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# Responses of forest carbon and water coupling to thinning treatments across multiple spatial scales

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23 **Abstract**

24 Background

25 Water-use efficiency (WUE) represents the coupling of forest carbon and water. Little is known  
26 about the responses of WUE to thinning at multiple spatial scales. The objective of this research  
27 was to use field measurements to understand short-term effects of two thinning treatments (T1:  
28 4,500 stems ha<sup>-1</sup>; and T2: 1,100 stems ha<sup>-1</sup>) and the control (C: 27,000 stems ha<sup>-1</sup>) on WUE (the  
29 ratio of leaf photosynthesis to leaf transpiration, or tree growth to tree transpiration, or net stand  
30 above-ground biomass (AGB) accumulation to stand transpiration) and the intrinsic WUE  
31 (WUE<sub>i</sub>, the ratio of leaf photosynthesis to stomatal conductance or the net stand AGB  
32 accumulation to canopy conductance) in a 16-year old natural lodgepole pine forest. Leaf-level  
33 measurements were conducted in 2017, while tree- and stand-level measurements were  
34 conducted in both 2016 (the normal year) and 2017 (the drought year).

35

36 Results

37 There was no significant effect of thinning on the tree- and stand-level WUE in 2016, while in  
38 2017, only T2 exhibited significantly higher tree-level WUE (0.63 mm<sup>2</sup> kg<sup>-1</sup>) than the C (0.06  
39 mm<sup>2</sup> kg<sup>-1</sup>), and the stand-level WUE values were significantly higher in the thinned stands, with  
40 the means of 0.34, 0.61 and 0.7 kg m<sup>-3</sup> for the control, T1 and T2, respectively. Stand-level  
41 WUE<sub>i</sub> was, however, significantly higher in the unthinned stands than in the thinned stands. In  
42 contrast, the leaf-level WUE values were not significantly different from each other, while the  
43 leaf-level WUE<sub>i</sub> was statistically higher in C than in the thinned stands. Thinning changed the  
44 WUE-VPD relationships at tree and stand levels, but not at the leaf level.

45

46 Conclusions

47 The effects of thinning on forest carbon and water coupling differed with the spatial scales and  
48 the metrics (WUE or WUEi) of water use efficiency. Lacking consistent responses of WUE  
49 metrics to thinning treatments across the spatial scales suggests that caution must be exercised  
50 when transferring and modeling WUE from one spatial scale to others. Both tree-level and stand-  
51 level WUE values in the more heavily thinning stands were significantly promoted under the  
52 drought condition, demonstrating that thinning can improve WUE and consequently support  
53 forests to cope with the drought effects.

54

55 **Keywords:** Water-use efficiency (WUE), thinning, *Pinus contorta*, gas exchange, upscaling,  
56 drought.

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## 70 **Background**

71 Water-use efficiency (WUE), representing the coupling between carbon assimilation and water  
72 consumption of vegetation, is an important parameter in modelling responses of terrestrial  
73 carbon and water cycles to climate and land cover changes (Gentine et al., 2019; Liu et al., 2015;  
74 Tang et al., 2014; Zhang et al., 2018; Zhen et al., 2017). At the leaf level, water-use efficiency  
75 (leaf-level WUE) is calculated as the ratio of net photosynthetic assimilation to leaf transpiration.  
76 As exchanges of CO<sub>2</sub> and water vapor share the same diffusion pathway via stomata (Perez-  
77 Harguindeguy et al., 2013), intrinsic water-use efficiency (leaf-level WUE<sub>i</sub>, the ratio of net  
78 photosynthesis to stomatal conductance) is an alternative index for the leaf-level carbon and  
79 water coupling, which excludes influences from evaporative demand on leaf transpiration  
80 (Wieser et al., 2018). At the individual tree level, WUE (tree-level WUE) is expressed as the  
81 ratio of tree growth (e.g., basal area increments (BAI)) to the whole tree transpiration  
82 (Wullschleger et al., 1998). And at the ecosystem level, WUE can be quantified as the ratio of  
83 gross primary production to evapotranspiration or the ratio of net primary production to  
84 transpiration (e.g., Petritsch et al. (2007)). The responses of WUE at finer spatial levels (e.g.,  
85 leaf and individual tree) provide valuable information for understanding and predicting behaviors  
86 of carbon and water processes of forest ecosystems at coarser spatial scales.

87 Holistic view on forest WUE across spatial scales is limited. Leaf-level studies are generally  
88 concentrated on the leaf-level WUE<sub>i</sub> that is detected from isotopic signatures of tree tissues,  
89 because when comparing with leaf-level WUE, the isotopic leaf-level WUE<sub>i</sub> only accounts for  
90 the ratio of intercellular and ambient CO<sub>2</sub> concentration, and can cover periods of low light, low  
91 temperature and dry conditions, while leaf-level WUE that is usually conducted by the gas  
92 exchange method, reflects optimal conditions of trees (near light saturation and optimal ranges of

93 temperature) due to limitations in conducting measurements in the field (e.g., during night)  
94 (Wieser et al., 2018). The leaf-level  $WUE_i$  can also be measured from the gas exchange  
95 technique, and the discrepancy between  $WUE_i$  of two different methods has been ascribed to the  
96 differences in the time scale (i.e., long term and short term) (Wieser et al., 2018) because the  
97 ratio of photosynthesis to stomatal conductance is positively linearly with the ratio of the leaf  
98 intercellular  $CO_2$  concentration ( $C_i$ ) to the atmospheric  $CO_2$  concentration ( $C_a$ ), and the  $C_i/C_a$  is  
99 also assumed to be linearly related to the carbon isotope discrimination by approximating the  
100 intercellular chloroplast concentration to  $C_i$  (Farquhar et al., 1989; Seibt et al., 2008). Some  
101 research have discovered that leaf-level  $WUE_i$  tended to be a homeostatic trait (Comstock and  
102 Ehleringer, 1992; Fernández-de-Uña et al., 2016), while others found that leaf-level  $WUE_i$   
103 responded to changes in plant morphology (Brienen et al., 2017) and climatic controls (Adams et  
104 al., 2019). A review by Cernusak et al. (2013) suggested that environmental factors modified  
105 leaf-level  $WUE_i$ , and internal physiology which varied with species, dampening its responses.  
106 However it remains unresolved the mechanism underlying the interactions between  
107 environmental and physiological determinants on leaf-level  $WUE_i$ . On the other hand, leaf-level  
108  $WUE$  is closer to the concept of net carbon and water exchange with atmosphere, especially in  
109 the context of climate change (Seibt et al., 2008). Besides, when scaling up from leaf to  
110 ecosystem levels there are more complications involved, including physical and physiological  
111 processes within the ecosystem, errors and uncertainties associated with measuring approaches  
112 and differences in the temporal and spatial resolutions, which lead to a lack of correspondence of  
113  $WUE$  between different spatial levels (Guerrieri et al., 2016; Medrano et al., 2015). For instance,  
114 Guerrieri et al. (2016) found opposing patterns of  $WUE$  at leaf and ecosystem scales across a  
115 broader range of American forests. Ponton et al. (2006), however, showed a good agreement

116 between ecosystem WUE and WUE<sub>i</sub> by studying Douglas fir forest, aspen forest and grassland  
117 in Canada, and the differences in WUE among the three sites were most determined by variations  
118 in VPD. Contrast evidences imply cautions are needed in choosing the most representative  
119 indicators of carbon and water coupling and in the applicability of scaling from leaf to ecosystem  
120 levels.

