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Additional Information

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

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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: 4,500 stems per ha; and T2: 1,100 stems per ha) and one control (C: 27,000 stems per ha), randomly assigned in three blocks. Sap flow and microclimatic variables were continuously monitered 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 mm^2/d), sap flow velocity (64.61 g/cm^2d), and highest stand transpiration (4.36 mm/d), while T2 had the highest tree radial growth (1.28 mm^2/d), sap flow velocity (149.14 g/cm^2d), 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 conditions (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

47   on how thinning can be used to manage ecological responses to forest practices in a changing

48   climate.

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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 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). 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

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94   2017) and slow response to thinning treatments unless being treated early (Bassman 1985, Cole

95   1973, Lotan and Critchfield 1990). Thinning treatments have been also considered as an effective

96   strategy to mitigate the effects of drought (Ambrose et al. 2018, Cabon et al. 2018, Del Río et al.

97   2017, Elkin et al. 2015, Kohler et al. 2010, Rodríguez-Calcerrada et al. 2011, Sohn et al. 2013). A

98   review of juvenile thinning experiments conducted in lodgepole pine forests in western Canada

99   concluded that the treatments improved individual tree growth in terms of diameter and volume

100   (Chase et al. 2016a, Johnstone and Van Thienen 2004), but the majority of treated stands still had

101   lower net stand basal area and total volume increments compared to untreated counterparts 20

102   years after juvenile thinning treatments were applied (Johnstone and Van Thienen 2004). More

103   interestingly, thinning can promote tree vigor that may thus be helpful in withstanding beetle

104   attacks (Mitchell et al. 1983), but tree mortality rate in some cases was actually increased under

105   juvenile thinning due to increased disturbances by snow, wind and certain pests (e.g. Atropellis

106   canker) (Johnstone and Van Thienen 2004). Therefore, whether juvenile thinning is an appropriate

107   measure for sustaining various ecological processes and functions is questionable (Daniel et al.

108   2017, Naudts et al. 2016), requiring more investigations.

109   Various studies have reported positive impacts of thinning on the growth performance of individual

110   trees and tree-water relations under non-drought and drought conditions (Cabon et al. 2018, Kohler

111   et al. 2010, Laurent et al. 2003, Park et al. 2018, Rodríguez-Calcerrada et al. 2011, Simonin et al.

112   2007, Sohn et al. 2013, Sohn et al. 2016a). The better performance of trees in the thinned stands

113   was mainly attributed to enhanced light, soil water, and nutrient availability (Lagergren et al. 2008,

114   Moreaux et al. 2011, Moreno and Cubera 2008, Skubel et al. 2017a). Therefore, it is reasonable to

115   assume that a higher thinning intensity can yield better drought resistance of trees in dry regions.

116   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 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

140   as steep, rugged terrain with cold and snowy conditions in the winter (Coupé et al. 1991). The

141   elevation is around 1675 m a.s.l, and snow cover lasts from early November through middle of

142   June. Seasonal droughts during the summer often occur. Historical climate records from 1986 to

143   2014 show that the mean annual precipitation was 763 mm with less than one-third precipitation

144   in the growing season (between June to October) and the mean annual temperature is1.9 ℃

145   (Winkler et al. 2017). The daily temperature in the studied growing seasons ranged from -8 to 28℃.

146   The study site is generally south aspect, occupied with even-aged lodgepole pine forests that are

147   regenerated after logging in 2002. Understory vegetation including *Rhodendron albiflorum*,

148   *Vaccinium scoparium*, *Valeriana sitchensis*, *Tiarella unifoliata*, and *Arnica latifolia* (Hope 2009)

149   is sparse. Soils were Luvisolic, and were derived from granite parent rock, coarse sandy-loam in

150   texture, with low water holding capacities. More detailed descriptions can be found in Hudson and

151   Golding (1997) and Winkler and Moore (2006).

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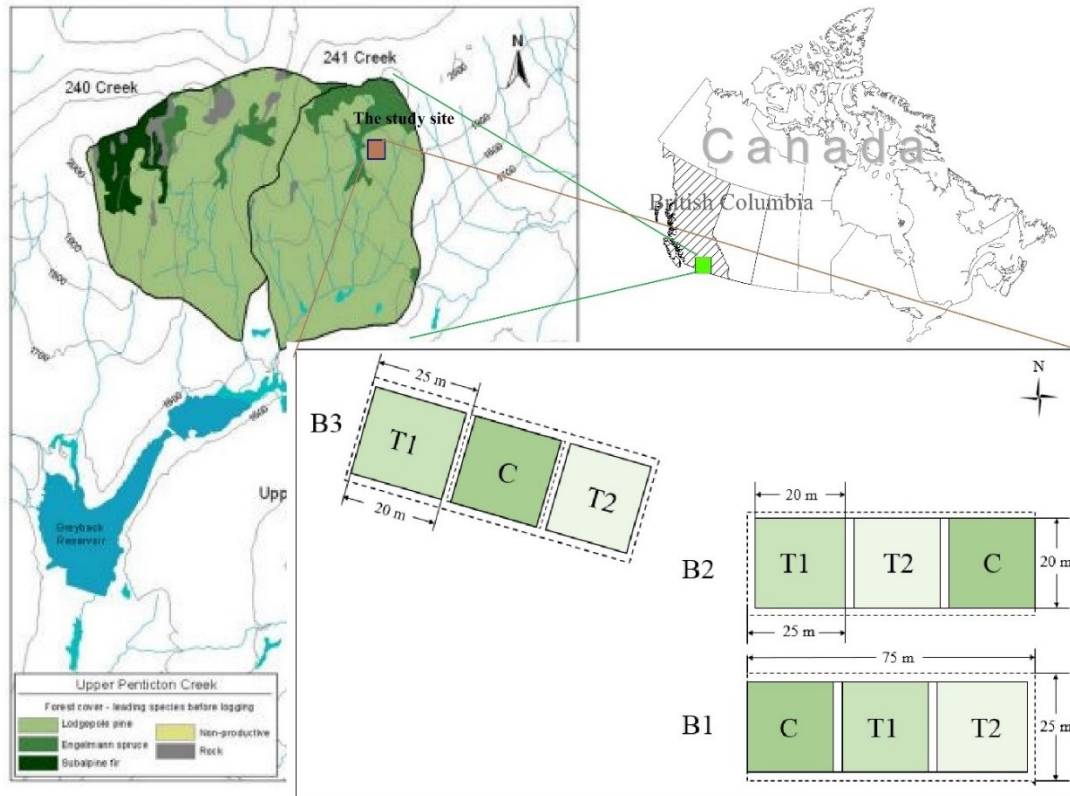
Figure 1. The study location and the experimental layout of three blocks (C: control; T1:

treatment 1 and T2: treatment 2)

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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.

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165   2.3 Monitoring of tree growth

166   Tree growth was quantified as basal area increment (BAI_D, mm^2). In each plot, 45 trees of similar

167   diameter size distributions were selected for measurement. Tree diameters at the breast height

168   (DBH) were measured monthly in the growing season of 2016 and 2017 with an electronic caliper

169   (Model: 500-196-30, Mitutoyo Corporation, Japan). The initial distribution of DBH frequencies

170   of the selected trees are showed in Table 1.

171   Table 1. Distributions of trees in DBH classes in C (control), T1 (treatment 1) and T2 (treatment

172   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%

173

174   In addition, home-made dendrometer sensors, following Cattelino et al. (1986), were installed in

175   five of the selected trees per plot in B1 (15 trees in total) to measure diameter changes (basal

176   perimeter) at 20 cm above ground. The selected trees cover proportionally the range of diameters

177   found in each plot. Basal perimeter (tree girth) was recorded every 20 minutes using a CR1000

178   (Campbell Scientific Inc., Logan, UT, USA). All trees were connected to a central datalogger unit

179   (CR1000, Campbell Scientific Inc., Logan, UT, USA) by using a multiplexer (AM16/32B,

180   Campbell Scientific Inc.) located in B1. Changes in areas at the basal height were recorded as

181   BAI_B (mm). A linear relationship between basal diameter and DBH based on additional

182   measurements from 180 trees in all three blocks is showed below ($R^2 = 0.83$):

183 $$DBH \, (mm) = 0.6935 \times basal \, diameter \, (mm) + 8.5685 \qquad (1)$$

184

185 2.4 Measurement of tree-level transpiration and stand-level transpiration

186 Granier-type sap flow probes (Model TDP-30, Dynamax, Inc., Texas, USA) were also inserted at

187 the breast height in the five previously selected trees that were equipped with home-made

188 dendrometers at each plot (15 trees in total) in B1. In consideration of the small DBHs of young

189 trees (Table 1), each tree was installed with one pair of TDP-30 probes assuming that there were

190 no systematic variations in sap flow density along the sapwood depth (Clausnitzer et al. 2011). All

191 the probes were oriented towards the southern exposure, and were fully insulated with thermal

192 insulation aluminum foil to minimize possible effects of ambient temperature gradients. The

193 installation and detailed description of the probes can be found in Granier et al. (1990). Sap flow

194 was calculated with empirical equations (2-4) calibrated from Granier (1987):

195 $$K = (\Delta T_{max} - \Delta T)/\Delta T \qquad (2)$$

196 $$SFD = 0.0119 \times K^{1.231} \qquad (3)$$

197 $$F = As \times SFD \times 3600 \qquad (4)$$

198 Where, K is a dimensionless variable calculated from the measured temperature difference

199 between two thermocouples of the probe (ΔT, ^{0}C). It was assumed that no sap flow occurs at night

200 when the temperature difference reached its maximum (ΔT_{max}, ^{0}C). SFD is the sap flow velocity

201 (g/cm^2), F denotes the sap flow rate, (g/h), and As stands for the sapwood area per tree (cm^2).

202 Sapwood area was inferred from the linear relationship between DBH and sapwood area (Equation

203 (5), $R^2 = 0.98$) derived from seven trees representing a range of diameters within the stand. This

204 relationship was assumed to be hold for trees in both the control and thinned plots (Bréda and

205 Granier 1996).

206   As (mm^2) = 102.81 × DBH (mm) − 3709.3   (5)

207   Daily mean SFD values for C, T1 and T2 were also upscaled to calculate daily stand-level

208   transpiration following by Bréda and Granier (1996). Stand sapwood areas were summed

209   according to the stand densities for the thinned and unthinned stands, DBH distributions (Table 1)

210   and the DBH-sapwood relationship (Equation (5)).

211     $E_S = \overline{SFD} \times As_g$ (6)

212   Where, Es is the daily stand transpiration (mm/d); $\overline{SFD}$ is the mean SFD of the five trees per each

213   plot for C, T1 and T2, respectively (g/cm^2); and As$_g$ is the estimated total stand sapwood area (cm^2)

214   for 400 m^2 plot.

215   Additional species-specific calibration of the empirical equations (2-4) was not considered, as the

216   original equations have been widely used in other sap flow studies on lodgepole pine stands (Reid

217   et al. 2006, Zhang et al. 2015).

