

**RESPONSES OF FOREST CARBON AND WATER COUPLING TO JUVENILE
THINNING AT BOTH THE LEAF AND INDIVIDUAL TREE LEVELS IN A 16-
YEAR OLD NATURAL PINUS CONTORTA STAND**

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RESPONSES OF FOREST CARBON AND WATER COUPLING TO JUVENILE
THINNING AT BOTH THE LEAF AND INDIVIDUAL TREE LEVELS IN A 16-YEAR
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Abstract

Large-scale mountain pine beetle infestation (MPB) has generated overstocking lodgepole pine stands in the interior of British Columbia. A critical need is to determine sustainable management strategies to ensure their healthy growth and provision of various ecological functions. The objective of this study is to assess the effects of juvenile thinning on various carbon and water processes (tree growth, tree-level and stand-level transpiration, and leaf-level and tree-level water-use efficiency (WUE)) in a 16-year old, naturally regenerated lodgepole pine stand using an experimental approach. An experiment involving two thinning treatments (T1: 4,500 stems per ha; and T2: 1,100 stems per ha) and one control (C: 27,000 stems per ha) that were randomly assigned in three blocks, was established in 2016 and has been continuously monitored since then. Data on tree diameter at the breast height, sap flow and environmental variables have been collected since the first growing season (June to October), while additional leaf-level measurements on photosynthesis and transpiration were included in the second growing season. The results showed that juvenile thinning significantly increased tree radial growth and tree-level transpiration, but the significant difference between T1 and T2 only occurred under drought conditions (in the summer season of 2017), with T2 being more resilient to the drought effect. At the stand-level, transpiration of the thinned stands were not statistically different before and during the drought, while that of the unthinned stand was significantly reduced over the drought period. Thinning increased the tree-level WUE (the ratio of tree growth to tree transpiration) with greater enhancement in the more heavily thinned stands (T2), but it did not affect the leaf-level WUE (the ratio of leaf photosynthesis to leaf transpiration). The leaf-level *i*WUE (the ratio of leaf photosynthesis to stomatal conductance) was significantly higher in the unthinned stand than the thinned stands, with no statistical

difference between the two thinned stands. We conclude that juvenile thinning had significant and positive effects on forest carbon and water processes at the individual tree level, and the heavier thinning was more effective for trees to cope with drought conditions.

Lay Summary

Using an experimental approach, this study examined the responses of carbon and water processes at the leaf and individual tree levels to two thinning treatments (T1: 4,500 stems per ha; and T2: 1,100 stems per ha) in a 16 year old, overstocked lodgepole pine forest in the southern interior of British Columbia over the period of 2016-2017. The results showed that the thinning treatments significantly promoted tree growth, transpiration, and water-use efficiency at the tree level. The enhancements were more pronounced in the more heavily-thinned stands during the summer drought season of 2017. Thinning also maintained stand-level transpiration during the 2017 drought. However, the responses of leaf-level water use efficiency (WUE) to thinning were not consistent with those at the tree-level, suggesting that caution must be exercised when evaluating and modelling forest carbon and water coupling processes.

Preface

This study was directed by Dr. Adam Wei in the Department of Earth, Environmental and Geographical Sciences. The field experiment was designed by Dr. Adam Wei, Dr. Antonio del Campo and Yi Wang. The data collection, analysis and thesis writing were conducted by Yi Wang. Part of the results have been published (listed below). The project was supported by Natural Sciences and Engineering Research Council of Canada (NSERC)'s Collaborative Research and Development (CRD) Grants.

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List of Abbreviations

B1	Block 1
B2	Block2
B3	Block3
C	The unthinned plot
iWUE	Intrinsic water-use efficiency
SPI	Standard Precipitation Index
T1	Juvenile thinning treatment with a intensity of 4,500 stems/ha
T2	Juvenile thinning treatment with a intensity of 1,100 stems/ha
WUE	Water-use efficiency
UPW	Upper Penticton Watershed

List of Symbols

As	Sapwood area per tree (cm ²)
As _g	Estimated total stand sapwood area for each plot with the plot area of 400 m ² (cm ²)
BAI _B	Basal area increment calculated from basal perimeter (mm ²)
BAI _{Bn}	BAI _B of a measured tree on the n th day (mm ²)
BAI _D	Basal area increment calculated from diameter at the breast height (mm ²)
BAI _{DN}	Total basal area change at breast height during the whole growing season (mm ²)
Ca	Atmospheric CO ₂ concentration (mol/mol)
Ci	Leaf intercellular CO ₂ concentration (mol/mol)
DBH	Diameter at breast height (mm)
Es	Daily stand transpiration with the plot area of 400 m ² (mm/d)
F	Sap flow rate (g/h)
F _N	Total transpiration per tree during the whole growing season (g)
F _n	Daily tree transpiration on the n th day (g)
K	Dimensionless variable calculated from the measured temperature difference between two thermocouples of the probe
N	Total days of each growing season
P	Precipitation (mm)
Rn	Solar radiation (W/m ²)
RH	Relative humidity (%)
SFD	Sap flow velocity (g/cm ²)
T	Temperature (°C)
ΔT	Temperature difference between two thermocouples of the TDP-30 probe (°C)
ΔT _{max}	Maximum ΔT (°C)
Wv	Wind velocity (m/s)
VWC	Soil volumetric water content (%)

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Dedication

*This work is dedicated to my beloved grandparents and
parents:*

陈祝同， 邓如惠

王国斌， 钟素娟

王荣杰， 陈虹微

Chapter 1: Introduction

Large-scale forest disturbances have severely impaired the structure and composition of forests across the world, and consequently affected various ecological processes such as carbon and water cycles (Bearup et al. 2014, Bonan 2008, Reichstein et al. 2013, Seidl et al. 2014). For example, forest fires in Canada led to an annual carbon emission of 27 ± 6 Tg C from 1959 to 1999 (Amiro et al. 2001, Bond-Lamberty et al. 2007), while mountain pine beetle outbreaks since 1999 in British Columbia, Canada have infested over 170,000 km² of forests, and turned them into net carbon sources (Kurz et al. 2008), with negative effects on hydrological processes (Bearup et al. 2014) and regional climate (Maness et al. 2012). The effects of natural forest disturbances and timber harvesting on forest carbon and water have been extensively studied (Seidl et al. 2017), but much less is known about the post-disturbance recovery process through regeneration of affected stands.

Following stand-replacing disturbances or intensive timber harvesting, lodgepole pine (*Pinus contorta* ssp. *latifolia*) forests, which were able to adapt to the poor soil and had a large number of active cones (Boateng et al. 2011, Kaufmann et al. 2008), could naturally regenerate with over-dense, uniform cohorts, of which the densities could be larger than 50,000 stems per ha (Johnstone and Van Thienen 2004, Kashian et al. 2004, Nyland 1998, Turner et al. 2013, Yang 1998). Such overstocking impedes healthy growth of trees, hampers their ability to produce merchantable volumes of woods, and seriously affects carbon sequestration and hydrological processes (Berryman 1982, Brix and Mitchell 1986, Eremko 1990). This problem could be further compounded by climate change induced droughts, as it might increase the risk and the frequency of forest fires (Siegert et al. 2001) and insect outbreaks (McDowell et al. 2008). As a result, carbon starvation (i.e., when carbon consumption by respiration, growth and defense

exceeds carbon assimilation from photosynthesis) and hydraulic failure (i.e., failed water transport when trees are under water stress), the two mechanisms of tree mortality, are commonly observed in affected forests (McDowell et al. 2008, McDowell 2011). Clearly, practical strategies or practices are needed to manage those highly dense forest stands, particularly in the context of future climate change impact (Seidl et al. 2017, Spittlehouse and Stewart 2003).

Juvenile thinning (or pre-commercial thinning), which reduces the stand density of immature forests, was suggested as an effective approach to deal with the overstocking problems of young lodgepole pine stands due mainly to their low effective self-thinning (Stewart and Salvail 2017) and slow response to thinning treatments unless being treated early (Bassman 1985, Cole 1973, Lotan and Critchfield 1990). Thinning treatments have been also considered as an effective strategy to mitigate the effects of drought (Ambrose et al. 2018, Cabon et al. 2018, Del Río et al. 2017, Elkin et al. 2015b, Gyenge et al. 2011, Kohler et al. 2010, Laurent et al. 2003, Park et al. 2018, Rodríguez-Calcerrada et al. 2011, Simonin et al. 2007, Sohn et al. 2013, Sohn et al. 2016b, Sohn et al. 2016c). Juvenile thinning had been applied for various coniferous species in western Canada since the 1920s but declined in recent decades (Eremko 1990). A review on juvenile thinning experiments conducted in lodgepole pine forests in western Canada concluded that the thinning treatment improved individual tree growth in terms of diameter and volume (Chase et al. 2016a, Johnstone and Van Thienen 2004), but the majority of treated stands still had lower net stand basal area and total volume increments compared to untreated counterparts 20 years after thinning treatments were applied (Johnstone and Van Thienen 2004). More interestingly, thinning can promote tree vigor that may thus be helpful in withstanding beetle attacks (Mitchell et al. 1983), but tree mortality rate was actually increased under

juvenile thinning due to increased disturbances by snow, wind and certain pests (e.g. Atropellis canker) (Johnstone and Van Thienen 2004). Therefore, whether juvenile thinning is an appropriate measure for sustaining various ecological processes and functions is questionable (Daniel et al. 2017, Naudts et al. 2016).

Various studies have assessed the effects of thinning treatments on either young stands or mature stands, and those studies generally reported positive impacts of thinning on the individual growth performance of trees and tree-water relations both under non-drought and drought periods (Cabon et al. 2018, Del Río et al. 2017, Kohler et al. 2010, Laurent et al. 2003, Park et al. 2018, Rodríguez-Calcerrada et al. 2011, Simonin et al. 2007, Sohn et al. 2013, Sohn et al. 2016a, Sohn et al. 2016c). The better performance of trees in the thinned stands during drought periods were attributed to abiotic factors (e.g. enhanced soil water availability) and biotic factors, (e.g., physiological adjustments of trees to droughts (Ambrose et al. 2018, Bréda et al. 2006, Zweifel et al. 2009) that were modified by thinning treatments (Cabon et al. 2018, Elkin et al. 2015a, Gyenge et al. 2011, Park et al. 2018, Rodríguez-Calcerrada et al. 2011, Simonin et al. 2007, Sohn et al. 2016c). However, only a few studies examined the effects of thinning on the coupling of carbon and water processes (e.g., water-use efficiency (WUE), the trade-off between carbon assimilation and water use) (Fernandes et al. 2016a, Forrester et al. 2012a, Park et al. 2018). As hydrological effects of forest management are a growing concern related to the protection of water resources and in coping with climate change impacts, evaluating the effects of thinning on the coupling of carbon and water processes is critically needed.

Although WUE is a key parameter in estimating and evaluating forest productivity and associated water use, little is known about the response of WUE to juvenile thinning across

various spatial scales. WUE has been quantified in various ways according to different research needs and spatial scales. For example, it can be denoted as intrinsic water-use efficiency (iWUE), the ratio of net photosynthetic assimilation to stomatal conductance, which can be either measured by the isotopic method on leaves or tree rings, or by the instantaneous gas exchange method on leaves (Guehl et al. 1995, Peñuelas et al. 2011); it can also be calculated as the ratio of net photosynthetic assimilation to leaf transpiration at the leaf scale (leaf-level WUE), or the ratio of tree growth (e.g., basal area increments (BAI)) to whole tree transpiration at the individual tree level (tree-level WUE) (Wullschleger et al. 1998); or the ratio of gross primary production to evapotranspiration at the ecosystem level (e.g., Hu et al. (2008)). The responses of WUE at finer spatial levels (e.g., leaf and individual tree) provides valuable information for understanding and predicting those at larger spatial scales.

From leaf to tree levels, the concept of iWUE was developed in considering that leaf-level WUE measured by instantaneous gas exchange systems can change dramatically on the same leaf over a certain short period of time, which increases the challenge in separating the effects of various experimental treatments and different responses of species (Perez-Harguindeguy et al. 2013). Therefore, iWUE, by replacing transpiration with stomatal conductance, is adopted, because exchanges of CO₂ and water vapor share the same diffusion pathway via stomata, which excludes the effect of fluctuations in vapor pressure on transpiration rate (Perez-Harguindeguy et al. 2013). According to the physiological model that simplifies the gas diffusion of stomatal conductance, iWUE is positively and linearly correlated with the ratio of the leaf intercellular CO₂ concentration (C_i) to the atmospheric CO₂ concentration (C_a). On the other hand, this ratio is also assumed to be linearly related to carbon isotope discrimination by approximating the intercellular chloroplast concentration to C_i. Therefore, iWUE can also be

determined by the isotopic method (Farquhar et al. 1989, Seibt et al. 2008). The gas exchange derived iWUE has been mainly adopted in short-term studies, while the isotope-based iWUE has been applied to longer-term studies over a longer time span (e.g. Junker et al. (2017) and Wieser et al. (2018)). Thus, the discrepancy between iWUE of the two different methods was ascribed to the difference in time scales (Wieser et al. 2018).

Spatial scales are important for understanding the sensitivity of WUE to climatic factors or human activities (Medrano et al. 2015, Niu et al. 2011, Tu et al. 2008). For example, Niu et al. (2011) found that precipitation was linearly and positively correlated with WUE at the tree and ecosystem levels, while negatively correlated with WUE at the leaf level. The contrast was due to the differences in ecohydrological processes incorporated in each WUE at different spatial scales, suggesting that caution must be taken in extrapolating the responses of WUE from one spatial scale to another when modelling the carbon and water processes. Even at the same spatial level, contrasting behaviors of WUE were also observed. For instance, Meinzer et al. (1992) reported that leaf-level WUE and the intrinsic WUE of a coffee plant (*Coffea arabica* L.) measured by the gas exchange system responded oppositely to two levels of the irrigation treatments, which highlighted the importance in considering the spatial aspects of WUE.

The above-mentioned divergent responses of WUE also lead to a lack of correspondence in WUE across various spatial scales, though all WUE shares the similar concept between carbon sequestration and water consumption from an eco-physiological point of view. For example, the lack of correlations between iWUE or leaf-level WUE with whole-plant WUE is commonly observed in crops, which introduces limitations in choosing the most representative indicators of WUE and in the applicability of scaling from single leaf to whole-plant (Medrano et al. 2015). There are fewer studies on trees, but the same discrepancies have been reported (Niu et al.

2011). For example, thinning could increase tree-level WUE (Forrester et al. 2012a, Park et al. 2018) but may not affect isotope-derived iWUE (Fernandes et al. 2016a, Martín-Benito et al. 2010). Furthermore, under the interaction of thinning and climate variability (e.g., drought), the behavior of WUE and isotope-derived iWUE has been reported inconsistently (Bréda et al. 2006, Del Río et al. 2017, González de Andrés et al. 2018, Park et al. 2018). Efforts have been made to explain potential linkages and discrepancies between WUE and iWUE (Battie-Laclau et al. 2016, Fernandes et al. 2016a), for example, Fernández-de-Uña et al. (2016) suggested that CO₂ and climate are the main drivers of the variability of tree-ring derived iWUE as iWUE was closely related to intercellular CO₂ concentration, while competition and climate are the major drivers of WUE fluctuations. The lack of correspondence in WUE across various spatial scales among current research impedes the interpretation and evaluation of forest carbon and water coupling in association with forest management and climate change.