121 Upscaling WUE from leaf to canopy levels requires knowledge of relationships between WUE  
122 and micrometeorological forcing. Ecosystems whose WUE exhibited good agreement across  
123 spatial scales, their WUE were fairly stable and mostly determined by VPD (Baldocchi et al.,  
124 1987; Lindroth and Cienciala, 1996; Morén et al., 2001; Ponton et al., 2006; Tang et al., 2006),  
125 which served as the basis for upscaling WUE from leaf to canopy levels. The relationship  
126 between WUE and VPD is also dependent on light intensity, because the stomata can react to  
127 decreases in photosynthesis under lower light intensity by closure, and thus lowering the  
128 transpiration processes (Bierhuizen and Slatyer, 1965; Linderson et al., 2012). Besides, water  
129 availability (e.g., soil water contents) can potentially influence the sensitivity of WUE to  
130 climatic variables through its effects on stomatal behaviors (Gimeno et al., 2016). Because of  
131 these WUE-micrometeorology relationships, it is generally expected that forest thinning  
132 treatments would affect the responses of WUE, because they affect the microclimate resulting in  
133 higher direct incident radiation reaching the ground, higher soil temperature, air temperature and  
134 wind speed, and lower air humidity within treated stands (Anderson et al., 2007; Bartos and  
135 Amman, 1989; Chen et al., 1999; Cutini and Mascia, 1996; Weng et al., 2007). To authors'  
136 knowledge, no previous studies have examined the effects of thinning on microclimate sensitivity  
137 of WUE and WUE<sub>i</sub> except for the one reported that the isotopic WUE<sub>i</sub> became sensitive to  
138 annual precipitation after thinning (Fernandes et al., 2016). However, a limited number of studies

139 examined the effects of thinning on growth-climate and transpiration-climate relationships. For  
140 instance, Magruder et al. (2013) found that overstory thinning in red pine (*Pinus resinosa* Ait.)  
141 stands in Michigan at either the high or moderate thinning intensity, had the highest number of  
142 significant correlation coefficients between the radial growth and precipitation and temperature,  
143 whereas the unthinned had the lowest number of significant correlation coefficients. And  
144 enhanced sensitivities of tree transpiration to microclimatic controls under thinning treatments  
145 have also been observed in the beech (*Nothofagus antarctica*) forests in Argentina, maritime pine  
146 (*Pinus pinaster* Ait.) stands in Spain and cypress (*Chamaecyparis obtusa* and *Cryptomeria*  
147 *japonica*) stands in Japan (Gyenge et al., 2011; Jimenez et al., 2008; Tateishi et al., 2015). To  
148 date, few studies have been carried out on the effects of thinning on WUE at multiple spatial  
149 levels and under ambient conditions (Linderson et al., 2012; Tsamir et al., 2019). Modelling the  
150 forest carbon dynamics by using WUE relies on the established functions between WUE and  
151 VPD (Zhou et al., 2014), and thus, it is important to know if thinning changes the relationship  
152 between WUE and microclimate.

153 In the separate prior study in the young lodgepole pine forests in the interior of British Columbia,  
154 Canada, we examined the effects of juvenile thinning on tree-level radial growth, sap flow  
155 velocity and stand transpiration under drought and non-drought years, and found that significant  
156 differences of tree growth and sap flow velocity between light and heavy thinning treatments  
157 only occurred in the drought year, with the heavier thinning having a higher sensitivity of sap  
158 flow velocity to VPD (Wang et al., 2019). Building on this prior study, we further assess in this  
159 work the effects of juvenile thinning on WUE across the multiple spatial scales during the  
160 growing seasons of 2016 and 2017. The drought occurred in 2017 provided an excellent  
161 opportunity of evaluating the responses of WUE to thinning treatments under the drought

162 condition. In this study, we hypothesized: (1) the juvenile thinning would significantly affects  
163 leaf-level WUE and WUE<sub>i</sub>, tree-level WUE and stand-level WUE and WUE<sub>i</sub> ; (2) there were  
164 consistent responses of WUE and WUE<sub>i</sub> to thinning treatments across various spatial scales; and  
165 (3) the thinning would alter the sensitivity of WUE to microclimatic variables at all three spatial  
166 scales.

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168

## 169 **Methods**

### 170 Study area and experiment design

171 The study was conducted in an even-aged 16 years old lodgepole pine (*Pinus contorta* Dougl.)  
172 forest in the Upper Pentiction Watershed (UPW) in the southern interior of British Columbia,  
173 Canada (49°39'34"N, 119°24'34"W). The site is around 1675 m a.s.l, generally south aspect, and  
174 have sparse understory vegetation. Soils were derived from granite parent rock, coarse sandy-  
175 loam in texture, with low water holding capacities, and were classified as Luvisol. Snow cover  
176 lasts from early November through middle of June. In June 2016, two thinning treatments  
177 (Treatment 1 (T1): 4,500 stems per ha; Treatment 2 (T2): 1,100 stems per ha) and one unthinned  
178 control (C: 27,000 stems per ha) were randomly assigned to three plots (20 m ×20 m each) of  
179 each block. There are 3 blocks, B1, B2 and B3 (25 m × 75 m each) and each block has 3 plots.

180 The leaf-level measurements were carried out in the growing season of 2017 (June to October)  
181 while the tree-level measurements were recorded since June 2016. The year of 2017 has been  
182 classified as a drought year based on the calculation of Standardized Precipitation Index (SPI).  
183 The mean daily temperature during the growing season of 2017 is 12.1°C, and the total growing

184 season precipitation is 37.4 mm. Detailed information on the study site and the experimental  
185 design can be found from Wang et al. (2019).

186

187 Leaf-level measurements

188 Leaf-level WUE ( $\mu\text{mol mmol}^{-1}$ ) was calculated as the ratio of leaf photosynthesis rate ( $\mu\text{mol CO}_2$   
189  $\text{m}^{-2}\text{s}^{-1}$ ) to leaf transpiration rate ( $\text{mmol H}_2\text{O m}^{-2}\text{s}^{-1}$ ). Leaf-level WUEi ( $\mu\text{mol mol}^{-1}$ ) was  
190 calculated as the ratio of leaf photosynthesis rate ( $\mu\text{mol CO}_2 \text{m}^{-2}\text{s}^{-1}$ ) to stomatal conductance  
191 ( $\text{mol H}_2\text{O m}^{-2}\text{s}^{-1}$ ). Leaf-level WUEi approximately equals to the product of leaf-level WUE and  
192 the leaf to air vapour pressure deficit (i.e., leaf-level WUEi = leaf-level WUE  $\times$  VPD, or  
193 alternatively, leaf-level WUE = leaf-level WUEi/VPD), because the ratio of leaf transpiration to  
194 VPD corresponds approximately to the conductance of water vapor via stomata (i.e., stomatal  
195 conductance ( $g_s$ )) (Gorthi et al., 2019; Linderson et al., 2012; Seibt et al., 2008; Wieser et al.,  
196 2018).

$$197 \quad \text{Leaf-level WUE} = \frac{\text{leaf photosynthesis}}{\text{leaf transpiration}}$$

198 (1)

$$199 \quad \text{Leaf-level WUEi} = \frac{\text{leaf photosynthesis}}{\text{stomatal conductance}} \quad (2)$$

200 All the variables were measured by the instantaneous photosynthesis measurement system  
201 (Model LI-6400XT, Licor, Lincoln, NE, USA) with an opaque conifer chamber (Model 6400-22)  
202 and an external RGB light source (6400-18A). The measurements took place between 10:00 am  
203 and 14:00 pm from June, 23<sup>rd</sup>, 2017, and were conducted approximately once per week in the  
204 three blocks until the end of the growing season (October 2017). When the measurement was

205 conducted each time, five trees in each plot were selected, and for each tree, four bunches of  
206 needles orienting north, south, east and west at the similar location of tree canopy (around 1.5-  
207 1.7 m height) were measured for three times. In order to mimic the natural surrounding  
208 environment of measured leaves when conducting the chamber measurement, the temperature  
209 was set as the ambient temperature, the light conditions were set to reflect the ambient light  
210 levels, and the leaf chamber was sealed with gum in case of gas leaking. Flow rate was set at 500  
211  $\mu\text{mol/s}$  to minimize the modifications on the environmental variables by the equipment  
212 (Medrano et al., 2010).

213

214 Tree-level measurements

215 Tree-level WUE ( $\text{mm}^2 \text{kg}^{-1}$ ) is calculated as the ratio of basal area increment (BAI,  $\text{mm}^2\text{d}^{-1}$ ) to  
216 tree transpiration (T,  $\text{kgd}^{-1}$ ).

$$217 \quad \text{Tree-level} \quad \text{WUE} \quad = \quad \frac{\text{BAI}}{T}$$

218 (3)

219 Tree transpiration was calculated based on the sap flow of 5 trees per plot in B1 (namely sap  
220 flow trees). Sap flow was continuously measured by the Granier-type sap flow probes (Model  
221 TDP-30, Dynamax, Inc., Texas, USA) at the breast height (15 trees in total). The detailed  
222 descriptions on DBH and sap flow measurement and their related quality control can be found  
223 in Wang et al. (2019). BAI were calculated based on the diameter at the breast height (DBH)  
224 measured on the five sap flow trees per plot in B1 by an electronic caliper (Model:500-196-30,  
225 Mitutoyo Corporation, Japan) at the beginning and the end of each growing season of 2016 and  
226 2017. Besides, DBH of 45 trees per plot across the three blocks were measured monthly by the

227 same electronic caliper in the two growing season.