218

219   2.5 Calculation of resistance index

220   The resistance of trees to drought was quantified using a resistance index. The resistance index of

221   tree growth, sap flow velocity and stand transpiration were calculated as the ratio of target variables

222   under the drought year (Y$_{dy}$) to that in the pre-drought year (Y$_{predy}$), following Lloret et al. (2011)

223   and Sohn et al. (2016b):

224     $\text{RI} = \dfrac{Y_{dy}}{Y_{predy}}$ (7)

225   Where, Y$_{dy}$ represents the target variables (i.e., tree mean daily BAI$_D$, mean daily SFD or mean

226   Es) during the drought year (2017), and Y$_{predy}$ represents the target variables during the pre-drought

227   year (2016).

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229   2.6 Collection of climate data

230   One climate station (HOBO weather station, Onset Computer, Bourne MA, USA) was installed in

231   each plot in B1 to collect climate data including transmitted solar radiation (Rn, W/m^2), relative

232   humidity (RH, %), temperature (T, ^oC), precipitation (P, mm) and wind velocity (Wv, m/s) at 10-

233   minute intervals during the study period. The sensors were placed at approximately 2.5 m height

234   which is just at the canopy level. VPD is calculated from RH and T according to Goff–Gratch

235   equation (Goff 1946).

236   Soil volumetric water content (VWC) in B1 was measured at two depths (20 cm and 40 cm) in

237   three randomly selected locations per plot by EC-5 sensors (Decagon, Pullman, WA, USA) at 20-

238   minute intervals for the study period. The selection of soil depths was based on studies reporting

239   that tree transpiration was associated with soil water content at the depth of 10 to 20 cm (Raz-

240   Yaseef et al. 2012, Sun et al. 2014a). Manual measurements of soil VWC at 20 cm depth in the

241   three blocks were also made weekly during the growing season of 2017 using a GS-1 portable

242   measuring system (Decagon, Pullman, WA, USA).

243

244   2.7 Statistical analysis

245   The BAI_D of selected trees were converted into daily means in order to adjust for different growing

246   season lengths in 2016 and 2017.

247   BAI_D among the three treatments was analyzed by ANCOVA with the initial DBH of the trees as

248   covariate, and the block, treatment and year (drought) as factors. Differences in sap flow velocity

249   (SFD) were analyzed with mixed-effect models considered the thinning treatments, drought and

250   date as fixed effects and the tree identity as a random effect on SFD.

251   In all cases, data were checked to meet the requirements of homogeneity of variance and normality

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252 (and homogeneity of the regression slopes in the ANCOVA). In most cases, the assumptions were

253 violated, even though multiple methods including log transformation, square roots and cubic roots

254 transformations and Box-Cox transformation were applied. Therefore, comparisons on BAI_D, SFD,

255 ES, and RI between treatments or between years were performed with independent-t test, if data

256 met the requirements of homogeneity of variance and normality. Otherwise, the Mann-Whitney U

257 test was employed.

258 We were also interested in the response of SFD to VPD, and the relationship between SFD and

259 VPD has been fitted into an exponential saturation equation (equation (8)) (Ewers et al. 2001,

260 Tang et al. 2006) or a parabolic equation (equation (9)) (Grossiord et al. 2018).

261 $\text{SFD} = a\,(1 - e^{-b\,\times VPD})$ (8)

262 $\text{SFD} = \text{mVPD}^2 + \text{nVPD}$ (9)

263 Where, a, b, m and n are fitted coefficients.

264 Therefore, the relationship between SFD and VPD were determined by comparing which equations

265 yielded the best fit (R^2). Coefficients of the equation (8) and the equation (9) and their goodness

266 of fit were listed in Table S5. As the equation (9) yielded higher R^2, the sensitivity of SFD to VPD

267 (S_{VPD}, g/cm^2·kPa) was denoted as:

268 $S_{VPD} = \dfrac{d\,SFD}{d\,VPD} = 2mVPD + n$ (10)

269 The extent of drought in 2017 was evaluated by the Standard Precipitation Index (SPI) (Guttman

270 1999) based on the long-term precipitation data (1953-2017) derived from the Penticton Airport

271 Climate Station around 20 km southwest of the study site. Correlation was examined using the

272 Spearman test. A significance level of $p < 0.05$ was used for all analyses. All data were processed

273 by R (R Core Team (2014) and SPSS for Windows (SPSS, Inc., USA).

274

3. Results

275

276   3.1 Difference in climatic conditions of the growing seasons in 2016 and 2017

277   Climatic conditions in the growing seasons varied between 2016 (Figure S1) and 2017 (Figure S2).

278   Average daily transmitted solar radiation across all blocks was 103.9 and 141.5 W/m^2 for the

279   growing seasons of 2016 and 2017, respectively. The average growing season temperature was 7.7

280   ^{0}C in 2016 versus 12.1 ^{0}C in 2017. Daily mean RH was 74.5% in 2016 and 56.5% in 2017. As a

281   result, the daily mean VPD in 2016 (0.34 kPa) was less than half of that in 2017 (0.72 kPa). Daily

282   mean precipitation over the growing season was nearly 5 times greater in 2016 (1.59 mm) than in

283   2017 (0.32 mm). Averaged daily soil VWC across blocks were 17.5% and 14.3% for the depths

284   of 20 and 40 cm in 2016, respectively, while those amounts were reduced to 12.9% and 11.3%,

285   respectively in 2017. All daily mean environmental variables in 2016 were significantly different

286   from those in 2017 (all p < 0.01). The Standardized Precipitation Index (SPI) showed that 2016

287   was a normal to humid year, while 2017 was a typical drought year (Table S1).

288

289   3.2 Transmitted solar radiation, soil volumetric water content and VPD between treatments

290   Transmitted solar radiation and averaged soil VWC across 20 cm and 40 cm depths were

291   consistently significantly higher in T2, followed by T1 and then C in both years. However, during

292   the drought year, the soil VWC at 20 cm was not statistically different between C and T1, and soil

293   VWC at 40 cm was not significantly different between T1 and T2. No significant differences in

294   VPD between C and T1 was found in the non-drought year. (Table 2).

295

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

297   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]

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

299

300   3.3 Tree growth

301   The mean daily BAI_D in the C, T1 and T2 during the two-year study period were significantly

302   different from each other, with the mean daily value of 0.14, 0.79 and 1.28 mm^2/d for C, T1 and

303   T2, respectively (all p <0.01). No significant reduction of BAI_D before and during drought was

304   detected for C, T1 and T2. When each growing season was considered separately, BAI_D of T2 was

305   significantly higher to that from C (both years) and T1 (only in the drought year), whilst C and T1

306   were statistically different only in the non-drought year (Figure 2).
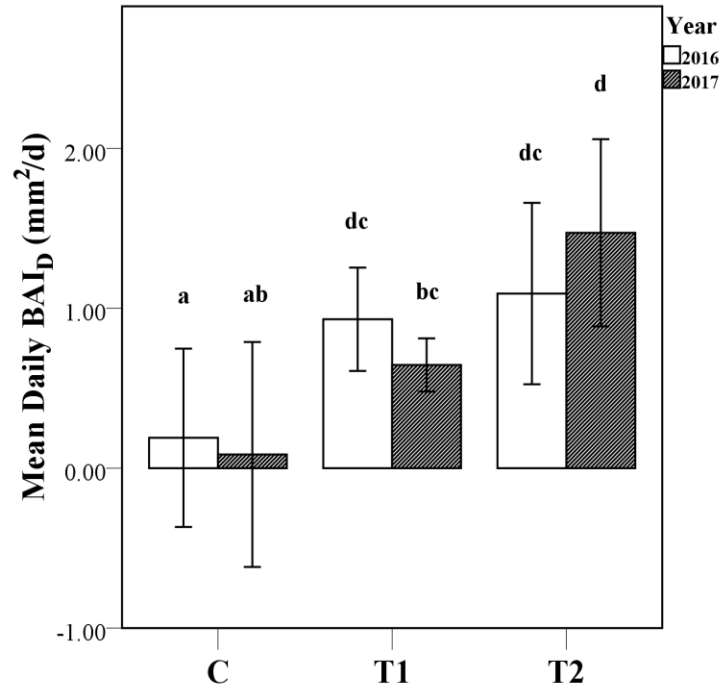
Figure. 2 Mean daily basal area increment (BAI_D) at the respective growing seasons of 2016 and 2017. Error bars denote the 95% confidence interval, and bars with different letters indicate significant differences between treatments and between years.

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 (Figure 3). However, there was no significant difference in the mean daily SFD between T1 and T2 in 2016, while the significant difference occurred in the drought season of 2017 (Figure 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.
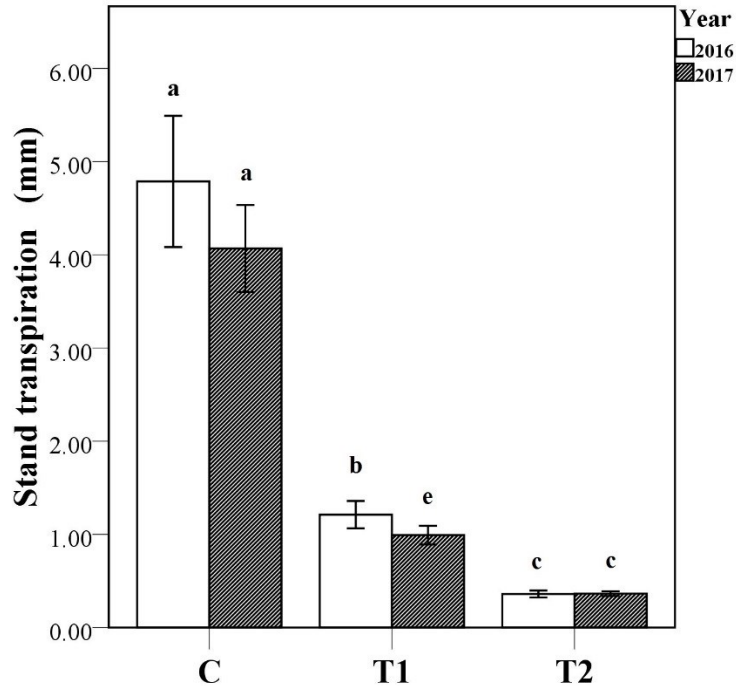
16
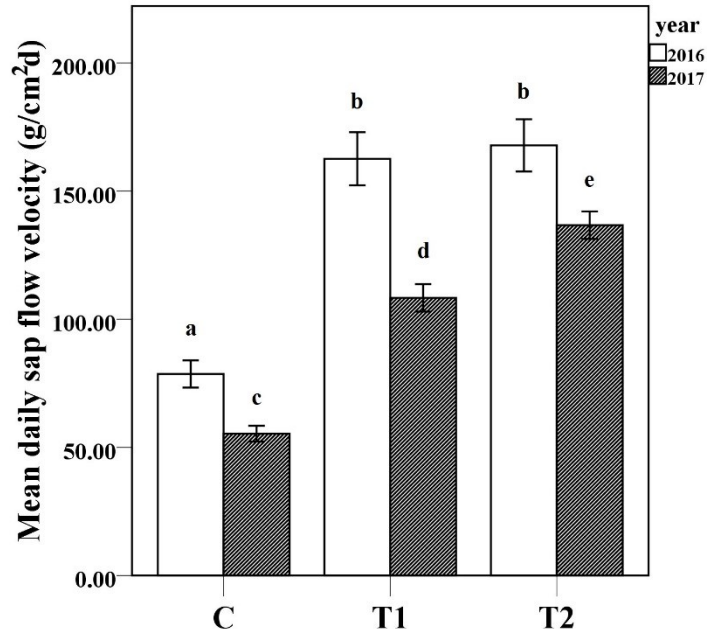
Figure 3. Mean daily sap flow velocity (SFD) at the respective growing seasons of 2016 and 2017. Error bars denote the 95% confidence interval, and bars with different letters indicate significant differences between treatments and between years.

