



Juvenile thinning can effectively mitigate the effects of drought on tree growth and water consumption in a young *Pinus contorta* stand in the interior of British Columbia, Canada

Yi Wang^{a,b}, Xiaohua Wei^{a,*}, Antonio D. del Campo^c, Rita Winkler^d, Jianping Wu^e, Qiang Li^a, Wanyi Liu^a

^a Department of Earth, Environmental and Geographic Sciences, University of British Columbia, Okanagan, 1177 Research Road, Kelowna, British Columbia V1V 1V7, Canada

^b Department of Geography and Environmental Management, University of Waterloo, 200 University Ave W, Waterloo, Ontario N2L 3G1, Canada

^c Research Institute of Water and Environmental Engineering (IIAMA), Universitat Politècnica de València, Camí de Vera s/n, E-46022 València, Spain

^d BC Ministry of Forests, Lands and Natural Resource Operations, 515 Columbia St., Kamloops, British Columbia V2C 2T7, Canada

^e Laboratory of Ecology and Evolutionary Biology, State Key Laboratory for Conservation and Utilization of Bio-Resources in Yunnan, Yunnan University, Kunming 650500, China



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ABSTRACT

Large-scale forest disturbances including mountain pine beetle infestation and forest fires have generated overstocked 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 under increased drought risk due to climate change. In 2016, a field experiment was established to study the effects of juvenile thinning on carbon assimilation and water use at the both tree- and stand-scales in a 16-year old lodgepole pine stand from June to October in 2016 and 2017. This study located northeast of Penticton, British Columbia, included two thinning treatments (T1: 4500 stems per ha; and T2: 1100 stems per ha) and one control (C: 27,000 stems per ha), randomly assigned in three blocks. Sap flow and microclimatic variables were continuously monitored in one plot of each treatment in one block, while tree diameter at breast height were measured across the three blocks. The results showed that C had the lowest tree radial growth (0.14 mm²/d), sap flow velocity (64.61 g/cm²/d), and highest stand transpiration (4.36 mm/d), while T2 had the highest tree radial growth (1.28 mm²/d), sap flow velocity (149.14 g/cm²/d), and lowest stand transpiration (0.36 mm/d) over the two-year study period. Significant differences of tree radial growth and sap flow velocity between T1 and T2 only occurred under the drought condition (in the summer season of 2017), with T2 having a significant higher resistant index of sap flow velocity than C and T1, by taking advantage of the change in microclimatic conditions following intense thinning. At the stand-level, only the stand transpiration of T1 statistically decreased in the drought year. We conclude that the thinning plays a significant and positive role in maintaining tree growth and water consumption in the short term, and the more heavily thinning (T2) would be more effective to mitigate the drought effect in young overstocking lodgepole pine forests in terms of water consumption. These findings improve our understanding on how thinning can be used to manage ecological responses to forest practices in a changing climate.

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). Following stand-replacing disturbances or intensive timber harvesting,

lodgepole pine (*Pinus contorta* ssp. *latifolia*) is commonly replanted and in many areas it also regenerates naturally in plantations, which often results in over-dense, uniform cohorts, of which the densities could be > 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

* Corresponding author.

E-mail address: adam.wei@ubc.ca (X. Wei).

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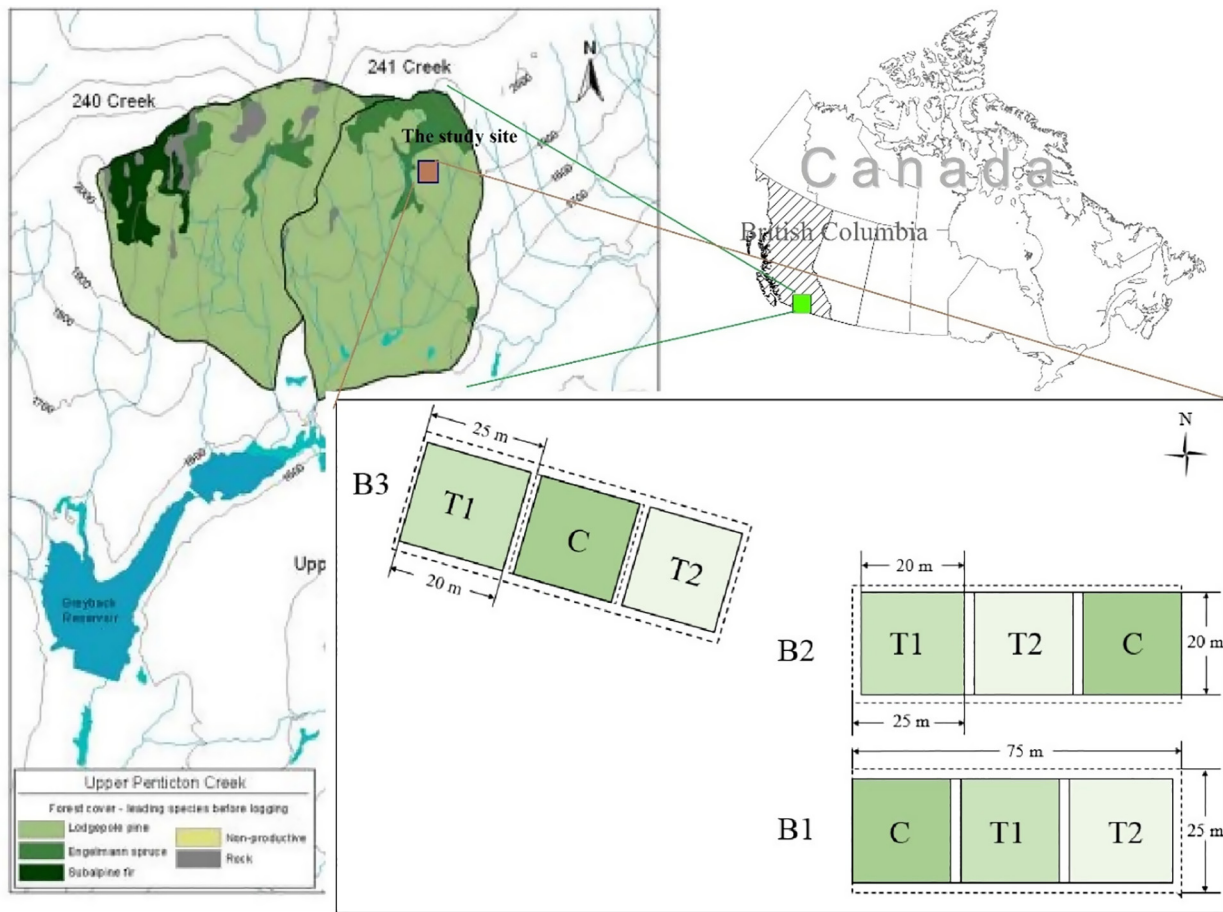


Fig. 1. The study location and the experimental layout of three blocks (C: control; T1: treatment 1 and T2: treatment 2).

sequestration and hydrological processes (Berryman 1982, Brix and Mitchell 1986). This problem could be further compounded by climate change induced droughts. As a result, two mechanisms of tree mortality, the carbon starvation (i.e., when carbon consumption by respiration, growth and defense exceeds carbon assimilation from photosynthesis) and the hydraulic failure (i.e., failed water transport when trees are under water stress), are often observed in affected forests (McDowell et al. 2008, McDowell 2011). In addition, hydraulic failure has been found to be more ubiquitous than carbon starvation in causing drought-induced mortality (Adams et al. 2017). Clearly, practical strategies are needed to manage those highly dense forest stands for wood production, carbon sequestrations and water conservation, particularly in the context of future climate change impacts (wildfires, droughts, and beetle attacks) (Seidl et al. 2017, Spittlehouse and Stewart 2003).

Juvenile thinning (or pre-commercial thinning), which reduces the stand density of immature forests, has been 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. 2015, Kohler et al. 2010, Rodríguez-Calcerrada et al. 2011, Sohn et al. 2013). A review of juvenile thinning experiments conducted in lodgepole pine forests in western Canada concluded that the treatments 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 juvenile 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 in some cases 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), requiring more investigations.

