

The paradox of defoliation: declining tree water status with increasing soil water content

Lorena Balducci¹, Angelo Fierravanti¹, Sergio Rossi^{1,2}, Sylvain Delzon³, Louis De Grandpré⁴, Daniel D. Kneeshaw⁵, Annie Deslauriers^{1*}

¹ Département des Sciences Fondamentales, Université du Québec à Chicoutimi, 555 boulevard de l'université, Chicoutimi, QC G7H 2B1, Canada.

² Key Laboratory of Vegetation Restoration and Management of Degraded Ecosystems, Provincial Key Laboratory of Applied Botany, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou, China.

³ Univ. Bordeaux, INRAE, BIOGECO, Bat B2, Allée Geoffroy St-Hilaire, 33615 Pessac, France.

⁴ Natural Resources Canada. Canadian Forest Service, Laurentian Forestry Centre, 1055 du P.E.P.S., Québec. QC G1V 4C7, Canada.

⁵ Centre d'étude de la forêt, Département des sciences biologiques, Université du Québec à Montréal, C.P. 8888, Succursale Centre-ville, Montréal, QC, H3C 3P8, Canada.

*Corresponding author: adeslaur@uqac.ca

Abstract

Defoliation can enhance tree water status by reducing canopy transpiration under drought. During long-lasting insect outbreaks however, this effect can be transient as reduced foliage affects not only transpiration but also the entire soil-plant-atmosphere continuum. In this study, we investigated the effects of defoliation and vapor pressure deficit (VPD) on plant and soil water status in balsam fir and black spruce defoliated by spruce budworm, *Choristoneura fumiferana* (Clemens). We sampled 48 fir trees and 36 spruce trees subjected to differing severities of defoliation. In May–September 2014 and 2015, we monitored the relative shoot water content (RWC) and soil volumetric water content (VWC), and midday shoot water potential (Ψ_{md} , only in 2015). We applied linear mixed models (LMMs) to assess changes in RWC, Ψ_{md} , and VWC to defoliation and VPD and we ran structural equation models (SEM) to determine the causal relationships between the measured variables in relation to defoliation and VPD. In LMMs models, defoliation and VPD, as individual factors, reduced Ψ_{md} in both balsam fir and pooled species models but did not affect RWC. Defoliation alone increased VWC in balsam fir and in pooled models. We observed no interaction between VPD and defoliation on tree water status, but significant effect on VWC (in balsam fir and pooled models), indicating that both factors had independent and additive effects on plants but not on soil. However, in SEM models, RWC was negatively correlated to defoliation, suggesting a hydraulic safety margin. Under conditions of multiple-years of natural defoliation during a spruce budworm outbreak, the decrease in Ψ_{md} reflects the amount of internal water capacitance that could be caused by both a lower Ψ_{md} due to larval feeding and a negative feedback between defoliation and xylem vulnerability.

Keywords: Relative water content, water potential, soil moisture, defoliation, vapor pressure deficit, *Picea mariana*, *Abies balsamea*, spruce budworm

Abbreviations: eastern spruce budworm (SBW); vapor pressure deficit (VPD, kPa); study areas [Gaspard (GAS), Girardville (GIR), Simoncouche (SIM), Toulouste–Lac Dionne (TLD)]; and shoot relative water content (RWC, %); midday shoot water potential (Ψ_{md} , MPa); minimal midday shoot water potential ($\Psi_{md\ min}$, MPa); soil volumetric water content (VWC, %), pressure inducing 50% loss of hydraulic conductance (P_{50} , MPa), embolism vulnerability (P_{12} , xylem air entry point,

MPa), slope of the vulnerability curve (S , % MPa⁻¹), and xylem hydraulic conductivity (k_s , m² MPa⁻¹ s⁻¹).

1. Introduction

Insect outbreaks, fire, and drought are major disturbances in forest ecosystems (Seidl et al., 2017). Globally, ~345 M ha of forest are affected annually by these disturbances (van Lierop et al., 2015). Climate change alters interactions between plants and insects (Fleming and Volney, 1995; Haynes et al., 2014; Singer and Parmesan, 2010), directly influencing the frequency of outbreaks and their spatial distribution (Despland, 2018; Foster et al., 2013) and indirectly influencing water availability (D'Orangeville et al., 2018). Given the ongoing global change, a 20%–40% reduction in soil water content is expected in eastern North America (Houle et al., 2015). Insect defoliation, however, may not necessarily lead to negative and cumulative impact when combined with water deficit in term of tree growth and vitality (Bouzidi et al., 2019; Itter et al., 2018). For example, a lower leaf area under defoliation reduces the leaf transpiration surface and increases water availability per leaf unit area (Schmid et al., 2017; Wiley et al., 2013) and, in young trees, improves water potential in the short-term (Bouzidi et al., 2019). At present, most studies have been conducted under controlled conditions, i.e., experiments with seedlings growing in pots e.g., Chen et al. (2002); Kolb et al. (1999); Quentin et al. (2010). Thus, the response of trees to long-term (>5 yr) defoliation in terms of water uptake and their ability to regulate water status remains poorly studied in field conditions in the boreal forest.

Depending on the specific plant-insect interactions, the direct effects of defoliation on plant water status can be positive or negative (Aldea et al., 2005; Nardini et al., 2012; Pittermann et al., 2014). Tree water potential improved at the onset of a defoliation event in partially defoliated *Eucalyptus* (Eyles et al., 2013; Quentin et al., 2012). In contrast, insect attacks on broadleaf species reduced leaf size (Wiley et al., 2013) and midday water potential (Ψ_{md}) (Quentin et al., 2011). This effect led to both morphological and physiological changes in the trees that were similar in terms of response to drought (Nabity et al., 2009; Peschiutta et al., 2016). Similarly, lower shoot water content was observed in defoliated conifer species, including balsam fir (Deslauriers et al., 2015) and Scots pine (Salmon et al., 2015), indicating a consequent decrease in indices of tree water status and an increased transpiration rate during defoliation.

In short-term controlled experiments, young plants exhibit lower Ψ_{md} during active defoliation, i.e., larval feeding, causing air to enter into the damaged needles (Bouzidi et al., 2019; Eyles et al., 2013), however, values of Ψ_{md} were less negative than the water potential threshold inducing loss of hydraulic conductivity (Balducci et al., 2015). When larvae cease to feed, an opposite response occurs with an increased Ψ_{md} in black spruce (Bouzidi et al., 2019), thereby indicating a time-dependent effect. Over five years, however, the negative effects of defoliation on tree water status, i.e. shoot relative water content, persist in highly defoliated natural stands of balsam fir (Deslauriers et al., 2015). There is thus a need to reassess the water status of defoliated conifers by considering the cumulative effect of defoliation over a long-lasting outbreak as the response in natural settings may differ from those observed in short-term (1–2 yr) controlled experiments.

During a long period of defoliation—as leaf area is gradually reduced—soil moisture content also affects the ability of trees to take up water. Models simulations of the impact of forests insects and pathogens on tree physiology suggest that the foliar losses due to defoliation result in a slight increase in soil water content (Dietze and Matthes, 2014). This increase stems from the greater loss of foliage than fine roots, leading to reduced transpiration and thus a reduced depletion of soil moisture (Dietze and Matthes, 2014). However, defoliation alone cannot fully explain this reduced transpiration as water status is largely driven by stomatal conductance, which declines as the vapor pressure deficit (VPD) increases (Oren et al., 1999). To resist to high VPD, plants respond by tightly regulating stomatal control and leaf water potential; most species close stomata in response to increased VPD and soil drought (Martin-StPaul et al., 2017). Generally, this mechanism allows trees to maintain leaf water potential above a minimum threshold, thereby avoiding water stress, reducing transpiration (Sperry et al., 1988; Tyree, 1997), and limiting a tree’s vulnerability to any subsequent biotic stress (Jactel et al., 2012).