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

17

Figure 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.

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 (Figure 5 (1)). RI of sap flow velocity, however, was not significantly different between C and T1 (Figure 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 RI of stand transpiration. Nevertheless, these results clearly suggest that T2 has the highest resistance to the drought.

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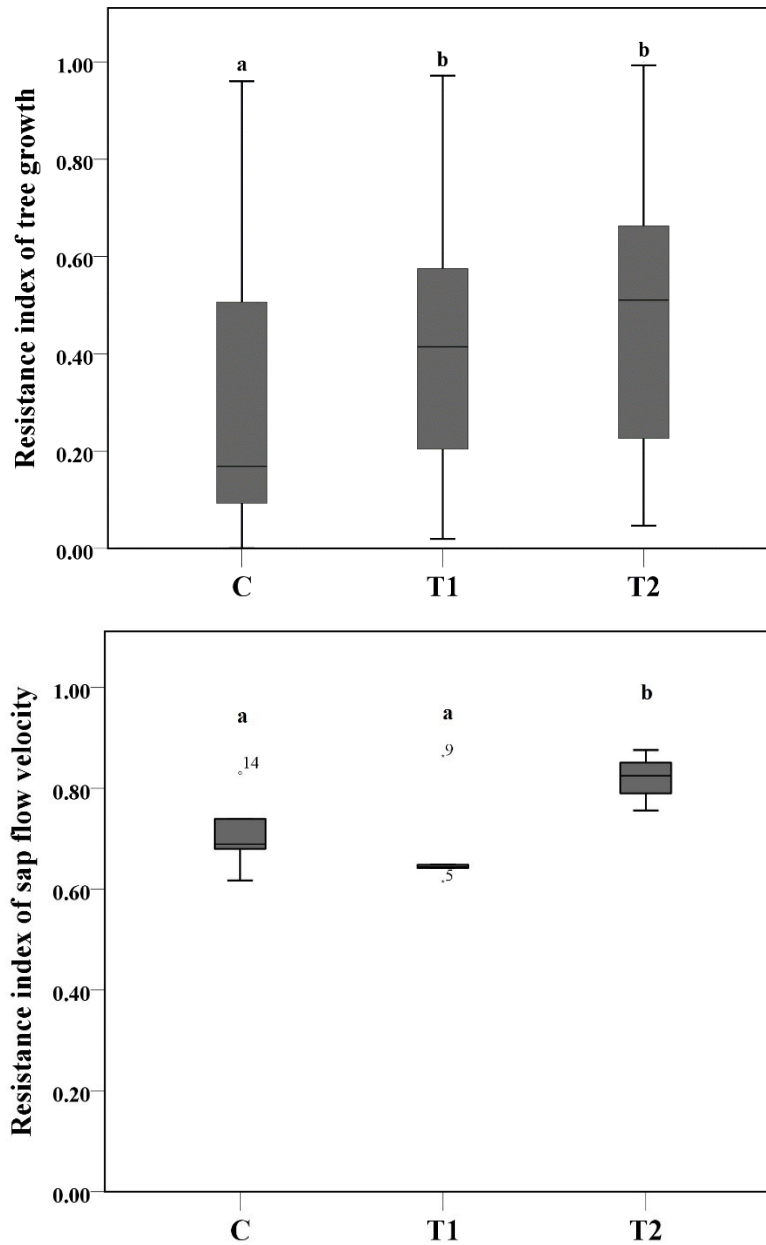
Figure 5. Resistance indices of tree growth (1) and sap flow velocity (2). Different letters

indice significant differences between treatments. Numbers indicate the tree outliers.

4. Discussion

Our results generally agree with other studies showing that thinning can greatly increase tree radial

345   growth (Chase et al. 2016b, Fernandes et al. 2016, Jimenez et al. 2008, Lindgren and Sullivan

346   2013, Martín-Benito et al. 2010, Sullivan et al. 2006) and sap flow velocity (del Campo et al. 2014,

347   Fernandes et al. 2016, Gebhardt et al. 2014, Medhurst et al. 2002, Simonin et al. 2007, Skubel et

348   al. 2017b), while decreasing stand-level transpiration due to the decrease in stand density

349   (Forrester et al. 2012, Gebhardt et al. 2014, Moreaux et al. 2011, Simonin et al. 2007, Skubel et al.

350   2017b, Sun et al. 2014b). Stand-scale transpiration decreased 75.3% and 91.7% in T1 and T2,

351   where stand densities had been reduced by 83.3% and 95.9%, respectively, in comparison to C.

352   This relatively smaller percentage reduction in stand transpiration than the percentage decrease in

353   stand density is due to the enhanced transpiration of individual trees following the thinning

354   treatments, which is consistent with the finding from Simonin et al. (2007).

355   The above-mentioned positive effects of thinning on tree radial growth and sap flow velocity are

356   mainly due to more availability of resources (e.g., light, soil nutrients, soil water content), as a

357   result of reduced competition after thinning (González de Andrés et al. 2018, Park et al. 2018,

358   Skubel et al. 2017a). Increased light penetration promotes carbon assimilation processes (Aussenac

359   2000), and open canopy exposure causes higher negative values of leaf water potential, leading to

360   higher individual tree transpiration (Simonin et al. 2007). On the other hand, decreased

361   interception of rainfall and total stand transpiration can lead to higher soil moisture that exerts

362   stronger regulation in maintaining higher stomatal conductance, and thus both higher

363   photosynthesis and transpiration rates (Giuggiola et al. 2016). Soil nutrients (e.g., N, P, and K

364   nutrition) have been observed to be increased under juvenile thinning treatments by increasing soil

365   moisture, temperature and thus microbial activitivies (Carlyle 1995, Chase et al. 2016a, Thibodeau

366   et al. 2000). Significant differences in some soil nutrients may not occur immediately after thinning

367   treatments were applied (e.g., NO_3-N in Hope (2009) and mineral N and N mieralization rate in

368   Carlyle (1995)), but in the long term, enhanced soil nutrients play an important role in tree growth

369   (Chase et al. 2016a, Jokela et al. 2004). Unfortunately, we did not measure soil nutrients in this

370   short term study, and thus were not able to account for the effects of changed soil nutrients resulted

371   from juvenile thinning treatments on tree radial growth and sap flow velocity. Therefore, the

372   following discussion focused on the effects of increased availability of light and soil water after

373   thinning for explaining greater growth and transpiration at the individual tree level.

374   Our two-year results demonstrate that the more heavily thinned treatment (T2) had the more

375   pronounced effect on tree growth, sap flow velocity, and stand-level transpiration. Significant

376   improvements in radial growth and tree transpiration in the heavily thinned stand corresponded

377   with higher light and soil water availabilities, as well as the higher evaporative demand (VPD) in

378   T2 than the other two stands (Table 2). This finding is consistent with those of Park et al. (2018)

379   who studied two thinning treatments (light-thinning: 320 tree/ha, and heavy-thinning: 240 tree/ha)

380   in a 50-year-old Korean pine (*Pinus koraiensis*) forest. Based on their 4-year study, Park et al.

381   (2018) found that heavy thinning greatly increased tree growth and sap flow velocity with the

382   effects being increased over time, while the light thinning had little effect on site water availability

383   and tree growth, and the resultant enhancement on sap flow velocity declined over time. Thus,

384   Park et al. (2018) concluded that the heavier thinning was an appropriate management practice for

385   mature pine plantations in their region.

386   However, the effects of thinning intensity are subject to interplay among various factors. For

387   example, Jimenez et al. (2008) failed to find significant differences in tree-level transpiration and

388   soil water availability under two intensities of thinning treatments (3,850 trees/ha and 1,925

389   trees/ha) in a 8-year-old *Pinus pinaster* stand. They attributed those insignificant differences to the

390   similar reduction in the absolute basal area instead of the percentage area reduction (Jimenez et al.

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391 2008). Gebhardt et al. (2014), who studied moderate (removal of 43% basal area) and heavy

392 thinning treatments (removal of 67% basal area) in a 26 year old Norway spruce *(Picea abies)*

393 stand, suggested that the effects of heavy thinning would be larger if the understory did not respond

394 promptly to the increased light and water availability resulted from thinning, and indicated that

395 repeated moderate thinning was a better option than the heavy thinning, because: (1) wood biomass

396 production was not maximized by the heavy thinning at the stand level; and (2) the heavy thinning

397 induced progressive development of understory which not only competed for resources with trees

398 but also hindered natural regeneration (Gebhardt et al. 2014). In our study, the understory was

399 sparse, so its effects are expected to be minor, but the role of the understory in the longer term

400 could become important affecting the difference between the two thinning treatments. This further

401 highlights a need to examine the long-term effects of the thinning treatments in our studied young

402 forest stands.

403 Surprisingly, we didn't detect significant reductions on the BAI_D of all the three groups caused by

404 the drought, even though the mean daily BAI_D was smaller in the drought year than the non-

405 drought year (except for T2), and the drought-induced earlier cessation of stem growth was

406 observed (Figure S3). We attributed this insignificance mainly to the great variance in our data of

407 DBH (high standard deviations in the Table S2) and possible delayed responses, as most studies

408 found significant decreases of tree growth during the drought period (Eilmann and Rigling 2012,

409 Julio Camarero et al. 2018). However, Sohn et al. (2013) also found that the more heavily thinned

410 stands can mantain growth rates during drought, probabaly due to higher soil water availability.