Various studies have reported positive impacts of thinning on the growth performance of individual trees and tree-water relations under non-drought and drought conditions (Cabon et al. 2018, 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). The better performance of trees in the thinned stands was mainly attributed to enhanced light, soil water, and nutrient availability (Lagergren et al. 2008, Moreaux et al. 2011, Moreno and Cubera 2008, Skubel et al. 2017). Therefore, it is reasonable to assume that a higher thinning intensity can yield better drought resistance of trees in dry regions. However, this is not always the case, in terms of the carbon assimilation (Sohn et al. 2013), sap flow rate (Jiménez et al. 2009, Medhurst et al. 2002), basal area growth and drought intensity (Kohler et al. 2010). A meta-data analysis by Sohn et al. (2016b) indicated that thinning had no significant effect on the radial growth of trees during or after drought. Thus, selecting optimal thinning intensities for sustaining ecological functions such as carbon sequestration and water conservation is urgently needed (Cabon et al. 2018).

The objective of this study was to evaluate the responses of tree growth, tree-level and stand-level transpiration under two juvenile

thinning treatments over two growing seasons of 2016–2017 in a young overstocked lodgepole pine (*Pinus contorta* ssp. *latifolia*) forest. Drought conditions during the summer of 2017 provided an excellent opportunity to assess whether thinning could mitigate the effects of drought. We hypothesized that (1) juvenile thinning could increase tree growth and tree-level transpiration, but reduce stand-level transpiration, with the more pronounced effects in more heavily-thinned stands; and that (2) more heavily-thinned stands would consistently maintain the highest tree growth and tree-level transpiration both under the non-drought and drought conditions. The results from this study could provide useful information for designing post-disturbance management strategies for large-scale overstocking young lodgepole forests under climate change impacts.

2. Materials and methods

2.1. Study area

The study area is located at the 241 Creek in the Upper Pentiction Watershed (UPW), approximately 26 km northeast of Pentiction in the southern interior of British Columbia, Canada (49°39'34"N, 119°24'34"W) (Fig. 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. Historical climate records from 1986 to 2014 show that the mean annual precipitation was 763 mm with less than one-third precipitation in the growing season (between June to October) and the mean annual temperature is 1.9 °C (Winkler et al. 2017). The daily temperature in the studied growing seasons ranged 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. Understorey vegetation including *Rhodendron albiflorum*, *Vaccinium scoparium*, *Valeriana sitchensis*, *Tiarella unifoliata*, and *Arnica latifolia* (Hope 2009) is sparse. Soils were Luvisolic, and were 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) and Winkler and Moore (2006).

2.2. Experiment design

Three experimental blocks, B1, B2 and B3 (25 m × 75 m each), were established in June 2016. Each block included two thinning treatments (20 m × 20 m each) and one unthinned control plot following the completely randomized block design (9 plots in total). Thinning was completed manually with the slash left on site. The tree densities in treatment 1 (T1) and treatment 2 (T2) are approximately 4,500 (1.5-m spaced) and 1,100 stems (3-m spaced) per ha, respectively. The control plots have an averaged density of around 27,000 stems per ha. Trees were counted if their heights were greater than or equal to 1.3 m.

2.3. Monitoring of tree growth

Tree growth was quantified as basal area increment (BAI_b, mm²). In each plot, 45 trees of similar diameter size distributions were selected for measurement. Tree diameters at the breast height (DBH) were measured monthly in the growing season of 2016 and 2017 with an electronic caliper (Model: 500-196-30, Mitutoyo Corporation, Japan). The initial distribution of DBH frequencies of the selected trees are showed in Table 1.

In addition, home-made dendrometer sensors, following Cattellino et al. (1986), were installed in five of the selected trees per plot in B1 (15 trees in total) to measure diameter changes (basal perimeter) at 20 cm above ground. The selected trees cover proportionally the range

Table 1

Distributions of trees in DBH classes 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%

of diameters found in each plot. Basal perimeter (tree girth) was recorded every 20 min using a CR1000 (Campbell Scientific Inc., Logan, UT, USA). All trees were connected to a central datalogger unit (CR1000, Campbell Scientific Inc., Logan, UT, USA) by using a multiplexer (AM16/32B, Campbell Scientific Inc.) located in B1. Changes in areas at the basal height were recorded as BAI_b (mm²). A linear relationship between basal diameter and DBH based on additional measurements from 180 trees in all three blocks is showed below ($R^2 = 0.83$):

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

2.4. Measurement of tree-level transpiration and stand-level transpiration

Granier-type sap flow probes (Model TDP-30, Dynamax, Inc., Texas, USA) were also inserted at the breast height in the five previously selected trees that were equipped with home-made dendrometers at each plot (15 trees in total) in B1. In consideration of the small DBHs of young trees (Table 1), each tree was installed with one pair of TDP-30 probes assuming 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 aluminum foil 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):

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

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

$$F = As \times SFD \times 3600 \quad (4)$$

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 occurs at night when the temperature difference reached its maximum (ΔT_{\max} , °C). SFD is the sap flow velocity (g/cm²), F denotes the sap flow rate, (g/h), and As stands for the sapwood area per tree (cm²).

Sapwood area was inferred from the linear relationship between DBH and sapwood area (Equation (5), $R^2 = 0.98$) derived from seven trees representing a range of diameters within the stand. This relationship was assumed to be hold for trees in both the control and thinned plots (Bréda and Granier 1996).

$$As(mm^2) = 102.81 \times DBH(mm) - 3709.3 \quad (5)$$

Daily mean SFD values for C, T1 and T2 were also upscaled to calculate daily stand-level transpiration following by Bréda and Granier (1996). Stand sapwood areas were summed according to the stand densities of the thinned and unthinned stands, DBH distributions (Table 1) and the DBH-sapwood relationship (Equation (5)).

$$E_s = \overline{SFD} \times As_g \quad (6)$$

where, E_s is the daily stand transpiration (mm/d); \overline{SFD} is the mean SFD of the five trees per each plot for C, T1 and T2, respectively (g/cm²); and As_g is the estimated total stand sapwood area (cm²) for 400 m² plot.

Additional species-specific calibration of the empirical equations (2–4) 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. Calculation of resistance index

The resistance of trees to drought was quantified using a resistance index. The resistance index of tree growth, sap flow velocity and stand transpiration were calculated as the ratio of target variables under the drought year (Y_{dy}) to that in the pre-drought year (Y_{predy}), following Lloret et al. (2011) and Sohn et al. (2016b):

$$RI = \frac{Y_{dy}}{Y_{predy}} \quad (7)$$

where, Y_{dy} represents the target variables (i.e., tree mean daily BAI_D , mean daily SFD or mean Es) during the drought year (2017), and Y_{predy} represents the target variables during the pre-drought year (2016).

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 transmitted solar radiation (R_n , W/m^2), relative humidity (RH, %), temperature (T , $^{\circ}C$), precipitation (P , mm) and wind velocity (W_v , m/s) at 10-minute intervals during the study period. The sensors were placed at approximately 2.5 m height which is just at the canopy level. VPD is calculated from RH and T according to Goff–Gratch equation (Goff and Gratch, 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-minute intervals for the study period. The selection of soil depths was based on studies reporting that tree transpiration was associated with soil water content at the depth of 10 to 20 cm (Raz-Yaseef et al. 2012, Sun et al. 2014a). Manual measurements of soil VWC at 20 cm depth in the three blocks were also made weekly during the growing season of 2017 using a GS-1 portable measuring system (Decagon, Pullman, WA, USA).

2.7. Statistical analysis

The BAI_D of selected trees were converted into daily means in order to adjust for different growing season lengths in 2016 and 2017.

BAI_D among the three treatments was analyzed by ANCOVA with the initial DBH of the trees as covariate, and the block, treatment and year (drought) as factors. Differences in sap flow velocity (SFD) were analyzed with mixed-effect models considered the thinning treatments, drought and date as fixed effects and the tree identity as a random effect on SFD.