Atmospheric vapor pressure deficit (VPD) is derived from air temperature and relative humidity, and this factor has been widely recognized as the evaporative driving force of water movement in trees (Earles et al., 2018; Williams et al., 2012; Zhang et al., 2017). However, the regulation of plant transpiration depends on internal coordination and also the availability of water in the soil and the efficiency of the hydraulic system (Tyree and Zimmermann, 2002). Thus, changes in both soil moisture and VPD have direct consequences on plant water status (Sperry et al., 1998; Tyree

and Zimmermann, 2002). Stress conditions predispose trees to pathogen attacks and reduce the vigor of trees (see the review in Niinemets (2010)), as observed for Douglas fir stands affected by the western spruce budworm (Flower et al., 2014). Because the development of insect damage depends of the feeding location on the leaves (top and bottom surfaces of a leaf), the negative effect of defoliation on cuticular permeability modifies water relations, increasing the water loss through adaxial leaf surface at midday VPD conditions (Wagner et al., 2008; Wagner et al., 2019). The effect of this coupling of the environmental factor (VPD) and defoliation on soil and plant water status has rarely been considered for boreal forests.

In this study, we investigated the long-term effects of both defoliation and VPD on the tree and soil water status in natural stands. We selected two conifer species, balsam fir (*Abies balsamea* (L.) Mill.) and black spruce (*Picea mariana* Mill. BSP), that are the respective primary and secondary hosts of spruce budworm [*Choristoneura fumiferana* (Clemens)] (Pureswaran et al., 2015). We tested whether physiological traits related to water stress—represented by Ψ_{md} and the relative water content of the shoots—and volumetric water content of the soil are affected by increased defoliation levels and VPD, as individual and interactive effects. We hypothesized that (i) defoliation exacerbates water stress (reductions in Ψ_{md} and relative shoot water content), and thus at the same time leads to an indirect increase of the soil volumetric water content as defoliation level rises; (ii) the interaction of VPD, soil and tree water status increases the sensitivity of both species to drought; (iii) interactive effects of defoliation and VPD alter the soil-plant-atmosphere continuum at high levels of defoliation.

2. Materials and methods

2.1. Study area

The study was conducted in natural boreal forests of eastern Quebec, Canada. The study area is located between the Saguenay-Lake St-John region and the North Shore of St-Lawrence River in Quebec. The natural stands are characterized by balsam fir (*Abies balsamea* (L.) Mill.) and black spruce (*Picea mariana* (Mill.) B.S.P.), as dominant or co-dominant species (Saucier et al., 2009). The topography of the study area is generally flat and uniform with low-elevation hills in the Saguenay-Lake St-Jean and tall hills in North Shore of St-Lawrence River, with an elevation ranging between 213 and 538 m above sea level (3% to 30% slope) (Figure S1). The superficial soil deposits of the soil consist mainly of thin glacial tills (Robitaille and Saucier, 1998).

The regional climate is cold with harsh winters and mild summers. The Saguenay-Lake St-Jean region has a mean annual temperature of 2.6 °C, with 176 days having a daily mean temperature >0 °C (Figure S2). Mean annual precipitation is 864 mm, with 31% falling as snow. From April to October, monthly average temperature and precipitation ranged between 1.2 and 18.7 °C and 100.4 and 270 mm, respectively. In the North Shore region of the St-Lawrence River, the mean annual temperature is 2.1 °C, and 165 days have with a daily mean temperature >0 °C. Mean annual precipitation at this site is 921 mm, 28% of this precipitation falling as snow (Environment Canada, 2018). During the growing season, mean monthly temperature and precipitation are ranged between 0.2 and 17.0 °C and 102 and 195 mm, respectively. The eastern spruce budworm (SBW) [*Choristoneura fumiferana* (Clemens)] is a major defoliator of balsam fir and black spruce in this study area. Cyclical SBW outbreaks during the 20th century caused a >50% annual loss of productivity and widespread mortality in spruce and fir species (Morin, 1994; Pureswaran et al., 2016). Since 2006, a new outbreak has been observed in Quebec, Canada, affecting >9 M ha of forest in 2019 (Bouchard et al., 2018; Ministère des forêts de la faune et des parcs, 2019).

2.2. Site and tree selection

Three sites, affected by the current spruce budworm outbreak, were selected in the study area. To verify the presence of SBW outbreak history in the sites, we used the forest inventory data of the Quebec Ministry of Forestry, Wildlife, and Parks that computed the defoliation level of the area (Ministère des Forêts de la Faune et des Parcs, 2015a; Ministère des Forêts de la Faune et des

Parcs, 2015b). Sampling was conducted in 0.4 ha plots in the study sites. In the first site, Gaspard (hereafter called, GAS), a single plot (1, Figure S1) was located within a mixed fir-spruce stand with low defoliation level ($< 10\%$), according to Ministère des Forêts de la Faune et des Parcs (2015a). We selected two plots in Girardville site (hereafter called, GIR (2–3), both representing mixed fir-spruce stands at from low to severe defoliation level (Ministère des Forêts de la Faune et des Parcs, 2015a). The third site, Tournestouc–Lac Dionne (hereafter called, TLD), in which we sampled at four plots (plots 4–7) were composed of different mixes of spruce and fir stand compositions. One of plot was located in a black spruce dominated stand one in a balsam fir dominated stand, and two in mixed fir-spruce stands with these stands having low to severe defoliation level (Ministère des Forêts de la Faune et des Parcs, 2015a). We randomly selected 6–18 dominant or co-dominant balsam fir and black spruce trees per plot, for a total of 84 trees (48 fir and 36 spruce).

2.3.Data collection

We measured shoot relative water content (RWC) and the soil volumetric water content (VWC) of the soil on a fortnightly basis between May and September in both 2014 and 2015. We monitored midday shoot water potential (Ψ_{md}) in 2015 only. One 20–30 cm long shoot per tree was sampled using a pruning shear at mid-crown, located generally at a height of 4 to 6 m above the ground (Régnière and Nealis, 2007). We sampled branches at mid-crown, based on a previous study that showed higher SBW larval density in the mid to upper crown (Régnière et al., 1989). Larvae were present at the time of sampling on the branches (GAS, GIR, TLD, data not shown), they were absent in the control site (SIM), also in accordance with the location of areas infested with Spruce Budworm in Quebec in 2013, 2014, 2015 (Ministère des Forêts de la Faune et des Parcs, 2015a; Ministère des Forêts de la Faune et des Parcs, 2015b). We visually assessed the defoliation levels of all existing shoots of the sampled branches within each plot and calculated the overall mean defoliation for each branch using the shoot-count method (MacLean and Lidstone, 1982; Piene et al., 1981), modified to be recorded as a percentage from 0% (absence of defoliation) to 100% (complete defoliation). In this study, the total defoliation level was representative of both sample years.

RWC was calculated from the fresh, rehydrated, and dried weights. We applied the following formula:

$$RWC = \frac{[Mf - Md]}{(Mr - Md)} \times 100.$$

where Mf and Md represent the fresh and dry mass, respectively. Mr represents rehydrated mass, which was obtained after a rehydration treatment lasting 24 h. Md was quantified after oven-drying at 80 °C for 48 h (Deslauriers et al., 2015; Tanentzap et al., 2015). In 2015 only, the shoots that were used to assess RWC, were also used for Ψ_{md} . In the field, we measured Ψ_{md} between 11:00 and 13:00 using a Scholander-type pressure chamber (Model 610, PMS Instruments Company, Albany, OR). Soil volumetric water content (VWC) was measured with a portable time domain reflectometry probe (Spectrum Technologies, Inc., Aurora, IL) at a depth of 12 cm in four orthogonal points at a distance of 1 m from the stem of each study tree. We then averaged the four measurements. We retrieved cumulative atmospheric vapor pressure deficit (VPD) over the 2014 and 2015 growing seasons for each sampling day using the BioSIM software 10.3 (Natural Resources Canada, Sainte-Foy, Canada) (Giguère-Croteau et al., 2019; Régnière et al., 2014). BioSIM is a software tool of temperature-driven simulation models and daily weather database, which can generate climate variables at different time resolution (Régnière, 1996); Régnière and St-Amant 2007). BioSIM interpolates climatic data from the nearest selected weather stations to a specific location, and adjusts the data based on the differences in latitude, longitude, and elevation between weather data sources and the study site (Régnière and Bolstad, 1994). We then adjusted the data using solar radiation and monthly thermal gradients (Beaulieu et al., 2011). We selected eight weather stations closest to our study sites (Environment Canada: <https://climate.weather.gc.ca/>).