411 Nevertheless, the significantly lower RI of tree growth in C indicated that the unthinned stands

412 were more vulnerable to the drought in term of radial growth. In addition, our results on the drought

413 resistance of tree growth of the thinned stands support the review by Sohn et al. (2016b) who found

414 that the RI of tree growth in coniferous species did not significantly vary with the thinning

415 intensities, based on up to 20 studies across the world. They indicated that the reduction of stomatal

416 conductance irrespective of thinning treatments, which was found in most of the studies, was likely

417 the reason. As stomatal conductance is highly influenced by atmospheric evaporative demand and

418 soil water availability (Edward Boyd Reid et al. 2006, Jiménez et al. 2009), higher soil water

419 availability and stronger atmospheric regulation in thinned stands can improve RI of tree growth,

420 as found in our study.

421 The drought reduction of SFD is consistent with findings reported in the literature for several tree

422 genera (e.g., *Ficus*, *Tilia*, *Pinus*, *Picea* and *Fraxinus*) that experienced droughts (Nadezhdina and

423 Cermak 2000, Stohr and Losch 2004). To our surprise, we did not find significant differences in

424 RI of sap flow velocity between C and T1. The explanations may lie in both the regulation of

425 microclimatic variables that influence stomatal behaviors, and the adjusted physiological

426 sensitivity of sap flow velocity to environmental regulations. As shown in Figure 3, SFD was not

427 significantly different between T1 and T2 in 2016, which may be explained by the combined

428 effects between the slightly higher sensitivity of SFD in T1 to VPD (Figure 6(1)) and the

429 significantly lower daily VPD in T1 than T2 (Table 2). The daily sensitivities of SFD to VPD (S_{VPD},

430 Table S5) were significantly different among the three groups in 2016, with daily averages of 155.4

431 $g/cm^2 \cdot kPa$, 364.4 $g/cm^2 \cdot kPa$ and 303.3 $g/cm^2 \cdot kPa$ in C, T1 and T2, respectively (all p<0.05). The

432 higher S_{VPD} but lower VPD in T1 led to similar magnitudes of SFD as T2 that had lower S_{VPD} but

433 higher VPD (e.g., the products of daily mean VPD and daily mean S_{VPD} are 116.6 g/cm^2 in T1 and

434 118.3 g/cm^2 in T2). In 2017, the daily S_{VPD} was statistically different among the three groups (all

435 p<0.1), but the mean daily value decreased from that in 2016 to 37.0 $g/cm^2 \cdot kPa$, 85.4 $g/cm^2 \cdot kPa$

436 and 128.4 $g/cm^2 \cdot kPa$ for C, T1 and T2, respectively. Clearly, the reduction of the daily S_{VPD} in T2

437   is the lowest. In addition, the significantly higher daily VPD in T2 might enlarge the differences

438   in tree sap flow velocity between T1 and T2, while the significantly lower daily VPD in T1 might

439   reduce the differences between T1 and C. All above explain significantly higher RI of sap flow

440   velocity in T2, even though there was no significant difference in RI of sap flow velocity between

441   T1 and C.

442   The sensitivity of SFD to VPD is greatly influenced by the soil water availability (Bovard et al.

443   2005, Gyenge et al. 2011), which was supported by our results, as the response of SFD to VPD

444   among treatments corresponded well with the magnitudes of the averaged soil VWC for each

445   treatment (Fig S4). The soil VWC of both thinned stands was less responsive to precipitation in

446   the non-drought year than in the drought year (Fig S4), indicating that soil VWC was not a limiting

447   factor for tree growth and tree-water consumption (range between 15-20%). In the drought year,

448   however, the reduction of soil VWC in T1 was steeper than in T2, reaching lower values by the

449   end of the drought spell (Fig S4), probably due to the higher tree density and stand tranpiration in

450   T1. As a result, SFD was greatly reduced in T1 compared to T2, as soil VWC in the former could

451   have been below 7-8% for several weeks (Fig S4), i.e., below the wilting point for this coarse

452   sandy-loam soil, consequently the RI of SFD was significantly lower in T1 than in T2, given the

453   high values recorded in the preceding wet year. This indicates that thinning intensity affects the

454   vulnerability of tree-water relations to drought, but also indicates the ability of T1 to adjust its

455   water use to changing soil moisture (shortage/abuncance), and hence a plastic response of the

456   species.

457   Thinning modifies microclimate conditions, and consequently leads to major changes in

458   physiological responses of trees (Aussenac 2000, Chen et al. 1993, Zobel et al. 1976).

459   Modifications on microclimates under thinning (Anderson et al. 2007, Weng et al. 2007) and

460   enhanced sensitivities of tree transpiration to VPD by thinning treatments (Gyenge et al. 2011,

461   Tateishi et al. 2015) have been previously reported, but little is known about their combined effects

462   on drought resistance of trees. Our study implies that such combined effects could be more

463   pronounced in the more heavily thinning stands. However, physiological mechanisms governing

464   these combined effects requires further investigation.
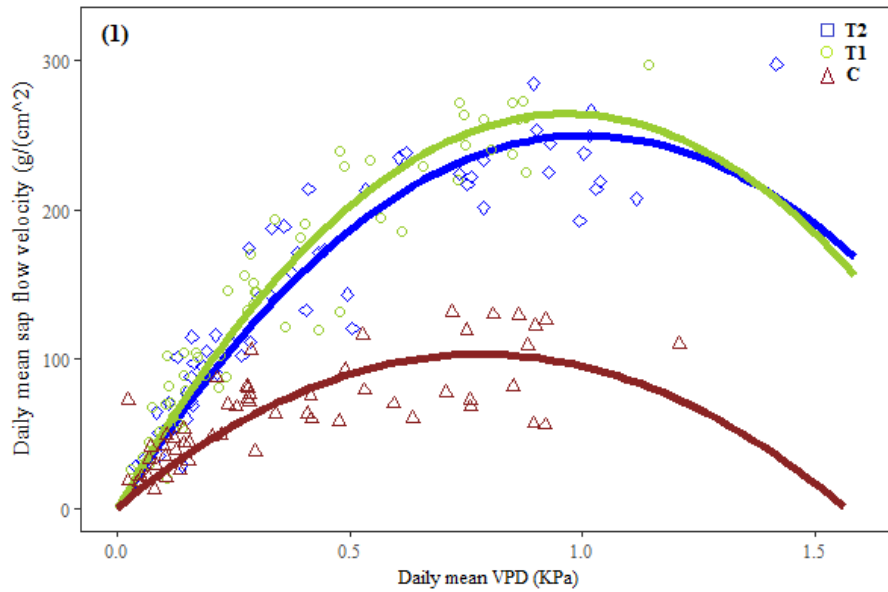
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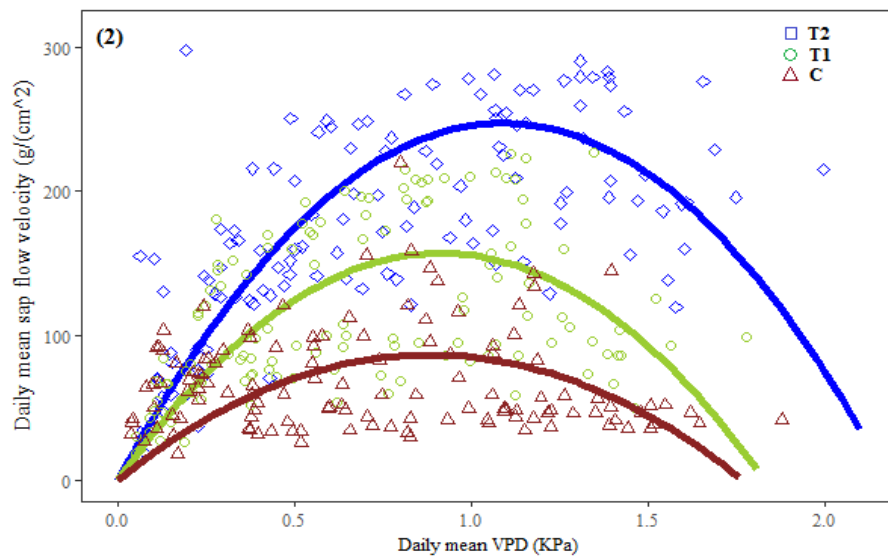
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467   Figure 6. The daily mean sap flow velocity as a function of VPD in 2016 (1) and 2017 (2). Blue,

468   green and red colors denote T2, T1 and C, respectively.

469   Interestingly, no significant reduction of the stand-level transpiration in the drought year in

470   comparison to the non-drought year was found in C and T2 in our study (Figure 4). This

471   observation is contrary to some previous studies showing that droughts greatly reduce stand-level

472   transpiration (Schäfer et al. 2014, Stojanović et al. 2017). The insignificance of stand transpiration

473   of C between 2016 and 2017 might be due to the greater variance in the dataset (Table S4), while

474   the insignificant differences of stand transpiration of T2 before and during the drought may be

475   attributed to the increased total basal area in the thinned stands in the two growing seasons

476   compensating for the decrease in SFD during the drought. Similar to our observation, Simonin et

477   al. (2007) discussed that the thinned stands might maintain relatively higher stand transpiration

478   rates than the unthinned counterparts during the drought period as the higher leaf-level

479   transpiration in thinned stands could compensate for the reduction of leaf area. Overall, the ability

480   of maintaining relatively high stand transpiration in the heavily thinned stands indicates the benefit

481   of heavy juvenile thinning in sustaining tree growth and transpiration under the drought in our

482   study area.

483

5. Conclusion

485   Our study presented the short-term benefits of the juvenile thinning in terms of increasing tree

486   radial growth, sap flow velocity, and reducing stand transpiration. Those effects were more

487   pronounced in the more heavily thinned stands, demonstrating that heavier thinning can produce

488   more ecological benefits, such as carbon sequestration and water conservation. Our results also

489   showed that the difference in the studied variables between the two thinning treatments was only

490   significant during the drought period, suggesting that heavier thinning can more effectively

491   mitigate the negative impacts of the drought. Thus, we conclude that the thinning treatments have

492 significantly provided short-term ecological benefits to young overstocking lodgepole pine forests

493 in the BC interior. More studies on long-term effects of thinning are still needed to support

494 development of sustainable management for wood production, carbon sequestration and water

495 conservation in lodgepole pine forests in the context of climate change impacts.