In all cases, data were checked to meet the requirements of homogeneity of variance and normality (and homogeneity of the regression slopes in the ANCOVA). In most cases, the assumptions were violated, even though multiple methods including log transformation, square roots and cubic roots transformations and Box-Cox transformation were applied. Therefore, comparisons on BAI_D , SFD, ES, and RI between treatments or between years were performed with independent- t test, if data met the requirements of homogeneity of variance and normality. Otherwise, the Mann-Whitney U test was employed.

We were also interested in the response of SFD to VPD, and the relationship between SFD and VPD has been fitted into an exponential saturation equation (equation (8)) (Ewers et al. 2001, Tang et al. 2006) or a parabolic equation (equation (9)) (Grossiord et al. 2018).

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

$$SFD = mVPD^2 + nVPD \quad (9)$$

where, a , b , m and n are fitted coefficients.

Therefore, the relationship between SFD and VPD were determined by comparing which equations yielded the best fit (R^2). Coefficients of the equation (8) and the equation (9) and their goodness of fit were listed in Table S5. As the equation (9) yielded higher R^2 , the sensitivity of SFD to VPD (S_{VPD} , $g/cm^2 \cdot kPa$) was denoted as:

$$S_{VPD} = \frac{dSFD}{dVPD} = 2mVPD + n \quad (10)$$

The extent of drought in 2017 was evaluated by the Standard Precipitation Index (SPI) (Guttman 1999) based on the long-term precipitation data (1953–2017) derived from the Penticton Airport Climate Station around 20 km southwest of the study site. Correlation was examined using the Spearman test. A significance level of $p < 0.05$ was used for all analyses. All data were processed by R (R Core Team (2014) and SPSS for Windows (SPSS, Inc., USA).

3. Results

3.1. Difference in climatic conditions of the growing seasons in 2016 and 2017

Climatic conditions in the growing seasons varied between 2016 (Figure S1) and 2017 (Figure S2). Average daily transmitted solar radiation across all blocks was 103.9 and 141.5 W/m^2 for the growing seasons of 2016 and 2017, respectively. The average growing season temperature was 7.7 $^{\circ}C$ in 2016 versus 12.1 $^{\circ}C$ in 2017. Daily mean RH was 74.5% in 2016 and 56.5% in 2017. As a result, the daily mean VPD in 2016 (0.34 kPa) was less than half of that 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 (0.32 mm). Averaged daily soil VWC across blocks were 17.5% and 14.3% for the depths of 20 and 40 cm in 2016, respectively, while those amounts were reduced to 12.9% and 11.3%, respectively in 2017. All daily mean environmental variables in 2016 were significantly different from those in 2017 (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 (Table S1).

3.2. Transmitted solar radiation, soil volumetric water content and VPD between treatments

Transmitted solar radiation and averaged soil VWC across 20 cm and 40 cm depths were consistently significantly higher in T2, followed by T1 and then C in both years. However, during the drought year, the soil VWC at 20 cm was not statistically different between C and T1, and soil VWC at 40 cm was not significantly different between T1 and T2. No significant differences in VPD between C and T1 was found in the non-drought year. (Table 2).

3.3. Tree growth

The mean daily BAI_D in the C, T1 and T2 during the two-year study period were significantly different from each other, with the mean daily value of 0.14, 0.79 and 1.28 mm^2/d for C, T1 and T2, respectively (all $p < 0.01$). No significant reduction of BAI_D before and during drought was detected for C, T1 and T2. When each growing season was considered separately, BAI_D of T2 was significantly higher to that from C (both years) and T1 (only in the drought year), whilst C and T1 were statistically different only in the non-drought year (Fig. 2).

3.4. Sap flow velocity and stand-level transpiration

The thinned stands had significantly higher mean daily SFD than the unthinned stands in each respective season (Fig. 3). However, there was no significant difference in the mean daily SFD between T1 and T2 in

Table 2
Mean daily transmitted solar radiation, soil volumetric water contents (VWC) and VPD in 2016 and 2017.

Mean daily variables	T2	T1	C
2016			
Transmitted solar radiation (W/m ²)	150.1 ^a	112.1 ^b	49.6 ^c
Soil VWC at 20 cm	19.1% ^a	18.4% ^b	15.1% ^c
Soil VWC at 40 cm	14.3% ^a	16.0% ^b	12.5% ^c
Averaged soil VWC across 20 cm and 40 cm depths	16.7% ^a	17.2% ^b	13.8% ^c
VPD (kPa)	0.39 ^a	0.32 ^b	0.32 ^b
2017			
Transmitted solar radiation (W/m ²)	213.1 ^a	149.3 ^b	62.2 ^c
Soil VWC at 20 cm	14.4% ^a	13.0% ^b	11.3% ^b
Soil VWC at 40 cm	12.1% ^a	13.7% ^a	8.0% ^b
Averaged soil VWC across 20 cm and 40 cm depths	13.2% ^a	13.3% ^b	9.7% ^c
VPD (kPa)	0.78 ^a	0.69 ^b	0.72 ^c

Different letters in a row indicate significant differences between treatments (P < 0.05).

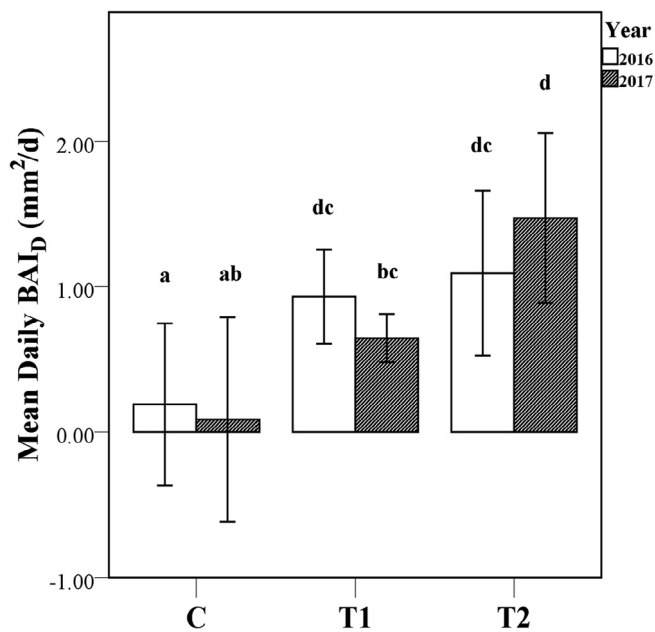


Fig. 2. Mean daily basal area increment (BAI_D) at the respective growing seasons of 2016 and 2017. Error bars denote the 95% confidence interval, and bars with different letters indicate significant differences between treatments and between years.

2016, while the significant difference occurred in the drought season of 2017 (Fig. 3). Unlike BAI_D, SFD of all the three groups significantly decreased during the drought, with the decline of 29.6%, 33.4% and 21.5% for C, T1 and T2, respectively.

At the stand-scale daily transpiration was the highest in C and lowest in T2 during the entire study period (P < 0.001, Fig. 4). When 2016 and 2017 were compared, only stand-scale transpiration of T1 exhibited a significant reduction due to drought (Fig. 4).