228

229 Stand-level estimations

230 Stand-level WUE ( $\text{kg m}^{-3}$ ) is calculated as the ratio of the stand net primary production (NPP,  $\text{kg}$

231  $\text{m}^{-2} \text{d}^{-1}$ ) to stand transpiration ( $T_{\text{stand}}$ ,  $\text{mm d}^{-1}$ ). And stand-level intrinsic WUE (stand-level WUEi,

232  $\text{kg m}^{-3}$ ) is calculated as the ratio of NPP to the canopy conductance ( $G_s$ ,  $\text{mm d}^{-1}$ ).

233 
$$\text{Stand-level WUE} = \frac{NPP}{T_{\text{stand}}} \quad (4)$$

234 
$$\text{Stand-level WUEi} = \frac{NPP}{G_s} \quad (5)$$

235 Given that the studied stand is even-aged and mono-species forest with sparse understory, NPP is

236 estimated by changes in the stand above-ground biomass ( $\text{AGB}_{\text{stand}}$ ,  $\text{g}$ ) in each growing season,

237 and  $T_{\text{stand}}$  ( $\text{mm d}^{-1}$ ) is estimated from the tree transpiration, stand density and DBH distribution,

238 which has been reported in our previous study (Wang et al., 2019). Tree AGB ( $\text{AGB}_{\text{tree}}$ ) is

239 estimated by the tree allometric equations based on 24-year-old lodgepole pine trees from a

240 range of stand densities across the Yellowstone subalpine plateaus (Copenhaver and Tinker,

241 2014).

242 
$$\text{AGB}_{\text{tree}} (\text{g}) = 98.85 \times \text{basal diameter (cm)}^{1.99} \quad (6)$$

243 
$$\text{AGB}_{\text{stand}} = \text{mean AGB}_{\text{tree}} \times \text{stand density} \quad (7)$$

244 
$$\text{NPP} = \Delta \text{AGB}_{\text{stand}} \quad (8)$$

245 Paired measurements of tree DBH and basal diameter from 180 trees across all three blocks were

246 used to build a linear relationship between basal diameter and tree DBH, which has been also

247 reported in our previous study (Wang et al., 2019).

248 Gs was used as a proxy to indicate the stomatal responses at the canopy level. It was calculated  
249 by the simplified inversion of Penman-Monteith equation by assuming that the VPD is close to  
250 the leaf to air vapor pressure deficit with no vertical gradient through canopy, and negligible  
251 water storage above the measurement point where sap flow probes were inserted (Ewers and  
252 Oren, 2000). This method have been applied in lodgepole pine forests (Reid et al., 2006). The  
253 conditions of our young lodgepole pine forests that have low canopy height (< 2.5m) and  
254 relatively open canopy (canopy closure <55%) generally satisfy the assumptions of the equation.

$$255 \quad G_s = \frac{\gamma \lambda E_{LA}}{\rho_a c_a VPD} \quad (9)$$

256 Where,  $\gamma$  is the psychrometric constant (0.067 kPa K<sup>-1</sup>);  $\lambda$  is the latent heat of vaporization  
257 calculated by Harrison's equation,  $\lambda = 2.501 - 2.361 \times 10^{-3} T_a$  (Harrison, 1963);  $E_{LA}$  is the  
258 transpiration per leaf area, E/LA (mms<sup>-1</sup>);  $\rho_a$  is air density (1.225 kg m<sup>-3</sup>);  $c_a$  is the specific heat  
259 of air (1.0 × 10<sup>-3</sup> MJ kg<sup>-1</sup> K<sup>-1</sup>); VPD is vapor pressure deficit (kPa). All VPD data used in the  
260 equation are greater than 0.6 kPa to minimize the relative errors (<10%) (Ewers and Oren, 2000).

261 Monthly leaf area (LA, m<sup>2</sup>) was also estimated from the tree allometric equations from  
262 Copenhaver and Tinker (2014).

$$263 \quad LA \text{ (in m}^2\text{)} = 0.02 \times \text{basal diameter (in cm)}^{2.34} \quad (10)$$

264 Leaf area index (LAI) was estimated by dividing LA by the projection coefficient (2.5) (Litton et  
265 al., 2004). The estimated mean monthly LAI in 2016 for C (0.99) matches relatively well with  
266 the field measurement (0.97).

267

268 Collection of climate data

269 Climatic variables including solar radiation ( $R_n$ ,  $W\ m^{-2}$ ), air relative humidity (RH, %),  
270 temperature (T,  $^{\circ}C$ ), precipitation (P, mm) and wind velocity ( $W_v$ ,  $m\ s^{-1}$ ) were continuously  
271 measured in each treatment in B1 by climate station (HOBO weather station, Onset Computer,  
272 Bourne MA, USA). The sensors were placed at the canopy level (approximately 2.5 m). VPD is  
273 calculated based on Goff–Gratch equation (Goff, 1946). Microclimate variables including leaf  
274 temperature, leaf VPD and incoming photosynthetically active radiation (PAR,  $\mu mol$  (photons)  
275  $m^{-2}\ s^{-1}$ ), at the height of approximately 1.5 -1.7 m, across three blocks (9 plots) at the mid-day on  
276 a weekly basis during the growing season, were recorded by the instantaneous photosynthesis  
277 measurement system (Model LI-6400XT, Licor, Lincoln, NE, USA). Soil volumetric water  
278 content (VWC) at two depth (20 and 40 cm) in three randomly selected locations per plot in B1  
279 was measured by EC-5 sensors (Decagon, Pullman, WA, USA) at the interval of 20 minutes. Soil  
280 VWC at the 20 cm depth was also manually measured in the three blocks weekly by GS-1  
281 portable measuring system (Decagon, Pullman, WA, USA).

282

### 283 Statistical analysis

284 Leaf-level WUE and  $WUE_i$  were analysed by multi-factor AVOVA to investigate the effects of  
285 branch aspect, thinning, date and their interactions. Tree-level WUE was analyzed by ANCOVA  
286 with the initial DBH of the trees as covariate, and the thinning treatment and year (drought) as  
287 factors. Stand-level WUE was log-transformed before the two-way ANOVA analysis (Table S4),  
288 and stand-level  $WUE_i$  was only analysed in 2017 due to the requirement of the canopy  
289 conductance model on VPD (which should be greater than 0.6kPa). Model residuals were  
290 checked to meet the requirements of normality and homoscedasticity of variance (Figure S1-S2,  
291 Table S2-S4). Besides, monthly tree-level WUE, stand-level WUE and  $WUE_i$  were also

292 calculated in order to examine their responses to microclimatic factors. However, the DBH  
293 measurements in the september of 2016 and the August of 2017 were systematically greater than  
294 the following months due to the misoperation, were thus excluded from analyses. Besides,  
295 monthly stand-level WUE<sub>i</sub> were only available in the August of 2016 and the July and the  
296 August of 2017 because their VPD conditions were allowed to apply the canopy conductance  
297 model. Comparisons between two groups were performed with independent-t test, if data met the  
298 requirements of homogeneity of variance and normality, otherwise, were tested by the Mann-  
299 Whitney U test. Correlation was tested by Spearman test. A significance level of  $p \leq 0.05$  was  
300 used for all analyses. All data were processed by R (R Core Team (2014) and SPSS for Windows  
301 (SPSS, Inc., USA).

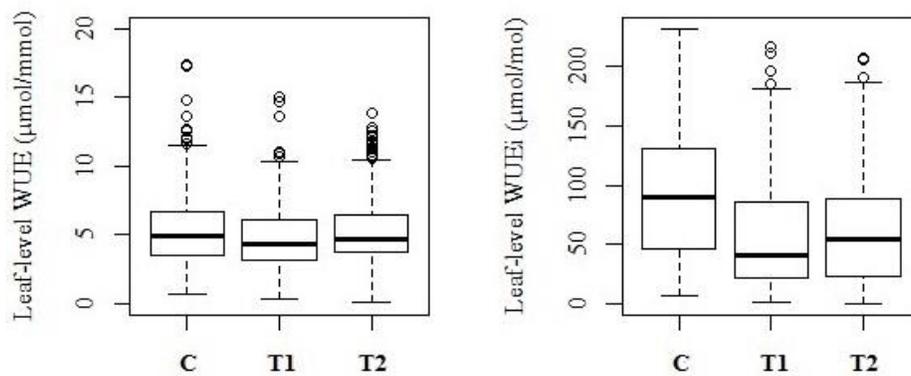
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303

## 304 **Results**

### 305 Effects of thinning on leaf-level WUE and WUE<sub>i</sub>

306 Thinning did not significantly affect leaf-level WUE ( $p=0.47$ , Table S1), with mean leaf-level  
307 WUE values for C, T1 and T2 being  $5.50 \pm 3.04$ ,  $4.99 \pm 3.40$  and  $5.31 \pm 2.96 \mu\text{mol mmol}^{-1}$ ,  
308 respectively. However, thinning did significantly influence leaf-level WUE<sub>i</sub> ( $p < 0.001$ , Table  
309 S1), with the averaged leaf-level WUE<sub>i</sub> for C, T1 and T2 being  $93.14 \pm 55.55$ ,  $57.24 \pm 47.23$  and  
310  $62.03 \pm 45.61 \mu\text{mol mol}^{-1}$ , respectively. Leaf-level WUE<sub>i</sub> in C was statistically higher than in T1  
311 and T2 (both  $p < 0.001$ ), while T1 and T2 did not significantly differ from each other ( $p=0.66$ ).  
312 (Figure 1, Table S1).