The objectives of this study were: (1) to evaluate the responses of tree growth, tree- and stand-level transpiration under two juvenile thinning treatments during the two growing seasons of 2016-2017; and (2) to study the responses of iWUE, and WUE to juvenile thinning from leaf to tree levels. A drought occurred in the second growing season providing an unique opportunity to compare the effect of juvenile thinning under non-drought and drought conditions. The results from this study not only provided useful information for designing post-disturbance management strategies for sustaining ecological functions under climate change, but also supported evaluation of forest carbon and water coupling across various spatial scales.

Chapter 2: Study Area and Methods

2.1 Study Area

The study area is located at the 241 Creek in the Upper Penticton Watershed (UPW), approximately 26 km northeast of Penticton in the southern interior of British Columbia, Canada (49°39'34"N, 119°24'34"W) (Figure 1). According to the biogeoclimate zones of British Columbia, UPW belongs to the drier part of the Engelmann Spruce-Subalpine Fir Zone which is characterized as steep, rugged terrain with cold and snowy conditions in the winter (Coupé et al. 1991). The elevation is around 1675 m a.s.l, and snow cover lasts from early November through middle of June. Seasonal droughts during the summer often occur. Climate records from 1992-2008 show that the mean annual precipitation was 697.2 mm with less than one-third precipitation in the growing season (between June to October). The mean annual temperature is 1.9 °C, with daily temperature in the growing season ranging from -8 to 28°C. The study site is generally south aspect, occupied with even-aged lodgepole pine forests that are regenerated after logging in 2002. Understory vegetation including *Rhodendron albiflorum*, *Vaccinium scoparium*, *Valeriana sitchensis*, *Tiarella unifoliata*, and *Arnica latifolia* (Hope 2009) is sparse. Soils are derived from granite parent rock, coarse sandy-loam in texture, with low water holding capacities. More detailed descriptions can be found in Hudson and Golding (1997), Winkler and Moore (2006).

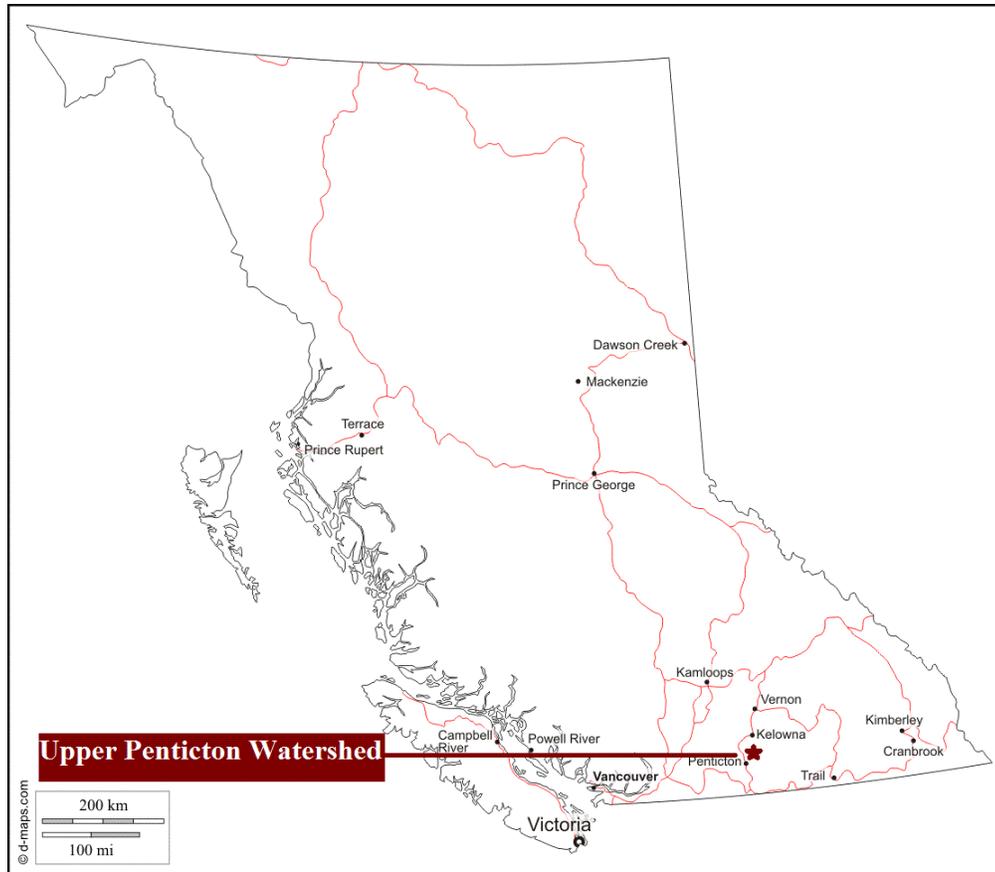


Figure 1. Map of the Upper Penticton Watershed.

2.2 Experimental Design

Three blocks including B1, B2 and B3 (25 m × 75 m each), with each having two thinning treatments and one unthinned control plot (20 m × 20 m each) were established in June 2016 following the randomized block design (9 plots in total) (Figure 2). Thinning was applied manually with the slash left on site. The tree densities in the first treatment (T1) and the second treatment (T2) are approximately 4,500 (1.5 m spacing) and 1,100 (3 m spacing) stems per ha, respectively. The controlled plots have an average density of 26,933 stems per ha. Trees were only counted if their heights are greater than or equal to 1.3 m.

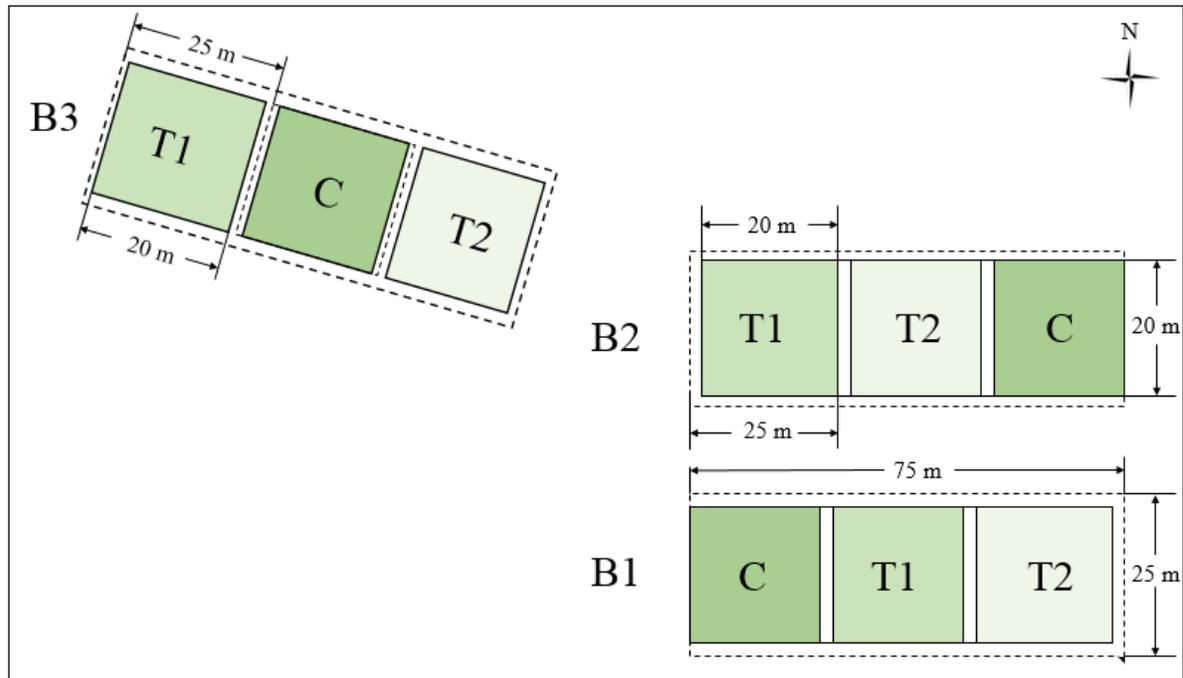


Figure 2. Layout of the study site

2.3 Monitoring of Tree Growth

Tree growth is regarded as the basal area increment (BAI_D , mm^2) (West 1980). In each plot, 45 trees were randomly selected to measure tree heights and diameters at breast height (DBH) with an electronic caliper (Model:500-196-30, Mitutoyo Corporation, Japan). The measurements were conducted monthly in the growing seasons of 2016 and 2017. The data on the initial DBH distribution of those selected trees are showed in Table 1. An effort was made to ensure those selected trees from each plot are comparable.

Table 1. Initial DBH Distributions of the selected trees in C (control), T1 (treatment 1) and T2 (treatment 2).

DBH (mm)	C	T1	T2
≤ 30	8.1%	11.0%	1.8%
>30 and ≤ 45	54.5%	44.1%	32.7%
>45 and ≤ 60	27.3%	36.4%	47.3%
>60	10.1%	8.5%	18.2%

In addition, home-made dendrometer sensors following the design by Cattelino et al. (1986), were installed in five of the selected trees per plot in B1 (15 trees in total) to continuously measure diameter changes at 20 cm above the ground. The selected trees cover proportionally the range of diameters found in each class. Those sensors measured basal perimeters (tree girth) every 20 minutes, and were connected to the multiplexer (CR1000, AM16/32B, Campbell Scientific Inc., Logan, UT, USA) installed in the central sap flow systems (FLGS-TDP XM1000, Dynamax, Inc., Texas, USA) located in B1. The increment of basal perimeter was denoted as BAI_B (mm). A linear equation between basal diameter and DBH was established based on additional measurements from 180 trees in all three blocks. The established equation (1) ($R^2 = 0.83$) is showed below.

$$DBH \text{ (mm)} = 0.6935 \times \text{basal diameter (mm)} + 8.5685 \quad (1)$$

2.4 Measurement of Tree-level and Stand-level Transpiration

Granier-type sap flow probes (Model TDP-30, Dynamax, Inc., Texas, USA) were also inserted at breast height in the five previously selected trees equipped with home-made dendrometers at each plot (15 trees in total). In consideration of the small DBHs of young trees (Table 1), each tree was installed with one pair of TDP-30 probes with the assumption that there were no systematic variations in sap flow density along the sapwood depth (Clausnitzer et al. 2011). All the probes were oriented towards the southern exposure, and were fully insulated with thermal insulation materials to minimize possible effects of ambient temperature gradients. The installation and detailed description of the probes can be found in Granier et al. (1990). Sap flow was calculated with empirical equations (2-4) calibrated from Granier (1987):

$$K = (\Delta T_{\max} - \Delta T) / \Delta T \quad (2)$$

$$\text{SFD} = 0.0119 \times K^{1.231} \quad (3)$$

$$F = A_s \times \text{SFD} \times 3600 \quad (4)$$

Where, K is a dimensionless variable calculated from the measured temperature difference between two thermocouples of the probe (ΔT , °C). It was assumed that no sap flow occurred at night when the temperature difference reached its maximum (ΔT_{max} , °C). SFD is the sap flux density (g/cm^2), F denotes the sap flow rate, (g/h), and A_s stands for the sapwood area per tree (cm^2).

Sapwood area was inferred from the linear relationship between DBH and sapwood area ($R^2 = 0.98$) derived from seven trees representing a range of diameters within the stand. This relationship was assumed to be held for trees in the controlled and thinned plots (Bréda and Granier 1996).

$$A_s (\text{mm}^2) = 102.81 \times \text{DBH} (\text{mm}) - 3709.3 \quad (5)$$

Daily tree transpiration for the selected sap flow trees was calculated by summing up half hourly sap flow rates from 0:00 to 23:30 each day. Total tree-level transpiration during the growing season was then used to extrapolate transpiration to other trees of similar DBH classes according to the established linear relationship between tree transpiration and DBH (Appendix C). Daily mean SFD values for C, T1 and T2 were also upscaled to calculate the daily stand transpiration following by Bréda and Granier (1996). Stand sapwood areas were summed up according to the stand densities for the thinned and unthinned stands, DBH distributions (Table 1) and the DBH-sapwood relationship (Equation (5)).

$$E_s = \overline{\text{SFD}} \times A_{s_g} \quad (6)$$

Where, E_s is the daily stand transpiration (mm/d); \overline{SFD} is the mean SFD for C, T1 and T2 (g/cm²); and A_{sg} is the estimated total stand sapwood area for each plot with the plot area of 400 m² (cm²).

However, the species-specific calibration of the empirical equations (2-4) for lodgepole pine was not considered, as the original equations have been widely used in other sap flow studies on lodgepole pine stands (Reid et al. 2006, Zhang et al. 2015).

2.5 Estimation of Leaf-level WUE and iWUE, and Tree-level WUE

Leaf-level WUE was calculated as the ratio of leaf photosynthesis to leaf transpiration, while leaf-level iWUE was calculated as the ratio of leaf photosynthesis to stomatal conductance. All the variables were measured by the instantaneous photosynthesis measurement system (Model LI-6400XT, Licor, Lincoln, NE, USA) with an opaque conifer chamber (Model 6400-22) and external RGB light source (6400-18A). The measurements took place between 10:00 am and 14:00 pm beginning on June, 23rd, 2017, and then once per week in all three blocks until the end of the growing season (October 2017). Each time the measurements were conducted, five trees in each plot were selected, and for each tree, four bunches of needles orienting north, south, east and west at a similar location in the tree canopy (around 1.5-1.7 m height) were measured for three times. The volume of the measured branches was kept the same, and no correction for the total needle area of each branch at every measurement was made, because leaf area was removed in the calculation of WUE. In order to mimic the natural surrounding environment of the selected leaves, the leaf chamber was sealed with gum in case of gas leaking, and the temperature and light inside the chamber were set as the ambient temperature and light.

Flow rate was set at 500 $\mu\text{mol/s}$ to minimize the modifications on the environmental variables by the equipment (Medrano et al. 2010).

The tree-level WUE of the treatments and the control were compared by using the mean daily tree-level WUE which was calculated as the ratio of total BAI_D to total transpiration during the whole growing seasons, divided by the total growing days in each year, with consideration of the greater sample size and the different durations of the growing season in each year. The relationships between tree-level WUE and leaf-level WUE and $i\text{WUE}$ were analyzed using the continuous daily tree-level WUE, with consideration of data continuity.

$$\text{Mean daily tree-level WUE} = \frac{\frac{\text{BAI}_{DN}}{F_N}}{N} \quad (7)$$

$$\text{Daily tree-level WUE} = \frac{\text{BAI}_{B_n}}{F_n} \quad (8)$$

Where, BAI_{DN} is the total basal area change at DBH per tree during the whole growing season for each year (mm^2); F_N is the total transpiration per tree during the whole growing season for each year (g); N is the total growing days for trees (d); BAI_{B_n} is the BAI_B of a measured tree on the n_{th} day (mm^2); and F_n is the daily transpiration for that measured tree on the n_{th} day (g).

2.6 Collection of Climate Data

One climate station (HOBO weather station, Onset Computer, Bourne MA, USA) was installed in each plot in B1 to collect climate data including solar radiation (R_n , W/m^2), air relative humidity (RH, %), temperature (T , $^{\circ}\text{C}$), precipitation (P , mm) and wind velocity (W_v , m/s) at 10 minutes intervals throughout the study period. The sensors were placed at approximately

2.5 m height which is just at the canopy level. VPD was calculated from RH and T according to Goff–Gratch equation (Goff 1946).

Soil volumetric water content (VWC) in B1 was measured at two depths (20 cm and 40 cm) in three randomly selected locations per plot by EC-5 sensors (Decagon, Pullman, WA, USA) at 20 minutes intervals for the study period. The selection of soil depths was based on the studies reporting that tree transpiration was mainly associated with soil water content at the depth of 10 to 20 cm (Raz-Yaseef et al. 2012, Sun et al. 2014a). Soil VWC at the 20 cm depth were also manually collected in all three blocks weekly during the growing season of 2017 by GS-1 portable measuring system (Decagon, Pullman, WA, USA).