3.5. The resistance indices of tree growth, sap flow velocity and stand transpiration

RI of tree growth of the three groups was significantly higher in the thinned stands than the control, but no significant difference were found between T1 and T2 (Fig. 5 (1)). RI of sap flow velocity, however, was not significantly different between C and T1 (Fig. 5(2)). RI of stand transpiration in T2 was 1.00, followed by C (0.85) and T1 (0.82). It is note that no statistical test were applied to test the effect of thinning on

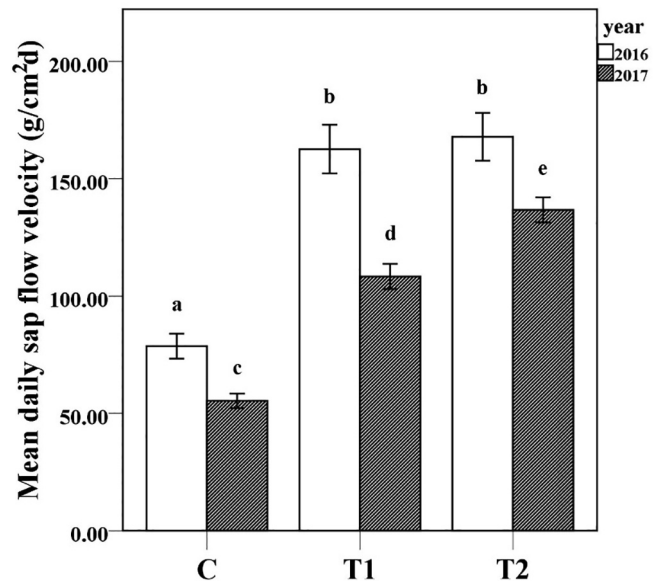


Fig. 3. Mean daily sap flow velocity (SFD) at the respective growing seasons of 2016 and 2017. Error bars denote the 95% confidence interval, and bars with different letters indicate significant differences between treatments and between years.

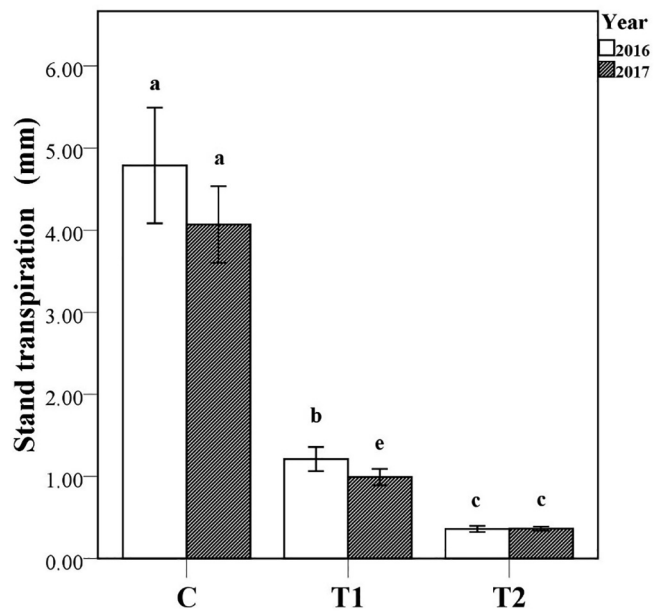


Fig. 4. Mean daily stand transpiration during the respective growing seasons of 2016 and 2017. Error bars denote the 95% confidence interval, and bars with different letters indicate significant differences between treatments and between years.

RI of stand transpiration. Nevertheless, these results clearly suggest that T2 has the highest resistance to the drought.

4. Discussion

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

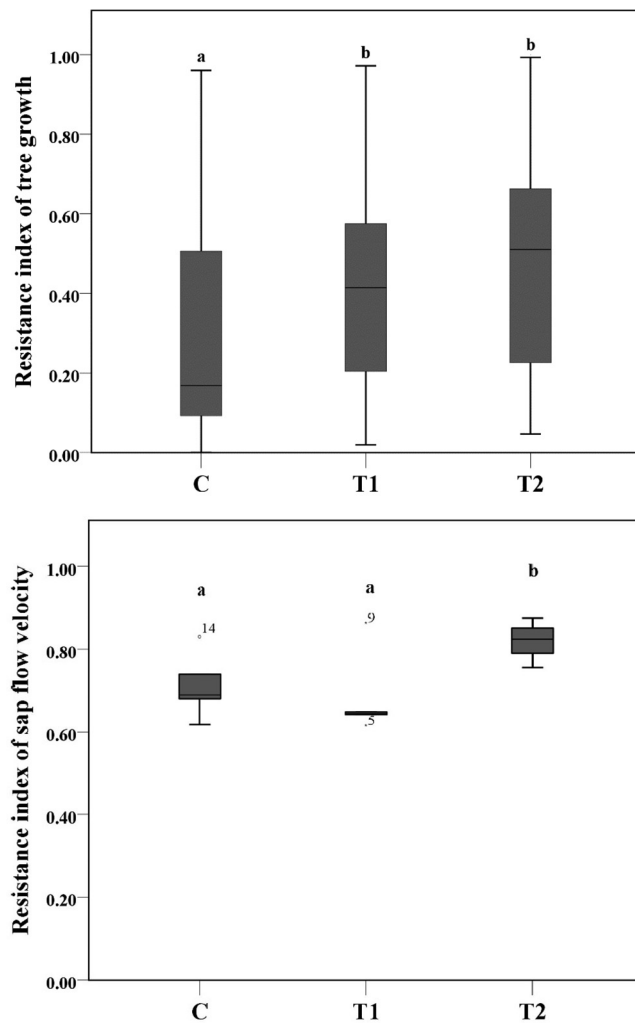


Fig. 5. Resistance indices of tree growth (1) and sap flow velocity (2). Different letters indicate significant differences between treatments. Numbers indicate the tree outliers.

(Forrester et al. 2012, Gebhardt et al. 2014, Moreaux et al. 2011, Simonin et al. 2007, Skubel et al., 2017, Sun et al. 2014b). Stand-scale transpiration decreased 75.3% and 91.7% in T1 and T2, where stand densities had been reduced by 83.3% and 95.9%, respectively, in comparison to C. This relatively smaller percentage reduction in stand transpiration than the percentage decrease in stand density is due to the enhanced transpiration of individual trees following the thinning treatments, which is consistent with the finding from Simonin et al. (2007).

The above-mentioned positive effects of thinning on tree radial growth and sap flow velocity are mainly due to more availability of resources (e.g., light, soil nutrients, soil water content), as a result of reduced competition after thinning (González de Andrés et al. 2018, Park et al. 2018, Skubel et al. 2017). Increased light penetration promotes carbon assimilation processes (Aussenac 2000), and open canopy exposure causes higher negative values of leaf water potential, leading to higher individual tree transpiration (Simonin et al. 2007). On the other hand, decreased interception of rainfall and total stand transpiration can lead to higher soil moisture that exerts stronger regulation in maintaining higher stomatal conductance, and thus both higher photosynthesis and transpiration rates (Giuggiola et al. 2016). Soil nutrients (e.g., N, P, and K nutrition) have been observed to be increased under juvenile thinning treatments by increasing soil moisture, temperature and thus microbial activities (Carlyle 1995, Chase et al.

2016a, Thibodeau et al. 2000). Significant differences in some soil nutrients may not occur immediately after thinning treatments were applied (e.g., $\text{NO}_3\text{-N}$ in Hope (2009) and mineral N and N mineralization rate in Carlyle (1995)), but in the long term, enhanced soil nutrients play an important role in tree growth (Chase et al. 2016a, Jokela et al. 2004). Unfortunately, we did not measure soil nutrients in this short term study, and thus were not able to account for the effects of changed soil nutrients resulted from juvenile thinning treatments on tree radial growth and sap flow velocity. Therefore, the following discussion focused on the effects of increased availability of light and soil water after thinning for explaining greater growth and transpiration at the individual tree level.

Our two-year results demonstrate that the more heavily thinned treatment (T2) had the more pronounced effect on tree growth, sap flow velocity, and stand-level transpiration. Significant improvements in radial growth and tree transpiration in the heavily thinned stand corresponded with higher light and soil water availabilities, as well as the higher evaporative demand (VPD) in T2 than the other two stands (Table 2). This finding is consistent with those of Park et al. (2018) who studied two thinning treatments (light-thinning: 320 tree/ha, and heavy-thinning: 240 tree/ha) in a 50-year-old Korean pine (*Pinus koraiensis*) forest. Based on their 4-year study, Park et al. (2018) found that heavy thinning greatly increased tree growth and sap flow velocity with the effects being increased over time, while the light thinning had little effect on site water availability and tree growth, and the resultant enhancement on sap flow velocity declined over time. Thus, Park et al. (2018) concluded that the heavier thinning was an appropriate management practice for mature pine plantations in their region.