313

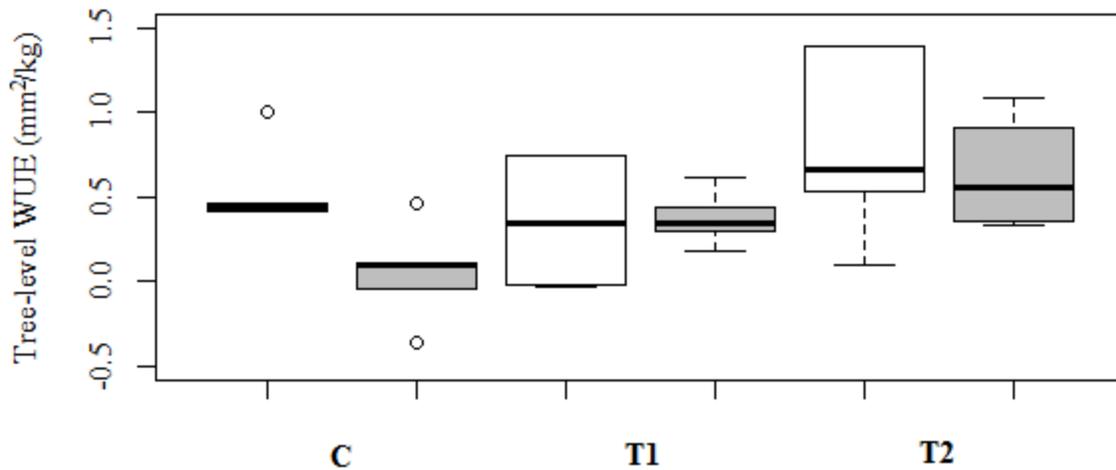
314 Figure 1. Leaf-level WUE (in left) and WUEi (in right) during the growing season of 2017.

315

316 Effects of thinning on tree-level WUE

317 The ANCOVA test showed that thinning significantly affected tree-level WUE ( $p = 0.033$ , Table  
 318 S2). The mean tree-level WUE for C, T1 and T2 in 2016 were  $0.14 \pm 1.01$ ,  $1.07 \pm 1.85$  and  
 319  $1.27 \pm 1.42 \text{ mm}^2 \text{ kg}^{-1}$ , respectively, and they were not significantly different from each other ( $p$   
 320  $= 0.45$ ). The values were reduced to  $0.06 \pm 0.30$ ,  $0.38 \pm 0.16$  and  $0.63 \pm 0.35 \text{ mm}^2 \text{ kg}^{-1}$  in 2017,  
 321 respectively, and only tree-level WUE between C and T2 was statistically different ( $p = 0.009$ ).  
 322 Thus, the heavier thinning significantly improved tree-level WUE in the drought year.

323 However, the ANCOVA test showed that the drought did not significantly affect tree-level WUE  
 324 ( $p = 0.4$ , Table S2). And for each of the three groups, their tree-level WUE also did not  
 325 statistically differ between years (all  $p > 0.1$ ). These were probably due to the large variances in  
 326 the tree-level WUE of T1 and T2 in the non-drought year (Figure 2). In addition, there was no  
 327 significant interaction effect between year (drought) and thinning ( $p = 0.84$ , Table S2).



328

329 Figure 2. Tree-level WUE during the growing season of 2016 (in white) and 2017 (in gray).

330

331 Effects of thinning on the stand-level WUE and WUEi

332 The ANOVA test showed that the thinning did not have significant impacts on the stand-level

333 WUE ( $p = 0.27$ , Table S4). In 2016, stand-level WUE was  $1.57 \pm 0.347$ ,  $1.73 \pm 0.245$ , and

334  $1.39 \pm 0.245 \text{ kg m}^{-3}$  for C, T1 and T2, respectively, and there was not any significant differences

335 among them ( $p = 0.89$ ). In 2017, stand-level WUE was reduced to  $0.339 \pm 0.20$ ,  $0.61 \pm 0.20$ , and

336  $0.75 \pm 0.20 \text{ kg m}^{-3}$  for C, T1, and T2, respectively, and C was significantly lower than T1 ( $p =$

337  $0.03$ ) and than T2 ( $p = 0.005$ ), suggesting the positive thinning effects only occurred in the

338 drought year. However, there was no statistical difference between T1 and T2 ( $p = 0.18$ ).

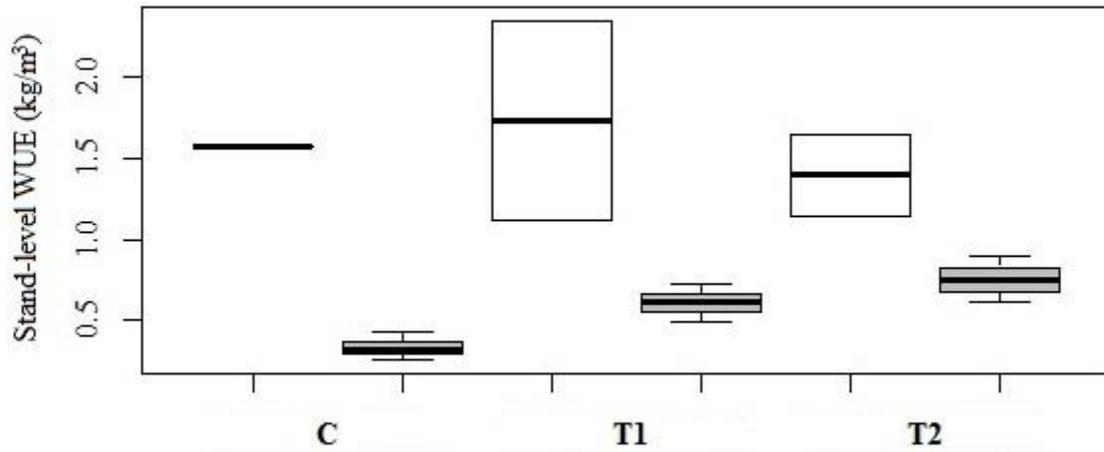
339 The drought significantly reduced stand-level WUE ( $p < 0.001$ , Table S4), while the interaction

340 between thinning and drought did not play a significant role (both  $p > 0.1$ ) (Table S4, Figure 3).

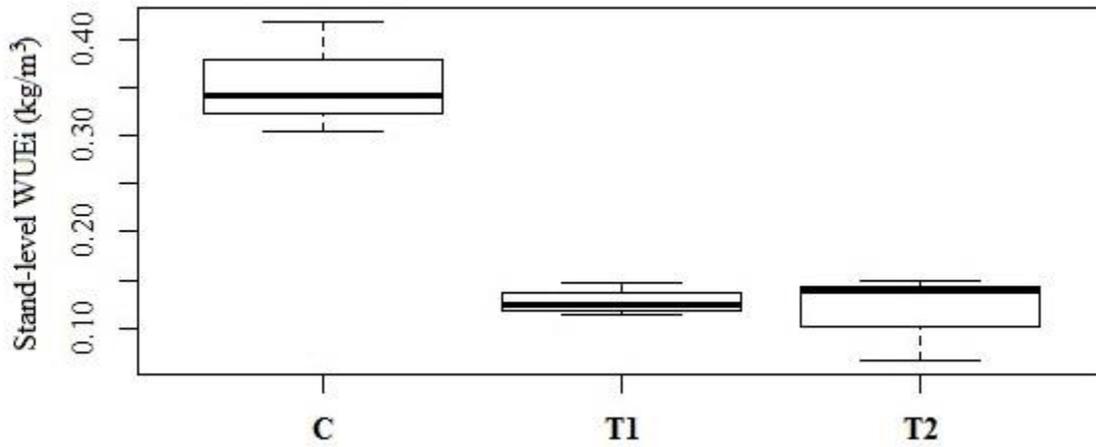
341 Stand-level WUEi in 2017 was  $0.36 \pm 0.06$ ,  $0.13 \pm 0.02$ , and  $0.12 \pm 0.04 \text{ kg m}^{-3}$  for C, T1 and T2

342 respectively. C was statistically higher than T1 and T2 (both  $p = 0.001$ ), and there was no

343 significant difference between T1 and T2 ( $p = 0.77$ ) (Figure 3).