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Supplementary Materials

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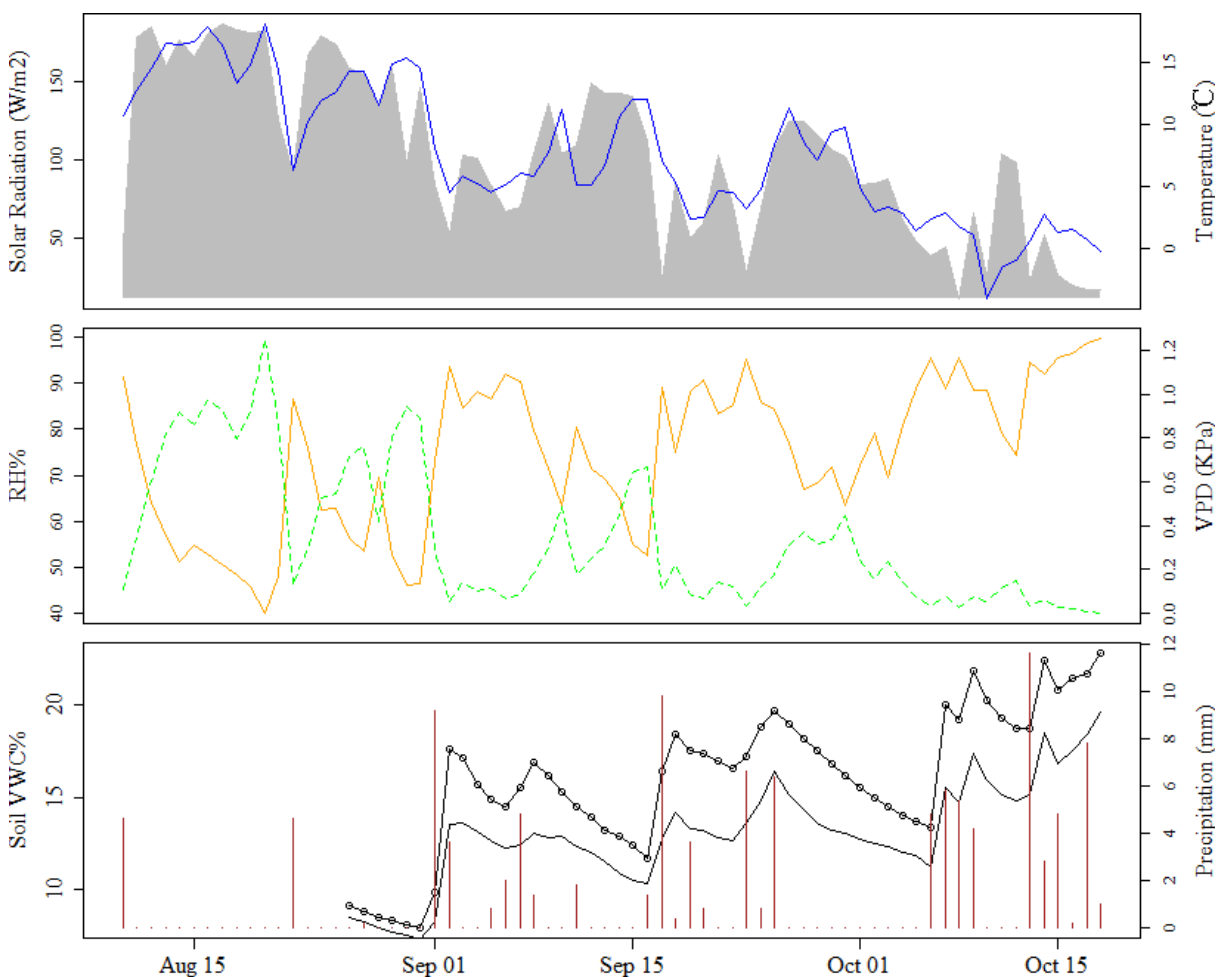
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518   Figure S1. Climate conditions in 2016. Climate variables includes temperature (in blue),

519 transmiteed solar radiation (in gray), RH (in orange), VPD (in green), soil VWC at 20 cm (black

520   dots), soil VWC at 40 cm (black line) and precipitation (in brown) in 2016.
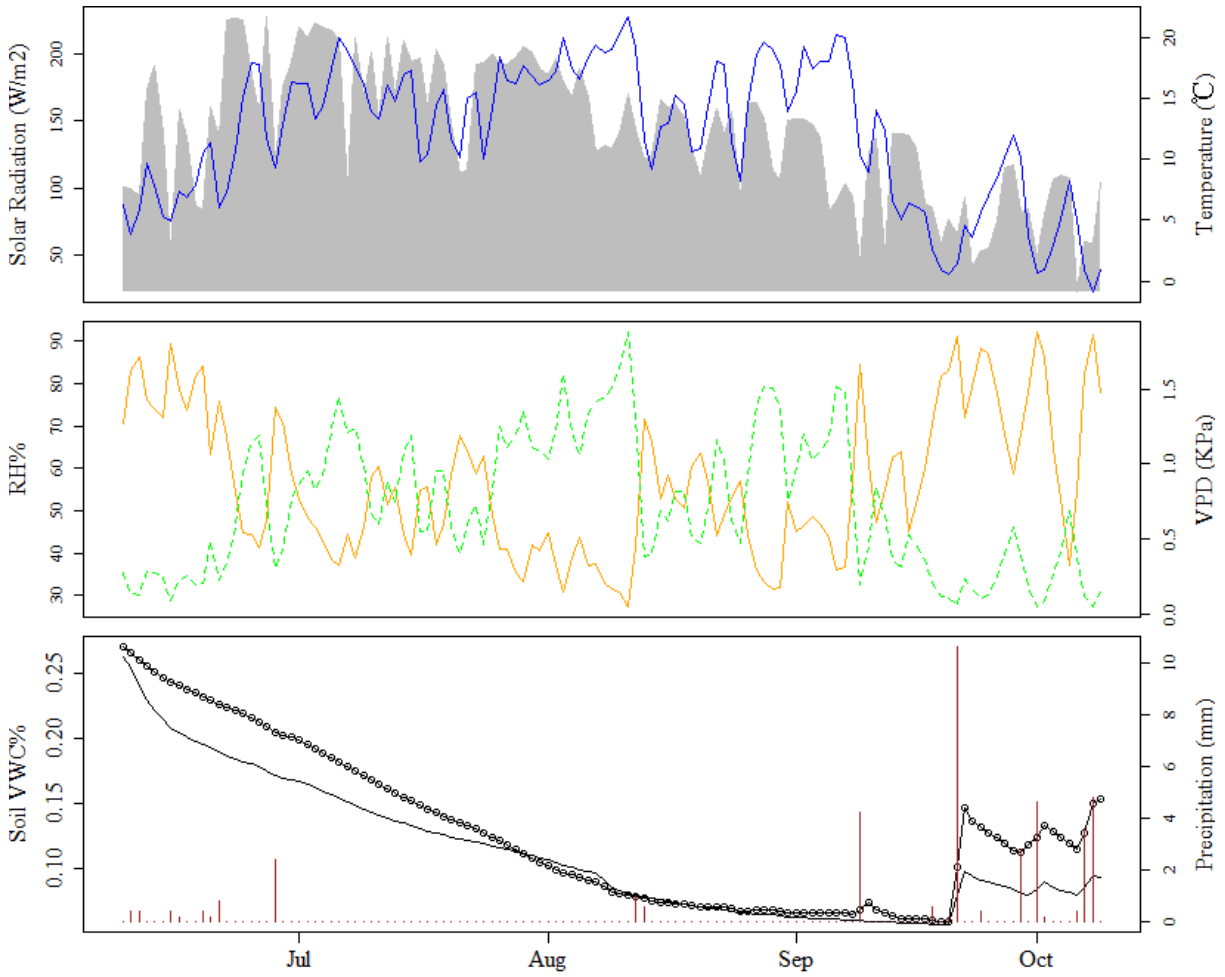
Figure S2. Climate conditions in 2017. Climate variables includes temperature (in blue), transmitted solar radiation (in gray), RH (in orange), VPD (in green), soil VWC at 20 cm (black dots), soil VWC at 40 cm (black line) and precipitation (in brown) in 2017.

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Table S1. Standardized Precipitation Index (SPI) for 2016 and 2017

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

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552   Table S2 (1). Summary of mean daily BAI_D for each treatment in the year 2016 and 2017.

553   Different letter represents statistically significant differences between treatments for a given year

554   and between years for a given treatment. Significance level is accepted at P<0.05.

Treatment		Mean Daily BAI (mm²/d)	Std. Deviation	N
C	2016	0.190^a	3.276	135
	2017	0.086^{ab}	4.133	135
	Total	0.138	3.723	270
T1	2016	0.931^{dc}	1.898	135
	2017	0.646^{bc}	0.979	135
	Total	0.788	1.514	270
T2	2016	1.095^{dc}	3.319	134
	2017	1.468^d	3.427	134
	Total	1.281	3.372	268

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556   Table S2 (2). Summary of p-values from Levene's test for equality of variances, independent t
557   test (for p-value Levene >0.05) and Mann-Whitney U test (for p-value of Levene <0.05) on daily
558   BAI_D among various groups.

Group		Levene's Test for equality of variances p-value	p-value
C-2016	T1-2016	<0.001	0.005
C-2016	T2-2016	0.197	0.026
C-2016	C-2017	0.001	0.904
C-2016	T1-2017	<0.001	0.039
C-2016	T2-2017	0.022	<0.001
T1-2016	C-2017	0.39	0.032
T1-2016	T1-2017	<0.001	0.186
T1-2016	T2-2017	0.45	0.11
T1-2016	T2-2016	0.029	0.542
T2-2016	C-2017	0.033	0.001
T2-2016	T1-2017	<0.001	0.104
T2-2016	T2-2017	0.308	0.357
C-2017	T1-2017	0.440	0.127
C-2017	T2-2017	0.222	0.003
T1-2017	T2-2017	0.003	<0.001

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561   Table S3 (1). Summary of mean daily sap flow velocity for each treatment in the year 2016 and

562   2017. Different letter represents statistically significant differences between treatments for a

563   given year and between years for a given treatment. Significance level is accepted at P<0.05.

Treatment		Mean daily sap flow velocity ($g/cm^2 d$)	Std. Deviation	N
	2016	78.98^a	44.43	77
C	2017	55.62^c	27.54	123
	Total	64.61	36.73	200
	2016	162.60^b	84.08	77
T1	2017	108.33^d	55.75	123
	Total	129.23	72.84	200
	2016	171.86^b	83.68	77
T2	2017	134.92^e	54.41	123
	Total	149.14	69.38	200

564

565   Table S3 (2). Summary of p-values from Levene's test for equality of variances, independent t
566 test (for p-value Levene >0.05) and Mann-Whitney U test (for p-value of Levene <0.05) on daily
567   sap flow velocity among various groups.

| Group		Levene's Test for equality of variances p-value	p-value
C-2016	T1-2016	<0.001	<0.001
C-2016	T2-2016	<0.001	<0.001
C-2016	C-2017	<0.001	<0.001
C-2016	T1-2017	0.001	<0.001
C-2016	T2-2017	0.014	<0.001
T1-2016	C-2017	<0.001	<0.001
T1-2016	T1-2017	<0.001	<0.001
T1-2016	T2-2017	<0.001	0.029
T1-2016	T2-2016	0.857	0.494
T2-2016	C-2017	<0.001	<0.001
T2-2016	T1-2017	<0.001	<0.001
T2-2016	T2-2017	<0.001	0.001
C-2017	T1-2017	<0.001	<0.001
C-2017	T2-2017	<0.001	<0.001
T1-2017	T2-2017	0.458	<0.001

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569   Table S4 (1). Summary of mean daily stand transpiration for each treatment in the year 2016 and

570   2017. Different letter represents statistically significant differences between treatments for a

571   given year and between years for a given treatment. Significance level is accepted at P<0.05.