In 2013, we conducted a preliminary study on non-defoliated balsam fir and black spruce in control site (hereafter called, SIM, 8, Figure S1), defoliation history was evaluated according to Ministère des Forêts de la Faune et des Parcs (2013). We collected 40 cm long branches (7 mm in diameter) at the mi-crown on 5 balsam fir and 6 black spruce. The branches were collected in the early morning and needles immediately removed to minimize xylem tension. Vulnerability curves, which express the percentage loss of hydraulic conductivity in relation to xylem pressure, were measured using the cavitron technique (Cochard *et al.*, 2005; Delzon *et al.*, 2010). The

centrifugation-based technique was used to establish negative pressure in the xylem and to provoke water stress-induced cavitation, using a custom-built honeycomb rotor (Precis 2000, Bordeaux, France) mounted on a high-speed centrifuge (Sorvall RC5, Asheville, NC, USA) (Delzon *et al.*, 2010). The pressure inducing 50% loss of hydraulic conductance (P_{50} , MPa), embolism vulnerability (P_{12} , xylem air entry point; MPa), slope of the vulnerability curve (S , % MPa⁻¹), and xylem hydraulic conductivity (k_s , m² MPa⁻¹ s⁻¹) of the stem were obtained by fitting the parameter model to vulnerability curves. For each sample, a sigmoid function (Pammenter and Willigen, 1998) was fitted to the vulnerability curve using proc NLIN in SAS according to the equation:

$$PLC = \frac{100}{1 + \exp\left(\frac{S}{25(P_i - P_{50})}\right)}$$

where P_{50} is the pressure inducing 50% loss of hydraulic conductance (MPa) and S is the slope of the vulnerability curve (% MPa⁻¹) of the stem at the inflection point (Urli *et al.*, 2013). For each specie, we also calculated the hydraulic safety margin (HSM) as the difference between the minimum midday twig water potential measured in field conditions during 2015 (Ψ_{\min}) and the water potential inducing 12 and 50% of embolisms (Choat, 2013; Delzon and Cochard, 2014).

2.4. Statistical analyses

We ran linear mixed models to evaluate the effects of defoliation and VPD on relative shoot water content (RWC, %), midday shoot water potential (Ψ_{md} , MPa), and the soil volumetric water content (VWC, %). In the models, defoliation and VPD were considered as continuous fixed factors, trees (nested in sites and plots) and years were included as random factors. The factor year was included as random only for RWC and VWC models. We evaluated normality and homoscedasticity graphically using the residuals. All models were run with data separated by species and with data pooled from species and the three study regions. We grouped VPD into ten classes from 0 to 1 kPa. The selection of the model structure was based on the lowest Akaike information criterion (AIC). Analyses of variance were performed with the PROC MIXED procedure of SAS 9.3 (SAS Institute, Cary, NC). We also ran Student's *t*-tests to compare means on P_{50} , P_{12} , S and k_s (Quinn and Keough, 2002).

We applied structural equation modeling (SEM, path analysis) to explore multiple pathways by which defoliation and VPD, as exogenous independent variables, simultaneously determined changes in plant and soil water status (endogenous dependent variables). SEM is a multivariate technique that simultaneously evaluates direct and indirect influences and responses (Grace, 2006). SEM also provides the sign, strength, and significance of the networks of relationships among variables (Grace, 2006). Based on our hypotheses we used the following assumptions to define the hypothetical structure of the model: (1) VPD influences defoliation, RWC, Ψ_{md} , and VWC; (2) defoliation influences RWC, Ψ_{md} , and VWC; (3) VWC influences RWC and Ψ_{md} ; and (4) Ψ_{md} influences RWC. To estimate the model fitting and validation, we followed the process proposed by Fan et al. (2016) and Grace (2006) that is based on the best maximum likelihood estimation procedure. We used chi-square (χ^2) tests, the root mean square error of approximation (RMSEA), and the comparative fit index (CFI) to evaluate the overall model fit (Fan et al., 2016; Grace, 2006). R^2 allowed a direct comparison of the paths. We retained a model when $\frac{\chi^2}{df} < 5.0$ with *P*-values > 0.05 (where χ^2 is the chi-square statistic and *df* is the degrees of freedom), $RMSEA < 0.06$, $CFI \geq 0.95$, and $R^2 > 0.20$ (Fan et al., 2016; Grace, 2006; Hooper et al., 2008). For the SEM analysis, we used Ω nyx 1.0-1010 (Omega.brandmaier.de) (Kievit et al., 2018; von Oertzen et al., 2015).

3. Results

3.1. Effect of defoliation on plant and soil water status

No significant effect of defoliation on RWC was observed in individual and pooled LMMs (Table 1). However, defoliation significantly affected the Ψ_{md} in individual-balsam fir and pooled LMMs, but not in individual-black spruce LMM (Table 1). In the pooled raw data, mean values of Ψ_{md} ranged from -1.01 MPa at 0% defoliation to a maximum of -1.78 MPa at 100% defoliation (Figure 1). Similarly, defoliation significantly affected VWC in individual-balsam fir and pooled LMMs, but not in black spruce one (Table 1). In the pooled raw data, mean values of soil VWC were close to 15% in lightly defoliated trees, whereas they increased to 25%–27% in completely defoliated trees (Figure 1).

3.2. Effect of VPD on plant and soil water status

VPD had no significant effect on RWC of the shoot in either species or in pooled LMMs (Table 1). The only significant effects of VPD were observed on Ψ_{md} in individual-balsam fir and pooled LMMs (Table 1). In the pooled raw data, mean values of Ψ_{md} fluctuated between -1.00 and -1.09 MPa with increasing VPD (0.1 to 0.8 kPa, Figure 1). However, these values were more negative (-1.36 MPa) in the middle values of VPD. We observed no significant effect of VPD on VWC in either species or in pooled LMMs (Table 1), although at VPD increase the VWC decreased by about 8.5% (Figure 1).

3.3. Interactions between defoliation and VPD on plant and soil water status

The interaction between defoliation and VPD was significant only for VWC in individual-balsam fir and pooled LMMs ($P = 0.0128$ and $P = 0.0066$, respectively, Table 1). In pooled predicted data, mean values of VWC increased as defoliation and VPD decreased (Figure 2). At lower defoliation levels as VPD increased, the overall change (increase-decrease) in predicted VWC was 2%–5%. At higher levels of defoliation with a similar increase in VPD, this difference was about 25% (Figure 2). According to the model predictions, for a combination of defoliation levels between 0% and 95% and VPD between 0 and 1 kPa, RWC decreased by 10% overall (Figure 2) with no significant interaction in any of the models (Table 1). Defoliation and VPD together did not cause a significant effect of interaction of biotic or abiotic factors in any of the LMM models (Table 1).