344



345

346 Figure 3. Stand-level WUE in 2016 and 2017, and stand-level WUEi in 2017.

347 (The upper panel showed stand-level WUE of 2016 in white, and that of 2017 in gray. The bottom panel

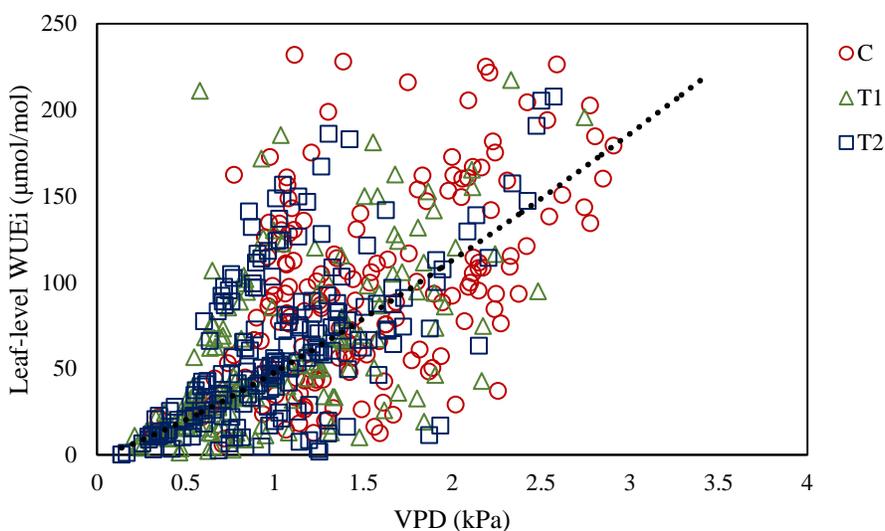
348 showed the stand-level WUEi in 2017.)

349

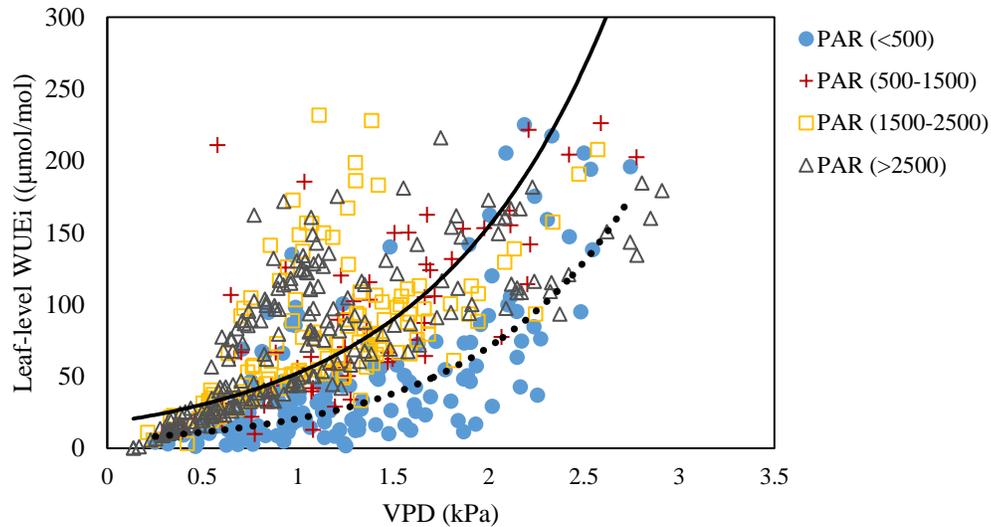
350 Responses of leaf level WUE and WUEi to VPD and PAR

351 Leaf-level WUE did not significantly correlate with VPD ( $p = 0.49$ ), while leaf-level WUEi

352 exhibited strongly positive relationship with VPD (spearman rho= 0.629, p<0.001). The  
353 responses of leaf-level WUE<sub>i</sub> to VPD did not apparently differ among C, T1 and T2, and were fit  
354 best with exponential equation ( $R^2 = 0.45$ ) (Figure 4). However, both the leaf-level WUE and  
355 WUE<sub>i</sub> were significantly correlated with PAR, with correlation coefficients of 0.47 and 0.23,  
356 respectively (both p< 0.001). But there were no any significant differences in the responses of  
357 leaf-level WUE and WUE<sub>i</sub> to PAR among C, T1, and T2 (Figure S3-S4). The responses of leaf-  
358 level WUE<sub>i</sub> to VPD were lower when PAR was less than 500  $\mu\text{mol}/\text{m}^2\text{s}$  (Figure 4). But when  
359 PAR was greater than 500  $\mu\text{mol}/\text{m}^2\text{s}$ , increasing PAR did not obviously enhance the responses of  
360 leaf-WUE<sub>i</sub> to VPD (Figure 4).



361



362

363 Figure 4. Leaf-level WUEi versus VPD for C, T1 and T2, and for the four PAR groups.

364 (The upper panel showed the leaf-level WUEi versus VPD for C, T1, and T2 with a fitted exponential

365 equation (leaf-level WUEi =  $47.894 \times \text{VPD}^{1.2356}$  ( $R^2=0.45$ )). The bottom panel shoed the leaf-level WUEi

366 versus VPD for the four PAR groups (unit:  $\mu\text{mol}/\text{m}^2\text{s}$ ) with fitted exponential equations (when PAR < 500:

367 leaf-level WUEi =  $6.1266e^{1.2208 \times \text{VPD}}$  ( $R^2=0.43$ ) and when PAR  $\geq 500$ : leaf-level WUEi =  $17.825e^{1.0788 \times \text{VPD}}$

368 ( $R^2=0.47$ )).)

369

### 370 Responses of tree-level WUE to VPD and transmited solar radiation

371 Tree-level WUE was significantly correlated with VPD ( $\rho=-0.63$ ,  $p=0.02$ ). The response of

372 tree-level WUE to VPD in C was slightly lower than those of T1 and T2, and there was no any

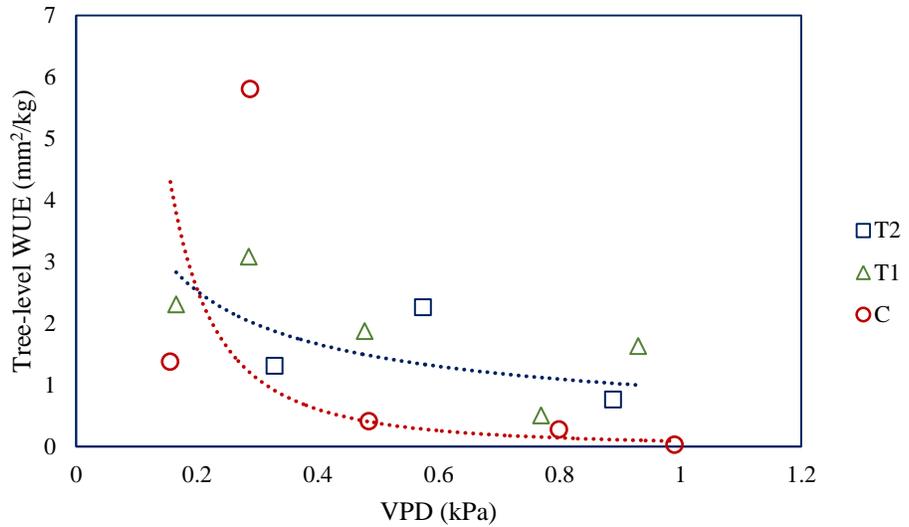
373 apparent difference between T1 and T2 (Figure 5). At each treatment group, however, there were

374 no significant correlations with VPD in C ( $\rho = -0.9$ ,  $p = 0.083$ ), T1 ( $\rho = -0.8$ ,  $p = 0.13$ ), and

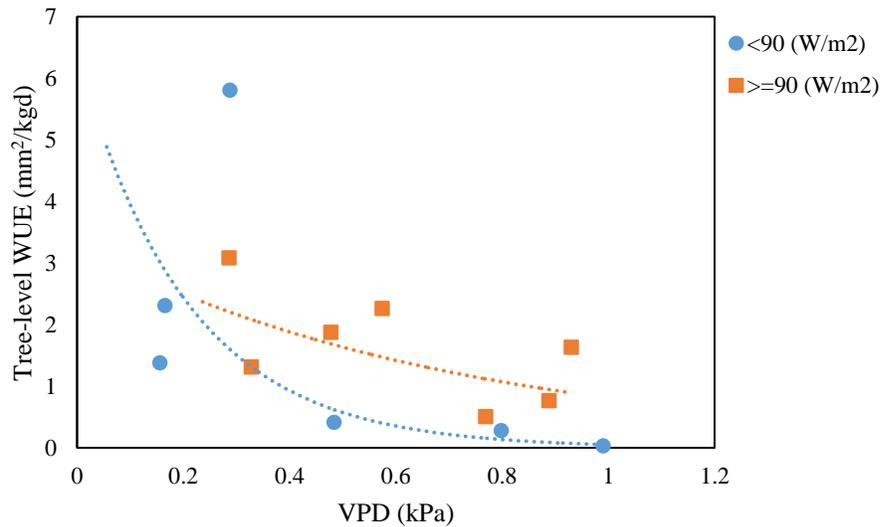
375 T2 ( $\rho = -0.5$ ,  $p = 1$ ), probably due to the limited sampling data. There were also no any

376 significant correlations between tree-level WUE and transmited solar radiation either when

377 pooling the three groups together ( $p=0.86$ ) or analysing the group individually (all  $p>0.1$ ), but  
 378 transmitted solar radiation influenced the responses of tree-level WUE to VPD (Figure 5).