Treatment		Mean daily stand transpiration (mm)	Std. Deviation	N
C	2016	4.79^a	3.11	77
	2017	4.07^a	2.52	123
	Total	4.36	2.78	200
T1	2016	1.21^b	0.65	77
	2017	0.99^e	0.54	123
	Total	1.08	0.59	200
T2	2016	0.36^c	0.16	77
	2017	0.36^c	0.14	123
	Total	0.36	0.15	200

572

573   Table S4 (2). Summary of p-values from Levene's test for equality of variances, independent t
574   test (for p-value Levene >0.05) and Mann-Whitney U test (for p-value of Levene <0.05) on daily
575   stand transpiration among various groups.

Stand transpiration		Levene's Test for equality of variances p-value	p-value
C-2016	T1-2016	<0.001	<0.001
C-2016	T2-2016	<0.001	<0.001
C-2016	C-2017	0.048	0.102
C-2016	T1-2017	<0.001	<0.001
C-2016	T2-2017	<0.001	<0.001
T1-2016	C-2017	<0.001	<0.001
T1-2016	T1-2017	0.062	0.012
T1-2016	T2-2017	<0.001	<0.001
T1-2016	T2-2016	<0.001	<0.001
T2-2016	C-2017	<0.001	<0.001
T2-2016	T1-2017	<0.001	<0.001
T2-2016	T2-2017	0.076	0.852
C-2017	T1-2017	<0.001	<0.001
C-2017	T2-2017	<0.001	<0.001
T1-2017	T2-2017	<0.001	<0.001

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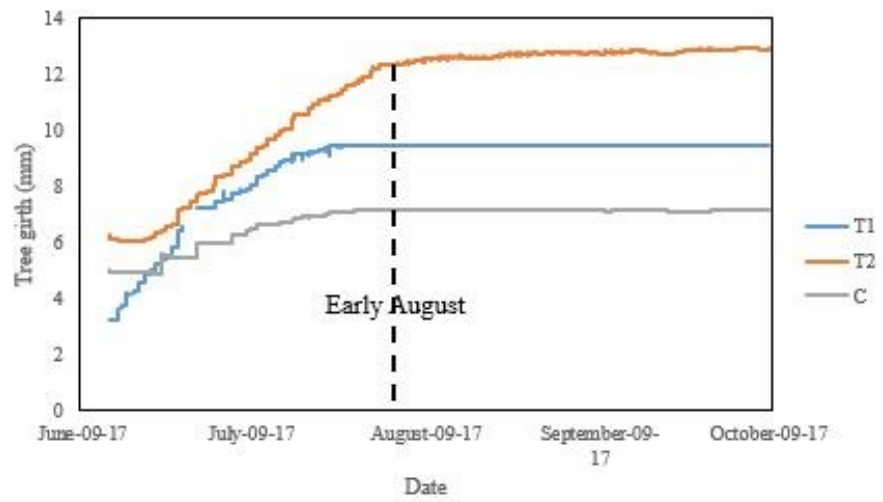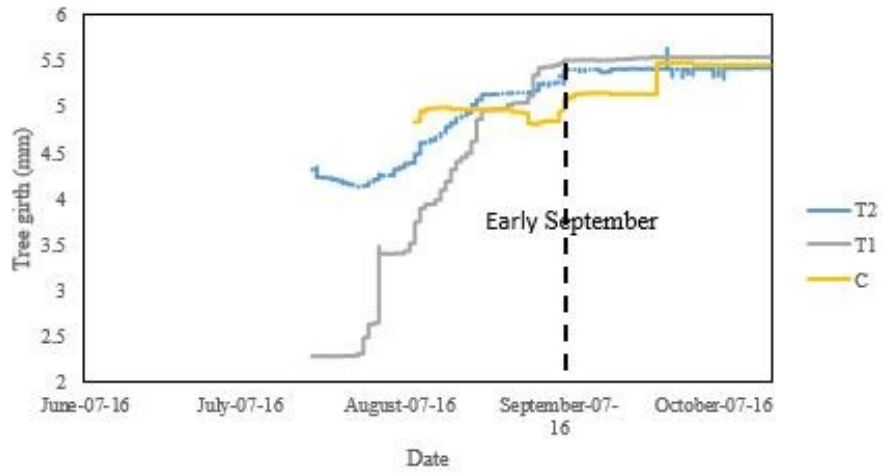
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580   Figure S3 Continuously tree girth data from home-made electronic band dendrometer.

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588   Table S5(1) The coefficients of the fitted relationships according to equation (8).

Group	2016			2017		
	a	b	R^2	a	b	R^2
C	97.9***	4.3***	0.60	68.5***	21.7*	0.02
T1	310.2***	2.1***	0.92	139.2***	4.5***	0.30
T2	264.1***	2.4***	0.89	213.0***	5.6***	0.12

589

590   Table S5(2) The coefficients of the fitted relationships according to equation (9).

Group	2016			2017		
	m	n	R^2	m	n	R^2
C	-168.5***	263.6***	0.90	-111.1***	196.3***	0.74
T1	-282.9***	547.0***	0.98	-188.3***	343.9***	0.87
T2	-245.9***	495.7***	0.97	-208.4***	454.0***	0.80

591   Note: Significant level at 0.01***, 0.05**, and 0.1*.

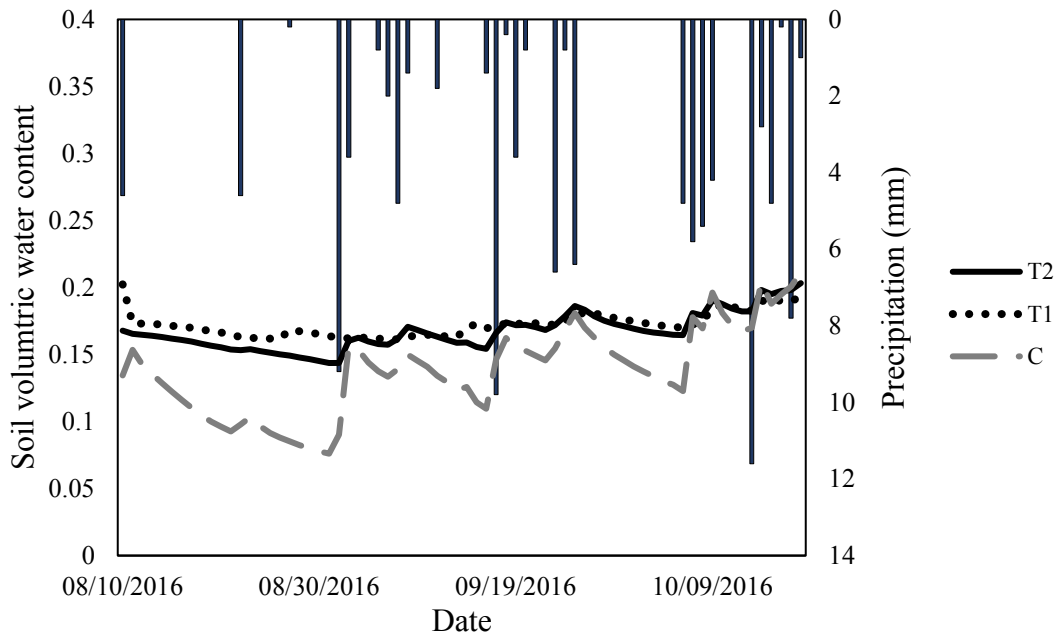592

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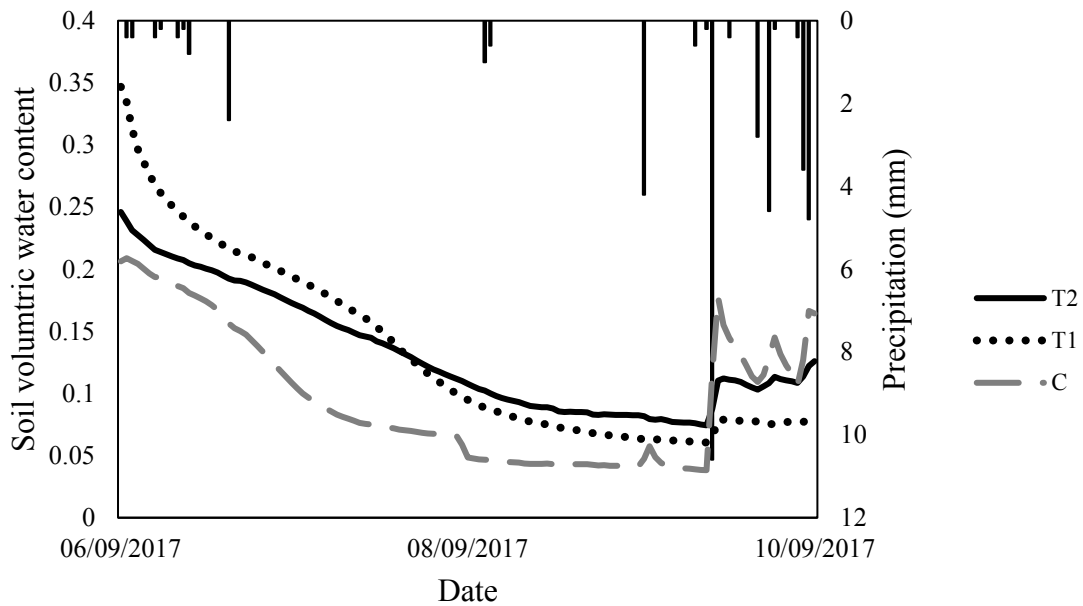598

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608 Figure S4 Averaged daily soil volumetric water contents of C, T1 and T2 with daily precipitation

609 in 2016 and 2017.

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Refences:

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. and Allen, C.D. (2017) A multi-species synthesis of physiological mechanisms in drought-induced tree mortality. Nature ecology & evolution 1(9), 1285.

Ambrose, A.R., Baxter, W.L., Martin, R.E., Francis, E., Asner, G.P., Nydick, K.R. and Dawson, T.E. (2018) Leaf- and crown-level adjustments help giant sequoias maintain favorable water status during severe drought. Forest Ecology and Management 419-420, 257-267.

Anderson, P.D., Larson, D.J. and 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. and McCray, J.E. (2014) Hydrological effects of forest transpiration loss in bark beetle-impacted watersheds. Nature Climate Change 4, 481.

Berryman, A. (1982) Mountain pine beetle outbreaks in Rocky Mountain lodgepole pine forests. Journal of Forestry 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.

635 Bovard, B.D., Curtis, P.S., Vogel, C.S., Su, H.B. and Schmid, H.P. (2005) Environmental
636   controls on sap flow in a northern hardwood forest. Tree Physiology 25(1), 31-38.