3.4. What is the margin of stem vulnerability to defoliation?

Minimum leaf water potential values ($\Psi_{\min \text{ md}}$) in defoliated trees were of -2.3 MPa and -2.95 MPa in black spruce and balsam fir, respectively. The hydraulic safety margin (HSM) at P_{12} was negative in balsam fir (-0.11 MPa), but positive in black spruce ($+1.02$ MPa). The hydraulic safety margin (HSM) at P_{50} was smaller in balsam fir than in black spruce, however in both species HSMs were positive. In non-defoliated trees, the xylem tension inducing 50% loss in conductivity (P_{50}) significantly differed between the species ($F = 26.97$, $P = 0.0006$), ranging from -3.27 MPa for balsam fir to -3.89 MPa for black spruce (Figure 3, Table 2). The embolism vulnerability at air point entry (P_{12}) was significantly lower with average values of -2.84 MPa in balsam fir compared to -3.32 MPa in black spruce ($F = 12.76$, $P = 0.0060$, Figure 3, Table 2). The xylem specific hydraulic conductance (k_s) was equal between the species ($F = 3.189$, $P = 0.1078$), ranging from $0.00072 \text{ m}^2 \text{ MPa}^{-1} \text{ s}^{-1}$ for balsam fir to $0.00061 \text{ m}^2 \text{ MPa}^{-1} \text{ s}^{-1}$ for black spruce (Table 2). The slope of the vulnerability curve (S) was not significantly different between species ($F = 2.7957$, $P = 0.1289$), ranging between $93.50 \text{ \% MPa}^{-1}$ (black spruce) and $119.54 \text{ \% MPa}^{-1}$ (balsam fir) (Table 2).

3.5. Structural equation modeling (SEM)

SEM models illustrated multiple pathways by which defoliation and VPD modulated the response of plant and soil water status individually and globally for each species (Figure 4). All three SEM models exhibited a good fit ($\chi^2 < 5$ with P (χ^2) nonsignificant, RMSEA < 0.0001 , and CFI > 0.96). No direct relationship, i.e., non-significant linkage, was detected between defoliation and VPD in any of the three models, indicating that these variables were independent. These nonsignificant effects also suggest that the effects of VPD and defoliation on plant and soil water status were not connected each other. These two explanatory factors are represented via different colors in Figure 3 (black and red pathways for VPD and defoliation, respectively). Both factors had an additive effect on RWC, Ψ_{md} , and VWC.

The proportion of explained variance for RWC was higher in the black spruce SEM model ($R^2 = 0.50$) than either the balsam fir model ($R^2 = 0.28$) or the model of the two species pooled together ($R^2 = 0.12$) (Figure 4). Except for black spruce, defoliation negatively influenced RWC with standardized path coefficients ranging between -0.38 and -0.46 (Figure 4). Although the r -path

coefficient between defoliation and RWC was negative in black spruce, it was not significant (data not shown). In SEM models, all relationships between VPD and RWC were nonsignificant, which corresponds to the results of the mixed model.

The Ψ_{md} showed the highest proportion of observed variance R^2 (between 0.56 and 0.59, Figure 4) compared to RWC and VWC, indicating that it explained a larger percentage of the variability in the SEM models. Both defoliation and VPD had a direct negative relationship with Ψ_{md} , in agreement with the mixed model results. In the balsam fir SEM model, both variables VPD and defoliation, negatively influenced Ψ_{md} with standardized path coefficients of -0.52 and -0.53, respectively (Figure 4). In black spruce, the negative effect of defoliation on Ψ_{md} was greater than that of VPD; this probably influenced the results when the two species were pooled together.

Except for balsam fir ($R^2 = 0.43$), the proportion of variability explained for VWC was low, especially when the species were pooled together ($R^2 = 0.09$) (Figure 4). In all cases, defoliation had a positive effect on VWC; the highest (positive) correlation was observed in balsam fir (standardized path coefficient = 0.63), while we observed a standardized path coefficient of 0.45 for black spruce. The effect of VPD on VWC remained negative, but the correlations were not significant (data not shown). Finally, we found no direct relationship between RWC, Ψ_{md} , and VWC. The exception was for the black spruce SEM model, where VWC negatively influenced RWC (standardized path coefficient = -0.35).

4. Discussion

4.1. Until what point was tree water status negatively influenced by defoliation?

The significant decrease in shoot Ψ_{md} with increasing defoliation reflected one signal of water loss, however the total amount of internal water capacitance in defoliated trees (represented here, as RWC) was not completely affected much by defoliation. Needle damage and death due to defoliation constrain transpiration directly (Pincebourde et al., 2006) and can be caused by both (1) a lower Ψ_{md} due to active larval feeding and (2) the feedback between reduced leaf area (i.e., after defoliation) and hydraulic conductivity.

Recent studies have already found that, over the short term, the mechanical chewing of larvae as they feed, induces air to enter the hydraulic system because of tissue injuries (Eyles et al., 2013). The Ψ_{md} in young defoliated black spruce saplings was lower than that of control plants but only during the six week period larvae feed (Bouzidi et al., 2019). As the physiological mechanisms involved in the resistance to cavitation are species-specific (Delzon et al., 2010), the Ψ_{min} informs on whether the threshold of hydraulic failure has been crossed or not (Benito Garzón et al., 2018; Brodribb and Cochard, 2009). In the present study, changes in Ψ_{md} and Ψ_{min} during the period of active defoliation were above water potential inducing 12% of xylem embolism in black spruce, but not in balsam fir. The minimum leaf water potential reached -2.95 MPa which corresponds to the onset of xylem embolism in balsam fir (xylem air entry pressure, P_{12} , being on average around -2.8 MPa in non-defoliated trees). This species might have therefore experienced xylem embolism during defoliation. In view of P_{12} and P_{50} average values in non-defoliated black spruce, (-3.3 and -3.9 MPa, respectively), Ψ_{min} of defoliated black spruce showed a greater hydraulic safety margin under defoliation and thus a lower risk of hydraulic failure compared to balsam fir. The results in black spruce are in line with previous observations in young trees of this species under drought conditions (Balducci et al., 2015). Moreover, black spruce showed lower levels of defoliation compared to balsam fir and this could explain the non-significant effect of defoliation on Ψ_{md} in black spruce in the mixed model, while a significant effect was observed in balsam fir. The reduction in leaf surface after defoliation was not strong enough (using RWC as direct measurement of outcome of water supply (Martínez-Vilalta et al., 2019)).

Contrary to our expectation, we observed negative significant correlations between Ψ_{md} , RWC and defoliation in the SEM models. In our study, SEM models detected changes in leaf water potential (an increase at lower % defoliation vs a decrease at higher % defoliation levels) reflecting the gradual loss of water in shoots. Contrasting results have been observed in other studies, for example, in two oak species—*Quercus marilandica* Muench and *Quercus rubra* Lam.—the short-term response to foliar reduction also improved plant water status due to a change in VPD–stomatal conductance (Reich and Hinckley, 1989). Several authors have found that defoliation in young trees either does not affect (Quentin et al., 2012) or does not increase (i.e., less negative) water potential (Quentin et al., 2011; Vanderklein and Reich, 2000; Wiley et al., 2013) compared to non-defoliated trees. However, the reported increases in Ψ_{md} were derived from measurements after only a single year of defoliation. This result may not reflect the tree defoliation gradient caused by several years of defoliation in adult evergreen trees, i.e., multiple years of foliage loss as it is primarily the current year foliage that is consumed by larvae in any given year. Our observations may thus partially explain the contrasting observations of improved and decreased tree-soil water status by showing that the relationship changes with the severity of defoliation (and length of defoliation event) in natural stands. Our results suggest that the severity and duration of defoliation could be critical factors to consider in conifers that are defoliated over years, and thus that twig water potential can still be considered as an early indicator of water loss.