379



380

381 Figure 5. Tree-level WUE versus VPD for C, T1 and T2, and for the two transmitted solar  
 382 radiation groups.

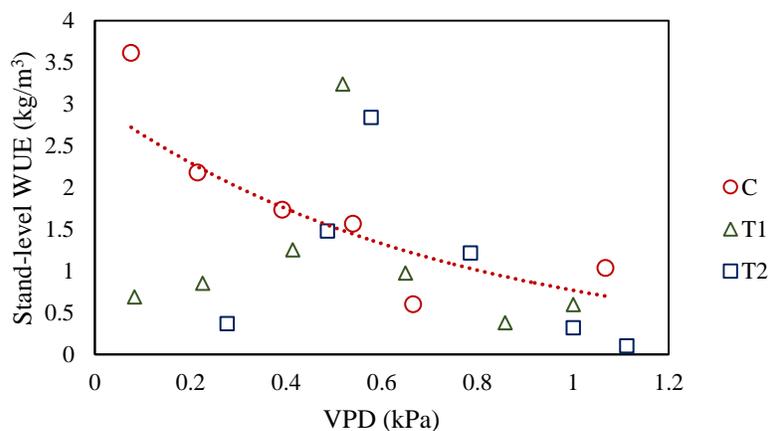
383 (The upper panel showed the tree-level WUE versus VPD with fitted exponential equations for C (tree-  
 384 level WUE =  $7.3514e^{-4.992 \times \text{VPD}}$  ( $R^2=0.79$ )), and for T1 and T2 (tree-level WUE =  $0.143e^{-3.336 \times \text{VPD}}$  ( $R^2 =$

385 0.47)). The bottom panel showed the tree-level WUE versus VPD for the two transmitted solar radiation  
 386 groups (unit:  $W/m^2$ ) with fitted exponential equations (when the transmitted solar radiation < 90: tree-level  
 387  $WUE = 6.3938e^{-4.818 \times VPD}$  ( $R^2=0.81$ ) and when the transmitted solar radiation  $\geq 90$ : tree-level  $WUE =$   
 388  $3.3011e^{-1.405 \times VPD}$  ( $R^2=0.34$ )).

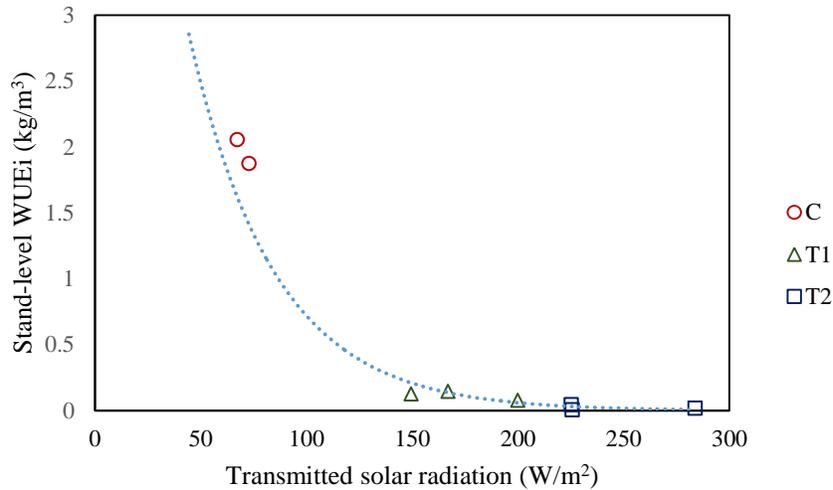
389

390 Responses of the stand-level WUE and WUEi to VPD and transmitted solar radiation

391 The stand-level WUE was statistically correlated with VPD ( $\rho=-0.51$ ,  $p = 0.03$ , Figure 9) and  
 392 transmitted solar radiation ( $\rho=-0.72$ ,  $p = 0.002$ ) when C, T1 and T2 were analysed together, but  
 393 when the three groups were analyzed individually, only C exhibited a significant correlation  
 394 between the stand-level WUE and VPD ( $\rho=-0.94$ ,  $p = 0.02$ ), and no significant correlations  
 395 with transmitted solar radiation were found in any of the three groups. Due to data deficiency,  
 396 stand-level WUEi was only analyzed by pulling the three groups together, and it was only  
 397 significantly correlated with transmitted solar radiation ( $\rho=-0.95$ ,  $p = 0.001$ , Figure 6).



398



399

400 Figure 6. Stand-level WUE versus VPD, and stand-level WUEi versus transmitted solar radiation  
 401 for C, T1 and T2.

402 (The upper panel showed the stand-level WUE versus VPD with a fitted exponential equation for C  
 403 (stand-level WUE =  $3.0195e^{-1.368 \times VPD}$  ( $R^2=0.61$ )). The bottom panel showed the stand-level WUEi versus  
 404 transmitted solar radiation with a fitted exponential equation (stand-level WUEi =  $8.5971e^{-0.025 \times VPD}$   
 405 ( $R^2=0.86$ )).

406

407

408 **Discussion**

409 The effects of thinning on WUE across the spatial scales

410 Contrast to our hypothesis, the leaf-level WUE values were not significantly different among C,  
 411 T1 and T2, while the leaf-level WUEi was statistically higher in C than in the thinned stands, and  
 412 there were no significant differences between the two thinning intensities. Our result on the leaf-  
 413 level WUEi is in accordance with some studies showing that thinning had no effects on WUEi

414 based on the isotope method for Scots pine (*Pinus Sylvestris*) and maritime pine (*Pinus pinaster*)  
415 (Navarro-Cerrillo et al., 2016), Aleppo pine (*Pinus halepensis* Mill.) (Fernandes et al., 2016), and  
416 black pine (*Pinus nigra* Arn.) (Martín-Benito et al., 2010) stands in Mediterranean forests. But  
417 our result is in contrast to the studies which were conducted by the leaf gas-exchange  
418 measurements in young paper birch (*Betula papyrifera* Marsh.) stands (Wang et al., 1995) and  
419 saplings of oak (*Quercus cerris* L.) and ash (*Fraxinus ornus* L.) forests (D'Alessandro et al.,  
420 2006). They attributed the increased leaf-level WUE<sub>i</sub> to increased PAR induced by their thinning  
421 treatments (D'Alessandro et al., 2006; Wang et al., 1995).

422 In our study, VPD, instead of PAR, might explain the discrepancy between the responses of leaf-  
423 level WUE and WUE<sub>i</sub>, and the significant higher leaf-level WUE<sub>i</sub> in C. It is because that leaf-  
424 level WUE<sub>i</sub> approximates the product of leaf-level WUE and VPD (Linderson et al., 2012;  
425 Wieser et al., 2018), and VPD during the leaf measurement periods was statistically higher in C  
426 than in T1 and T2 (both  $p < 0.001$ ) with no significant differences between T1 and T2 ( $p = 0.29$ ,  
427 Figure S5). Besides, in comparison with temperature and PAR, VPD is the only microclimate  
428 variable that exhibited significant differences between the control and the thinned stands during  
429 the leaf measurement periods (Figure S5). As VPD is determined by temperature and RH, and  
430 RH is influenced by soil evaporation and plant transpiration (Arx et al., 2013; Danehy and  
431 Kirpes, 2000; Fischer et al., 2007), higher VPD in C can be attributed to a lower soil water  
432 content and a higher stand transpiration in C, both of which were shown in our previous study at  
433 the same site (Wang et al., 2019). Besides, VPD indicates the atmospheric drought (Burkhardt  
434 and Pariyar, 2016), and increased WUE<sub>i</sub> were commonly observed under drought conditions  
435 (Andrés et al., 2018; Fernandes et al., 2016; Linares and Camarero, 2012). Therefore, higher  
436 leaf-level WUE<sub>i</sub> in C suggests that the unthinned stand experienced severer water stress than the

437 thinned stands.