637 Bréda, N. and Granier, A., A. (1996) Intra- and interannual variations of transpiration, leaf area
638   index and radial growth of a sessile oak stand (Quercus petraea). Annales des sciences
639   forestières 53(2-3), 521-536.

640 Brix, H. and Mitchell, A.K. (1986) Thinning and nitrogen fertilization effects on soil and tree
641   water stress in a Douglas-fir stand. Canadian Journal of Forest Research 16(6), 1334-
642   1338.

643 Cabon, A., Mouillot, F., Lempereur, M., Ourcival, J.-M., Simioni, G. and Limousin, J.-M.
644   (2018) Thinning increases tree growth by delaying drought-induced growth cessation in
645   a Mediterranean evergreen oak coppice. Forest Ecology and Management 409, 333-342.

646 Carlyle, J.C. (1995) Nutrient management in a Pinusradiata plantation after thinning: the effect
647   of thinning and residues on nutrient distribution, mineral nitrogen fluxes, and extractable
648   phosphorus. Canadian Journal of Forest Research 25(8), 1278-1291.

649 Cattelino, P.J., Becker, C.A. and Fuller, L.G. (1986) Construction and installation of homemade
650   dendrometer bands. Northern Journal of Applied Forestry 3(2), 73-75.

651 Chase, C.W., Kimsey, M.J., Shaw, T.M. and Coleman, M.D. (2016a) The response of light,
652   water, and nutrient availability to pre-commercial thinning in dry inland Douglas-fir
653   forests. Forest Ecology and Management 363(Supplement C), 98-109.

654 Chase, C.W., Kimsey, M.J., Shaw, T.M. and Coleman, M.D. (2016b) The response of light,
655   water, and nutrient availability to pre-commercial thinning in dry inland Douglas-fir
656   forests. Forest Ecology and Management 363, 98-109.

657 Chen, J., Franklin, J.F. and Spies, T.A. (1993) Contrasting microclimates among clearcut, edge,

658   and interior of old-growth Douglas-fir forest. Agricultural and Forest Meteorology

659   63(3), 219-237.

660 Clausnitzer, F., Köstner, B., Schwärzel, K. and Bernhofer, C. (2011) Relationships between

661   canopy transpiration, atmospheric conditions and soil water availability—Analyses of

662   long-term sap-flow measurements in an old Norway spruce forest at the Ore

663   Mountains/Germany. Agricultural and Forest Meteorology 151(8), 1023-1034.

664 Cole, D.M. (1973) Culture of immature lodgepole pine stands for timber objectives, pp. 9-11.

665 Coupé, R., Stewart, A. and Wikeem, B. (1991) Engelmann spruce–subalpine fir zone.

666   Ecosystems of British Columbia. D. Meidinger and J. Pojar (editors). BC Ministry of

667   Forests, Research Branch, Victoria, BC. Special Report Series (6), 223-236.

668 Daniel, C.J., Ter-Mikaelian, M.T., Wotton, B.M., Rayfield, B. and Fortin, M.-J. (2017)

669   Incorporating uncertainty into forest management planning: Timber harvest, wildfire

670   and climate change in the boreal forest. Forest Ecology and Management

671   400(Supplement C), 542-554.

672 del Campo, A.D., Fernandes, T.J.G. and Molina, A.J. (2014) Hydrology-oriented (adaptive)

673   silviculture in a semiarid pine plantation: How much can be modified the water cycle

674   through forest management? European Journal of Forest Research 133(5), 879-894.

675 Del Río, M., Bravo-Oviedo, A., Pretzsch, H., Löf, M. and Ruiz-Peinado, R. (2017) A review of

676   thinning effects on Scots pine stands: From growth and yield to new challenges under

677   global change. Forest Systems 26(2), eR03S.

678 Edward Boyd Reid, D., Silins, U. and James Lieffers, V. (2006) Sapwood hydraulic recovery

679   following thinning in lodgepole pine. Annals of Forest Science 63(4), 329-338.

680   Eilmann, B. and Rigling, A. (2012) Tree-growth analyses to estimate tree species' drought

681   tolerance. Tree Physiology 32(2), 178-187.

682   Elkin, C., Giuggiola, A., Rigling, A. and Bugmann, H. (2015) Short- and long-term efficacy of

683   forest thinning to mitigate drought impacts in mountain forests in the European Alps.

684   Ecological Applications 25(4), 1083-1098.

685   Ewers, B.E., Oren, R., Johnsen, K.H. and Landsberg, J. (2001) Estimating maximum mean

686   canopy stomatal conductance for use in models. Canadian Journal of Forest Research

687   31(2), 198-207.

688   Fernandes, T.J.G., Del Campo, A.D., Herrera, R. and Molina, A.J. (2016) Simultaneous

689   assessment, through sap flow and stable isotopes, of water use efficiency (WUE) in

690   thinned pines shows improvement in growth, tree-climate sensitivity and WUE, but not

691   in WUEi. Forest Ecology and Management 361, 298-308.

692   Forrester, D.I., Collopy, J.J., Beadle, C.L., Warren, C.R. and Baker, T.G. (2012) Effect of

693   thinning, pruning and nitrogen fertiliser application on transpiration, photosynthesis and

694   water-use efficiency in a young Eucalyptus nitens plantation. Forest Ecology and

695   Management 266, 286-300.

696   Gebhardt, T., Häberle, K.-H., Matyssek, R., Schulz, C. and Ammer, C. (2014) The more, the

697   better? Water relations of Norway spruce stands after progressive thinning. Agricultural

698   and Forest Meteorology 197, 235-243.

699   Giuggiola, A., Ogee, J., Rigling, A., Gessler, A., Bugmann, H. and Treydte, K. (2016)

700   Improvement of water and light availability after thinning at a xeric site: which matters

701   more? A dual isotope approach. New Phytol 210(1), 108-121.

702 Goff, J.A., and S. Gratch (1946) Low-pressure properties of water from −160 to 212 °F. Goff,

703   J.A. (ed), pp. 95-122, New York.

704 González de Andrés, E., Camarero, J.J., Blanco, J.A., Imbert, J.B., Lo, Y.-H, Sangüesa-

705   Barreda, G., Castillo, F.J. and Turnbull, M. (2018) Tree-to-tree competition in mixed

706   European beech-Scots pine forests has different impacts on growth and water-use

707   efficiency depending on site conditions. Journal of Ecology 106(1), 59-75.

708 Granier, A. (1987) Evaluation of transpiration in a Douglas-fir stand by means of sap flow

709   measurements. Tree Physiol 3(4), 309-320.

710 Granier, A., Bobay, V., Gash, J.H.C., Gelpe, J., Saugier, B. and Shuttleworth, W.J. (1990)

711   Vapour flux density and transpiration rate comparisons in a stand of Maritime pine

712   (Pinus pinaster Ait.) in Les Landes forest. Agricultural and Forest Meteorology 51(3-4),

713   309-319.

714 Grossiord, C., Sevanto, S., Limousin, J.-M., Meir, P., Mencuccini, M., Pangle, R.E., Pockman,

715   W.T., Salmon, Y., Zweifel, R. and McDowell, N.G. (2018) Manipulative experiments

716   demonstrate how long-term soil moisture changes alter controls of plant water use.

717   Environmental and Experimental Botany 152, 19-27.

718 Guttman, N.B. (1999) Accepting the standardized precipitation index: A calculation algorithm1.

719   JAWRA Journal of the American Water Resources Association 35(2), 311-322.

720 Gyenge, J., Fernández, M.E., Sarasola, M. and Schlichter, T. (2011) Stand density and drought

721   interaction on water relations of Nothofagus antarctica: contribution of forest

722   management to climate change adaptability. Trees 25(6), 1111-1120.

723   Hope, G.D. (2009) Clearcut harvesting effects on soil and creek inorganic nitrogen in high

724   elevation forests of southern interior British Columbia. Canadian Journal of Soil Science

725   89(1), 35-44.

726   Hudson, R.O. and Golding, D.L. (1997) Controls on groundwater chemistry in subalpine

727   catchments in the southern interior of British Columbia. Journal of Hydrology 201(1-4),

728   1-20.

729   Jimenez, E., Vega, J.A., Perez-Gorostiaga, P., Cuinas, P., Fonturbel, T., Fernandez, C.,

730   Madrigal, J., Hernando, C. and Guijarro, M. (2008) Effects of pre-commercial thinning

731   on transpiration in young post-fire maritime pine stands. Forestry 81(4), 543-557.

732   Jiménez, E., Vega, J.A., Pérez-Gorostiaga, P., Fonturbel, T. and Fernández, C. (2009)

733   Relationships between watre use and environmental papameters in a young post-fire

734   martime pine stand after precommercial thinning, pp. 303-308, International Society for

735   Horticultural Science (ISHS), Leuven, Belgium.

736   Johnstone, W.D. and Van Thienen, F. (2004) A summary of early results from recent lodgepole

737   pine thinning experiments in the British Columbia interior, Ministry of Forests, Forest

738   Science Program.

739   Jokela, E.J., Dougherty, P.M. and Martin, T.A. (2004) Production dynamics of intensively

740   managed loblolly pine stands in the southern United States: a synthesis of seven long-

741   term experiments. Forest Ecology and Management 192(1), 117-130.

742   Julio Camarero, J., Gazol, A., Sangüesa-Barreda, G., Cantero, A., Sánchez-Salguero, R.,

743   Sánchez-Miranda, A., Granda, E., Serra-Maluquer, X. and Ibáñez, R. (2018) Forest

744   Growth Responses to Drought at Short- and Long-Term Scales in Spain: Squeezing the

745   Stress Memory from Tree Rings. Frontiers in Ecology and Evolution 6(9).

746   Kashian, D.M., Tinker, D.B., Turner, M.G. and Scarpace, F.L. (2004) Spatial heterogeneity of

747   lodgepole pine sapling densities following the 1988 fires in Yellowstone National Park,

748   Wyoming, USA. Canadian Journal of Forest Research 34(11), 2263-2276.

749   Kohler, M., Sohn, J., Nägele, G. and Bauhus, J. (2010) Can drought tolerance of Norway spruce

750   (Picea abies (L.) Karst.) be increased through thinning? European Journal of Forest

751   Research 129(6), 1109-1118.

752   Lagergren, F., Lankreijer, H., Kučera, J., Cienciala, E., Mölder, M. and Lindroth, A. (2008)

753   Thinning effects on pine-spruce forest transpiration in central Sweden. Forest Ecology

754   and Management 255(7), 2312-2323.

755   Laurent, M., Antoine, N. and Joël, G. (2003) Effects of different thinning intensities on drought

756   response in Norway spruce (Picea abies (L.) Karst.). Forest Ecology and Management

757   183(1-3), 47-60.

758   Lindgren, P.M.F. and Sullivan, T.P. (2013) Long-term responses of tree and stand growth of

759   young lodgepole pine to pre-commercial thinning and repeated fertilization. Forest

760   Ecology and Management 307, 155-164.

761   Lloret, F., Keeling, E.G. and Sala, A. (2011) Components of tree resilience: effects of

762   successive low-growth episodes in old ponderosa pine forests. Oikos 120(12), 1909-

763   1920.