RWC of balsam fir was negatively affected by defoliation in SEM compared to mixed models. The reduction of RWC after defoliation is consistent with previous observations in Deslauriers et al. (2015). One explanation for this difference between the models could be due to the negative HSM at P_{12} observed in balsam fir compared to black spruce, inducing xylem embolism. A recent study has shown that larval feeding damage on adaxial epidermis reduces relative water content, while the damage on the abaxial epidermis increased relative water content, modifying the stomatal function and cuticular permeability (Wagner et al., 2019). As balsam fir and black spruce have different leaf morphology (DeLucia and Berlyn, 1984), balsam fir could be more predisposed to adaxial damage than black spruce. Our SEM models also suggest that balsam fir is more vulnerable than black spruce. Another recent study has found that defoliation caused significant reduction on less negative P_{50} and k_s , increasing the vulnerability to embolism of defoliated trees

(Hillabrand et al., 2019). Although we did not measure these parameters on defoliated trees, this suggests that transport safety and efficiency could be compromised after defoliation.

4.2. Direct and indirect effects of VPD on water status

Our findings also highlight the negative and direct effect of VPD on Ψ_{md} , observations that are consistent with our second hypothesis. We found a negative relationship between VPD and midday shoot water potential in both species. As VPD increased, the midday water potential decreased, i.e., an increase in water tension in the xylem. Trees having a more negative water potential due to an increase of VPD are also more likely to lose hydraulic conductivity decreases following xylem embolism (Tyree and Sperry, 1989) and eventual death (Adams et al., 2017; Anderegg et al., 2013). In our study, however, we did not observe $VPD > 1$ kPa. Previous studies showed that a range of 2–4 kPa greatly increased the sensitivity of stomata, and the step-change between 1 and 2 kPa is important to define the slope of change (Brodribb and Jordan, 2008; Grossnickle and Russell, 1991). A lower range of VPD therefore maintained smaller fluctuations of midday water potential, and it could be maintained relatively constant transpiration, although we did not measure the latter parameter. In wetter conditions (lower VPD), Ψ_{atmo} could contribute to rebalancing (refilling) water movement to lower Ψ_{stem} (Goldsmith, 2013).

The fluctuations of VPD and Ψ_{md} measured in this study cannot fully explain the feedback between defoliation and hydraulic conductivity. In our SEM model, we observed that the partial contribution of biotic factors was greater than that of abiotic factors in black spruce, whereas the partial contributions of biotic and abiotic factors were similar in balsam fir. Because we observed a difference between the species in their thresholds of hydraulic failure, and because balsam fir is more vulnerable to defoliation, we suggest that both defoliation and VPD might affect hydraulic conductivity in balsam fir. This could explain the similar partial contribution of defoliation and VPD in balsam fir in SEM model. However, as response to VPD depended on leaf sensitivity to VPD. Previous studies have found that this response has been associated with water relation strategies of species through the regulation by stomatal conductance, i.e., conservative *versus* risk-taking strategies (Domec and Johnson, 2012). The conservative strategy is defined by small fluctuations in water content to daily variations in VPD (Hochberg et al., 2018)— i.e. the ability to maintain constant midday leaf water potential when soil water content decreases (Domec and Johnson, 2012; Hochberg et al., 2018). Both species were previously considered as resistant to

plant dehydration (Ewers et al., 2007; Grossnickle and Blake, 1987; Grossnickle and MacDonald, 2018), although, the water balance in black spruce is highly time dependent (Balducci et al., 2013; Bouzidi et al., 2019). Our SEM models, however, suggest that defoliation affects the relationship between stomatal conductivity and VPD, increasing the hydraulic conductivity in the needle, making black spruce a more resistant species to hydraulic failure than balsam fir.

4.3. Consequences for soil water status

We observed an increase in soil water content around defoliated trees, again supporting our first hypothesis. Furthermore, our SEM models showed a positive influence of defoliation on soil water content around both species. Therefore, our results regarding the plant and soil water content of defoliated trees suggest a reduced water transfer throughout the soil-plant-air continuum. As observed by Dietze and Matthes (2014), a slight increase in soil water content follows defoliation. Such an increase in soil water content could be explained by reduced transpiration. Defoliated trees alter the water balance of a stand largely by changing the ratio between water input (precipitation) and output (evapotranspiration) (Dietze and Matthes, 2014; Hata et al., 2016).

As observed in the mixed model, the interaction between defoliation and VPD predispose the stand to greater fluctuations of volumetric water content in the soil. When defoliation increases canopy transparency (Hata et al., 2016), less precipitation is intercepted by the canopy and, consequently, the soil receives more water (Sun et al., 2015). Defoliation thus changes the water yield, i.e., the difference between precipitation and evapotranspiration (Viglizzo et al., 2016) through reduced interception and reduced canopy evaporation. Canopy transparency at higher defoliation levels may increase soil transpiration (Dietze and Matthes, 2014) under increasing VPD, thus decreasing the VWC. In the SEM models, VPD was not linked directly to VWC, suggesting that defoliation had a larger effect. However, in the boreal forest of eastern Quebec, temperatures are generally low, and precipitation is abundant and exceed soil transpiration (Gauthier et al., 2015), and thus also suggests that other environmental factors should be considered.

5. Conclusions

Defoliation negatively influences one of two physiological traits of tree water status (decreasing plant water potential rather than relative water content in the mixed model) while having a positive effect on soil water status. Atmospheric vapor pressure deficit (VPD) contributes to the decrease in plant water status, particularly for midday shoot water potential. Defoliation and VPD independently alter the soil-plant-atmosphere continuum during spruce budworm (SBW) outbreaks in both fir and spruce trees. In black spruce, however, the decrease in leaf water potential is driven more by defoliation than VPD, whereas the reduction of tree water potential in balsam fir is explained by both biotic and abiotic factors. When considering the overall duration and geographical extent (millions of ha) of insect outbreaks, water exchanges between terrestrial ecosystems and surrounding environments (atmosphere, hydrosphere, pedosphere-lithosphere) could be strongly affected during severe outbreaks.

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List of tables

Table 1.

Results of the mixed models for relative water content (RWC, %), midday shoot water potential (Ψ_{md} , MPa), and soil volumetric water content (VWC, %) for black spruce and balsam fir (pooled species) using defoliation (%), vapor pressure deficit (VPD, kPa), and their interaction. The results of RWC and VWC are based on data collected in 2014–2015; Ψ_{md} data was collected in 2015 only. For each effect, the results include the degree of freedom of the numerator (df), F -statistic (F), and probability (P). Significant effects ($P \leq 0.05$) are highlighted in bold.

| Black spruce | RWC | | | Ψ_{md} | | | VWC | | |
|---------------------------|-----|------|--------|--------------------|------|---------------|-----|------|---------------|
| | df | F | P | df | F | P | df | F | P |
| Defoliation | 1 | 1.70 | 0.1940 | 1 | 0.04 | 0.8386 | 1 | 2.52 | 0.1131 |
| VPD | 1 | 0.31 | 0.5805 | 1 | 1.59 | 0.2098 | 1 | 1.24 | 0.2669 |
| Defoliation \times VPD | 1 | 2.23 | 0.1369 | 1 | 0.53 | 0.4697 | 1 | 0.53 | 0.4686 |
| Balsam fir | RWC | | | Ψ_{md} | | | VWC | | |
| | df | F | P | df | F | P | df | F | P |
| Defoliation | 1 | 2.08 | 0.1500 | 1 | 7.29 | 0.0074 | 1 | 5.88 | 0.0156 |
| VPD | 1 | 0.35 | 0.5523 | 1 | 6.41 | 0.0120 | 1 | 1.24 | 0.2667 |
| Defoliation \times VPD | 1 | 0.00 | 0.9455 | 1 | 1.08 | 0.3000 | 1 | 6.24 | 0.0128 |
| Black spruce & balsam fir | RWC | | | Ψ_{md} | | | VWC | | |
| | df | F | P | df | F | P | df | F | P |
| Defoliation | 1 | 1.43 | 0.2327 | 1 | 7.03 | 0.0084 | 1 | 9.76 | 0.0018 |
| VPD | 1 | 0.40 | 0.5280 | 1 | 9.43 | 0.0023 | 1 | 2.97 | 0.0854 |
| Defoliation \times VPD | 1 | 0.20 | 0.6532 | 1 | 0.22 | 0.6426 | 1 | 7.41 | 0.0066 |

Table 2.