However, the effects of thinning intensity are subject to interplay among various factors. For example, Jimenez et al. (2008) failed to find significant differences in tree-level transpiration and soil water availability under two intensities of thinning treatments (3,850 trees/ha and 1,925 trees/ha) in a 8-year-old *Pinus pinaster* stand. They attributed those insignificant differences to the similar reduction in the absolute basal area instead of the percentage area reduction (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 year old Norway spruce (*Picea abies*) stand, suggested that the effects of heavy thinning would be larger if the understory did not respond promptly to the increased light and water availability resulted from thinning, and indicated that repeated moderate thinning was a better option than the heavy thinning, because: (1) wood biomass production was not maximized by the heavy thinning at the stand level; and (2) the 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 understory was sparse, so its effects are expected to be minor, but the role of the understory in the longer term could become important affecting the difference between the two thinning treatments. This further highlights a need to examine the long-term effects of the thinning treatments in our studied young forest stands.

Surprisingly, we didn't detect significant reductions on the BAI_D of all the three groups caused by the drought, even though the mean daily BAI_D was smaller in the drought year than the non-drought year (except for T2), and the drought-induced earlier cessation of stem growth was observed (Figure S3). We attributed this insignificance mainly to the great variance in our data of DBH (high standard deviations in the Table S2) and possible delayed responses, as most studies found significant decreases of tree growth during the drought period (Eilmann and Rigling 2012, Julio Camarero et al. 2018). However, Sohn et al. (2013) also found that the more heavily thinned stands can maintain growth rates during drought, probably due to higher soil water availability. Nevertheless, the significantly lower RI of tree growth in C indicated that the unthinned stands were more vulnerable to the drought in term of radial growth. In addition, our results on the drought resistance of tree growth of the thinned stands support the review by Sohn et al.

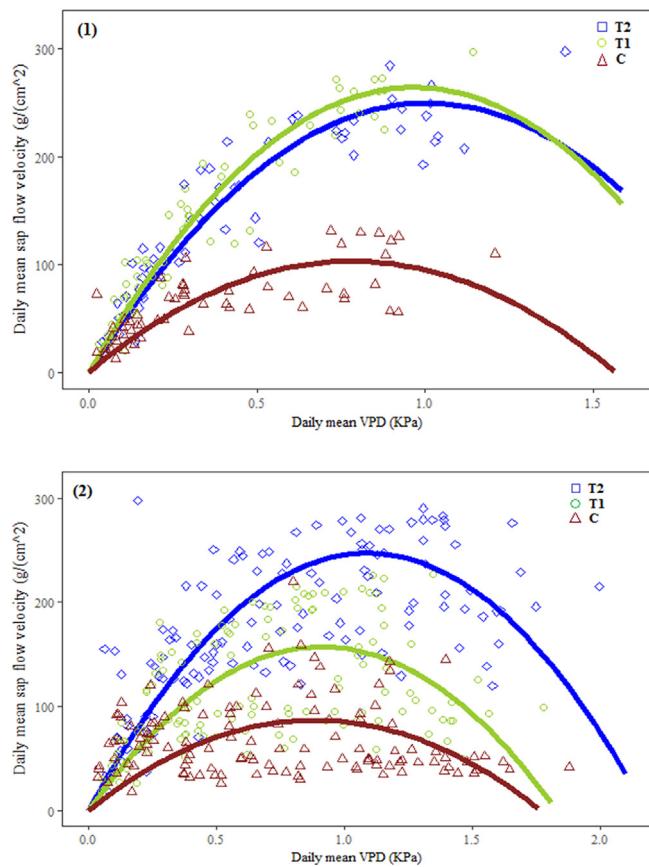


Fig. 6. The daily mean sap flow velocity as a function of VPD in 2016 (1) and 2017 (2). Blue, green and red colors denote T2, T1 and C, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(2016b) who found that the RI of tree growth in coniferous species did not significantly vary with the thinning intensities, based on up to 20 studies across the world. They indicated that the reduction of stomatal conductance irrespective of thinning treatments, which was found in most of the studies, was likely the reason. As stomatal conductance is highly influenced by atmospheric evaporative demand and soil water availability (Edward Boyd Reid et al. 2006, Jiménez et al. 2009), higher soil water availability and stronger atmospheric regulation in thinned stands can improve RI of tree growth, as found in our study.

The drought reduction of SFD is consistent with findings reported in the literature for several tree genera (e.g., *Ficus*, *Tilia*, *Pinus*, *Picea* and *Fraxinus*) that experienced droughts (Nadezhdina and Cermak 2000, Stohr and Losch 2004). To our surprise, we did not find significant differences in RI of sap flow velocity between C and T1. The explanations may lie in both the regulation of microclimatic variables that influence stomatal behaviors, and the adjusted physiological sensitivity of sap flow velocity to environmental regulations. As shown in Fig. 3, SFD was not significantly different between T1 and T2 in 2016, which may be explained by the combined effects between the slightly higher sensitivity of SFD in T1 to VPD (Fig. 6(1)) and the significantly lower daily VPD in T1 than T2 (Table 2). The daily sensitivities of SFD to VPD (S_{VPD} , Table S5) were significantly different among the three groups in 2016, with daily averages of 155.4 g/cm²·kPa, 364.4 g/cm²·kPa and 303.3 g/cm²·kPa in C, T1 and T2, respectively (all $p < 0.05$). The higher S_{VPD} but lower VPD in T1 led to similar magnitudes of SFD as T2 that had lower S_{VPD} but higher VPD (e.g., the products of daily mean VPD and daily mean S_{VPD} are 116.6 g/cm² in T1 and 118.3 g/cm² in T2). In 2017, the daily S_{VPD} was statistically different among the three groups (all $p < 0.1$), but the mean daily value decreased from that in

2016 to 37.0 g/cm²·kPa, 85.4 g/cm²·kPa and 128.4 g/cm²·kPa for C, T1 and T2, respectively. Clearly, the reduction of the daily S_{VPD} in T2 is the lowest. In addition, the significantly higher daily VPD in T2 might enlarge the differences in tree sap flow velocity between T1 and T2, while the significantly lower daily VPD in T1 might reduce the differences between T1 and C. All above explain significantly higher RI of sap flow velocity in T2, even though there was no significant difference in RI of sap flow velocity between T1 and C.

The sensitivity of SFD to VPD is greatly influenced by the soil water availability (Bovard et al. 2005, Gyenge et al. 2011), which was supported by our results, as the response of SFD to VPD among treatments corresponded well with the magnitudes of the averaged soil VWC for each treatment (Fig S4). The soil VWC of both thinned stands was less responsive to precipitation in the non-drought year than in the drought year (Fig S4), indicating that soil VWC was not a limiting factor for tree growth and tree-water consumption (range between 15 and 20%). In the drought year, however, the reduction of soil VWC in T1 was steeper than in T2, reaching lower values by the end of the drought spell (Fig S4), probably due to the higher tree density and stand transpiration in T1. As a result, SFD was greatly reduced in T1 compared to T2, as soil VWC in the former could have been below 7–8% for several weeks (Fig S4), i.e., below the wilting point for this coarse sandy-loam soil, consequently the RI of SFD was significantly lower in T1 than in T2, given the high values recorded in the preceding wet year. This indicates that thinning intensity affects the vulnerability of tree-water relations to drought, but also indicates the ability of T1 to adjust its water use to changing soil moisture (shortage/abundance), and hence a plastic response of the species.

Thinning modifies microclimate conditions, and consequently leads to major changes in physiological responses of trees (Aussenac 2000, Chen et al. 1993, Zobel et al. 1976). Modifications on microclimates under thinning (Anderson et al. 2007, Weng et al. 2007) and enhanced sensitivities of tree transpiration to VPD by thinning treatments (Gyenge et al. 2011, Tateishi et al. 2015) have been previously reported, but little is known about their combined effects on drought resistance of trees. Our study implies that such combined effects could be more pronounced in the more heavily thinning stands. However, physiological mechanisms governing these combined effects requires further investigation.