Climatic conditions varied between 2016 and 2017 (Appendix A). The average daily solar radiation was 102.68 and 141.20 W/m² for the growing seasons of 2016 and 2017, respectively. The average temperature was 7.68 °C in 2016 versus 12.14 °C in 2017. Daily mean RH was 74.47% in 2016 and 56.45% in 2017. As a result, the daily mean VPD was more than twice smaller in 2016 (0.34 KPa) than in 2017 (0.72 KPa). Daily mean precipitation over the growing season was nearly 5 times greater in 2016 (1.59 mm) than in 2017 (0.32mm). Averaged daily soil VWC were 15.98% and 13.03% for the depths of 20 and 40 cm in 2016, respectively, while those amounts were reduced to 12.91% and 11.25%, respectively in 2017. All daily mean environmental variables in 2016 were significantly different from those in 2017 (independent t test, all p < 0.01). The Standardized Precipitation Index (SPI) showed that 2016 was a normal to humid year, while 2017 was a typical drought year (Appendix B).

2.7 Statistical Analysis

All hourly data were averaged or summed to the daily scale. Although there were 135 trees selected for each treatment (T1 and T2) or control (C), trees with monthly growths in DBH that were greater than 5 mm or less than negative 5 mm were regarded as measurement errors and deleted from analyses. As a result, 111, 119 and 100 trees were kept for analyzing tree growth for C, T1 and T2, respectively. BAI_D among the three groups were analyzed by ANCOVA with the initial DBH of trees as a covariate.

Daily tree-level transpiration, daily stand-level transpiration and daily tree-level WUE for the treatments and control were compared by repeated measured ANOVA and Tukey HSD, if data met the requirements of homogeneity of variance and normality. Otherwise, a non-parametric test such as Independent K-sample Kruskal-Wallis test was implemented, and Wilcoxon Signed-Rank test for pair samples and Mann-Whitney test for independent two groups were applied for post-hoc comparisons. Sap flow velocity, leaf-level WUE and $iWUE$ were analyzed using linear mixed models (LMMs) considering the random effects of measuring times and the blocks. Daily tree-level WUE derived from BAI_B were only used in correlation analysis with leaf-level WUE and $iWUE$. Correlation was examined using spearman test. All data were processed by R (R Core Team (2014) and SPSS for Windows (SPSS, Inc., USA).

Chapter 3: Results

3.1 The Responses of Tree Growth, Transpiration and WUE to Juvenile Thinning at Various Spatial Scales

3.1.1 Tree Growth

Thinning had a significantly positive impact on average tree growth throughout the two growing seasons of 2016-2017 (Figure 3 (1)). The mean daily BAI_D in the three groups were significantly different from each other, with the value of 0.06, 0.50 and 0.90 mm^2/d for C, T1 and T2, respectively ($p < 0.001$).

When each growing season was considered separately, thinning also had a significant impact on tree growth ($p = 0.001$ in 2016, and $p = 0.003$ in 2017, Figure 3 (2), Appendix D). The mean daily BAI_D in 2016 was 0.08, 0.66 and 1.00 mm^2 in C, T1, and T2, respectively. Those values were greatly decreased in 2017 (0.04, 0.36 and 0.81 mm^2 in C, T1 and T2, respectively) due to the drought in the growing season in that year (Appendix B and D). However, the reduction was only 19% in T2 in comparison to 45% in both C and T1 (Figure 3 (2)).

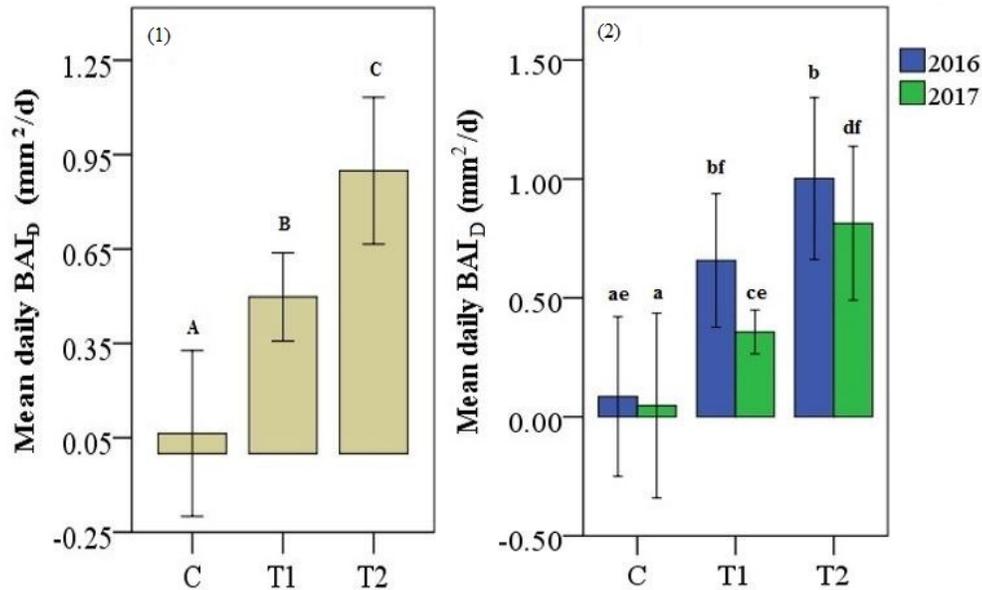


Figure 3. Mean daily BAI_D during the whole study period (1), and during the respective growing seasons of 2016 and 2017 (2). Error bars denote the 95% confidence interval, and letters denote the post-hoc comparison within and between the two years.

3.2.2 Transpiration at the Individual Tree and Stand Levels

Mean daily SFD values in C, T1 and T2 during the two growing seasons were significantly different from each other, with the highest in T2 and the lowest in C (Figure 4 (1), $p < 0.001$).

In each respective season, the thinned stands had significantly higher mean daily SFD than the unthinned stands (Figure 4 (2), $p < 0.001$). However, there was no significant difference in the mean daily SFD between T1 and T2 in 2016 ($p = 0.135$, Appendix G), while the significant difference occurred in the drought season of 2017 ($p < 0.001$, Appendix G). Their magnitudes were decreased to 55.41, 108.33 and 136.70 g/cm²d in 2017, from their corresponding values 78.63, 162.60 and 167.84 g/cm²d of C, T1 and T2 in 2016, respectively (Figure 4 (2)).

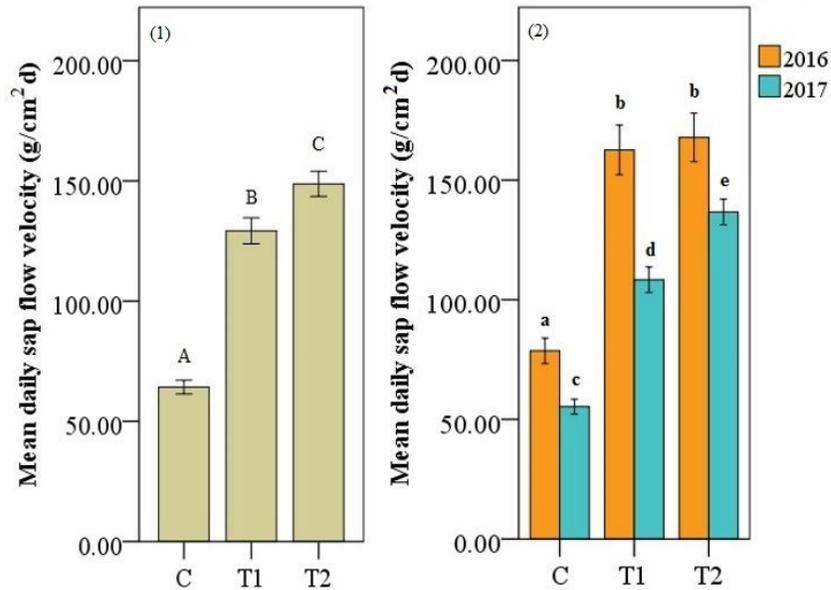


Figure 4. Mean daily sap flow velocity (SFD) during the whole study period (1) and at the respective growing seasons of 2016 and 2017 (2). Error bars denote the 95% confidence interval, and letters denote the post-hoc comparison within and between the two years.

Individual tree-level transpiration varied with tree sizes, with larger trees having greater daily transpiration. Therefore, to remove the possible influence of tree size, trees that have DBH ranges from 30 to 60 mm, which comprise the majority of the stands, were selected to statistically compare the average mean daily individual tree transpiration between the control and the thinning treatments (Table 2). The DBH of the selected groups of trees among C, T1 and T2 were not statistically different from each other (one-way ANOVA $p = 0.248$ and 0.131 for 2016 and 2017, respectively), suggesting that our selected trees from all the experimental plots are comparable in terms of individual tree-level transpiration.

Figure 5 shows that the mean daily tree transpiration values of C, T1 and T2 over the whole study period were significantly different from each other, with the highest value occurring in T2 and the lowest in C ($p < 0.05$, Figure 5 (1)). However, comparing the mean daily tree

transpiration in each study season, the values in the thinned groups (T1 and T2) were significantly higher than that in C, but no statistical difference was detected between T1 and T2 in both seasons ($p = 0.109$ for 2016 and $p = 0.159$ for 2017, Appendix H) (Figure 5 (2)). There was also no significant difference in tree transpiration between 2016 and 2017 for each group ($p > 0.1$).

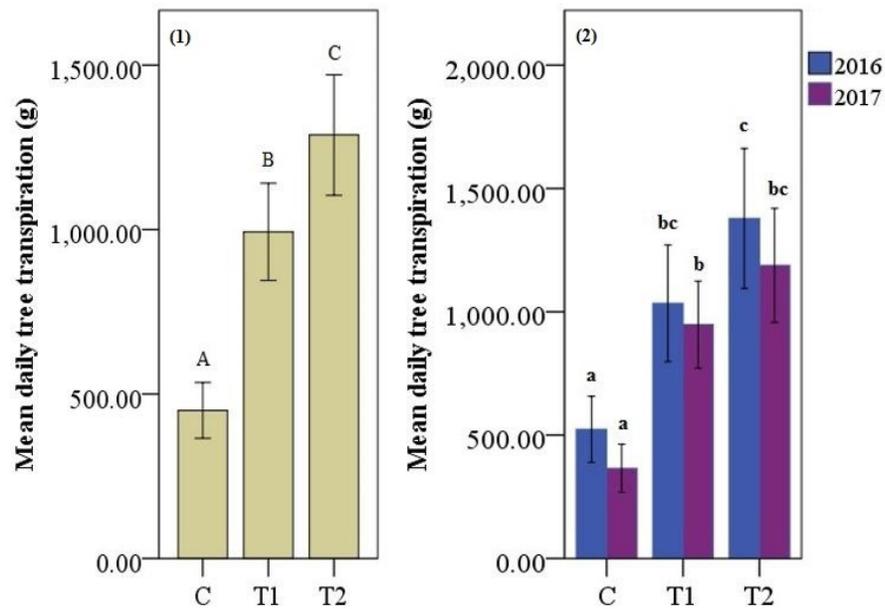


Figure 5. Mean daily tree transpiration during the whole study period (1) and during the respective growing seasons of 2016 and 2017 (2). Error bars denote the 95% confidence interval, and letters denote the post-hoc comparison within and between the two years.

On the contrary, the stand-level daily transpiration was the highest in C and the lowest in T2 during the entire study period as well as in each respective season (MANOVA, $P < 0.001$, Appendix I, Figure 6 (1)). But when compared between 2016 and 2017, only the stand-level transpiration in C exhibited a significant reduction ($p < 0.01$, Figure 6 (2)).

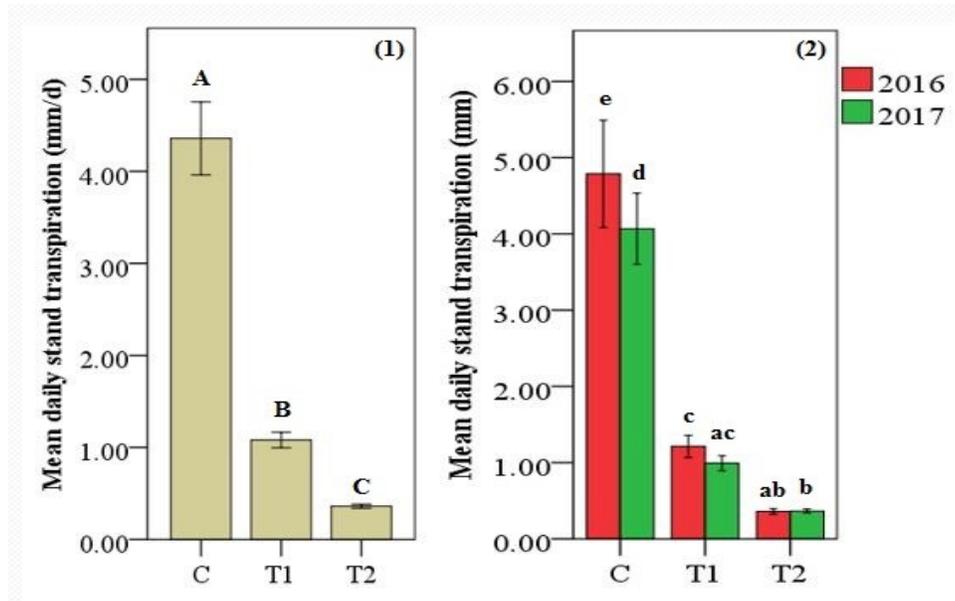


Figure 6. Mean daily stand transpiration during the whole study period (1) and during the respective growing seasons of 2016 and 2017 (2). Error bars denote the 95% confidence interval, and letters denote the post-hoc comparison within and between the two years.

3.2.3 Leaf-level WUE and iWUE

Figure 7 showed that the temporal variations of leaf-level WUE and iWUE were similar. During the early growing season (from June, 23rd to July, 23rd), both leaf-level WUE and iWUE remained relatively low, probably because of high soil moisture contents as a result of snow melting. However, during the mid-August when soil VWC continuously decreased and VPD became higher, both the leaf-level WUE and iWUE in C, T1 and T2 all increased. At the

end of the September 2017 when precipitation alleviated the soil water deficit and decreased the VPD, both the leaf-level WUE and iWUE in all three groups decreased (Figure 7).

