



1 **Unexpected water uptake under drought conditions and thinning treatments in young and**
2 **overstocked lodgepole pine (*Pinus contorta*) forests**

3 Emory C. Ellis¹, Robert D. Guy², Xiaohua A. Wei³

4 ¹School of Forestry, Northern Arizona University, Flagstaff, Arizona, 86001, USA

5 ²Department of Forestry and Conservation Sciences, University of British Columbia, Vancouver, British Columbia,
6 V6T1Z4, Canada

7 ³Department of Earth, Environmental and Geographic Sciences, University of British Columbia (Okanagan
8 Campus), Kelowna, British Columbia, V1V 1V7, Canada

9 Correspondence to: Emory C. Ellis (ece58@nau.edu)

10 **Abstract:**

11 As drought and prolonged water stress become more prevalent in dry regions under climate
12 change, understanding and preserving water resources has become the focal point of many
13 conversations. Forest regeneration after deforestation or disturbance can lead to over-populated
14 juvenile stands with high water demands and low water use efficiency. Forest thinning improves
15 tree health, carbon storage, and water use while decreasing stand demands in arid and semi-arid
16 regions. However, little is known about the impacts of over-population on seasonal variation in
17 depth to water uptake nor the magnitude of the effect of growing season drought conditions on
18 water availability, and existing reports are highly variable by climatic region, species, and
19 thinning intensity. In this study, stable isotope ratios of hydrogen ($\delta^2\text{H}$) and oxygen ($\delta^{18}\text{O}$) in
20 water collected from soil varying depths and from twigs of lodgepole pine (*Pinus contorta*)
21 under different degrees of thinning (control: 27,000 stems per ha; moderately thinned: 4,500
22 stems per ha; heavily thinned: 1,100 stems per ha) over the growing season and analyzed using
23 the MixSIAR Bayesian mixing model to calculate the relative contributions of different water
24 sources in the Okanagan Valley in the interior of British Columbia, Canada. We found that
25 lodgepole pine trees shift their depth to water uptake depending on water availability under
26 drought conditions and rely more heavily on older precipitation events that percolate through the
27 soil profile when shallow soil water becomes less accessible. Interestingly, forest thinning did
28 not cause a significant change in depth to water uptake. Our results support other findings by
29 indicating that although lodgepole pines are drought tolerant and have dimorphic root systems,
30 they cannot shift from deep water sources when shallow water becomes more available at the
31 end of the growing season.

32 **Keywords:** *Pinus contorta*; stable water isotopes; forest thinning; water use strategies;
33 preferential water uptake; dual-isotope analysis; Bayesian isotope mixing model; soil water
34 uptake; transpiration; the interior of British Columbia



35 1. Introduction

36 As forests recover after harvesting, carbon and water demands change, and future climate
37 projections of increased drought severity will further complicate biogeochemical cycling and
38 carbon-water trade-offs (Giles-Hansen et al., 2021; Wang et al., 2019). Regenerating stands add
39 further stress on ecosystems; for example light competition in dense juvenile stands increases
40 stand water demands by driving vertical growth and stand leaf area (Liu et al., 2011a). To
41 mitigate this stress, management strategies such as systemic thinning of high-density juvenile
42 stands promotes forest regeneration while decreasing competition and providing remaining
43 vegetation with increased light availability, rooting space, nutrient access, and space for
44 horizontal branch growth (Giuggiola et al., 2016). Over a variety of forest ecosystems,
45 reductions in stand density have been shown to increase light availability, tree water use, carbon
46 storage, and water use efficiency, an indication of improved tree health, and to decrease stand
47 water use, reducing the intensity of water stress under drought conditions (Belmonte et al., 2022;
48 Fernandes et al., 2016; Giuggiola et al., 2016; Liu et al., 2011b; Manrique-Alba et al., 2020;
49 Molina & del Campo, 2012; Park et al., 2018; Sohn et al., 2012, 2016; Wang et al., 2019).
50 Because the primary goal of forest thinning is to decrease stand water use and increase
51 productivity, literature reporting the effects of this management strategy often focuses on
52 changes in carbon storage, tree growth, transpiration, and water use efficiency (Giuggiola et al.,
53 2016; Manrique-Alba et al., 2020; Park et al., 2018; Sohn et al., 2016). However, few studies
54 have reported sources of water use and their shifting in association with thinning treatments in
55 overstocked naturally-regenerating forests, particularly under drought conditions.