Interestingly, no significant reduction of the stand-level transpiration in the drought year in comparison to the non-drought year was found in C and T2 in our study (Fig. 4). This observation is contrary to some previous studies showing that droughts greatly reduce stand-level transpiration (Schäfer et al. 2014, Stojanović et al. 2017). The insignificance of stand transpiration of C between 2016 and 2017 might be due to the greater variance in the dataset (Table S4), while the insignificant differences of stand transpiration of T2 before and during the drought may be attributed to the increased total basal area in the thinned stands in the two growing seasons compensating for the decrease in SFD during the drought. Similar to our observation, Simonin et al. (2007) discussed that the thinned stands might maintain relatively higher stand transpiration rates than the unthinned counterparts during the drought period as the higher leaf-level transpiration in thinned stands could compensate for the reduction of leaf area. Overall, the ability of maintaining relatively high stand transpiration in the heavily thinned stands indicates the benefit of heavy juvenile thinning in sustaining tree growth and transpiration under the drought in our study area.

5. Conclusion

Our study presented the short-term benefits of the juvenile thinning in terms of increasing tree radial growth, sap flow velocity, and reducing stand transpiration. Those effects were more pronounced in the more heavily thinned stands, demonstrating that heavier thinning can produce more ecological benefits, such as carbon sequestration and

water conservation. Our results also showed that the difference in the studied variables between the two thinning treatments was only significant during the drought period, suggesting that heavier thinning can more effectively mitigate the negative impacts of the drought. Thus, we conclude that the thinning treatments have significantly provided short-term ecological benefits to young overstocking lodgepole pine forests in the BC interior. More studies on long-term effects of thinning are still needed to support development of sustainable management for wood production, carbon sequestration and water conservation in lodgepole pine forests in the context of climate change impacts.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2019.117667>.

References

- Adams, H.D., Zeppel, M.J., Anderegg, W.R., Hartmann, H., Landhäusser, S.M., Tissue, D.T., Huxman, T.E., Hudson, P.J., Franz, T.E., Allen, C.D., 2017. A multi-species synthesis of physiological mechanisms in drought-induced tree mortality. *Nat. Ecol. Evol.* 1 (9), 1285.
- Ambrose, A.R., Baxter, W.L., Martin, R.E., Francis, E., Asner, G.P., Nydick, K.R., Dawson, T.E., 2018. Leaf- and crown-level adjustments help giant sequoias maintain favorable water status during severe drought. *For. Ecol. Manage.* 419–420, 257–267.
- Anderson, P.D., Larson, D.J., Chan, S.S., 2007. Riparian buffer and density management influences on microclimate of young headwater forests of western Oregon. *Forest Science* 53 (2), 254–269.
- Aussenac, G., 2000. Interactions between forest stands and microclimate: Ecophysiological aspects and consequences for silviculture. *Ann. For. Sci.* 57 (3), 287–301.
- Bassman, J.H., 1985. Selected physiological characteristics of lodgepole pine. Washington State University, Cooperative Extension.
- Bearup, L.A., Maxwell, R.M., Clow, D.W., McCray, J.E., 2014. Hydrological effects of forest transpiration loss in bark beetle-impacted watersheds. *Nat. Clim. Change* 4, 481.
- Berryman, A., 1982. Mountain pine beetle outbreaks in Rocky Mountain lodgepole pine forests. *J. Forest.* 80 (7), 410–419.
- Bonan, G.B., 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* 320 (5882), 1444–1449.
- Bovard, B.D., Curtis, P.S., Vogel, C.S., Su, H.B., Schmid, H.P., 2005. Environmental controls on sap flow in a northern hardwood forest. *Tree Physiol.* 25 (1), 31–38.
- Bréda, N., Granier, A., 1996. Intra- and interannual variations of transpiration, leaf area index and radial growth of a sessile oak stand (*Quercus petraea*). *Annales des sciences forestières* 53 (2–3), 521–536.
- Brix, H., Mitchell, A.K., 1986. Thinning and nitrogen fertilization effects on soil and tree water stress in a Douglas-fir stand. *Can. J. For. Res.* 16 (6), 1334–1338.
- Cabon, A., Mouillot, F., Lempereur, M., Ourcival, J.-M., Simioni, G., Limousin, J.-M., 2018. Thinning increases tree growth by delaying drought-induced growth cessation in a Mediterranean evergreen oak coppice. *For. Ecol. Manage.* 409, 333–342.
- Carlyle, J.C., 1995. Nutrient management in a *Pinus radiata* plantation after thinning: the effect of thinning and residues on nutrient distribution, mineral nitrogen fluxes, and extractable phosphorus. *Can. J. For. Res.* 25 (8), 1278–1291.
- Cattelin, P.J., Becker, C.A., Fuller, L.G., 1986. Construction and installation of homemade dendrometer bands. *North. J. Appl. For.* 3 (2), 73–75.
- Chase, C.W., Kimsey, M.J., Shaw, T.M., Coleman, M.D., 2016a. The response of light, water, and nutrient availability to pre-commercial thinning in dry inland Douglas-fir forests. *Forest Ecology and Management* 363(Supplement C), 98–109.
- Chase, C.W., Kimsey, M.J., Shaw, T.M., Coleman, M.D., 2016. The response of light, water, and nutrient availability to pre-commercial thinning in dry inland Douglas-fir forests. *For. Ecol. Manage.* 363, 98–109.
- Chen, J., Franklin, J.F., Spies, T.A., 1993. Contrasting microclimates among clearcut, edge, and interior of old-growth Douglas-fir forest. *Agric. For. Meteorol.* 63 (3), 219–237.