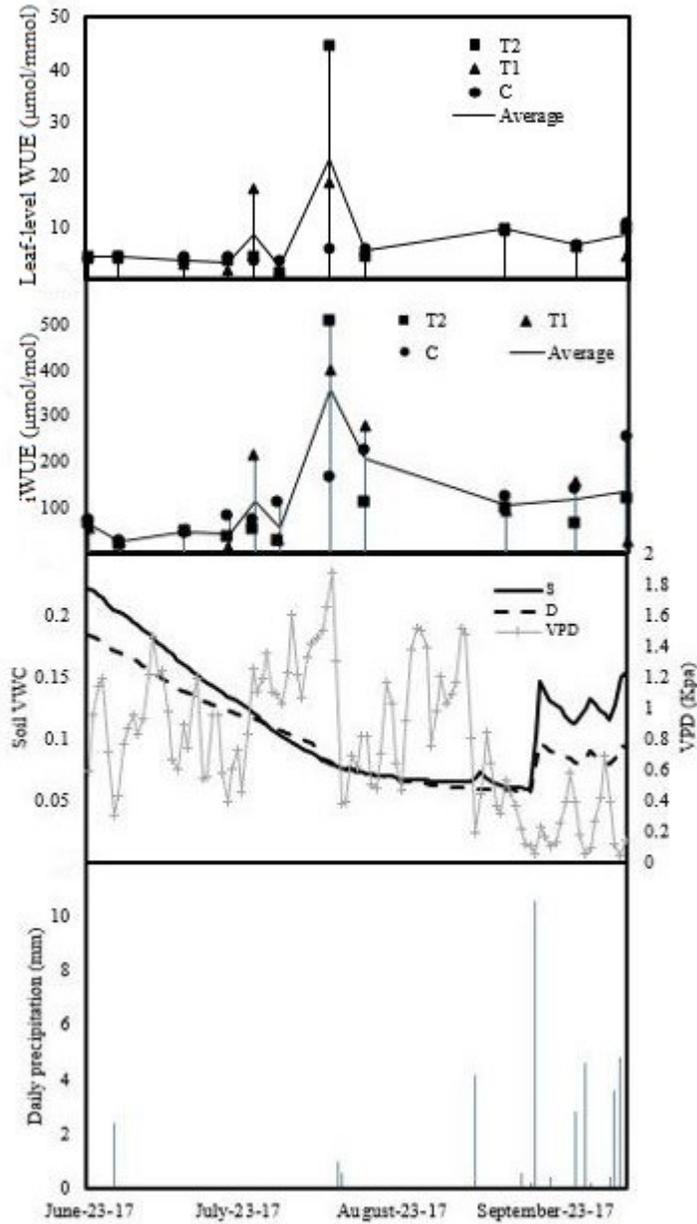


Figure 7. The mid-day leaf-level WUE and iWUE with daily precipitation, VPD and soil volumetric water content in 2017. S and D denote the soil depths of 20 cm and 40 cm, respectively; and daily precipitation, VPD and soil volumetric water content were the averaged values from all three groups.

At the leaf level, the mid-day WUE in 2017 were not significantly different between the treatments and the control, and between T1 and T2 ($p = 0.1$, Appendix J), but iWUE was significantly higher in C than T1 and T2 ($p < 0.001$) (Figure 8, Appendix J), with no significant difference between T1 and T2 ($p = 0.829$). Besides, no significant effects of the branch orientation, and the interactions of thinning treatment and branch orientation were found (Appendix J).

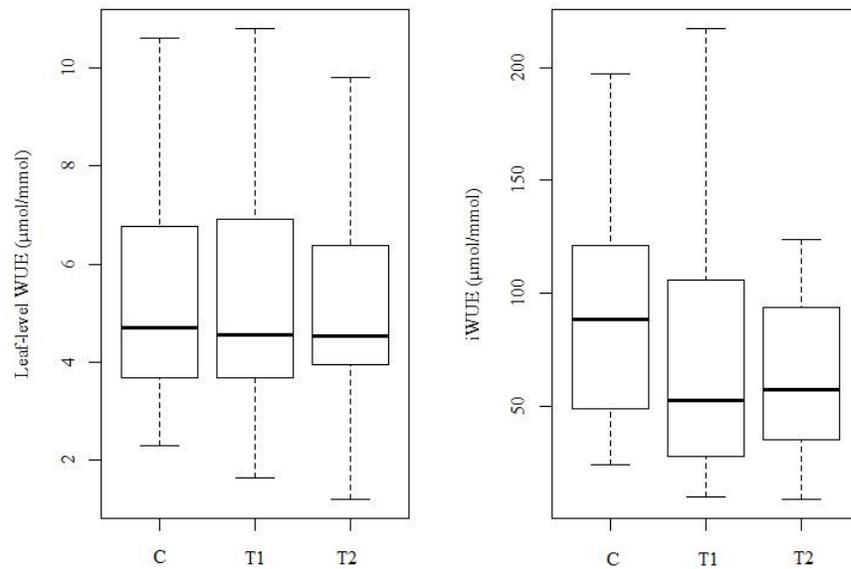


Figure 8. The midday leaf-level WUE and iWUE in the growing season of 2017.

3.2.4 Individual Tree-level WUE

Although BAI and individual tree transpiration were significantly different between the thinned and the unthinned stands, their ratios (the averaged daily individual tree-level WUE values) during the two growing seasons were not statistically different among the three groups ($p = 0.117$). The averaged daily tree-level WUE values of C, T1 and T2 were also not significantly different from each other in 2016 ($p = 0.742$, Table 2). However, significant differences in the individual tree-level WUE were detected in 2017, with T2 having the highest value, and C

having the least (Table 2). Although the averaged daily tree-level WUE values were greatly reduced in 2017 as compared with 2016, there were no statistical difference between the two years ($p > 0.1$, Appendix K).

Table 2. Averaged daily transpiration and daily WUE of the selected trees between the treatments and the control.

Group	ANCOVA test				Independent K-sample Kruskal-Wallis test					
	Sample No.	Mean Daily BAI _D (mm ²)	SD	P-value	Mean daily transpiration per tree (g)	SD	P-value	Mean Daily WUE per tree (mm kg ⁻¹ day ⁻¹)	SD	P-value
2016:										
T2	68	0.97	1.56	0.003	1378.21	1172.52	<0.001	0.11	1.13	0.742
T1	87	0.67	1.57		1034.55	1111.57		0.014	0.10	
C	81	0.080	1.59		523.35	604.48		0.0037	0.12	
2017:										
T2	62	0.83	1.89	0.001	1188.39	911.92	<0.001	0.0073	0.021	0.007
T1	81	0.40	0.40		947.94	797.30		0.0028	0.0053	
C	70	0.072	0.25		365.39	410.36		0.0010	0.017	

3.2 Correlations of Leaf-level WUE and iWUE, and Tree-level WUE with Environmental Factors

Table 3 shows that the leaf-level WUE and iWUE were significantly related to the studied environmental variables (temperature, RH, photosynthetically active radiation (PAR) and VPD), except PAR in T1. In addition, consistent but contrasted responses of the leaf-level WUE and iWUE to VPD were also found (Table 3). By pooling data from C, T1 and T2 together, it is clear that the leaf-level WUE was negatively correlated with VPD, while iWUE positively with it (Figure. 9).

Table 3. Correlation coefficients between leaf-level WUE and iWUE under juvenile thinning treatment with environmental factors.

Correlation Coefficient	C		T1		T2	
	Leaf-level WUE	iWUE	Leaf-level WUE	iWUE	Leaf-level WUE	iWUE
Temperature	-0.46 ***	-0.09	-0.06	0.16 **	-0.54 ***	-0.27 ***
RH	-0.38 ***	-0.67 ***	-0.17 **	-0.54 ***	-0.28 ***	-0.66 ***
PAR	-0.22 ***	-0.2 ***	0.05	0.11	-0.13 *	-0.2 ***
VPD	-0.28 ***	0.4 ***	-0.25 ***	0.41 ***	-0.26 ***	0.36 ***

Note: significance levels at 0.1, 0.05, and 0.01 are denoted as “*”, “**” and “***”, respectively.

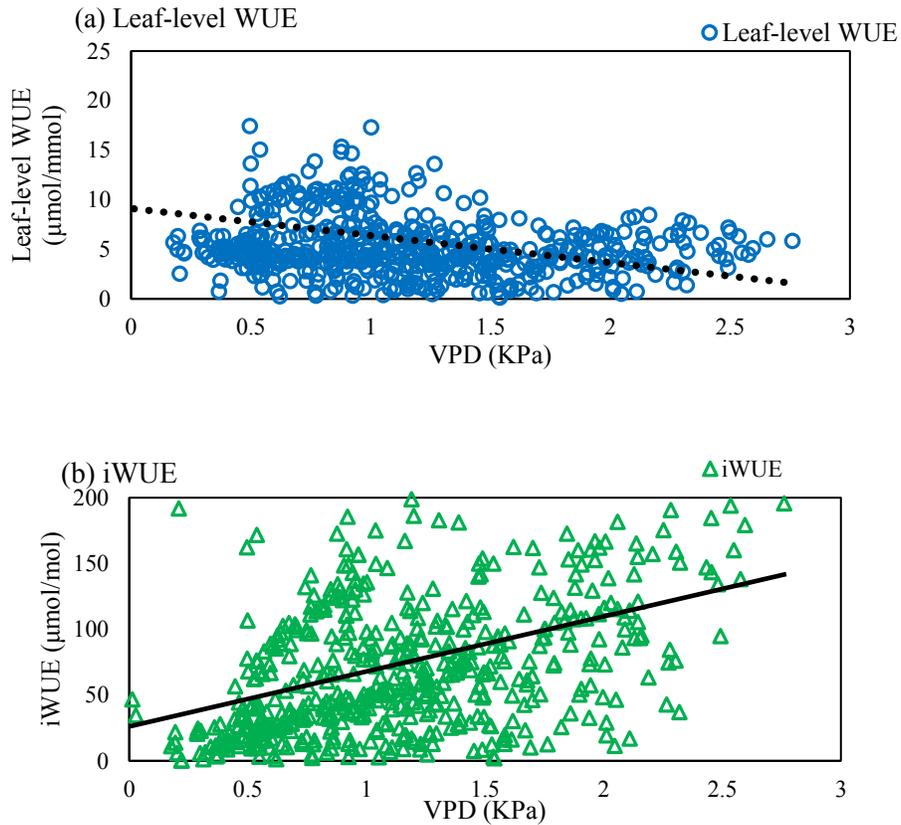


Figure 9. The contrasted responses of the leaf-level WUE (a) and iWUE (b) to VPD.

Table 4 shows that at the individual tree level, no significant correlation between WUE and the all studied environmental variables were found in the unthinned stands, while WUE values

were significantly and positively correlated with soil VWC at the soil depths of 20 and 40 cm in the thinned stands. WUE was also positively correlated with wind speed in T2 (Table 4).

Table 4. Correlation coefficients between tree-level WUE under juvenile thinning treatments with environmental factors.

Correlation Coefficient	C	T1	T2
	Tree-level WUE	Tree-level WUE	Tree-level WUE
Temperature	-0.12	-0.14	-0.22
RH	0.28	0.09	0.30
Solar Radiation	-0.18	0.03	0.004
VPD	-0.25	-0.10	-0.28
Wind Speed	0.18	0.02	0.60 ***
Soil VWC% at 20 cm	0.048	0.42 **	0.40 **
Soil VWC% at 40 cm	0.052	0.42 **	0.40 **

Note: significance levels at 0.1, 0.05, and 0.01 are denoted as “*”, “**” and “***”, respectively.

3.3 Linkage between Leaf-level WUE and iWUE with Tree-level WUE

As electronic band dendrometers were installed at the end of June 2017, and trees stopped growing at the beginning of August (Appendix E), paired data at two spatial scales (leaf and tree levels) were only available for one month (July 2017). As a result, there were not enough pairs of WUE at two spatial scales available for each group (C, T1 and T2) for comparing the correlations among groups. However, by pooling all data together, we showed that the midday leaf-level WUE was not significantly correlated with the tree-level WUE (Spearman rho = -0.27, p = 0.394, Figure 10 (1)), but iWUE was significantly negatively correlated it (Spearman rho = -0.780, p = 0.004, Figure 10 (2)), with a fitted linear equation: tree-level WUE = -0.1518 × iWUE + 25.32 (R²=0.3541).

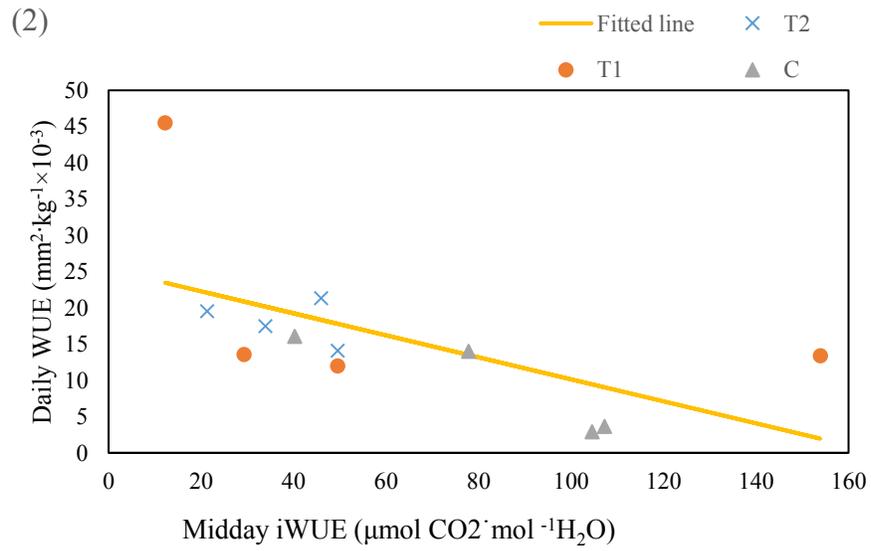
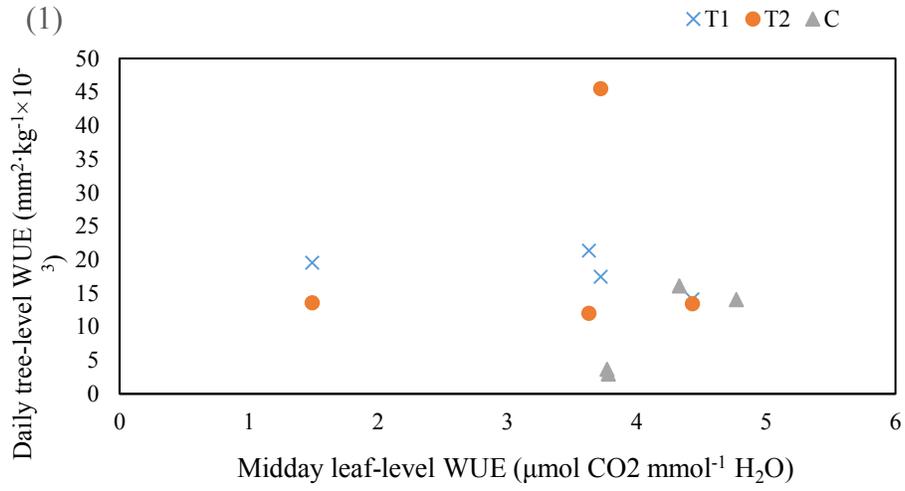


Figure 10. Correlations between the leaf-level WUE (1) and iWUE (2) with the tree-level WUE.

Chapter 4: Discussion

4.1 The Effect of Juvenile Thinning on Tree Growth, Sap Flow Velocity, Tree Transpiration and Stand Transpiration

Our results agree generally with other studies showing that thinning can greatly increase tree radial growth (Chase et al. 2016b, Fernandes et al. 2016b, Jimenez et al. 2008, Lindgren and Sullivan 2013, Martín-Benito et al. 2010, Sullivan et al. 2006), sap flow velocity and individual tree transpiration (del Campo et al. 2014, Fernandes et al. 2016b, Gebhardt et al. 2014, Medhurst et al. 2002, Simonin et al. 2007, Skubel et al. 2017b), while decrease stand-level transpiration (Forrester et al. 2012b, Gebhardt et al. 2014, Moreaux et al. 2011, Simonin et al. 2007, Skubel et al. 2017b, Sun et al. 2014b).