56 Quantifying stand water use is imperative to predicting the future of water availability in our
57 ecosystems. However, various studies indicate that trees do not always use the most recent
58 precipitation, and that vegetation can utilize different sources of water at different soil depths
59 depending on availability or stress (Dawson & Pate, 1996; Grossiord et al., 2017; Wang et al.,
60 2017). Many studies also report the depth of water uptake of various species and the relationship
61 between co-existing species and shared water sources (Andrews et al., 2012; Brinkmann et al.,
62 2019; Grossiord et al., 2017; Langs et al., 2020; Liu et al., 2015; Maier et al., 2019; Meinzer
63 et al., 2007; Sánchez-Pérez et al., 2008; Szymczak et al., 2020; Wang et al., 2017; Warren et al.,
64 2005). In arid and semi-arid regions where water is the limiting factor, some species have
65 adapted to derive water from various depths depending on seasonal water variability and have
66 higher ecological plasticity and drought tolerance (Langs et al., 2020; Wang et al., 2017).
67 Understanding where in the soil profile plants use water over prolonged dry periods and at
68 different stand densities is essential in assessing the impact of forest thinning and the relative
69 importance of different seasonal water sources under future climate conditions and shifts in
70 water availability in arid regions (Evaristo et al., 2015; Prieto et al., 2012; Sohn et al., 2016).

71 Stable isotope ratios can be used as powerful natural tracers to identify distinct water sources
72 such as rainfall, snow, groundwater, and stream flow (Brinkmann et al., 2018; Lin & da S. L.
73 Sternberg, 1993; Sprenger et al., 2017; Stumpp et al., 2018). The isotopic signature of
74 precipitation events is altered by elevation, temperature, and evaporative fractionation creating
75 distinctive layers within the soil profile (Kleine et al., 2020; Sprenger et al., 2017; Stumpp et al.,
76 2018). More specifically, soil water reflects precipitation events as they infiltrate through the soil
77 layer with the influence of evaporative fractionation until mixing with older groundwater and
78 depleted isotopes creating individualized isotopic signatures throughout the soil profile (Andrews



79 & Science, 2009; Brinkmann et al., 2018; Dawson & Pate, 1996; Sprenger et al., 2017; Stumpp
80 et al., 2018). The isotopic composition of plant water corresponds to the water uptake depth in
81 the soil profile (Brinkmann et al., 2019; Langs et al., 2020; Meinzer et al., 2007; Stumpp et al.,
82 2018; Wang et al., 2017). Due to these unique characteristics, stable water isotopes have been
83 used by researchers to assess sources of water use by plants and their possible shifts under
84 altered environmental conditions (Evaristo et al., 2015; Flanagan & Ehleringer, 1991; Meinzer et
85 al., 2001; Stumpp et al., 2018).

86 Lodgepole pine (*Pinus contorta* Douglas) is an early successional montane conifer with a deep
87 tap root, fine roots in shallow layers, and advantageous rooting system which allow this species
88 to access water throughout the soil profile (Fahey & Knight, 1986; Halter & Chanway, 1993).
89 Depending on the species, root structures have two components, lateral roots to increase their
90 soil surface area and tap root to reach deeper soil water or groundwater when surface water is
91 limited. Some species have also adapted to have dimorphic rooting habits, or the ability to access
92 water from different depths in the soil profile depending on soil moisture content and water
93 availability making them more resilient to water scarcity or prolonged drought conditions
94 (Dawson & Pate, 1996; Meinzer et al., 2013). One study, comparing Douglas-fir (*Pseudotsuga*
95 *menziesii* (Mirb.) Franco and lodgepole pine in southern Alberta, found that lodgepole pines are
96 able to minimize seasonal variations in stem water potential and that tap roots are deep enough to
97 access groundwater (Andrews et al., 2012). This finding is consistent with other literature that
98 lodgepole pines can access water from different depths depending on moisture availability and
99 can access bound soil water when there is low water potential (Meinzer et al., 2007a; Warren et
100 al., 2005). The literature indicates that lodgepole pines can access water from different soil layers
101 even under extreme or prolonged drought conditions, but little is known about the shifting of
102 water use under different stand densities as a result of thinning treatments and drought
103 conditions.