- Clausnitzer, F., Köstner, B., Schwärzel, K., Bernhofer, C., 2011. Relationships between canopy transpiration, atmospheric conditions and soil water availability—analyses of long-term sap-flow measurements in an old Norway spruce forest at the Ore Mountains/Germany. *Agric. For. Meteorol.* 151 (8), 1023–1034.
- Cole, D.M., 1973. Culture of immature lodgepole pine stands for timber objectives, pp. 9–11.
- Coupé, R., Stewart, A., Wikeem, B., 1991. Engelmann spruce–subalpine fir zone. Ecosystems of British Columbia. D. Meidinger and J. Pojar (editors). BC Ministry of Forests, Research Branch, Victoria, BC. Special Report Series 6, 223–236.
- Daniel, C.J., Ter-Mikaelian, M.T., Wotton, B.M., Rayfield, B., Fortin, M.-J., 2017. Incorporating uncertainty into forest management planning: Timber harvest, wildfire and climate change in the boreal forest. *Forest Ecology and Management* 400(Supplement C), 542–554.
- del Campo, A.D., Fernandes, T.J.G., Molina, A.J., 2014. Hydrology-oriented (adaptive) silviculture in a semiarid pine plantation: How much can be modified the water cycle through forest management? *Eur. J. Forest Res.* 133 (5), 879–894.
- Del Río, M., Bravo-Oviedo, A., Pretzsch, H., Löf, M., Ruiz-Peinado, R., 2017. A review of thinning effects on Scots pine stands: From growth and yield to new challenges under global change. *Forest Systems* 26 (2), eR03S.
- Edward Boyd Reid, D., Silins, U., James Lieffers, V., 2006. Sapwood hydraulic recovery following thinning in lodgepole pine. *Annals of Forest Science* 63 (4), 329–338.
- Eilmann, B., Rigling, A., 2012. Tree-growth analyses to estimate tree species' drought tolerance. *Tree Physiol.* 32 (2), 178–187.
- Elkin, C., Giuggiola, A., Rigling, A., Bugmann, H., 2015. Short- and long-term efficacy of forest thinning to mitigate drought impacts in mountain forests in the European Alps. *Ecol. Appl.* 25 (4), 1083–1098.
- Ewers, B.E., Oren, R., Johnsen, K.H., Landsberg, J., 2001. Estimating maximum mean canopy stomatal conductance for use in models. *Can. J. For. Res.* 31 (2), 198–207.
- Fernandes, T.J.G., Del Campo, A.D., Herrera, R., Molina, A.J., 2016. Simultaneous assessment, through sap flow and stable isotopes, of water use efficiency (WUE) in thinned pines shows improvement in growth, tree-climate sensitivity and WUE, but not in WUEi. *For. Ecol. Manage.* 361, 298–308.
- Forrester, D.I., Collopy, J.J., Beadle, C.L., Warren, C.R., Baker, T.G., 2012. Effect of thinning, pruning and nitrogen fertilizer application on transpiration, photosynthesis and water-use efficiency in a young *Eucalyptus nitens* plantation. *For. Ecol. Manage.* 266, 286–300.
- Gebhardt, T., Häberle, K.-H., Matussek, R., Schulz, C., Ammer, C., 2014. The more, the better? Water relations of Norway spruce stands after progressive thinning. *Agric. For. Meteorol.* 197, 235–243.
- Giuggiola, A., Ogee, J., Rigling, A., Gessler, A., Bugmann, H., Treyde, K., 2016. Improvement of water and light availability after thinning at a xeric site: which matters more? A dual isotope approach. *New Phytol* 210 (1), 108–121.
- Goff, J.A., Gratch, S., 1946. Low-pressure properties of water from –160 to 212 °F. Goff, J.A. (ed), pp. 95–122, New York.
- González de Andrés, E., Camarero, J.J., Blanco, J.A., Imbert, J.B., Lo, Y.-H., Sangüesa-Barreda, G., Castillo, F.J., Turnbull, M., 2018. Tree-to-tree competition in mixed European beech-Scots pine forests has different impacts on growth and water-use efficiency depending on site conditions. *J. Ecol.* 106 (1), 59–75.
- Granier, A., 1987. Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. *Tree Physiol* 3 (4), 309–320.
- Granier, A., Bobay, V., Gash, J.H.C., Gelpé, J., Saugier, B., Shuttleworth, W.J., 1990. Vapour flux density and transpiration rate comparisons in a stand of Maritime pine (*Pinus pinaster* Ait.) in Les Landes forest. *Agric. For. Meteorol.* 51 (3–4), 309–319.
- Grossiord, C., Sevanto, S., Limousin, J.-M., Meir, P., Mencuccini, M., Pangle, R.E., Pockman, W.T., Salmon, Y., Zweifel, R., McDowell, N.G., 2018. Manipulative experiments demonstrate how long-term soil moisture changes alter controls of plant water use. *Environ. Exp. Bot.* 152, 19–27.
- Guttman, N.B., 1999. Accepting the standardized precipitation index: A calculation algorithm. *JAWRA J. Am. Water Resour. Assoc.* 35 (2), 311–322.
- Gyenge, J., Fernández, M.E., Sarasola, M., Schlichter, T., 2011. Stand density and drought interaction on water relations of *Nothofagus antarctica*: contribution of forest management to climate change adaptability. *Trees* 25 (6), 1111–1120.
- Hope, G.D., 2009. Clearcut harvesting effects on soil and creek inorganic nitrogen in high elevation forests of southern interior British Columbia. *Can. J. Soil Sci.* 89 (1), 35–44.
- Hudson, R.O., Golding, D.L., 1997. Controls on groundwater chemistry in subalpine catchments in the southern interior of British Columbia. *J. Hydrol.* 201 (1–4), 1–20.
- Jimenez, E., Vega, J.A., Perez-Gorostiaga, P., Cuinas, P., Fonturbel, T., Fernandez, C., Madrigal, J., Hernando, C., Guijarro, M., 2008. Effects of pre-commercial thinning on transpiration in young post-fire maritime pine stands. *Forestry* 81 (4), 543–557.
- Jiménez, E., Vega, J.A., Pérez-Gorostiaga, P., Fonturbel, T., Fernández, C., 2009. Relationships between water use and environmental parameters in a young post-fire maritime pine stand after precommercial thinning. *International Society for Horticultural Science (ISHS), Leuven, Belgium*, pp. 303–308.
- Johnstone, W.D., Van Thienen, F., 2004. A summary of early results from recent lodgepole pine thinning experiments in the British Columbia interior. Ministry of Forests, Forest Science Program.