Mean values and SE of xylem pressure inducing 50% loss in conductance (P_{50} , MPa), xylem air entry point (P_{12} , MPa), vulnerability curve slope (Slope, % MPa⁻¹) and xylem specific hydraulic conductance (k_s , m² MPa⁻¹ s⁻¹) of the stem measured on branches of non-defoliated trees for balsam fir (*Abies balsamea*) and black spruce (*Picea mariana*). Different letters between species indicate significant differences between species at $P < 0.05$ (Student's test).

| Species | Balsam fir | Black spruce |
|----------|--------------------------------|-------------------------------|
| P_{50} | -3.27 ^b ± 0.05 | -3.89 ^a ± 0.27 |
| P_{12} | -2.84 ^b ± 0.04 | -3.32 ^a ± 0.32 |
| Slope | 119.54 ^a ± 17.40 | 93.50 ^a ± 9.17 |
| k_s | 0.00072 ^a ± 0.00009 | 0.00061 ^a ± 0.0001 |

Figure captions

Figure 1. Relative water content (RWC, %), midday shoot water potential (Ψ_{md} , MPa), and soil volumetric water content (VWC, %) expressed as a function of vapor pressure deficit (VPD, kPa) and defoliation (%) in 2014 and 2015 for black spruce and balsam fir. Dotted points represent the mean of raw data and the vertical bars represent the standard error of the mean.

Figure 2. Surface plot of predicted relative water content (RWC, %), midday shoot water potential (Ψ_{md} , MPa), and soil volumetric water content (VWC, %) expressed as function of defoliation (%) and vapor pressure deficit (VPD, kPa) in 2014 and 2015 for black spruce and balsam fir. Surface plots were obtained by the mixed model equation (n trees = 48 for RWC, n trees = 34 for Ψ_{md} , n trees = 48 for VWC).

Figure 3 Mean percentage loss of hydraulic conductance (PLC, %) versus xylem pressure (MPa) of non-defoliated trees for balsam fir (gray closed circles) and black spruce (black closed circles). The stem vulnerability curves were fitted based on raw data, obtained with the cavitron technique. Balsam fir was represented with a gray line and black spruce with a black line.

Figure 4. Path diagram of the structural equation models (SEM), showing the studied variables in the square boxes. The RWC is the shoots' relative water content (%); the Ψ_{md} is the shoots' midday water potential (MPa), and VWC is the volumetric water content (%). The solid pathway represents positive relationships; the dashed pathways are negative relationships. The black pathway is linked to vapor pressure deficit (VPD) as an assumption of the effect, the red pathways are linked to defoliation (DEF) as an assumption of the effect. and the gray pathways are among the soil-plant-water status variables. The RSMEA, chi-square, CFI, and its probability (P) are used to test the model. Values near the arrow represent the standardized path coefficients. The underlined values next to the response dependent variable boxes indicate the proportion of explained variance (R^2) of each variable. Differences in line thickness reflect the varying degrees of significance (thick, medium, and fine lines correspond to: ***, $P < 0.0001$; **, $P < 0.001$; *, $P < 0.05$, respectively).

Figures

Figure 1.

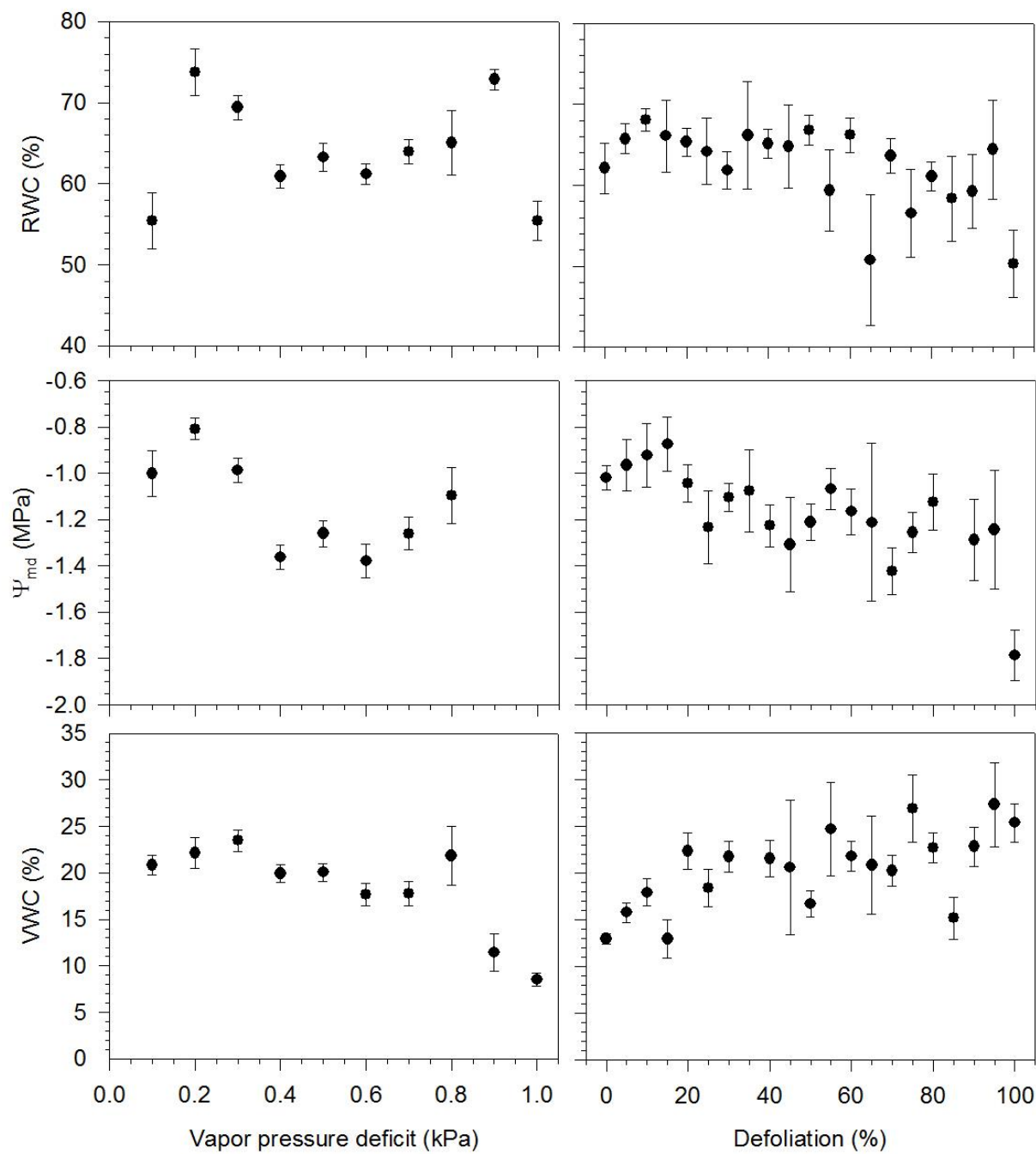


Figure 2.