104 In this study, we used the stable isotope ratios ($\delta^2\text{H}$ and $\delta^{18}\text{O}$) of soil and xylem water to evaluate
105 how overpopulated stands and thinned stands use water over the growing season to further our
106 understanding of the ecosystem-level impacts of thinning as a management strategy. We
107 hypothesized that lodgepole pine primarily relies on spring snowmelt but reductions in shallow
108 source water during the growing season (along with the low soil water holding capacity) would
109 drive lodgepole pines to utilize deeper sources of water. Prolonged aridity was expected to push
110 trees to depend on different water sources towards the end of the growing season. We also
111 hypothesized that overpopulated stands may be limited in their rooting depth and unable to
112 access deep soil water under extremely dry conditions, and that thinning can effectively mitigate
113 these stresses. Through a detailed partitioning of tree water sources, we can better understand
114 how lodgepole pine uses water, estimate proportional dependence of lodgepole pine on specific
115 source waters, and determine if thinning affects tree water use and uptake strategies under
116 drought conditions.

117

118 2. Methods

119 2.1. Study Site



120 The study was conducted in the Upper Pentiction Creek experimental watershed (UPC) northeast
121 of Pentiction in the interior of British Columbia, Canada (49°39'34" N, 119°24',34" W). The site
122 elevation is approximately 1675 m a.s.l. with steep, rocky terrain and a southern aspect (Wang et
123 al., 2019). The Luvisolic soils were formed from granite; the texture is course sandy-loam and is
124 well drained with a low water holding capacity (Hope, 2011; Winkler et al., 2021; Winkler &
125 Moore, 2006). The biogeoclimatic region is the Engelmann Spruce-Subalpine Fir zone with cold,
126 snowy conditions from November
127 to early June and seasonal drought
128 conditions during the summer
129 months, June to October (Coupe et
130 al., 1991; Wang et al., 2019). This
131 research site was initially
132 established as a paired watershed
133 experiment in the early 1980s to
134 quantify the impact of forest
135 harvesting on water resources
136 (Creed et al., 2014; Moore &
137 Wondzell, 2005; Winkler et al.,
138 2021).

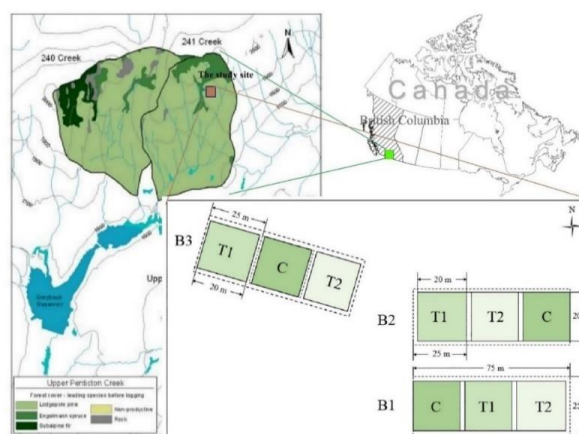


Figure 1 Watershed location and treatment plots of moderately thinned (T1), heavily thinned (T2), and the controlled (C) over-populated stands across the three replicate blocks (Wang et al., 2019)

139 The juvenile thinning experiment
140 began in 2016 when 16-year-old,
141 evenly aged, regenerating lodgepole
142 pine stands were thinned to different
143 densities than a control (C: 27,000
144 stem ha⁻¹, T1: 4,500 stems ha⁻¹, and T2: 1,100 stems ha⁻¹) where C represents the control stands,
145 T1 represents the lightly thinned stands, and T2 represents the heavily thinned stands (Figure 1).
146 The three treatments were repeated across three replicate blocks. Each block was 75 m long and
147 25 m in width with three 20 m² plots and 5 m between treatment plots. After the initial thinning,
148 all debris was left on site. The first two years' post-thinning results showed increased tree-level
149 water use and decreased stand-level water use in the thinned stands (Wang et al., 2019). Wang et
150 al. (2019) concluded that thinning positively influenced tree growth and water use and that
151 moderate and heavy thinning are effective management strategies for drought mitigation of
152 lodgepole pine in the UPC watershed.

153 Climate stations (HOBO weather station, Onset Computer, Bourne MA, USA) were deployed
154 across Block 1 treatments and have measured meteorological data since 2016 (ambient
155 temperature, relative humidity (rH), wind speed, precipitation, and solar radiation) in 10-minute
156 intervals. From this, we calculated daily vapor pressure deficit (VPD) as well as daily and
157 monthly potential evapotranspiration (PET) using temperature fluxes, relative humidity, and
158 precipitation (Flint & Childs, 1991; Russell, 1960; Streck, 2003). Recorded historical precipitation
159 (1997-2008) was acquired from a long-term climate station in a lodgepole pine forest in the 241
160 experimental watershed (climate station P7) (Moore et al., 2021).