- Jokela, E.J., Dougherty, P.M., Martin, T.A., 2004. Production dynamics of intensively managed loblolly pine stands in the southern United States: a synthesis of seven long-term experiments. *For. Ecol. Manage.* 192 (1), 117–130.
- Julio Camarero, J., Gazol, A., Sangüesa-Barreda, G., Cantero, A., Sánchez-Salguero, R., Sánchez-Miranda, A., Granda, E., Serra-Maluquer, X., Ibáñez, R., 2018. Forest Growth Responses to Drought at Short- and Long-Term Scales in Spain: Squeezing the Stress Memory from Tree Rings. *Frontiers in Ecology and Evolution* 6 (9).
- Kashian, D.M., Tinker, D.B., Turner, M.G., Scarpace, F.L., 2004. Spatial heterogeneity of lodgepole pine sapling densities following the 1988 fires in Yellowstone National Park, Wyoming, USA. *Can. J. For. Res.* 34 (11), 2263–2276.
- Kohler, M., Sohn, J., Nägele, G., Bauhus, J., 2010. Can drought tolerance of Norway spruce (*Picea abies* (L.) Karst.) be increased through thinning? *Eur. J. Forest Res.* 129 (6), 1109–1118.
- Lagergren, F., Lankreijer, H., Kučera, J., Cienciala, E., Mölder, M., Lindroth, A., 2008. Thinning effects on pine-spruce forest transpiration in central Sweden. *For. Ecol. Manage.* 255 (7), 2312–2323.
- Laurent, M., Antoine, N., Joël, G., 2003. Effects of different thinning intensities on drought response in Norway spruce (*Picea abies* (L.) Karst.). *For. Ecol. Manage.* 183 (1–3), 47–60.
- Lindgren, P.M.F., Sullivan, T.P., 2013. Long-term responses of tree and stand growth of young lodgepole pine to pre-commercial thinning and repeated fertilization. *For. Ecol. Manage.* 307, 155–164.
- Lloret, F., Keeling, E.G., Sala, A., 2011. Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests. *Oikos* 120 (12), 1909–1920.
- Lotan, J.E., Critchfield, W.B., 1990. *Pinus contorta* Dougl. ex Loud. *Silvics of North America* 1, 302–315.
- Martín-Benito, D., Del Río, M., Heinrich, I., Helle, G., Cañellas, I., 2010. Response of climate-growth relationships and water use efficiency to thinning in a *Pinus nigra* afforestation. *For. Ecol. Manage.* 259 (5), 967–975.
- McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G., Yezpe, E.A., 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytol* 178 (4), 719–739.
- McDowell, N.G., 2011. Mechanisms Linking Drought, Hydraulics, Carbon Metabolism, and Vegetation Mortality. *Plant Physiol.* 155 (3), 1051–1059.
- Medhurst, J.L., Battaglia, M., Beadle, C.L., 2002. Measured and predicted changes in tree and stand water use following high-intensity thinning of an 8-year-old *Eucalyptus nitens* plantation. *Tree Physiol.* 22 (11), 775–784.
- Mitchell, R.G., Waring, R.H., Pitman, G.B., 1983. Thinning Lodgepole Pine Increases Tree Vigor and Resistance to Mountain Pine Beetle. *Forest Science* 29 (1), 204–211.
- Moreaux, V., Lamaud, E., Bosc, A., Bonnefond, J.M., Medlyn, B.E., Loustau, D., 2011. Paired comparison of water, energy and carbon exchanges over two young maritime pine stands (*Pinus pinaster* Ait.): effects of thinning and weeding in the early stage of tree growth. *Tree Physiol* 31 (9), 903–921.
- Moreno, G., Cubera, E., 2008. Impact of stand density on water status and leaf gas exchange in *Quercus ilex*. *For. Ecol. Manage.* 254 (1), 74–84.
- Nadezhkina, N., Cermak, J., 2000. In: *The Supporting Roots of Trees and Woody Plants: Form, Function and Physiology*. Springer, Netherlands, Dordrecht, pp. 227–238.
- Naudts, K., Chen, Y., McGrath, M.J., Ryder, J., Valade, A., Otto, J., Luysaert, S., 2016. Europe's forest management did not mitigate climate warming. *Science* 351 (6273), 597.
- Nyland, R.D., 1998. Patterns of lodgepole pine regeneration following the 1988 Yellowstone fires. *For. Ecol. Manage.* 111 (1), 23–33.
- Park, J., Kim, T., Moon, M., Cho, S., Ryu, D., Seok Kim, H., 2018. Effects of thinning intensities on tree water use, growth, and resultant water use efficiency of 50-year-old *Pinus koraiensis* forest over four years. *For. Ecol. Manage.* 408, 121–128.
- Raz-Yaseef, N., Yakir, D., Schiller, G., Cohen, S., 2012. Dynamics of evapotranspiration partitioning in a semi-arid forest as affected by temporal rainfall patterns. *Agric. For. Meteorol.* 157, 77–85.
- Reichstein, M., Bahn, M., Ciais, P., Frank, D., Mahecha, M.D., Seneviratne, S.I., Zscheischler, J., Beer, C., Buchmann, N., Frank, D.C., Papale, D., Rammig, A., Smith, P., Thonicke, K., van der Velde, M., Vicca, S., Walz, A., Wattenbach, M., 2013. Climate extremes and the carbon cycle. *Nature* 500 (7462), 287–295.
- Reid, D.E.B., Silins, U., Lieffers, V.J., 2006. Sapwood hydraulic recovery following thinning in lodgepole pine. *Ann. For. Sci.* 63 (4), 329–338.
- Rodríguez-Calcerrada, J., Pérez-Ramos, I.M., Ourcival, J.-M., Limousin, J.-M., Joffre, R., Rambal, S., 2011. Is selective thinning an adequate practice for adapting *Quercus ilex* coppices to climate change? *Annals of Forest Science* 68 (3), 575–585.
- Schäfer, K.V.R., Renninger, H.J., Clark, K.L., Medvigy, D., 2014. Hydrological responses to defoliation and drought of an upland oak/pine forest. *Hydrol. Process.* 28 (25), 6113–6123.
- Seidl, R., Schelhaas, M.-J., Rammer, W., Verkerke, P.J., 2014. Increasing forest disturbances in Europe and their impact on carbon storage. *Nat. Clim. Change* 4, 806.
- Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M.J., Trotsiuk, V., Mairota, P., Svoboda, M., Fabrika, M., Nagel, T.A., Reyser, C.P.O., 2017. Forest disturbances under climate change. *Nat. Clim. Change* 7, 395.
- Simonin, K., Kolb, T.E., Montes-Helu, M., Koch, G.W., 2007. The influence of thinning on components of stand water balance in a ponderosa pine forest stand during and after extreme drought. *Agric. For. Meteorol.* 143 (3–4), 266–276.
- Skubel, R.A., Khomik, M., Brodeur, J.J., Thorne, R., Arain, M.A., 2017. Short-term selective thinning effects on hydraulic functionality of a temperate pine forest in eastern Canada. *Ecohydrology* 10 (1), e1780.
- Sohn, J.A., Gebhardt, T., Ammer, C., Bauhus, J., Häberle, K.-H., Matyssek, R., Grams, T.E.E., 2013. Mitigation of drought by thinning: Short-term and long-term effects on growth and physiological performance of Norway spruce (*Picea abies*). *For. Ecol. Manage.* 308, 188–197.
- Sohn, J.A., Hartig, F., Kohler, M., Huss, J., Bauhus, J., 2016a. Heavy and frequent thinning promotes drought adaptation in *Pinus sylvestris* forests. *Ecol Appl* 26 (7), 2190–2205.
- Sohn, J.A., Saha, S., Bauhus, J., 2016b. Potential of forest thinning to mitigate drought stress: A meta-analysis. *For. Ecol. Manage.* 380, 261–273.
- Spittlehouse, D., Stewart, R.B., 2003. *Adaptation to climate change in forest management*. Stewart, J.D., Salvail, J., 2017. *Evaluation of Precommercial Thinning of Lodgepole Pine from Long-term Research Installations in Alberta, Natural Resources Canada = Ressources naturelles Canada*.
- Stohr, A., Losch, R., 2004. Xylem sap flow and drought stress of *Fraxinus excelsior* saplings. *Tree Physiol.* 24 (2), 169–180.
- Stojanović, M., Szatniewska, J., Kyselová, I., Pokorný, R., Čater, M., 2017. Transpiration and water potential of young *Quercus petraea* (M.) Liebl. coppice sprouts and seedlings during favourable and drought conditions. *J. For. Sci.* 63, 313–323.
- Sullivan, T.P., Sullivan, D.S., Lindgren, P.M.F., Ransome, D.B., 2006. Long-term responses of ecosystem components to stand thinning in young lodgepole pine forest: III. Growth of crop trees and coniferous stand structure. *For. Ecol. Manage.* 228 (1–3), 69–81.
- Sun, X., Onda, Y., Kato, H., Otsuki, K., Gomi, T., 2014a. Partitioning of the total evapotranspiration in a Japanese cypress plantation during the growing season. *Ecohydrology* 7 (3), 1042–1053.
- Sun, X., Onda, Y., Otsuki, K., Kato, H., Hirata, A., Gomi, T., 2014b. The effect of strip thinning on tree transpiration in a Japanese cypress (*Chamaecyparis obtusa* Endl.) plantation. *Agric. For. Meteorol.* 197, 123–135.
- Tang, J., Bolstad, P.V., Ewers, B.E., Desai, A.R., Davis, K.J., Carey, E.V., 2006. Sap flux-upscaled canopy transpiration, stomatal conductance, and water use efficiency in an old growth forest in the Great Lakes region of the United States. *Journal of Geophysical Research. Biogeosciences* 111 (G2), n/a-n/a.
- Tateishi, M., Xiang, Y., Saito, T., Otsuki, K., Kasahara, T., 2015. Changes in canopy transpiration of Japanese cypress and Japanese cedar plantations because of selective thinning. *Hydrol. Process.* 29 (24), 5088–5097.
- Thibodeau, L., Raymond, P., Camiré, C., Munson, A.D., 2000. Impact of precommercial thinning in balsam fir stands on soil nitrogen dynamics, microbial biomass, decomposition, and foliar nutrition. *Can. J. For. Res.* 30 (2), 229–238.
- Turner, M., Romme, W., Tinker, D., Whitby, T., 2013. Landscape patterns of early postfire lodgepole pine regeneration dominate stand structure and function 24 years after the 1988 Yellowstone Fire.
- Weng, S.-H., Kuo, S.-R., Guan, B.T., Chang, T.-Y., Hsu, H.-W., Shen, C.-W., 2007. Microclimatic responses to different thinning intensities in a Japanese cedar plantation of northern Taiwan. *For. Ecol. Manage.* 241 (1), 91–100.
- Winkler, R., Spittlehouse, D., Boon, S., 2017. Streamflow response to clear-cut logging on British Columbia's Okanagan Plateau. *Ecohydrology* 10 (2), e1836.
- Winkler, R.D., Moore, R.D., 2006. Variability in snow accumulation patterns within forest stands on the interior plateau of British Columbia. *Canada. Hydrological Processes* 20 (17), 3683–3695.
- Yang, R.C., 1998. Foliage and stand growth responses of semimature lodgepole pine to thinning and fertilization. *Can. J. For. Res.* 28 (12), 1794–1804.
- Zhang, J.-G., He, Q.-Y., Shi, W.-Y., Otsuki, K., Yamana, N., Du, S., 2015. Radial variations in xylem sap flow and their effect on whole-tree water use estimates. *Hydrol. Process.* 29 (24), 4993–5002.
- Zobel, D.B., McKee, A., Hawk, G.M., Dyrness, C.T., 1976. Relationships of Environment to Composition, Structure, and Diversity of Forest Communities of the Central Western Cascades of Oregon. *Ecol. Monogr.* 46 (2), 135–156.