The above-mentioned positive effects of thinning on tree radial growth, sap flow velocity and individual tree-level transpiration are mainly due to more availability of resources (e.g., light, soil nutrients, soil moisture), as a result of reduced competition after thinning (González de Andrés et al. 2018, Park et al. 2018, Skubel et al. 2017a). For example, increased light penetration by thinning not only promotes carbon assimilation processes (Aussenac 2000), but also increases tree transpiration through its regulation on photosynthesis (Asbjornsen et al. 2007). Open canopy exposure also causes higher negative values of leaf water potential, leading to higher transpiration (Simonin et al. 2007). Furthermore, the influence of increased light availability on tree growth and transpiration was suggested to be less important than the effect of increased soil water availability. This is a result of decreased interception and stand transpiration after thinning in the dry forest stands, because higher soil extractable water exerts stronger regulation in maintaining higher stomatal conductance and thus both higher photosynthesis and transpiration rates (Giuggiola et al. 2016). As shown in Table 5,

significantly higher solar radiation and soil volumetric water contents at the soil depths of 20 and 40 cm in the thinned stands were detected in our study. Thus, more availability of resources (light and soil water contents) after thinning is likely the key reason for greater growth and transpiration at the individual tree level.

Table 5. Mean daily solar radiation and soil volumetric water contents (VWC) in 2016 and 2017 with the post-hoc test.

Variables	Daily mean			Independent -t test		
	T2	T1	C	T2 and T1	T2 and C	T1 and C
2016						
Solar radiation (W/m ²)	150.13	112.13	49.59	<0.001	<0.001	<0.001
Soil VWC at 20 cm	19.1%	18.4%	15.1%	0.0732	<0.001	<0.001
Soil VWC at 40 cm	14.3%	16.0%	12.5%	<0.001	<0.001	<0.001
2017						
Solar radiation (W/m ²)	213.06	149.34	62.20	<0.001	<0.001	<0.001
Soil VWC at 20 cm	14.4%	13.0%	11.3%	<0.001	<0.001	<0.001
Soil VWC at 40 cm	12.1%	13.7%	8.0%	<0.001	<0.001	<0.001

Our results also show that the thinning significantly decreased stand-level transpiration (Figure 6). The daily stand transpiration was only 0.36 mm/d in T2, in comparison with 4.36 mm/d in C. Similar negative impacts of thinning on stand transpiration were also found, and were attributed to the decrease of stand density, by Moreno and Cubera (2008). However, such a decrease in the stand-level transpiration in the thinned stands is usually smaller than the decrease in basal area or leaf area (Breda et al. 1995, Gyenge et al. 2011, Wang et al. 2008). Our study confirmed this pattern, as stand transpiration decreased 75.3% and 91.7% in T1 and T2, while the stand densities of T1 and T2 were reduced by 83.3% and 95.9%, respectively, in comparison to C. The relatively smaller reduction in stand transpiration than the decrease in stand density is due to the enhanced transpiration of individual trees following thinning treatments (Simonin et al. 2007).

As expected, our results clearly demonstrate that the more heavily thinned treatment (T2) had more pronounced effects on tree growth, sap flow velocity, tree-level transpiration, and stand-level transpiration. These effects corresponded with the highest improvement in solar radiation and soil water availability in T2 (Table 5). These findings are consistent with the study by Park et al. (2018) who studied the two thinning treatments (light-thinning: 320 tree/ha, and heavy-thinning: 240 tree/ha) in a 50-year-old Korean pine (*Pinus koraiensis*) forest for four years. In their study, Park et al. (2018) found that the light thinning had little effect on tree growth with the enhancement on sap flow velocity declining with time, whereas the heavy thinning greatly increased tree growth and sap flow velocity with the effects increasing over time (Park et al. 2018). Based on their results, Park et al. (2018) concluded the heavier thinning was an appropriate management practice for mature pine plantations in their region.

On the contrary, Jimenez et al. (2008) failed in finding significant differences in tree-level transpiration under two intensities of thinning treatments (3,850 trees/ha and 1,925 trees/ha) in a 8-year-old *Pinus pinaster* stand. They also did not observe a significant difference in soil water availability, and attributed the non-significant difference in both tree transpiration and soil water availability to the similar reduction in the absolute basal area, including changes in both overstory and understory vegetation (Jimenez et al. 2008).

Gebhardt et al. (2014), who studied moderate (removal of 43% basal area) and heavy thinning treatments (removal of 67% basal area) in a 26 years old Norway spruce (*Picea abies*) stand, observed similar patterns of tree growth and transpiration as in our results. However, they suggested that repeated moderate thinning was a better option than heavy thinning, because: (1) wood biomass production was not maximized by heavy thinning at the stand level; and (2) heavy thinning induced progressive development of understory which not only competed for

resources with trees but also hindered natural regeneration (Gebhardt et al. 2014). In our study, the sparse understory did not play an important role in our short study period, so the heavier thinning (T2) was most beneficial to tree growth and transpiration as well as stand water consumption over the short term. However, a longer duration of the study is necessary to examine the long-term effect of our different thinning intensities.

Juodvalkis et al. (2005) investigated 10–60 year-old stands of *Betula pendula*, *Betula pubescens*, *Fraxinus excelsior*, *Picea abies*, *Pinus sylvestris*, *Populus tremula*, and *Quercus robur* under various intensities of thinning treatment, and found that the effect of thinning intensity not only varied with tree species, but also with stand age (the volume increment in younger stands increased with thinning intensity, whereas the opposite was observed in the older stand). Thus, from a management point of view, thinning intensity, understory development, tree species and stand age should be taken into consideration for designing management strategies.

4.2 The Effect of the Drought on Tree Growth, Transpiration and WUE at Several Selected Scales

As shown in Table 2 and Figures 2 and 3, the reduction in BAI_D , SFD and tree-level WUE in the second year, as well as the significant difference between T1 and T2 that was only observed in the second year (under the drought condition) clearly demonstrate the significant effects of the drought on forest carbon and water processes. To better determine the effects of drought, it is important to consider possible delayed responses of trees to environmental variables caused by thinning treatments in the previous years (also Case and Peterson, 2007; Chhin et al., 2008). Given the significant differences of tree growth, sap flow velocity, tree transpiration and stand transpiration between the unthinned and thinned stands in the first growing season, and the

remarkable reduction in the second year, we believe that the studied variables, especially the tree radial growth, responded to thinning and drought directly. Therefore, the drought in the summer of 2017 is regarded as the predominant factor in the different responses of trees to thinning treatments between the two years. The followings discuss the detailed effects of the drought on various processes.

4.2.1 The Drought Greatly Affected Tree Growth, Sap Flow Velocity and Tree-level WUE, But Not Tree Transpiration and Stand Transpiration.

Our results showed that drought significantly reduced the BAI_D of T1 and T2, and the reduction was greater in T1 than T2. The smaller decrease in T2 may be attributed to the released soil water stress (Table 5) and delayed drought-induced cessation of stem growth in this thinning treatment (Appendix E). Similar observations have been reported in Norway spruce (*Picea abies*) and Scot pine (*Pinus sylvestris* L.) forests (Giuggiola et al. 2013, Sohn et al. 2013), and in a Mediterranean evergreen oak coppice (*Quercus ilex* L.) forest (Cabon et al. (2018)). However, different observations show no significant effects of thinning on the magnitude of growth reduction during droughts, or higher reductions in tree growth in the more heavily-thinned stands were also reported (Kohler et al. 2010, Sohn et al. 2013). The following may be the key reasons for these different results. Firstly, some reported droughts occurred a long time after thinning treatments were applied, so the long-term effects of thinning and droughts were interacting. Secondly, possible changes in carbon allocation from stem diameter growth to flowers and cones coincided with the droughts in the thinned stands. Thirdly, the favorable climatic conditions before the droughts as well as the delayed responses of tree radial growth to environmental changes might lead to the lagged effects during the droughts. Finally, the drought effects might not have been severe enough to cause an apparent reduction in tree

growth, or may have been severe but were not mitigated by thinning (Kohler et al. 2010, Sohn et al. 2013). In our study, the lack of significant differences in BAI_D in the control (C) before and during the drought might suggest that the unthinned trees may have already experienced growth stagnation due to the very high stocking densities before the drought.

Our results also showed that the drought significantly decreased SFD in all our treatments and the control, which conforms with various studies on several tree genera (e.g., *Ficus*, *Tilia*, *Pinus*, *Picea* and *Fraxinus*) (Nadezhdina and Cermak 2000, Stohr and Losch 2004), which showed that the reduction was mainly due to stomal closure. However, tree transpiration in our study did not show significant differences between 2016 and 2017 for all the three groups, a result which is similar to the studies by Lagergren and Lindroth (2002) who explained that the large variations of the responses of tree transpiration among individual tree might mask the significant differences between the non-drought and drought years (also Cermak and Kucera, 1990; Lu et al., 1995). But this explanation does not work for our study, as the standard deviation of tree transpiration was smaller in 2017 than in 2016 (Table 2). The reason for our result may be that the tree sizes of the selected trees ranging from 30-60 mm are slightly larger in 2017 than 2016, as the mean DBH of the selected trees were 42.55, 42.27 and 44.06 mm in 2016, and 42.50, 44.59 and 44.54 mm in 2017, for C, T1 and T2, respectively (although the groups were not statistically different from each other (the independent-t test, all $p > 0.1$, except for $p = 0.037$ when comparing the selected trees in T1 between 2016 and 2017)). Therefore, slightly larger sizes of trees might compensate for the decrease of SFD during the drought, leading to the insignificance of tree transpiration among the three groups. In addition, as explained above, tree-level transpiration calculated in our study was subject to the stand structures and the sizes of selected tree samples, so this variable is more useful for explaining

the behavior of tree-level WUE than demonstrating tree water consumption under juvenile thinning.

To our surprise, the drought significantly reduced stand transpiration in C, but had no significant impacts on those in the thinned stands in our study. This observation is contrary to some previous studies showing that droughts greatly reduced stand transpiration (Granier 1987, Schäfer et al. 2014, Stojanović et al. 2017). One possible explanation is that the increased total basal area in the thinned stands in the first growing season might compensate for the decrease in SFD during the drought. Besides, it is possible that the thinned stands might maintain relatively high stand transpiration during the drought period to compensate for the reduction of leaf area by thinning during the drought (Simonin et al. (2007). Overall, maintaining high stand transpiration in the thinned stands indicates the benefit of juvenile thinning in sustaining tree-water relations under water stresses caused by the drought in our study area.

Although we did not observe significant changes in the magnitude of tree-level WUE before and during the drought for all the three groups, which may be due to the large variations of tree-level WUE in 2016, the averaged values and the standard deviations of tree-level WUE for all the three groups were greatly reduced in the drought year (2017) (Table 2). This result is consistent with some previous studies showing that the tree-level WUE decreased because of the greater reduction of tree growth during the droughts (Ma et al. 2014, Park et al. 2018).

4.2.2 The Drought Enlarged the Differences in Tree Growth, Transpiration and Tree-level WUE between the Moderately-thinned and Heavily-thinned Stands.

The significant differences in BAI_D, SFD and tree-level WUE between the moderately-thinned (T1) and heavily-thinned stands in our study (T2) occurred only under the drought condition

(2017). The reason for this result may be attributed to a lower water stress as a result of a more intense thinning (Cabon et al. 2018, del Campo et al. 2014, Gebhardt et al. 2014, Park et al. 2018), as shown in Table 5. Park et al. (2018) suggested that thinning increased tree-level WUE in a light-limited environment rather than a water-limited environment. Considering light was not a limiting factor in our thinning treatment sites, as well as the year 2016 was characterized as a normal year, tree growth and water use might be more subject to genetic regulation and less to the environmental control. Moreno and Cubera (2008) have also suggested that tree-level WUE responded more to genetic differentiation than to the acclimation to site conditions, when they failed to observe any significant difference in WUE in the stands of various densities. Besides, it is also possible that the increase in tree growth and transpiration were at the similar magnitude under the thinning treatments, so their ratio (WUE) did not change (Martín-Benito et al. 2010). When water availability became limited in 2017 due to the drought in our study, the significant higher soil water content resulted from the thinning led to markedly greater tree growth than tree transpiration (as mentioned in the section of 4.1 and 4.2.1), and thus higher tree-level WUE.

Besides the above-mentioned abiotic factors that explain the differences between the two years, the adjusted physiological sensitivity to environmental regulations may also be a potential reason for the differences. In our study, strong correlations of VPD and soil water conditions on tree transpiration were found, which were strongly influenced by the thinning treatments. The relationship between SFV and VPD was also suggested as an exponential saturation equation (Ewers et al. 2001, Tang et al. 2006).

$$SFD = a (1 - e^{-b \times VPD}) \quad (8)$$

Where, a and b are fitted coefficients. For a better comparison between different thinning intensities, and for minimizing possible confounding effects caused by the variations of individual tree sizes, SFD was normalized (denoted as NSFD) by dividing all SFD data for each replicate tree by its maximum throughout the whole growing season of each year (Du et al. 2011).

Figure 11 clearly shows that the correlations between NSFD and VPD were higher in the thinned stands than in the control in both years. There was only a slight difference between T1 and T2 in the non-drought year (2016), while there were dramatical distinctions among the three groups in 2017. The slight difference between T1 and T2 in 2016, which might explain the insignificant difference in sap flow velocity and tree transpiration in 2016, can be attributed to the insignificant difference in the soil VWC at the depth of 20 cm (Table 5), as soil water availability was suggested to dominate the response of SFV to VPD (Lagergren and Lindroth 2002, Pataki et al. 2000, Renquist et al. 1994).

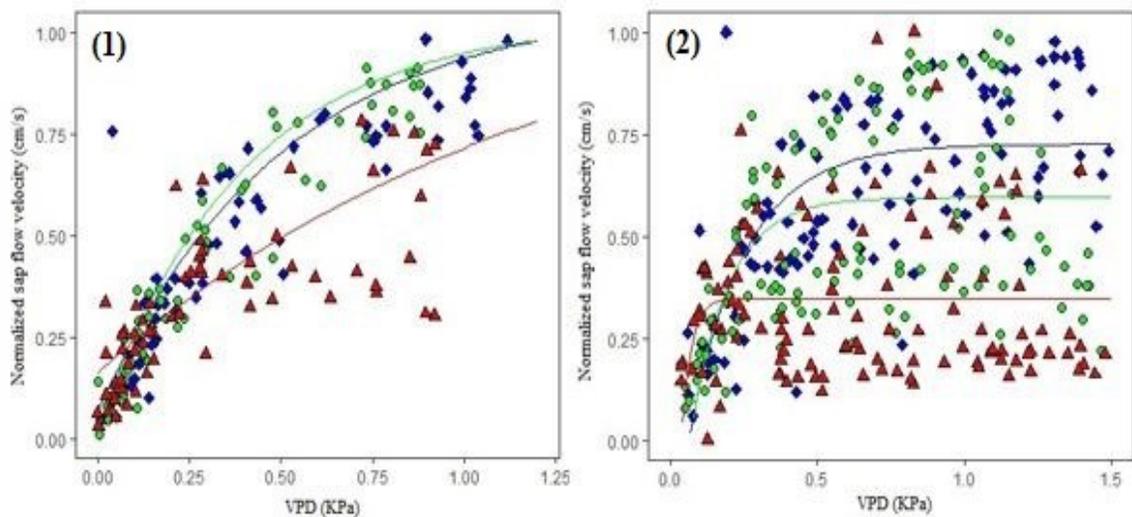
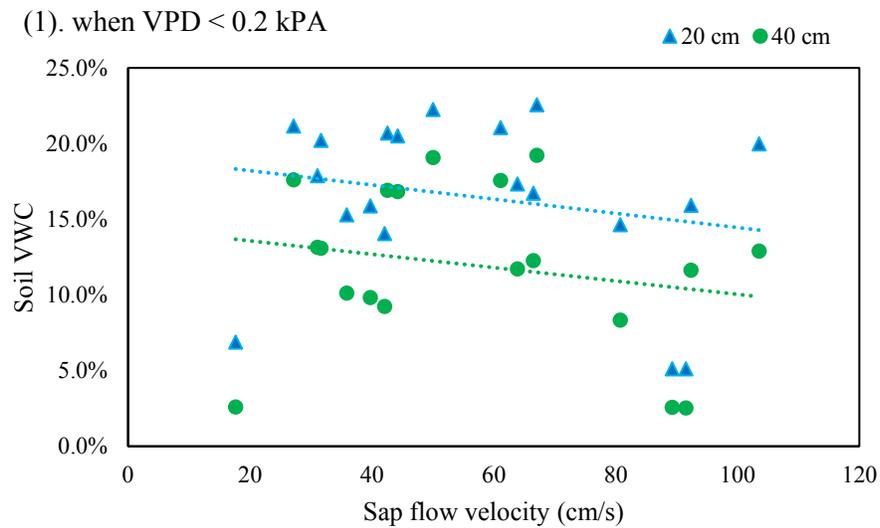


Figure 11. The daily normalized sap flow velocity as a function of VPD in 2016 (1) and 2017 (2). Blue, green and red colors denote T2, T1 and C, respectively.