764   Lotan, J.E. and Critchfield, W.B. (1990) Pinus contorta Dougl. ex. Loud. Silvics of North

765   America 1, 302-315.

766   Martín-Benito, D., Del Río, M., Heinrich, I., Helle, G. and Cañellas, I. (2010) Response of

767   climate-growth relationships and water use efficiency to thinning in a Pinus nigra

768   afforestation. Forest Ecology and Management 259(5), 967-975.

769 McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J.,

770   Sperry, J., West, A., Williams, D.G. and Yepez, E.A. (2008) Mechanisms of plant

771   survival and mortality during drought: why do some plants survive while others

772   succumb to drought? New Phytol 178(4), 719-739.

773 McDowell, N.G. (2011) Mechanisms Linking Drought, Hydraulics, Carbon Metabolism, and

774   Vegetation Mortality. Plant Physiology 155(3), 1051-1059.

775 Medhurst, J.L., Battaglia, M. and Beadle, C.L. (2002) Measured and predicted changes in tree

776   and stand water use following high-intensity thinning of an 8-year-old Eucalyptus nitens

777   plantation. Tree Physiology 22(11), 775-784.

778 Mitchell, R.G., Waring, R.H. and Pitman, G.B. (1983) Thinning Lodgepole Pine Increases Tree

779   Vigor and Resistance to Mountain Pine Beetle. Forest Science 29(1), 204-211.

780 Moreaux, V., Lamaud, E., Bosc, A., Bonnefond, J.M., Medlyn, B.E. and Loustau, D. (2011)

781   Paired comparison of water, energy and carbon exchanges over two young maritime

782   pine stands (Pinus pinaster Ait.): effects of thinning and weeding in the early stage of

783   tree growth. Tree Physiol 31(9), 903-921.

784 Moreno, G. and Cubera, E. (2008) Impact of stand density on water status and leaf gas

785   exchange in Quercus ilex. Forest Ecology and Management 254(1), 74-84.

786 Nadezhdina, N. and Cermak, J. (2000) The Supporting Roots of Trees and Woody Plants:

787   Form, Function and Physiology. Stokes, A. (ed), pp. 227-238, Springer Netherlands,

788   Dordrecht.

789 Naudts, K., Chen, Y., McGrath, M.J., Ryder, J., Valade, A., Otto, J. and Luyssaert, S. (2016)

790   Europe's forest management did not mitigate climate warming. Science 351(6273), 597.

791   Nyland, R.D. (1998) Patterns of lodgepole pine regeneration following the 1988 Yellowstone

792   fires. Forest Ecology and Management 111(1), 23-33.

793   Park, J., Kim, T., Moon, M., Cho, S., Ryu, D. and Seok Kim, H. (2018) Effects of thinning

794   intensities on tree water use, growth, and resultant water use efficiency of 50-year-old

795   Pinus koraiensis forest over four years. Forest Ecology and Management 408, 121-128.

796   Raz-Yaseef, N., Yakir, D., Schiller, G. and Cohen, S. (2012) Dynamics of evapotranspiration

797   partitioning in a semi-arid forest as affected by temporal rainfall patterns. Agricultural

798   and Forest Meteorology 157, 77-85.

799   Reichstein, M., Bahn, M., Ciais, P., Frank, D., Mahecha, M.D., Seneviratne, S.I., Zscheischler,

800   J., Beer, C., Buchmann, N., Frank, D.C., Papale, D., Rammig, A., Smith, P., Thonicke,

801   K., van der Velde, M., Vicca, S., Walz, A. and Wattenbach, M. (2013) Climate extremes

802   and the carbon cycle. Nature 500(7462), 287-295.

803   Reid, D.E.B., Silins, U. and Lieffers, V.J. (2006) Sapwood hydraulic recovery following

804   thinning in lodgepole pine. Ann. For. Sci. 63(4), 329-338.

805   Rodríguez-Calcerrada, J., Pérez-Ramos, I.M., Ourcival, J.-M., Limousin, J.-M., Joffre, R. and

806   Rambal, S. (2011) Is selective thinning an adequate practice for adapting Quercus ilex

807   coppices to climate change? Annals of Forest Science 68(3), 575-585.

808   Schäfer, K.V.R., Renninger, H.J., Clark, K.L. and Medvigy, D. (2014) Hydrological responses

809   to defoliation and drought of an upland oak/pine forest. Hydrological Processes 28(25),

810   6113-6123.

811   Seidl, R., Schelhaas, M.-J., Rammer, W. and Verkerk, P.J. (2014) Increasing forest disturbances

812   in Europe and their impact on carbon storage. Nature Climate Change 4, 806.

813   Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J.,

814   Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M.J., Trotsiuk, V., Mairota, P., Svoboda,

815   M., Fabrika, M., Nagel, T.A. and Reyer, C.P.O. (2017) Forest disturbances under

816   climate change. Nature Climate Change 7, 395.

817   Simonin, K., Kolb, T.E., Montes-Helu, M. and Koch, G.W. (2007) The influence of thinning on

818   components of stand water balance in a ponderosa pine forest stand during and after

819   extreme drought. Agricultural and Forest Meteorology 143(3-4), 266-276.

820   Skubel, R.A., Khomik, M., Brodeur, J.J., Thorne, R. and Arain, M.A. (2017a) Short-term

821   selective thinning effects on hydraulic functionality of a temperate pine forest in eastern

822   Canada. Ecohydrology 10(1), e1780.

823   Skubel, R.A., Khomik, M., Brodeur, J.J., Thorne, R. and Arain, M.A. (2017b) Short-term

824   selective thinning effects on hydraulic functionality of a temperate pine forest in eastern

825   Canada. Ecohydrology 10(1), e1780.

826   Sohn, J.A., Gebhardt, T., Ammer, C., Bauhus, J., Häberle, K.-H., Matyssek, R. and Grams,

827   T.E.E. (2013) Mitigation of drought by thinning: Short-term and long-term effects on

828   growth and physiological performance of Norway spruce (Picea abies). Forest Ecology

829   and Management 308, 188-197.

830   Sohn, J.A., Hartig, F., Kohler, M., Huss, J. and Bauhus, J. (2016a) Heavy and frequent thinning

831   promotes drought adaptation in Pinus sylvestris forests. Ecol Appl 26(7), 2190-2205.

832   Sohn, J.A., Saha, S. and Bauhus, J. (2016b) Potential of forest thinning to mitigate drought

833   stress: A meta-analysis. Forest Ecology and Management 380, 261-273.

834   Spittlehouse, D. and Stewart, R.B. (2003) Adaptation to climate change in forest management.

835 Stewart, J.D. and Salvail, J. (2017) Evaluation of Precommercial Thinning of Lodgepole Pine

836 from Long-term Research Installations in Alberta, Natural Resources Canada=

837 Ressources naturelles Canada.

838 Stohr, A. and Losch, R. (2004) Xylem sap flow and drought stress of Fraxinus excelsior

839 saplings. Tree Physiology 24(2), 169-180.

840 Stojanović, M., Szatniewska, J., Kyselová, I., Pokorný, R. and Čater, M. (2017) Transpiration

841 and water potential of young Quercus petraea (M.) Liebl. coppice sprouts and seedlings

842 during favourable and drought conditions. J. For. Sci 63, 313-323.

843 Sullivan, T.P., Sullivan, D.S., Lindgren, P.M.F. and Ransome, D.B. (2006) Long-term

844 responses of ecosystem components to stand thinning in young lodgepole pine forest:

845 III. Growth of crop trees and coniferous stand structure. Forest Ecology and

846 Management 228(1–3), 69-81.

847 Sun, X., Onda, Y., Kato, H., Otsuki, K. and Gomi, T. (2014a) Partitioning of the total

848 evapotranspiration in a Japanese cypress plantation during the growing season.

849 Ecohydrology 7(3), 1042-1053.

850 Sun, X., Onda, Y., Otsuki, K., Kato, H., Hirata, A. and Gomi, T. (2014b) The effect of strip

851 thinning on tree transpiration in a Japanese cypress (Chamaecyparis obtusa Endl.)

852 plantation. Agricultural and Forest Meteorology 197, 123-135.

853 Tang, J., Bolstad, P.V., Ewers, B.E., Desai, A.R., Davis, K.J. and Carey, E.V. (2006) Sap flux-

854 upscaled canopy transpiration, stomatal conductance, and water use efficiency in an old

855 growth forest in the Great Lakes region of the United States. Journal of Geophysical

856 Research: Biogeosciences 111(G2), n/a-n/a.

857   Tateishi, M., Xiang, Y., Saito, T., Otsuki, K. and Kasahara, T. (2015) Changes in canopy

858   transpiration of Japanese cypress and Japanese cedar plantations because of selective

859   thinning. Hydrological Processes 29(24), 5088-5097.

860   Thibodeau, L., Raymond, P., Camiré, C. and Munson, A.D. (2000) Impact of precommercial

861   thinning in balsam fir stands on soil nitrogen dynamics, microbial biomass,

862   decomposition, and foliar nutrition. Canadian Journal of Forest Research 30(2), 229-

863   238.

864   Turner, M., Romme, W., Tinker, D. and Whitby, T. (2013) Landscape patterns of early postfire

865   lodgepole pine regeneration dominate stand structure and function 24 years after the

866   1988 Yellowstone Fire.

867   Weng, S.-H., Kuo, S.-R., Guan, B.T., Chang, T.-Y., Hsu, H.-W. and Shen, C.-W. (2007)

868   Microclimatic responses to different thinning intensities in a Japanese cedar plantation

869   of northern Taiwan. Forest Ecology and Management 241(1), 91-100.

870   Winkler, R., Spittlehouse, D. and Boon, S. (2017) Streamflow response to clear-cut logging on

871   British Columbia's Okanagan Plateau. Ecohydrology 10(2), e1836.

872   Winkler, R.D. and Moore, R.D. (2006) Variability in snow accumulation patterns within forest

873   stands on the interior plateau of British Columbia, Canada. Hydrological Processes

874   20(17), 3683-3695.

875   Yang, R.C. (1998) Foliage and stand growth responses of semimature lodgepole pine to

876   thinning and fertilization. Canadian Journal of Forest Research 28(12), 1794-1804.

877   Zhang, J.-G., He, Q.-Y., Shi, W.-Y., Otsuki, K., Yamanaka, N. and Du, S. (2015) Radial

878   variations in xylem sap flow and their effect on whole-tree water use estimates.

879   Hydrological Processes 29(24), 4993-5002.

880   Zobel, D.B., McKee, A., Hawk, G.M. and Dyrness, C.T. (1976) Relationships of Environment

881   to Composition, Structure, and Diversity of Forest Communities of the Central Western

882   Cascades of Oregon. Ecological Monographs 46(2), 135-156.

883