161 Rainfall and temperature data from Block 1 was related to historical data to calculate the
162 monthly dryness (PET/P), standardized precipitation index (SPI), and standardized precipitation
163 evapotranspiration index (SPEI) (Beguería et al., 2014; Stagge et al., 2014; Wu et al., 2005). In



164 the middle of the growing season in 2021, four soil moisture probes (HOBO TEROS 11 Soil
165 Moisture/Temp Probes) were deployed in each treatment in Block 1 to measure changes in soil
166 moisture and temperature at 5 cm and 35 cm at 15-minute increments (n=12).

167 2.2 Sample collection

168 We sampled three trees per treatment across the three blocks and three in the mature plot (n = 30)
169 four times over the 2021 growing season in approximately six-week intervals (June 11-12, July
170 21-22, September 10-11, and October 7-8) around noon to capture peak transpiration time. We
171 used a pole pruner to cut a mid-canopy branch in the live crown. We peeled the bark off branch
172 segments with no needle coverage to remove outer bark and phloem, placed them into a glass
173 tube, sealed it with Parafilm wrap, covered it in aluminum foil, and set them in a cooler until the
174 end of the day when they were transferred to a freezer at -18°C. During the last two sampling
175 periods, some trees had red needles, likely an indication of dryness or higher temperatures from
176 an early growing season heat dome that began in June.

177 Soil samples were collected horizontally from 40 cm soil pits randomly dug across each
178 treatment plot at 5 and 35 cm depths from the surface. Large rocks were removed from the
179 profile. Soils were then sealed in freezer seal bags and frozen until cryogenic distillation for
180 water extraction. In the middle of the field season, 1 m pits were dug to sample the vertical
181 profile in 20 cm intervals in each treatment of Block 2. From the vertical pit, samples were
182 collected in 20 cm increments to determine the depth of tree water access. After samples were
183 collected, the larger rocks and soils were used to fill the pits.

184 Precipitation samples were collected when available during field collection days. Snow from a
185 late spring event was collected on June 11th and another snow event on October 11th. A rain event
186 was collected on September 10th. Groundwater and stream samples were collected from the creek
187 241 watershed at the end of the growing season and beginning of the seasonal hydraulic
188 recovery. Groundwater was collected using a hand pump. Groundwater and stream samples were
189 collected at the end of the growing season as stream beds were dry and groundwater was
190 inaccessible during the dry period. Once the well had been pumped and cleared, test tubes were
191 rinsed with ground water three times before being filled. Precipitation, groundwater and stream
192 samples were collected into test tubes, sealed with parafilm and foil, and stored in a fridge at
193 4°C.

194

195 2.3 Cryogenic extraction and isotopic analysis

196 Before extraction, samples were thawed, and weighed. For stable isotope analysis, water was
197 extracted from stem and soil samples using cryogenic distillation (Orlowski et al., 2013; Percy
198 et al., 2012). The test tube and branch sample segment of the line was immersed in liquid
199 nitrogen for 10 minutes until frozen (Chillakuru, 2009). Soils were frozen for 45 minutes in a
200 500 mL round-bottom flask using a dry-ice and 95% ethanol mixture before pumping out the air.
201 Frozen samples were pumped down to 60 mTorr, not disturbing the sample (Tsuruta et al.,
202 2019). The vacuum-sealed extraction unit was detached from the pump and transferred to a
203 boiling water bath; the extraction tube was submerged in liquid nitrogen. Branch samples were
204 set to distill for 1 hour and soil samples for 2 hours or until the tubing was clear to ensure all



205 mobile and bound source water was extracted (Orlowski et al., 2013; Tsuruta et al., 2019; Vargas
206 et al., 2017; West et al., 2006). Samples were also weighed after extraction and compared to
207 oven dried samples to ensure distillation was complete. Water extracted from branch and soil
208 samples accounted for $47.9 \pm 3.2\%$ and $9 \pm 6\%$ of mean sample weight.