In the drought season (2017), the control of soil VWC on the sap flow velocity was more distinct. As shown in Figure 11 (1), the increasing NSFD with increasing VPD almost reached saturation when VPD values were about 0.2, 0.5 and 0.6 KPa for C, T1 and T2, respectively, during the drought (the coefficients of a and b in the fitted equations, as well as the R^2 for each group in 2016 and 2017 were listed in Appendix L). By separating the dataset at the tipping points of VPD to determine if there were any changes in the responses of SFD to environmental regulators, the only significant change was the response of SFD to soil VWC. Taking the dataset from C as an example: when VPD was less than 0.2 KPa, there was no significant correlation between SFD and soil VWC at the soil depths of 20 and 40 cm ($p = 0.37$ and $p = 0.39$, respectively) (Figure 12 (1)); however, when VPD was greater than 0.2 KPa, soil VWC at both depths were significantly and positively correlated with SFD (both $p < 0.001$) (Figure 12 (2)).



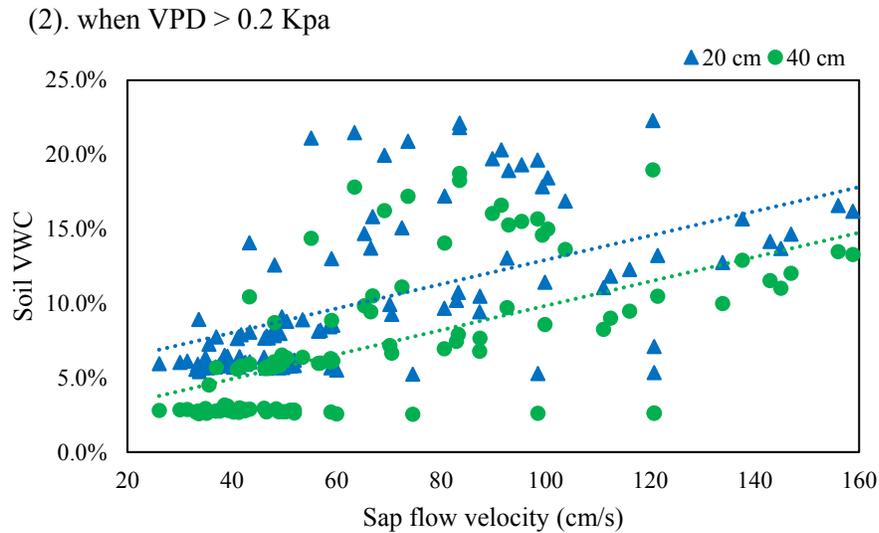


Figure 12. Linear correlations between daily SFD and soil VWC at the soil depths of 20 cm and 40 cm in the Control when VPD < 0.2 KPa (1), and VPD > 0.2 KPa (2) in 2017.

The above results suggested that the drought-induced differences in sap flow velocity among the three groups were likely due to the fact that the heavier thinned stands (T2) were more sensitive to VPD and soil VWC, as these two environmental variables were both significantly higher in T2 under the drought condition as compared with T1. The increased sensitivity of sap flow velocity to the environmental variables by thinning was also reported by Breda et al. (1995) who studied the tree-water relations in an oak forest. Furthermore, the responses of SFD to soil water conditions differed before and after the asymptote occurred (Laiju et al. (2012). The responses of SFD to soil water content influenced by VPD under drought in our study also agree with some studies on other tree species (e.g., sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*) and hemlock (*Tsuga canadensis*)) (Meinzer et al. 1999, O'Brien et al. 2004, Tang et al. 2006).

In summary, thinning can modify microclimatic conditions, and consequently lead to the changes in forest carbon and water processes. It is important to understand how thinning modifies microclimate and consequently the physiological sensitivity of trees to climate and treatments. The contrasted effects of the moderate and heavy thinning treatments in the non-drought and drought years in our study clearly show the pronounced effects of the heavier thinning (T2) during the drought period, suggesting that the heavier thinning would be more effective in mitigating the drought effects (Del Río et al. 2017). However, how heavy is sufficiently heavy is beyond the scope of this study, and should be a further study in the future.

Like many other studies, the enhancements in BAI_D , SFD and tree-level WUE were mainly attributed to a lower water stress under the more intense thinning treatment (Capon et al. 2018, del Campo et al. 2014, Gebhardt et al. 2014, Park et al. 2018). However, it should be noted that the mitigation of the heavier thinning to droughts may not be sustained for a long time because the enhanced water availability may be offset by increasing water demand from a more progressive development of overstory canopy and understory vegetation in the young stands (Gebhardt et al. 2014, Sohn et al. 2013).

4.3 The Effect of Juvenile Thinning on Leaf-level WUE and $iWUE$ during the Drought

Our results showed that leaf-level WUE was not significantly different among C, T1 and T2, while leaf-level $iWUE$ was significantly higher in C than in the unthinned stands with no significant difference between T1 and T2. The lack of the significant responses of leaf-level WUE to thinning may be explained by the observed increase of both leaf photosynthesis and transpiration in the thinned stands, with T2 having the greatest increments (Mann-Whitney test, all $p < 0.05$, except for $p = 0.051$ from the comparison on leaf photosynthesis between T1 and

T2). The effects of thinning on leaf-level WUE have been rarely examined in the literature. The only exception is the study by Tang et al. (2004) which showed that the leaves positioned higher in the crown in the thinned stands did not have statistically higher photosynthesis and transpiration rates, and they further concluded that the responses of leaf-level photosynthesis and transpiration to thinning may be subject to crown positions. The limited studies on this subject highlight a critical need for more future studies.

Although leaf photosynthesis was increased in the thinned stand, leaf-level iWUE was higher in the unthinned stand than in the thinned stands in our study. This may be attributed to the stomatal regulation, as a strong stomatal regulation on leaf photosynthesis was observed (Figure 13). When stomatal conductance was below around $1.0 \text{ molH}_2\text{O/m}^2\text{s}$, the increases in stomatal conductance led to sharp increase of leaf photosynthesis, causing higher iWUE; but when it exceeded approximately $2.0 \text{ molH}_2\text{O/m}^2\text{s}$, leaf photosynthesis gradually decreased (Figure 13). Because C had more lower values in stomatal conductance as compared with T1 and T2 (Mann-Whitney test, both $p < 0.001$) due to environmental suppression (e.g., lowest soil VWC (Table 5) and higher mid-day VPD (Figure 14), iWUE in C was thus greater. In contrast, similar magnitudes of iWUE between T1 and T2 were due to their insignificant difference in stomatal conductance (Mann-Whitney test, $p = 0.901$). However, this inverse exponential relationship requires cautious interpretation and more future studies.

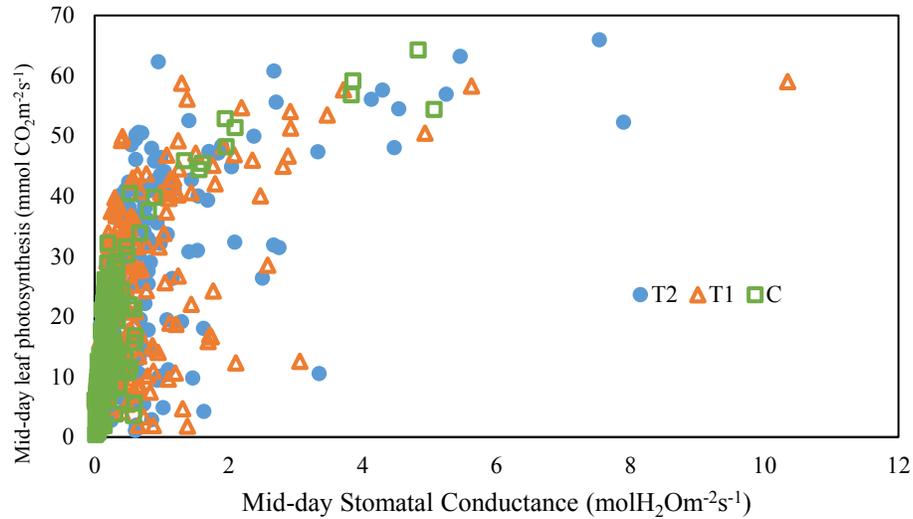


Figure 13. Stomatal regulations on leaf photosynthesis among C, T1 and T2.

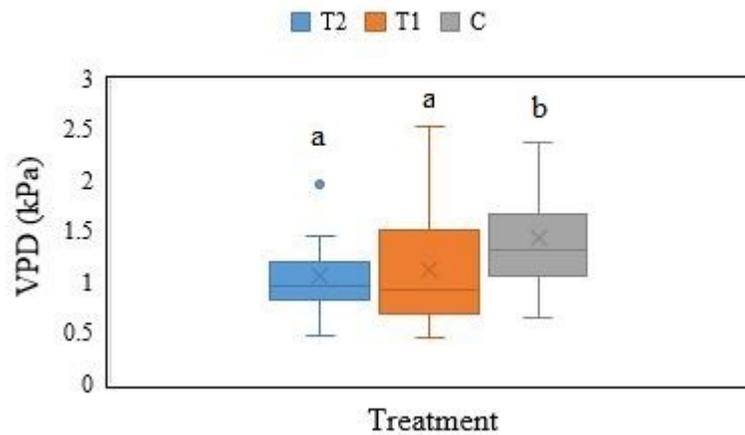


Figure 14. Boxplot of Midday VPD in C, T1 and T2 (letters denote the comparison by Tukey post hoc test).

In spite of limited studies in this subject, the change in stomatal conductance was regarded as the dominant factor in controlling the responses of *iWUE* to thinning for *pinus* species, and increasing of thinning intensity reduced *iWUE* in Mediterranean forests (Navarro-Cerrillo et al. 2016). However, the contradictory responses of *iWUE* to thinning were also reported. For example, Martín-Benito et al. (2010) found that *iWUE* remained unchanged in a *Pinus nigra*

afforestation stand before and after thinning, suggesting that stomatal conductance and photosynthesis either changed in similar magnitudes or remained unchanged after thinning. Wang et al. (1995) reported that thinning increased iWUE for paper birch (*Betula papyrifera* Marsh.). Therefore, the responses of iWUE to thinning treatments may be dependent on species-specific physiological responses and the microclimate conditions that regulate stomatal conductance, which are further discussed in the subsequent sections.

4.4 The Contrasted Responses of Leaf-level WUE and iWUE to Climatic Factors

Our results showed the discrepancy between the responses of leaf-level WUE and iWUE to climatic factors, which may be due to the distinct sensitivities of leaf transpiration and stomatal conductance to water vapor, as leaf transpiration is regulated jointly by stomatal conductance and boundary layer conductance (Defraeye et al. 2014). While the former depends on the density, size and degree of stomatal opening, the latter is determined by air movement and leaf morphology (Martin et al. 1999). The most contrasting couplings of leaf-level WUE and iWUE with climatic factors were found in their responses to VPD. Increasing VPD can result in stomatal closure directly (Turner et al. 1984), which also reduces leaf photosynthesis and transpiration (Farquhar and Sharkey 1982). However, the leaf transpiration, as is subject to stomatal conductance and boundary layer conductance, may be decreased to a lesser extent compared with the reduction in stomatal conductance (Martin et al. 1999), leading to the opposite correlations between VPD and different WUE. Since stomata is regarded as the main channel for leaf transpiration (Gu et al. 2017), our study not only underscores the importance of stomata in regulating leaf transpiration, but also suggests that the effect of boundary layer conductance should not be ignored, especially under droughts, for stomatal conductance and leaf transpiration was decoupled when VPD is high. In addition, modelling forest carbon

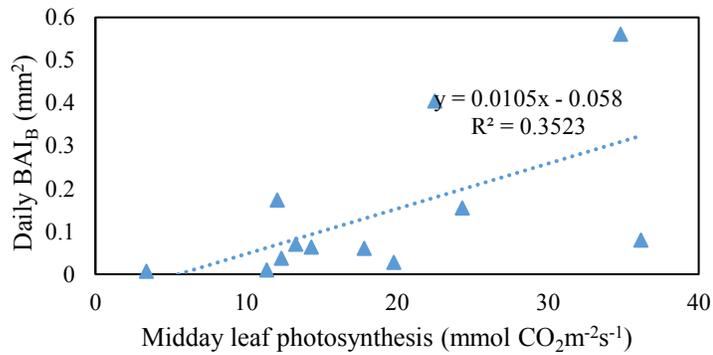
dynamics using WUE relies on the established functions between WUE and VPD (Zhou et al. 2014), the contrasted responses of WUE to forest management and climatic variables suggest that caution must be taken in selecting proper WUE for predicting the impact of climate change on the forest carbon and water coupling.