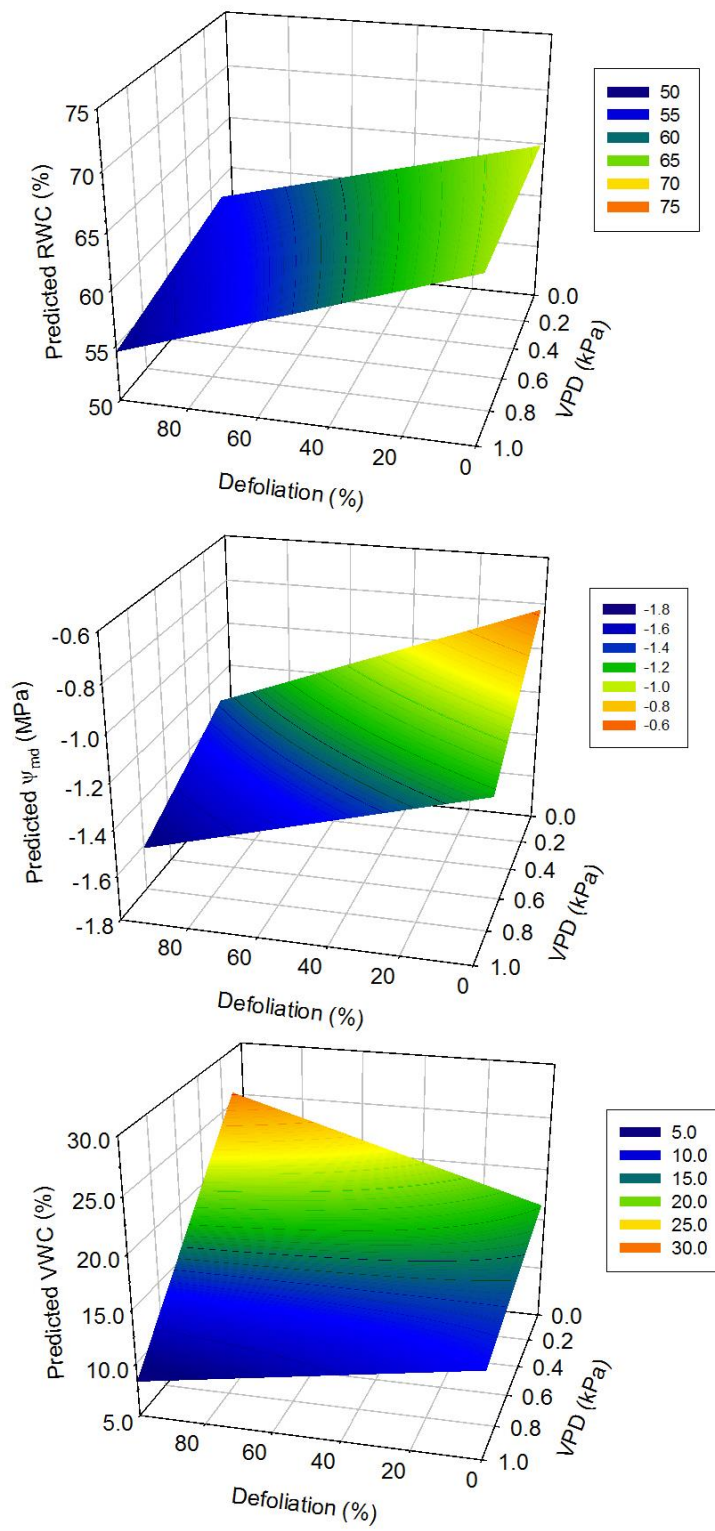


Figure 3.

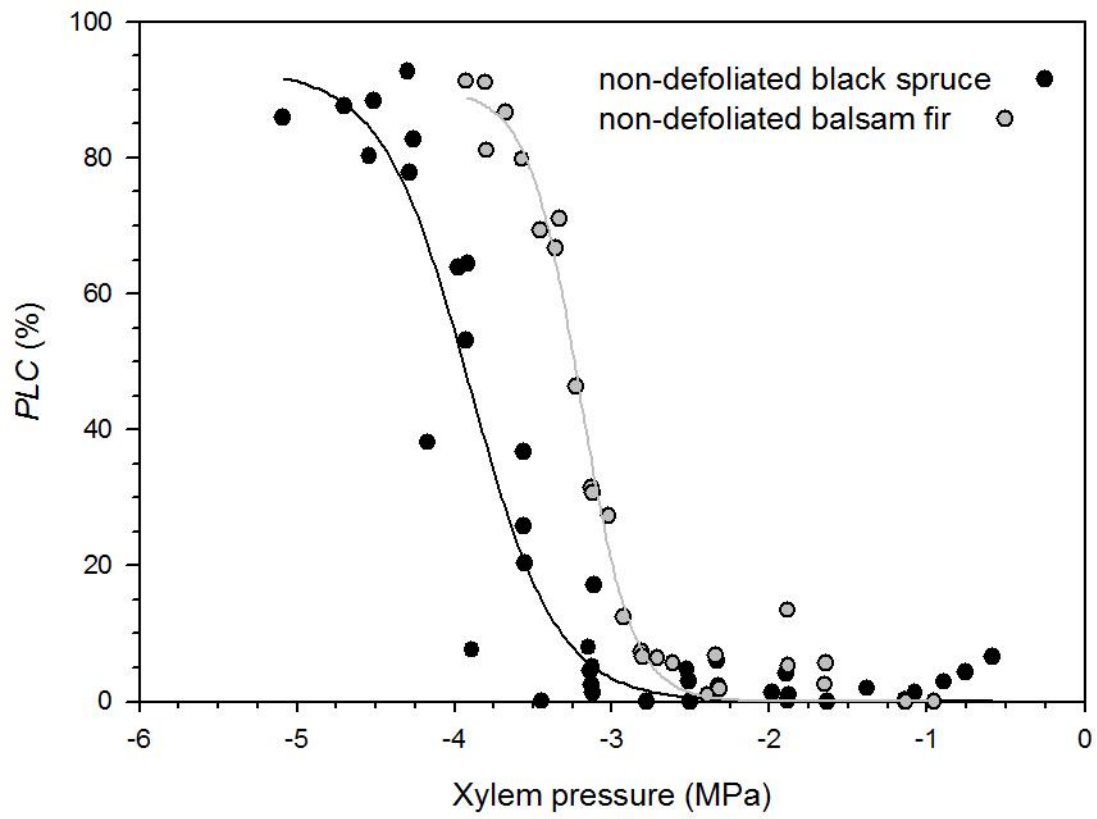
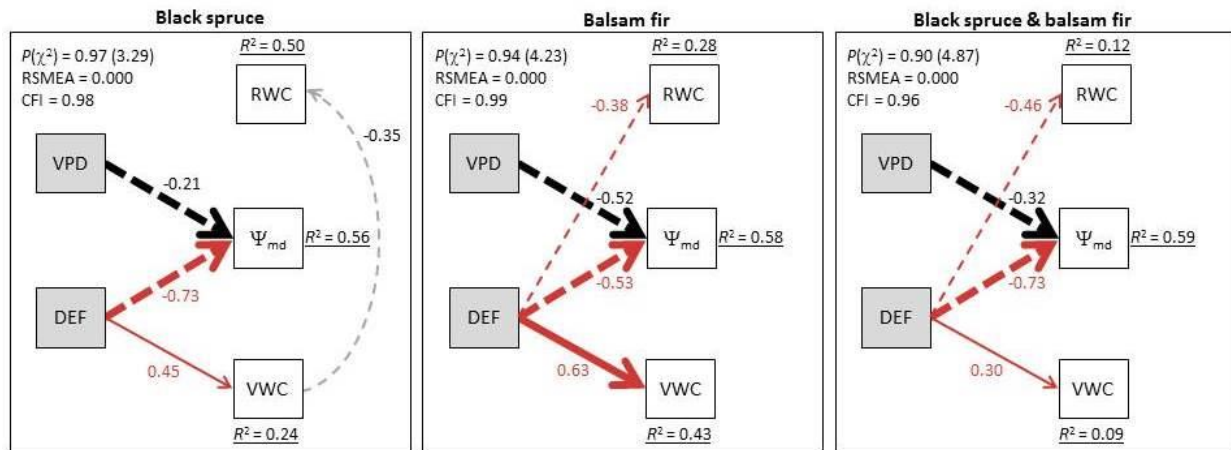
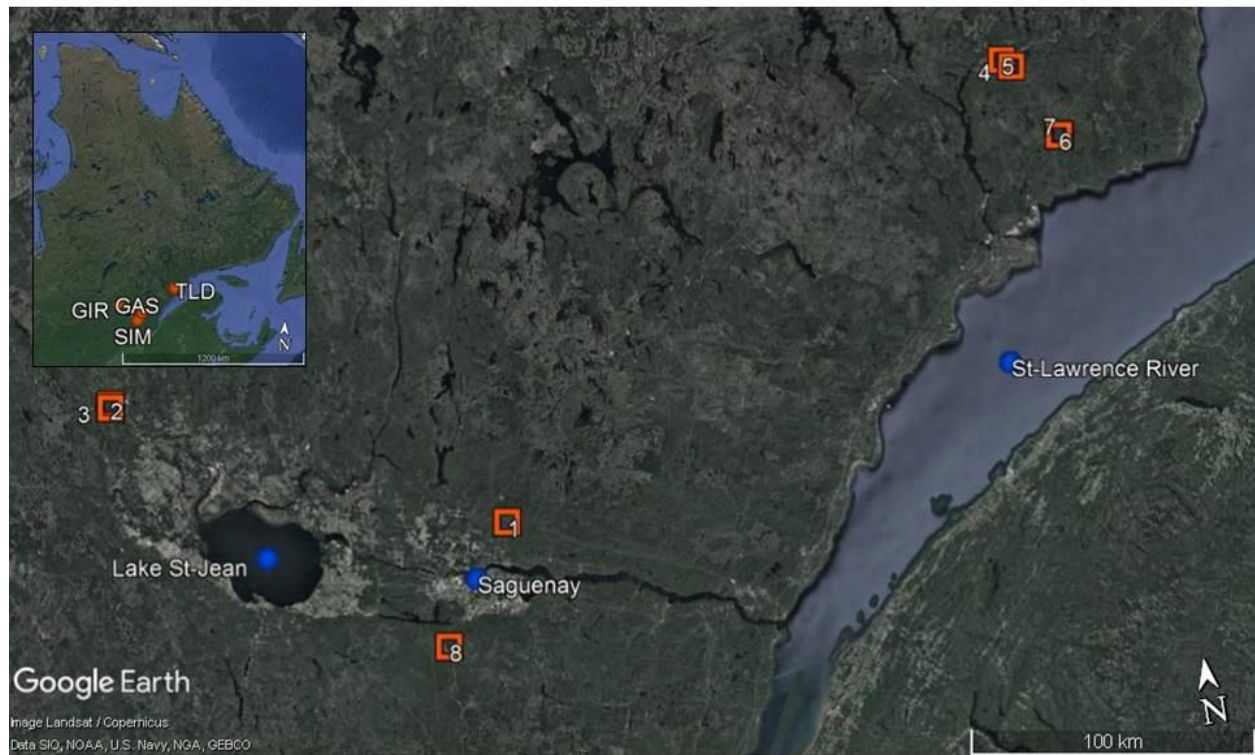