438 However, VPD could either increase (Arx et al., 2013; Guenther et al., 2012; Weng et al., 2007),  
439 or remain unchanged (Chan et al., 2004; Meyer et al., 2001; Monteith et al., 1991; Porté et al.,  
440 2004) with increasing thinning intensity. Therefore, though microclimates play important roles in  
441 determining leaf-level WUE<sub>i</sub>, their effects may be site specific. We also acknowledge that the  
442 field measurements in our study were conducted from 10 am to 14 pm, and consequently, the  
443 results may not fully represent the effects of thinning on mean daily leaf-level WUE and WUE<sub>i</sub>  
444 at the 24-hour basis. Such a shortcoming could be addressed by the isotopic method, which will  
445 be considered in our future study.

446 At the tree level, we found significant and positive impacts of thinning on tree-level WUE (p  
447 =0.03). Our result agrees with the studies showing that thinning increased tree-level WUE in  
448 Aleppo pine (*Pinus halepensis* Mill.), Silvertop (*Eucalyptus nitens*) (Deane and Maiden) and  
449 Norway spruce (*Picea abies* [L.] Karst.) forests (Fernandes et al., 2016; Forrester et al., 2012;  
450 Gebhardt et al., 2014), by observing the enhanced tree transpiration accompanied with a higher  
451 increase of tree growth. Besides, Park et al. (2018) found that the significant difference of tree-  
452 level WUE between the heavy thinning and the control stands occurred only in high growth years  
453 in a 50-year-old Korean pine (*Pinus koraiensis*) stands. The enhancement of tree-level WUE was  
454 mainly attributed to a lower water stress under a more intense thinning treatment (Capon et al.,  
455 2018; del Campo et al., 2014; Gebhardt et al., 2014; Park et al., 2018). Therefore, the effects of  
456 thinning on tree-level WUE depend on how thinning releases tree competition for resources (e.g.,  
457 water, light and nutrients) as indicated by Fernández-de-Uña et al. (2016), and thus they can be  
458 more pronounced in the drought year, as observed by Park et al. (2018). This has been confirmed  
459 by our study that increasing tree-level WUE accompanied with thinning intensity was more

460 obvious in the drought year (2017) than in the normal year (2016), and the magnitude of tree-  
461 level WUE was generally higher in the normal year (Figure 2).

462 The discrepancy of WUE between the tree and leaf levels in 2017 may be attributed to the  
463 respiratory processes (Medrano et al., 2015), the tree carbon allocation pattern under droughts  
464 (Pretzsch et al., 2012), and the night transpiration (Escalona et al., 2013; Medrano et al., 2015).  
465 Stem respiration, however, was greater in the thinned stands (Lavigne, 1988), and thus is  
466 unlikely to contribute to possible explanation of our observation. Under water stress, lodgepole  
467 pine tends to allocate more biomass to their root system to improve water acquisition (Pretzsch et  
468 al., 2012), which may serve as a potential explanation. Besides, in order to infer the effect of the  
469 night transpiration, we calculated the percentage of the tree daily nocturnal sap flow (from 1 h  
470 after sunset to 1 h before dawn according to the local time (Medrano et al., 2015)) to the tree  
471 daily total sap flow, for the night sap flow is usually partitioned into the night transpiration and  
472 the stem refilling (Forster, 2014). We found that tree daily night sap flow accounted for  $29.7 \pm$   
473  $26.1\%$ ,  $11.9 \pm 14.1\%$  and  $6.5 \pm 11.9\%$  of the total tree daily sap flow in 2017 for C, T1 and T2,  
474 respectively, and they were significantly different from each other (all  $p < 0.001$ ). If the stomata  
475 was open during night for tree transpiration in our study site during the experiment period, it was  
476 possible that the trees in C had the highest daily non-productive water consumption, while those  
477 in T2 had the lowest, contributing to a significantly low tree-level WUE in C but high tree-level  
478 WUE in T2. The fact that nocturnal transpiration reduced whole-plant WUE and consequently  
479 caused lack of correspondences of WUE between leaf and whole-plant scales have been well  
480 documented (Escalona et al., 2013; Medrano et al., 2015), in which the higher tree night  
481 transpiration corresponded to higher atmospheric water deficits and soil water contents mainly

482 through their effects on stomata (Dawson et al., 2007; Kavanagh et al., 2007). But in our study,  
483 the night-time VPD was generally highest in T2, followed by C, and then T1 (Figure S5), and  
484 soil water contents were sustainably higher in the thinned stands (Wang et al., 2019), so that  
485 VPD and soil water contents alone can not explain the patterns of nocturnal tree sap flow found  
486 in our study. However, under drought condition, stomata conductance can be unrelated to VPD  
487 and soil water contents, which leads to a great amount of unavoidable water loss through  
488 epidermis (e.g., 6-8% of daily transpiration under well-watered condition in comparison with 19-  
489 20% of daily transpiration under droughts) (Cavender-Bares et al., 2007). This may be the  
490 explanation for our study. Nevetheless, our further study will examine the mechnismes behind the  
491 phenomenon in more details.

492 The responses of the stand-level WUE to the thinning treatments were slightly different from the  
493 tree-level WUE in this study. The lack of significance of the overall thinning effects on the  
494 stand-level WUE was probably due to the large variations of the stand-level WUE in 2016.  
495 Except for that, the stand-level WUE exhibited good correspondences with the tree-level WUE.  
496 As expected, the unthinned stand had the least tree growth but the highest stand transpiration  
497 during the two growing seasons (Wang et al., 2019), and the difference between the unthinned  
498 and thinend stands was more pronounced in the drought year. Besides, our result on the stand-  
499 level WUE is within the range of the AGB-based WUE (Forrester et al., 2012), and agrees well  
500 with the studies reporting that thinning increased stand-level WUE (Forrester et al., 2012) and  
501 droughts decreased WUE (ecosystem WUE or GPP/ET) (Gao et al., 2017). In fact, stand-level or  
502 ecosystem WUE can either increase (Sinacore et al., 2019), remain unchanged (Sinacore et al.,  
503 2019) or even decrease (Gao et al., 2017) under drought conditions, which is subject to various  
504 factors including forest characteristics (e.g., mixed or monospecific), tree species and

505 environmental conditions. The reduced stand-level WUE in the drought year in our study is  
506 attributed to the fact that the decrease in stand transpiration accompanied with greater reduction  
507 in net accumulation of the stand aboveground biomass under the drought.

508 Surprisingly, the stand-level WUE<sub>i</sub> was significantly higher in C than in the thinned stands with  
509 no significant difference between T1 and T2. The net accumulation of the stand above-ground  
510 biomass was significantly higher in C than T1 ( $p = 0.004$ ) and T2 ( $p = 0.001$ ), and there was no  
511 significant difference between T1 and T2 ( $p = 0.11$ ). Canopy conductances, however, were not  
512 significantly different among the three groups (all  $p > 0.1$ , except for the comparison between  
513 T1 and T2 ( $p = 0.053$ )). Therefore, the pattern of the stand-level WUE<sub>i</sub> in our study was driven  
514 by the net stand above-ground biomass accumulation during the growing season. This indicates  
515 that the higher stand density in C compensated for the decreased individual tree growth, leading  
516 to a higher net stand above-ground biomass accumulation in the unthinned stands than the  
517 thinned ones. Although T2 had the highest individual tree growth, the low density in T2  
518 counterbalanced the improved individual tree growth under the thinning treatment.