4.5 The Correlations between Tree-level WUE and Leaf-level WUE and iWUE

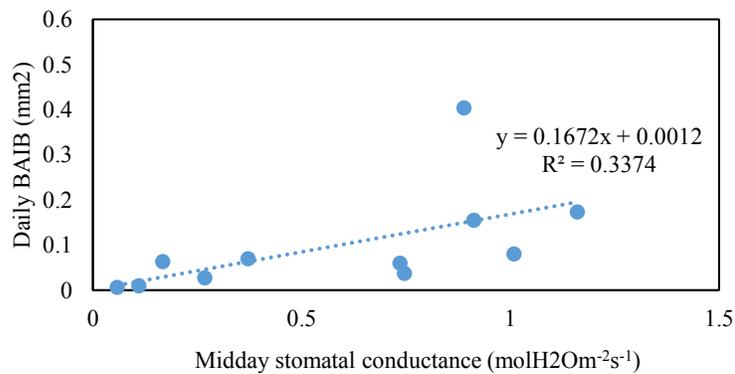
The results from this study showed that the leaf-level iWUE was significantly related to the tree-level WUE (Figure 10). The significant and negative correlation between daily tree-level WUE and mid-day leaf-level iWUE can be explained using the inverse exponential relationship between stomatal conductance and leaf photosynthesis (Figure 13). Both leaf photosynthesis and stomatal conductance exhibited significant and positive correlations with daily BAI (Spearman test, $\rho = 0.59$, $p = 0.04$) and tree-level transpiration (Spearman test, $\rho = 0.61$, $p = 0.03$) in July 2017 (Figure 15), confirming that photosynthesis and stomatal conductance can be used as proxies for radial growth and water use, respectively, as also proposed by Scheidegger et al. (2000) for the dual-isotope conceptual model. But increases in stomatal conductance lead to greater increases in the daily transpiration than daily BAI (Figure 15), and thus to a decreasing trend of tree-level WUE. In contrast, the resulted enhancement in leaf photosynthesis sharply increased with increasing stomatal conductance (when stomatal conductance was mostly between 0 and 1.0 molH₂O/m²s), which caused an increasing trend of leaf-level iWUE (Figure 13). Nevertheless, whether this correlation can be maintained when stomatal conductance is higher than approximately 2.0 molH₂O/m²s requires further investigation, as at that point in the increasing of leaf photosynthesis started to decline (Figure 13). Generally, trees allocate more carbon to roots (Oberhuber et al. 2017) and less to radial growth (Thomas 2015) under drought stresses. As the year of 2017 is characterized as a drought

year (Appendix B), the higher iWUE that occurred under severer water shortage, corresponded to a lower tree-level WUE, because of the shifting in carbon allocation caused by the drought. However, this result needs further confirmation when more data become available, and such studies on linkages between different WUE will facilitate the comparison among various thinning studies focusing on contrasted WUE, and the understanding on the responses of WUE to thinning treatments, incorporating different physiological processes of trees.

a. Leaf photosynthesis-Daily BAI_B



b. Stomatal conductance - Daily BAI_B



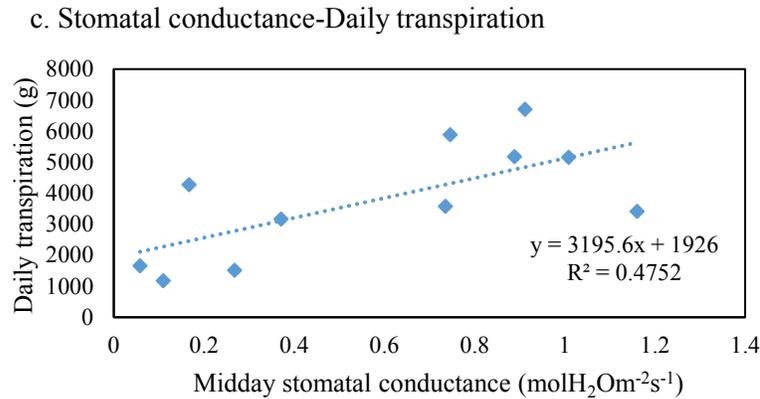


Figure 15. Correlations between daily BAI_B and leaf photosynthesis, and between stomatal conductance and daily transpiration in July 2017.

In contrast to this study, Fernandes et al. (2016b) observed no correlation between tree-level WUE and isotope-based iWUE. They ascribed this to the variations of isotopic signals corresponding to the changing microclimate, and thus, questioned the credibility of isotope-based iWUE in determining the physiological impact of thinning (Fernandes et al. 2016b). In addition, some studies demonstrated that water scarcity may enhance iWUE, but reduce tree growth (Andreu-Hayles et al. 2011, Nock et al. 2011, Peñuelas et al. 2011, Peñuelas et al. 2008); while nutrient fertilization may increase WUE without affecting iWUE (Battie-Laclau et al. 2016). These different results were mainly attributed to nutrient limitations (Battie-Laclau et al. 2016), drought stresses (Fernandes et al. 2016b) and physiological long-term acclimations to elevated CO₂ (Peñuelas et al. 2011). They also underline the importance in changes of resource availability affecting carbon allocation strategies of trees (McMurtrie and Dewar 2013).

With respect to the relationship between the leaf-level and tree-level WUE, our analysis shows that the relationship was insignificant (Figure 10). In fact, the lack of significant

correspondence between the leaf-level and tree level WUE is common, because of the differences in their physiological processes and the measurement procedures. For example, Medrano et al. (2015) not only showed that there were great temporal and spatial variations in leaf-level WUE and iWUE, but also suggested that the night transpiration and the respiratory processes strongly affected the correspondences among different WUE at various spatial scales. Therefore, studying the mechanisms underlying the variations in the responses of WUE at different spatial scales is necessary to improve our understanding of the relationship between the leaf-level and tree-level WUE in the context of forest management (e.g., thinning) and climate change impacts.

Clearly, our study suggests that iWUE is a better indicator of tree-level WUE than leaf-level WUE, given its significant correlation with tree-level WUE. However, the mechanism underlining this significant relation requires further investigation. As thinning not only reduces the competition among trees, but also modifies microclimatic conditions surrounding the trees. Both effects could lead to the changes in resources availability that may consequently affect the behavior of WUE at the both spatial scales.

Chapter 5: Uncertainty Analysis

There are some uncertainties in this study. Firstly, although the field experiment followed the completely random block design, some data such as tree sap flows and basic climatic variables (e.g., temperature, relative humidity, solar radiation, wind speed) were monitored only in Block 1 (B1), and were extrapolated to the other two blocks. Such an extrapolation may introduce a level of uncertainty. However, given that all three blocks are close by with a relatively uniform topography, we expect that the error associated with our extrapolation would be minor. Another possible uncertainty in terms of our experimental design is that only 5 trees representing different diameter classes in each plot of Block 1 were selected to measure sap flows. The limited tree number may affect calculations of tree-level transpiration and WUE. In order to minimize this potential error, the possible influences of different tree sizes on calculation of sap flow velocity were removed by selecting the trees with similar sizes so that the effects of thinning on sap flow velocity and transpiration were comparable among all the three groups.

Secondly, there are potential uncertainties from the measuring methods. The monthly data on tree DBH were measured by an electronic caliper which could precisely record any values at the accuracy level of 0.01. However, due to the variations in the measuring positions on each tree trunk, even though we tried our very best to locate the same marked positions for consistence, the measurement errors were expected. For example, some trees had negative DBH growth between two successive months, which is unlikely. To deal with this uncertainty, data with monthly DBH values greater than 5 mm or less than -5 mm were not included in our analysis. The remaining sampled tree sizes of C, T1 and T2 are listed in Appendix B. In addition, some electronic dendrometers were used to monitor continuous tree growth on the trees that were inserted with sap flow probes in B1 since the first growing season. However,

due to interruption and damage by animals, only limited data were useful. In short, data on tree growth were not used to estimate tree growth at the monthly interval. Instead, they were used to calculate tree growth at the seasonal interval. Besides, integrating sap flow velocity to estimate tree-level transpiration requires the knowledge of radial variations of sap flow velocity. However, we did not have sufficient probes to capture these possible variations, which may also affect the data on tree-level transpiration and tree-level WUE. However, since all the sap flow probes were inserted at the 3 mm depth into the sapwood, and tree DBH does not vary much in the young, even-aged, and homogeneous stands, this uncertainty was believed to be negligible. The last potential source of uncertainty in our measuring methods is that the leaf areas used for measuring leaf-level photosynthesis, transpiration and stomatal conductance were not measured. While this does not affect leaf-level WUE and iWUE because leaf area in the denominator and numerator were removed from the ratio, it affects the data credibility of leaf-level photosynthesis, transpiration and stomatal conductance. Therefore, the results of leaf-level WUE and iWUE were presented in this study, while the responses of leaf photosynthesis, transpiration and stomatal conductance were served as supporting data to help interpretation of the results.

Thirdly, data analysis may also introduce some potential uncertainties. As mentioned above, the trees with monthly growths in DBH being greater than 5 mm or less than negative 5 mm were not included in our analysis, which may induce bias in the tree growth. Besides, there might be uncertainty on calculating the stand transpiration because the upscaling from individual tree-level transpiration and the distribution of tree DBH classes were used, instead of summing up transpiration from each tree. In addition, the possible delayed response of tree growth to the change in environmental factors caused by the thinning treatments as stated in

the previous chapters may confound our assessment on the effects of the drought in 2017. However, this delayed response would unlikely affect our results as the differences of tree growth among C, T1 and T2 were already detected at the end of the first growing season as well as significant growth reduction occurred in all the study plots in the second growing season. More detailed explanations can be found in the previous chapters.

In summary, although there are various uncertainties in this study, they were either managed to minimize their influences, or were judged to have limited or negligible effects on our results. Therefore, the conclusions derived from the study are robust.

Chapter 6: Conclusions and Management Implications

Juvenile thinning significantly affected forest carbon and water processes by increasing tree radial growth, tree-level transpiration and tree-level WUE. The enhancements were more pronounced in the more heavily-thinned stands under drought conditions. Stand-level transpiration, however, was reduced by the thinning treatments due to reduced numbers of trees per hectare. The 2017 drought did not cause a significant reduction in stand-level transpiration in the thinned stands, but did in the unthinned stands. The difference in various carbon and water processes between two thinning treatments became significant only under the drought condition, with the more heavy thinning treatment being more resilient. Therefore, the more heavy thinning is most effective to cope with the effects of the drought in our study area.

There were large variations in the responses of various WUE at different spatial scales. Thinning increased tree-level WUE with the greatest enhancement in the more heavily thinned stand, but it did not affect leaf-level WUE. On the contrary, leaf-level iWUE was significant higher in the unthinned stand than those in the thinned stands, with no statistical difference between the two thinned stands. WUE and iWUE at the leaf level exhibited opposite correlations with air vapor pressure deficit (VPD). The leaf-level iWUE was significantly and negatively correlated with tree-level WUE, but not with leaf-level WUE. Therefore, caution must be exercised when selecting representative WUE for evaluating and modelling forest carbon and water coupling processes.

The results from this study provide important implications to support management of overstocking young lodgepine forests in the interior of British Columbia. Given the large-scale distribution of this type of forest, an important and practical question for BC is if we need to

apply thinning, and if so, what suitable thinning intensities and associated benefits are. The results from this study, along with future modelling of various thinning intensities and climate change scenarios would greatly support designing of management strategies in dealing with the overstocking problem of lodgepole pine forests in the context of climate change.

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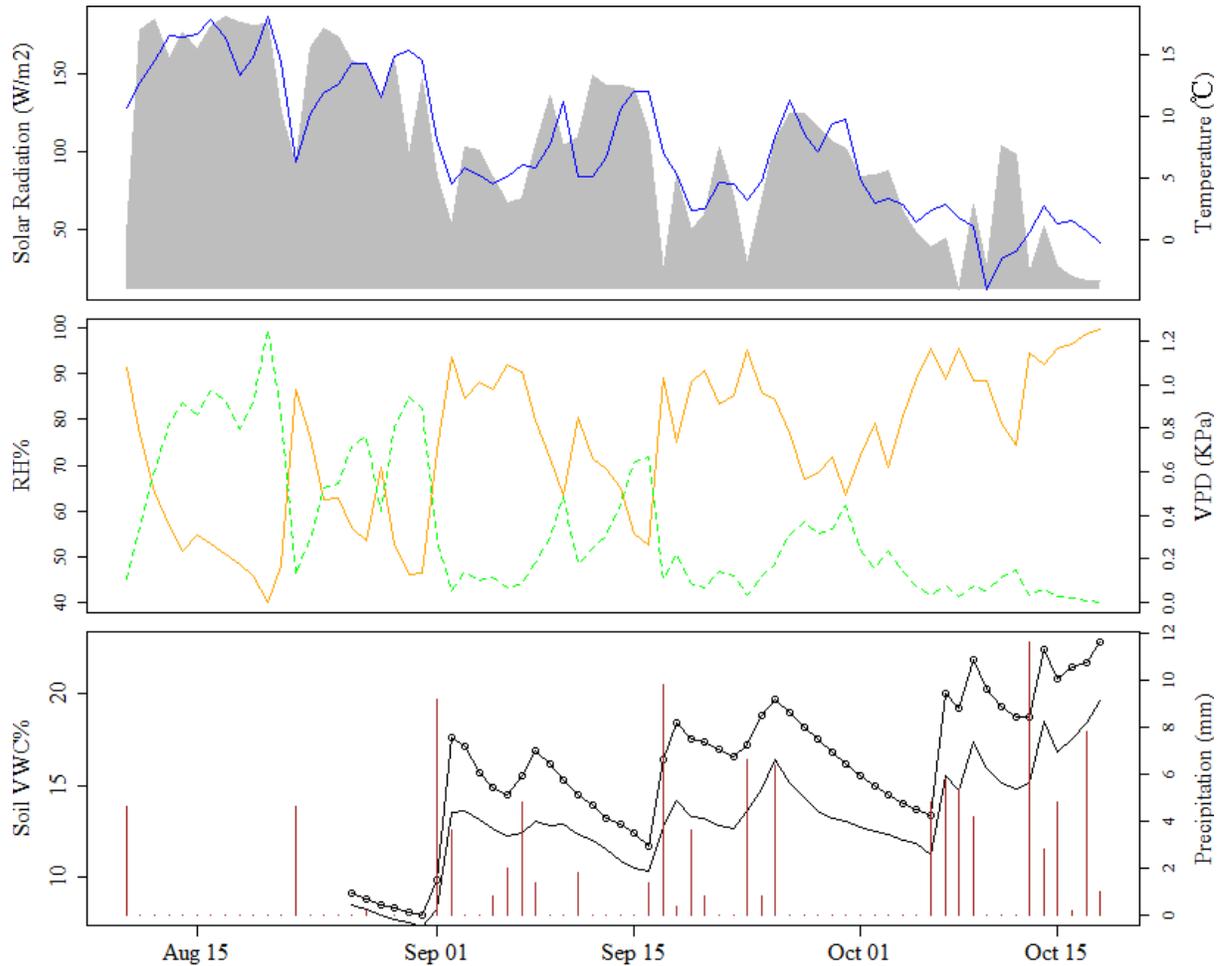
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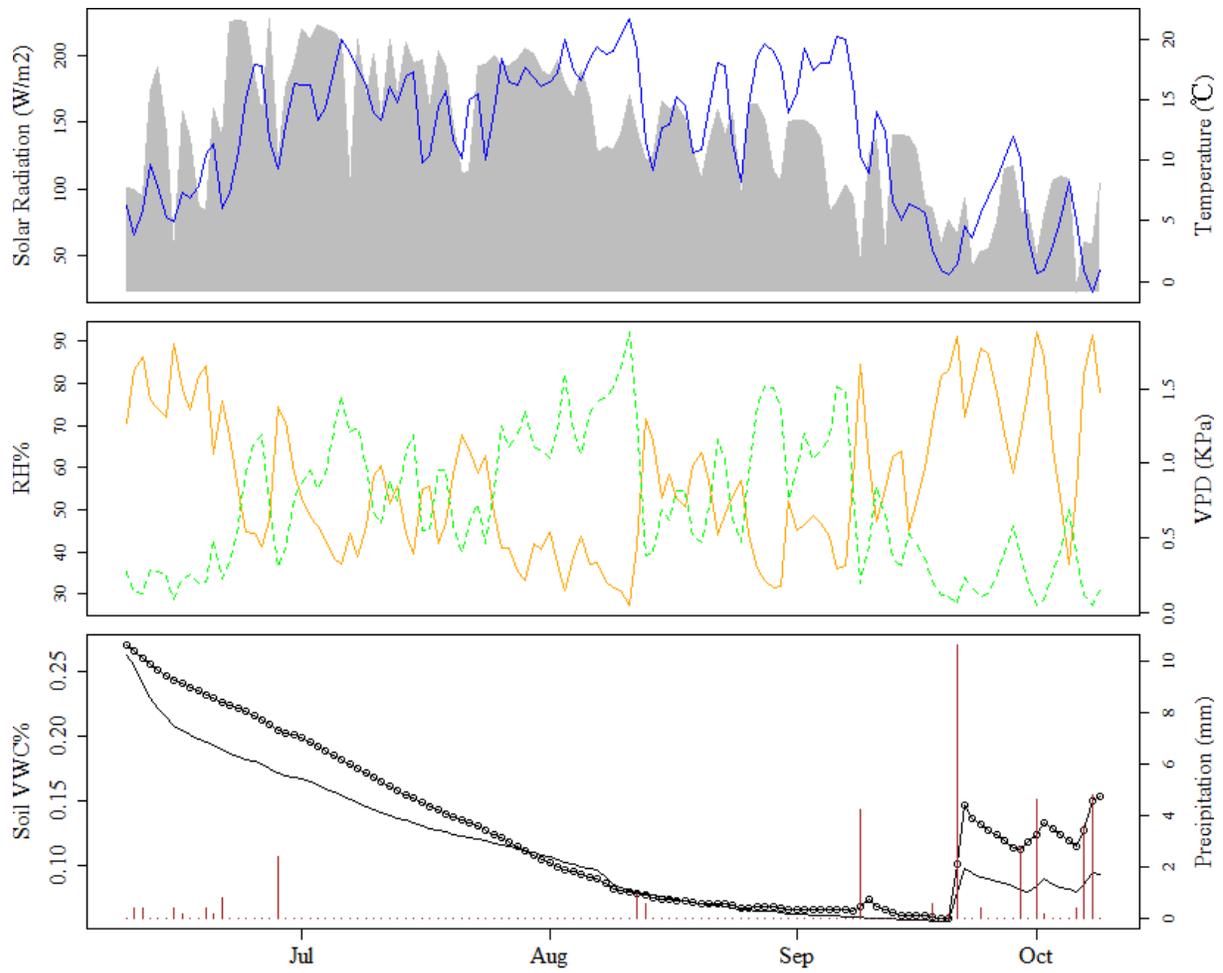
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Appendices

Appendix A – Climatic conditions during the growing seasons of 2016 (upper figure) and 2017 (bottom figure).