Figure 4.



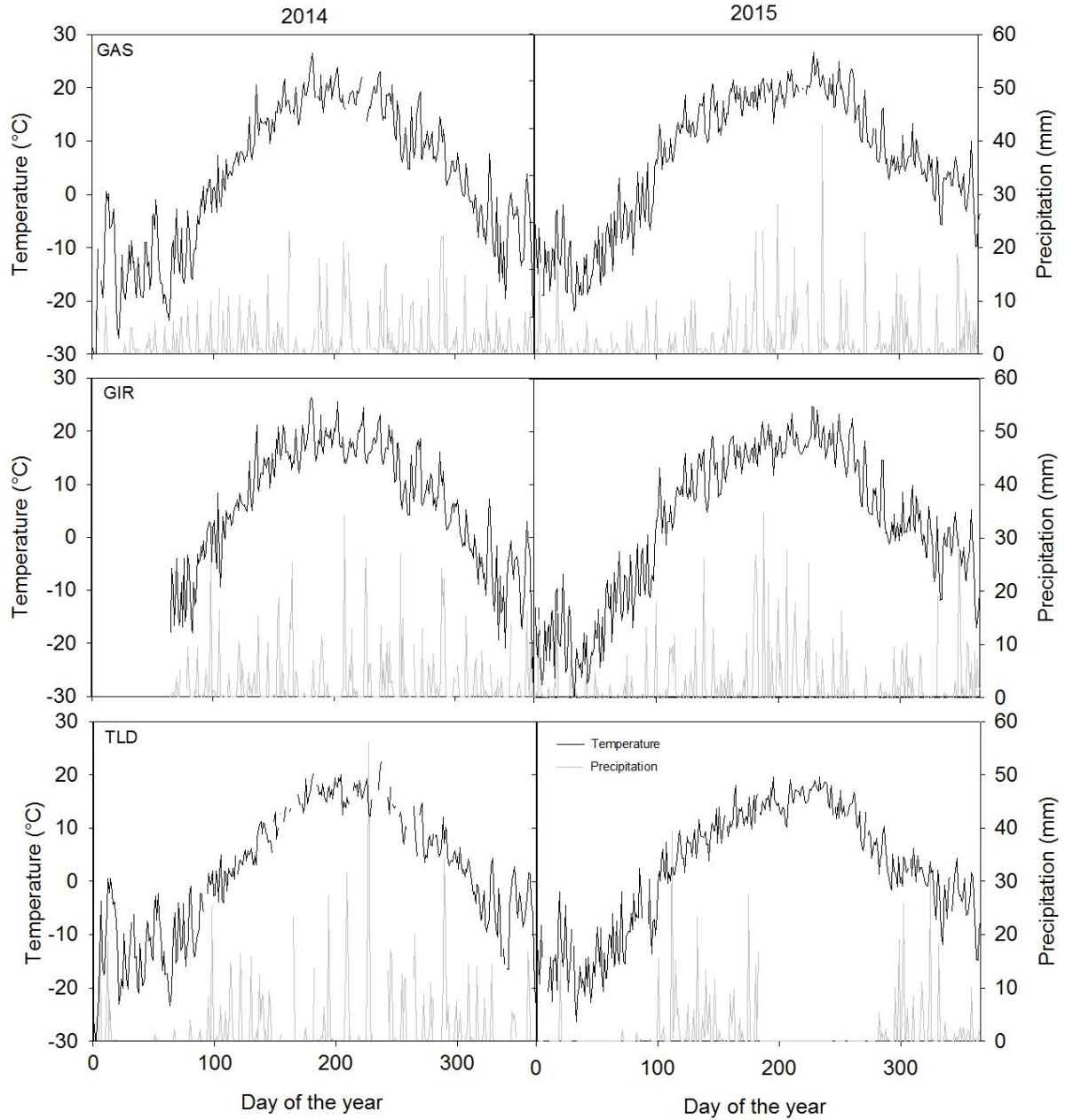
Supplementary material

Figure S1



Map of the study sites: Gaspard (GAS, 1), Girardville (GIR, 2, 3), and Toulnostouc–Lac Dionne (TLD, 4,5,6,7), Simoncouche (SIM, 8). Source: Google earth imagery was used as reference background image (Google Earth 2019).

Figure S2



Temperature (black curve) and precipitation (grey curve) in Gaspard (GAS), Girardville (GIR), Tournoustouc–Lac Dionne (TLD) during 2014-2015.