519

520 Responses of WUE and WUE<sub>i</sub> to microclimate under the thinning treatments and the  
521 implications for upscaling and modelling

522 Thinning changed the responses of WUE to microclimate at the tree and stand levels, but to our  
523 surprise, thinning did not change the sensitivity of the leaf-level WUE to PAR, and leaf-level  
524 WUE<sub>i</sub> to VPD and PAR. And the relationship between the leaf-level WUE with VPD fits the  
525 exponential increasing function (Figure 4), which is different from the exponential decay  
526 function established by Linderson et al. (2012) for beech (*Fagus sylvatica* L.) forests. The  
527 differences may be attributed to the differences between the studied conifer and deciduous species,

528 because we found that the exponential decay relations between WUE and VPD were mostly  
529 reported from the studies on deciduous species e.g., oak-hickory (*Quercus and Carya* spp.)  
530 (Baldocchi et al., 1987), sugar maple (*Acer saccharum*), hemlock (*Tsuga canadensis*), yellow  
531 birch (*Betula alleghaniensis*), basswood (*Tilia americana*), and American hophornbeam (*Ostrya*  
532 *virginiana*) (Tang et al., 2006), and basket willow (*Salix viminalis* L.) (Lindroth and Cienciala,  
533 1996), except for the Norway spruce (*Picea abies* L. Karst ) (Morén et al., 2001). It may also be  
534 due to the impacts of the drought in 2017: under the water stress, increasing VPD may result in  
535 greater reduction in stomatal conductance than photosynthesis, leading to a higher WUE<sub>i</sub>  
536 (Linares and Camarero, 2012).

537 The discrepancy between the leaf-level WUE and WUE<sub>i</sub> to microclimatic factors in this study  
538 was due to the distinct sensitivity of leaf transpiration and stomatal conductance, as leaf  
539 transpiration is regulated corroborely by stomatal conductance and boundary layer conductance  
540 to water vapor (Defraeye et al., 2014), the former of which depends on the density, size and  
541 degree of opening of stomata, while the latter is determined by the air movement and leaf  
542 morphology (Martin et al., 1999). The different responses of the leaf-level WUE and WUE<sub>i</sub> to  
543 VPD suggest that caution must be taken in selecting a proper WUE metric for upscaling from  
544 leaf to stand levels.

545 Similar with the leaf-level WUE<sub>i</sub>, the tree-level WUE was significantly correlated with VPD,  
546 and their relationship was modulated by the transmitted solar radiation (Figures 6 and 7). Such  
547 relationship between the tree-level WUE and VPD fits the exponential decay function, which is  
548 in agreement with the previous study (Lindroth and Cienciala, 1996). Although there was no  
549 significant correlation between tree-level WUE and leaf-level WUE and WUE<sub>i</sub> (both  $p > 0.1$ )  
550 probably due to limited sampling data, our study agrees with the research reporting that tree-

551 level WUE was primarily a function of VPD (Table 1) (Bierhuizen and Slatyer, 1965; Lindroth  
 552 and Cienciala, 1996; Park et al., 2018).

553 Thinning changed the responses of tree-level WUE to VPD, resulting in the apparent lower tree-  
 554 level WUE in C than in T1 and T2 at each VPD level (Figure 5). It is apparent in the Figure 5  
 555 that the lower responses of the tree-level WUE to VPD in C was because C generally had a lower  
 556 transmitted solar radiation, and thus lower responses of the tree-level WUE to VPD.

557 At the stand level, the response of the stand-level WUE to VPD was similar to the tree-level  
 558 response, exhibiting the exponential decay relationship in this study. This has also been  
 559 described by Lindroth and Cienciala (1996) and Kuglitsch et al. (2008). However, thinning  
 560 seemed to affect the response of the stand-level WUE to VPD, although the correlation was only  
 561 significant in C in our study. Besides, both the stand-level WUE and WUE<sub>i</sub> were significantly  
 562 correlated with transmitted solar radiation, which was probably because the stand-level WUE  
 563 and WUE<sub>i</sub> were primarily driven by the net above-ground biomass accumulation as discussed in  
 564 the previous section, and the net above-ground biomass accumulation is dependent on the light  
 565 availability (Jarčuška and Barna, 2011). Besides, we did not find any significant relationship  
 566 between the stand-level WUE and WUE<sub>i</sub> and the tree-level WUE (both  $p > 0.2$ ). Therefore,  
 567 whether the stand-level WUE can be predicted from the tree-level WUE requires further study.

568 Table 1. Correlation coefficient between WUE with VPD, light intensity and soil water content.

WUE across spatial scales	VPD	Light intensity (PAR or Transmitted solar radiation)	Soil water content at 20 cm	Soil water content at 40 cm
Leaf-level				
Leaf-level WUE	-0.03	0.47***	-0.25	-0.37**

Leaf-level WUEi	0.63***	0.23***	-0.47***	-0.55***
Tree-level				
Tree-level WUE	-0.63**	0.05	0.11	0
Stand-level				
Stand-level WUE	-0.51**	-0.72***	-0.16	-0.27
Stand-level WUEi	-0.37	-0.95***	-0.24	-0.48

569 Light intensity includes PAR at the leaf level and transmitted solar radiation at tree and stand  
570 levels. Star indicates the significant level at 0.01\*\*\*, 0.05\*\*, and 0.1\*;

571

572 Last but not least, although thinning did not affect the sensitivity of the leaf-level WUE and  
573 WUEi, the changes in microclimate resulting from thinning can still lead to the differences in  
574 WUE between the control and thinned stands (e.g., leaf-level WUEi and tree-level WUE).  
575 Clearly, microclimate is critical in evaluating the effects of thinning from the perspective of  
576 carbon and water coupling. It also plays an important role in other ecological functions of  
577 forests, such as seed germination (Dunlap and Helms, 1983; van Mantgem et al., 2006; Zald et  
578 al., 2008), species diversity (Dodson et al., 2008; Godefroid et al., 2006), soil nutrient cycling  
579 (Concilio et al., 2005; Gray et al., 2002; Moghaddas et al., 2008; Zhu et al., 2007), microhabitats  
580 for insects and animal (Chan et al., 2004; Chen et al., 1999; Meyer et al., 2001; Rambo and  
581 North, 2009) as well as reduction of wildfire (Bigelow and North, 2004; Whitehead et al., 2006)  
582 and mountain pine beetle attacks (Amman and Logan, 1998; Bartos and Amman, 1989). Previous  
583 research suggested that the changes of microclimate under forest management are predictable, as  
584 microclimate is closely related to vegetation structure, elevation and microtopography (Arx et  
585 al., 2013; Frey et al., 2016; Hardwick et al., 2015; Ma et al., 2010). It is very important for forest

586 silvicultural practices to create suitable microclimate conditions to improve forest ecological  
587 services. Our study provides the evidence of the short-term effects of thinning on WUE from leaf  
588 to stand levels. As juvenile thinning generates progressive crown and rooting system  
589 development and fast growing in understory vegetation (Aussenac, 2000; Bigelow and North,  
590 2004; Chan et al., 2004; Elkin et al., 2015; Sohn et al., 2013; Trentini et al., 2017), their effects  
591 are likely dynamic, and their long-term implications requires continuous investigation and  
592 monitoring.

593

594

## 595 **Conclusions**

596 Our study provided direct field evidences on the responses of WUE and WUE<sub>i</sub> to juvenile  
597 thinning treatments between the non-drought and drought conditions at the multiple spatial  
598 scales. We found that: (1) WUE and WUE<sub>i</sub> responded differently to the thinning treatments at the  
599 same spatial level as well as across the different spatial scales; (2) thinning affected the  
600 sensitivities of WUE to VPD at the tree and stand levels, but not the at the leaf level; (3) only  
601 under the drought condition, thinning significantly improved the tree- and stand-level WUE,  
602 demonstrating that thinning can promote forest resilience to the drought effects; and (4)  
603 microclimate played an important role in forest carbon and water coupling.

604

605

## 606 **Declarations**

607 Availability of data and materials

608 The data supporting this research are included within the article and its additional files.

609 Additional data are available upon request to corresponding author.

610

611 Competing interests

612 The authors declare that they have no competing interests.

613

614 Funding

615 The project was funded by the Collaborative Research and Development (CRD) Grants from

616 Natural Sciences and Engineering Research Council of Canada (NSERC). And Professor del

617 Campo was beneficiary of a “Salvador de Madariaga” grant (PR2015-00635) funded by the

618 Spanish Government.

619

620 Authors' contributions

621 Y. Wang, X. Wei and A. del Campo designed the study; Y. Wang and X. Wei led the field data

622 collection. Y. Wang did the data analyses; Y. Wang, X. Wei and A. del Campo led the writing of

623 the manuscript. All authors contributed to the drafts and gave final approval for publication.

624

625 Acknowledgement

626 We thank Dr. Guang Qi, Dr. Xin Yang, Dr. Peng Zhang, Dr. Yingchun Liao for help in the field

627 works, Dr. Trevor Blenner, Dr. Russell Smith and Dr. David Spittlehouse for providing forest

628 inventory and long-term climate data, and Dr. David Scott, Dr. Tongli Wang and Krysta Giles-

629 Hansen for valuable comments on the manuscript. We are thankful to Dr. Rita Winkler and the  
630 rest of the management faculty of Upper Penticton Watershed for the access to the study site and  
631 for their support toward our ecohydrological research programs.

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