Note: Environmental conditions including temperature (in blue), solar radiation (in gray), RH (in orange), VPD (in green), soil VWC at 20 cm (black dots), soil VWC at 40 cm (black line) and precipitation (in brown) in 2016.



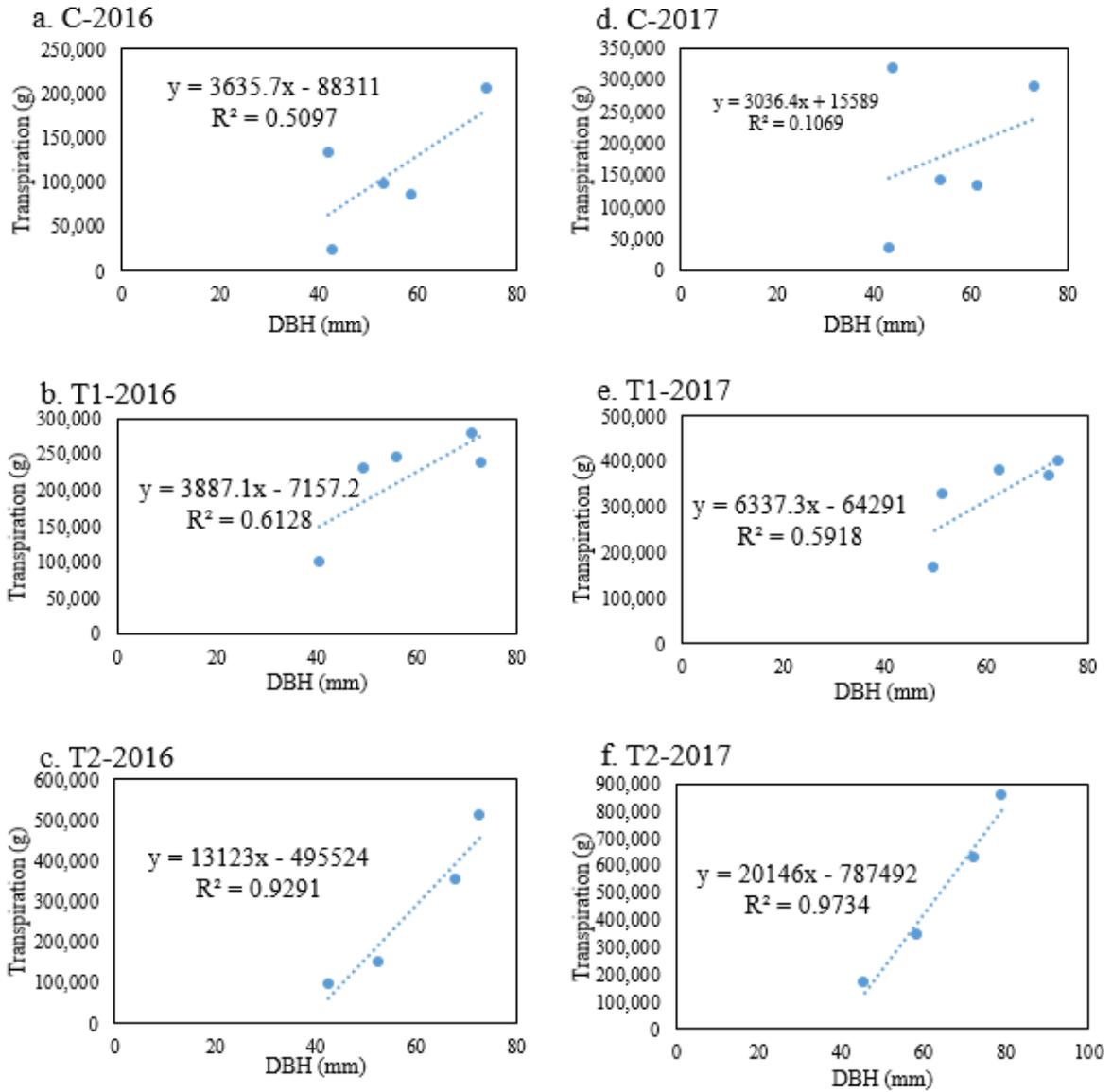
Note: Environmental conditions including temperature (in blue), solar radiation (in gray), RH (in orange), VPD (in green), soil VWC at 20 cm (black dots), soil VWC at 40 cm (black line) and precipitation (in brown) in 2017.

Appendix B - Standardized Precipitation Index (SPI) for 2016 and 2017

Month	SPI	Category
2016		
June	0.91	Near normal
July	0.17	Near normal
August	-0.37	Near normal
September	0.75	Near normal
October	1.95	Very wet
2017		
June	-1.69	Severely dry
July	-1.28	Moderately dry
August	-1.50	Severely dry
September	-0.76	Near normal
October	-1.04	Moderately dry

Note: SPI was calculated by the 30 years precipitation data derived from the Penticton Airport Climate Station around 20 km southwest of our study site.

Appendix C - Linear relationship between tree transpiration during the whole growing season of 2016 and 2017



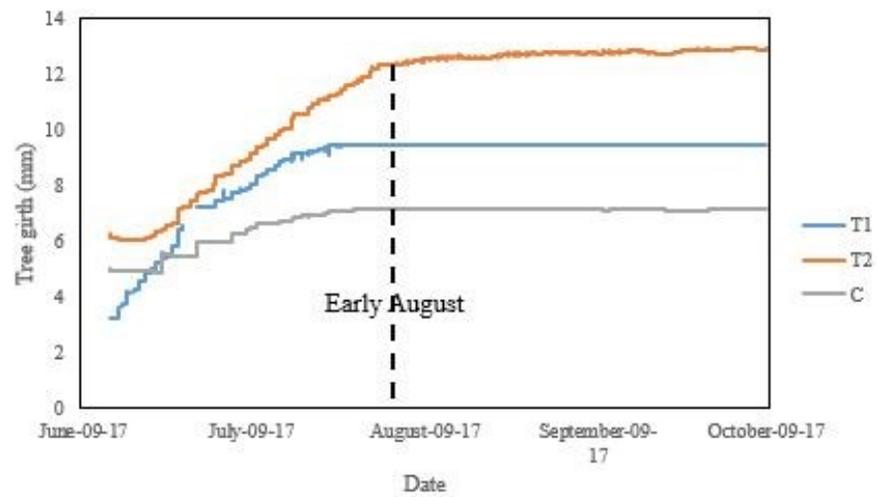
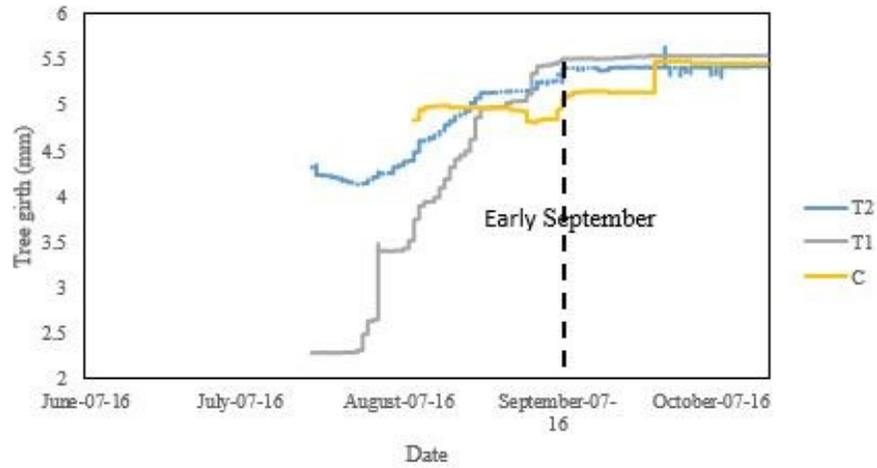
Note: one sap flow probe in T2 was broken since 2017, and was eliminated from the analysis on the both years.

Appendix D - ANOVA table on BAI_D for the growing season of 2016 (top) and 2017 (bottom)

Sample basal area increment			ANOVA Table for 2016					
Treatment type	Sample numbers	BAI _D (mm ²)	Sources	df	Sum of Squares	Mean squares	F	P-value
T2	111	77.15						
T1	119	50.63						
C	100	6.58						
			Corrected model	3	266426.354	88808.784	5.285	0.001
			Intercept	1	27204.205	27204.205	1.619	0.204
			Initial tree DBH	1	795.860	795.860	0.047	0.828
			Thinning	2	248016.468	124008.234	7.380	0.001
			Error	326	5477847.743	16803.214		
			Total	330	6448636.682			
			Corrected total	329	5744274.097			

Sample basal area increment			ANOVA Table for 2017					
Treatment type	Sample numbers	BAI _D (mm ²)	Sources	df	Sum of Squares	Mean squares	F	P-value
T2	134	92.75						
T1	135	40.67						
C	135	5.40						
			Corrected model	3	519936.193	173312.064	4.391	0.005
			Intercept	1	63163.702	63163.702	1.600	0.207
			Initial tree DBH	1	685.880	685.880	0.017	0.895
			Thinning	2	480115.493	240057.747	6.082	0.003
			Error	400	15788813.42	39472.034		
			Total	404	17169520.14			
			Corrected total	403	16308749.61			

Appendix E - Continuously tree girth data from home-made electronic band dendrometer



Appendix F - Post hoc test on BAI_D of 2016 and 2017

Post hoc comparison by the independent-sample Mann-Whitney U test		p
C-2016	T1-2016	0.031
C-2016	T2-2016	0.001
C-2016	C-2017	0.679
C-2016	T1-2017	0.346
C-2016	T2-2017	0.023
T1-2016	C-2017	<0.001
T1-2016	T1-2017	0.031
T1-2016	T2-2017	0.154
T1-2016	T2-2016	0.379
T2-2016	C-2017	<0.001
T2-2016	T1-2017	<0.001
T2-2016	T2-2017	0.022
C-2017	T1-2017	<0.001
C-2017	T2-2017	<0.001
T1-2017	T2-2017	0.001

Appendix G - Post hoc test on sap flow velocity of 2016 and 2017

Post hoc comparison by the independent-sample Mann-Whitney U test		p
C-2016	T1-2016	<0.001
C-2016	T2-2016	<0.001
C-2016	C-2017	<0.001
C-2016	T1-2017	<0.001
C-2016	T2-2017	<0.001
T1-2016	C-2017	<0.001
T1-2016	T1-2017	<0.001
T1-2016	T2-2017	0.029
T1-2016	T2-2016	0.135
T2-2016	C-2017	<0.001
T2-2016	T1-2017	<0.001
T2-2016	T2-2017	<0.001
C-2017	T1-2017	<0.001
C-2017	T2-2017	<0.001
T1-2017	T2-2017	<0.001

Appendix H - Post hoc test on tree transpiration for selected trees in 2016 and 2017

Post hoc comparison by the independent-sample Mann-Whitney U test		p
C-2016	T1-2016	0.001
C-2016	T2-2016	<0.001
C-2016	C-2017	0.210
C-2016	T1-2017	<0.001
C-2016	T2-2017	<0.001
T1-2016	C-2017	<0.001
T1-2016	T1-2017	0.525
T1-2016	T2-2017	0.410
T1-2016	T2-2016	0.109
T2-2016	C-2017	0.001
T2-2016	T1-2017	0.027
T2-2016	T2-2017	0.383
C-2017	T1-2017	<0.001
C-2017	T2-2017	<0.001
T1-2017	T2-2017	0.159

Appendix I - Mixed-effect ANOVA on stand transpiration

Sources	numDF	denDF	F-value	p-value
<i>Model formula: lme(stand transpiration~ Thinning*year, random=~1 Date)</i>				
Intercept	1	380	626.77	<0.001
Thinning	1	380	541.96	<0.001
Year	1	189	4.12	0.04
Thinning × Year	1	380	4.56	0.03

Appendix J - Mixed-effect ANOVA test on leaf-level WUE and iWUE

Sources	numDF	denDF	F-value	p-value
Leaf-level WUE				
<i>Model formula: lme(leaf-level WUE~ Thinning*Direction, random=~1 Block/Date)</i>				
Intercept	1	96	43.88	<0.001
Thinning	1	96	2.79	0.10
Direction	1	96	0.04	0.83
Thinning × Direction	1	96	0.06	0.81
iWUE				
<i>Model formula: lme(iWUE~ Thinning*Direction, random=~1 Block/Date)</i>				
Intercept	1	96	31.64	<0.001
Thinning	1	96	26.29	<0.001
Direction	1	96	0.01	0.92
Thinning × Direction	1	96	0.46	0.50

Note: this is the direct output from R. On each measuring data, only one block was measured, therefore, the date was nested within the block, as each block contains measurements from different dates.

Appendix K - Post hoc test on tree-level WUE for selected trees in 2016 and 2017

Post hoc comparison by the independent-sample Mann-Whitney U test		p
C-2016	T1-2016	0.811
C-2016	T2-2016	0.706
C-2016	C-2017	0.994
C-2016	T1-2017	0.694
C-2016	T2-2017	0.538
T1-2016	C-2017	0.103
T1-2016	T1-2017	0.397
T1-2016	T2-2017	0.929
T1-2016	T2-2016	0.837
T2-2016	C-2017	0.022
T2-2016	T1-2017	0.085
T2-2016	T2-2017	0.762
C-2017	T1-2017	<0.001
C-2017	T2-2017	<0.001
T1-2017	T2-2017	0.004

Appendix L - Coefficients of the fitted relationships between normalized sap flow velocity and VPD, and the explained variations of the models.

Group	2016			2017		
	a	b	R²	a	b	R²
C	1.16	0.55	0.56	0.35	84.45	0.02
T1	1.02	1.97	0.92	0.60	12.95	0.27
T2	1.07	1.52	0.85	0.73	7.13	0.46