit.

Other important traits conferring tree resistance to water stress and determining tree internal water storage dynamics are those related to the stem wood anatomical structure [19]. Water transport might be slow due to higher hydraulic resistance in the tracheids of the conifers (i.e., black spruce and especially jack pine here) compared to the vessels of angiosperm trees (i.e., trembling aspen), even after accounting for the efficient water transport in the porous margo region of the conifer pits [65]. Alternatively, a high solute concentration in the root xylem sap during drought can reduce water movement [66]. Consequently, our results may derive from this differential xylem hydraulic resistance, resulting in pine trees being more adjusted to depend on their own stem water storage during drought and to use a "hold my breath" strategy by rapidly closing their stomata.

4.2. Conifer Responses on Contrasting Soils

Soil properties can strongly influence tree resistance and recovery during and after drought [67], including specific soil–tree–mycorrhizal associations [68]. Our results are thus important because they provide a better understanding of the potential acclimation and vulnerability to drought of boreal trees based on local soil properties. While the tree water deficit of jack pine and black spruce was generally more sensitive to soil water depletion on sandy soils, the relative tree water storage was higher on such soil types under high and moderate soil water contents (approximately above 20%). Trees growing in resource-limited conditions, such as drier sandy soils, may develop structural/physiological acclimation over the long term [69]. Examples of structural acclimation include enhanced xylem resistance to cavitation or increased allocation of biomass to roots [12,70]. Granier et al. [41] identified a relative extractable water threshold of 40%, which remained constant across both angiosperm and coniferous species, below which transpiration gradually decreases due to stomatal closure during water deficit. This threshold could explain the stabilization of relative tree water deficit that we observed between 20% and 60% of field capacity on sandy soils.

On clay sites, we did not observe any flattening in the slopes of the models. Clay soils typically maintain high moisture conditions throughout normal growing seasons due to factors such as abundant precipitation, low soil porosity, low permeability, high electrochemical water bonding, and anisotropic flow [28]. Consequently, we could anticipate the observed relative insensitivity of tree water storage to variations in soil water content on clay sites until reaching very low values of relative extractable water. The relative tree water deficit of all trees increased rapidly, especially on sandy soils, only when the relative extractable water was below the threshold value of 20%.

4.3. Implications of the Study

Our findings better define tree-specific and site-specific tree water relations over short-term droughts in the boreal forest of eastern Canada. We have shown within this study that species known to have strict stomatal regulation during dry periods may display high variability of stem water storage during drought. Consequently, water storage dynamics, which are critical for tree growth [19], are not solely defined by what happens at the leaf level. Here, jack pine trees experienced significant water storage depletion during the drought. Consequently, although pines are generally tolerant to water stress, our results suggest that this species may face substantial reductions in woody biomass increment in the future in similar sites. We have also shown some amount of acclimation of tree water relations to dry conditions for trees growing on soil surficial deposits characterized by fast water drainage at least until low thresholds of soil water content are reached. Jack pine and black spruce trees on sandy soils experienced an increase in tree water deficit only when soil water dropped below 20% of the remaining relative extractable water. Above this threshold, their stem water storage was even greater than on clay soil surficial deposits. Despite these findings, further research is needed on water movement along the soil–plant–atmosphere continuum and on the use of internal water reserves by trees to clarify expected drought impacts. To better understand tree water use strategies during drought, future studies should integrate dendrometer measurements with other parameters, such as stomatal conductance and sap flow data [71,72]. Additionally, water isotope analyses and other complementary data may help in determining how the results we obtained are dependent on species-specific rooting depths and root water uptake dynamics at the study sites [73].

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/f16091448/s1, Dataset S1: Half-hourly time series of dendrometer and weather data (dataset_s1.csv.zip); Dataset S2: Daily time series of dendrometer and weather data (dataset_s2.csv); Table S1: Average air temperature and precipitation at the sites; Table S2: Diameter at breast height (DBH) of the trees surveyed by point dendrometers; Table S3: GAMM parameters for $RTWD_{max}$ in black spruce; Table S4: GAMM parameters for $RTWD_{min}$ in black spruce; Table S5: GAMM parameters for $RTWD_{max}$ in trembling aspen; Table S6: GAMM parameters for $RTWD_{min}$ in trembling aspen; Table S7: GAMM parameters for $RTWD_{max}$ in jack pine; Table S8: GAMM parameters for $RTWD_{min}$ in jack pine; Figure S1: Time series of precipitation at nearby weather stations; Figure S2: Time series of relative extractable water; Figure S3: Time series of tree water deficit; Figure S4: Time series of air temperature; Figure S5: Time series of vapor pressure deficit; Figure S6: Time series of SPEI over the summer of 2021; Figure S7: Time series of dendrometer data; Figure S8: Time series of relative minimum tree water deficit over the summer of 2021; Figure S9: Time series of relative maximum tree water deficit over the summer of 2021; Figure S10: Randomization test comparing $RTWD_{min}$ between species; Figure S11: Randomization test comparing $RTWD_{max}$ between species; Figure S12: Predicted response of RTWDmax to VPD and REW; Figure S13: Observed $RTWD_{min}$ and $RTWD_{max}$ as a function of VPD and REW.

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Data Availability Statement: The half-hourly (Dataset S1) and daily (Dataset S2) time series of dendrometer and weather data on which the conclusions of this study are based are available in the Supporting Information.

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Abbreviations

The following abbreviations are used in this manuscript:

AMS	Amos sand site
AUC	Authier clay site
AUS	Authier sand site
BEC	Berry clay site
GAMM	Generalized additive mixed model
REW	Relative extractable water
$RTWD_{max}$	Relative daily maximum tree water deficit
$RTWD_{min}$	Relative daily minimum tree water deficit
SPEI	Standardized precipitation-evapotranspiration index
TWD	Tree water deficit
TWD_{max}	Daily maximum tree water deficit
TWD_{min}	Daily minimum tree water deficit
VPD	Vapor pressure deficit
VWC	Volumetric water content

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