209 All samples were pipetted and sealed into glass vials with screw tops and shipped to the
210 University of California Davis Stable Isotope Facility (Davis, CA, USA) for analysis using
211 headspace gas equilibration on a GasBench-II device (Thermo-Finnigan, Bremen, Germany) for
212 ^{18}O and ^2H analysis. Precision was less than or equal to 2.0% for $\delta^2\text{H}$ and 0.2% for $\delta^{18}\text{O}$. Results
213 were returned in the "delta" notation expressing the isotopic composition of each sample as a
214 ratio in parts per million over to a standardized range of reference waters calibrated against
215 IAEA reference waters and reported relative to VSMOW (Vienna-Standard Mean Ocean Water)
216 where:

217
$$\delta(\text{‰}) = \left(\frac{R_{\text{Sample}}}{R_{\text{Standard}}} - 1 \right)$$

218 Sample extract was situated in an isotope biplot and compared to the global meteoric waterline
219 (GMWL) along with a local meteoric waterline (OMWL) ($\delta^2\text{H} = 6.6$ ($\delta^{18}\text{O}$)-22.7) and local
220 evaporative line (LEL) ($\delta^2\text{H} = 5$ ($\delta^{18}\text{O}$) - 48.4) calculated for the Okanagan Valley by Wassenaar
221 et al. (2011).

222 To test the variance between thinning treatments, block replicates, dates collected, and soil
223 depth, we first tested the normality of the subsets using the Shapiro-Wilk test and found that all
224 subgroups were approximately normally distributed. Repeated measures ANOVAs were used to
225 compare effects of date and treatment on $\delta^2\text{H}$ and $\delta^{18}\text{O}$ in branches, soils and groundwater to
226 determine if changes in lodgepole pine uptake patterns occur over time, if soil signatures vary
227 between different depths (0-100 cm and groundwater) and densities, and if thinning juvenile
228 stands changes seasonal shifts. All statistical analysis was conducted in R Studio (version
229 1.3.1073) using the appropriate tests to determine site distinctions and seasonal variability in
230 depth to uptake (RStudio Team, 2020).

231 2.4 MixSIAR model scenarios

232 Process-based models (PBM) with a Bayesian approach include integrating other processes or
233 existing information as priors allowing for a more informed approach than a simple linear model
234 (Ogle et al., 2014). To accurately partition potential lodgepole pine water sources, we used the
235 MixSIAR modeling package, a Bayesian mixing model (BMM) based on the Markov Chain
236 Monte Carlo method (MCMC) (Langs et al., 2020; Stock, 2013/2022, p. 201; Stock et al., 2018;
237 Wang et al., 2017; Wang et al., 2019). The MixSIAR modeling package was selected over the
238 previous iterations of dual-isotope BMM (SIAR and Simmr) and other partitioning models
239 because of the accuracy in the analysis of covariates and the ability of the model to include
240 source-specific uncertainties and discrimination factors (Stock et al., 2018; Wang et al., 2017).
241 We partitioned potential water sources for five different scenarios using a combination of single
242 and dual isotope approaches and different potential sources: scenario 1- single isotope $\delta^{18}\text{O}$ two
243 sources 5 cm and 35 cm depth; scenario 2-single-isotope $\delta^2\text{H}$ two sources 5 cm and 35 cm depth;
244 scenario 3- dual-isotope two sources 5 cm and 35 cm depth; scenario 4- dual isotope three
245 sources 5 cm, 35 cm and 45-100 cm depth; scenario 5 – dual isotope three sources 5 cm, 35-100



246 cm and groundwater; and scenario 6 – dual isotope four sources 5 cm, 35 cm, 45-100 cm and
247 groundwater. In scenarios using deep soil water (35-100 cm depths), the isotopic composition
248 was calculated as a weighted average between seasonally collected soil water from depth 35 and
249 average soil water at depths collected in 10 cm intervals during the early growing season (n=38
250 per season). There were no source concentration dependencies, and the discrimination was set to
251 zero for both isotopes in the analysis. The run length of the Markov chain Monte Carlo (MCMC)
252 was set to ‘normal’ (chain length = 100,000; burn =50,000; thin = 50; chains = 3). The Gelman-
253 Rubin and Geweke diagnostic tests included in the model package were used to determine
254 convergence (Gelman-Rubin score < 1.01). Scenarios that did not converge were run again with
255 a longer runtime (chain length: 300,000; burn: 200,000; thin: 100; chains = 3). No priors were
256 used, so each water source was considered equally ($\alpha = 1$).

257

258 3. Results

259 3.1. Meteorological droughts

260 The ambient temperature peaked in the moderately thinned plot (T1) on June 29th with a
261 maximum temperature of 36.3°C in an abnormally hot and dry summer. Relative humidity (rH)
262 and subsequently vapor pressure deficit (VPD) recorded in T1 showed the most variability and
263 highest evaporative capacity during July. Atmospheric water vapor was higher in late September
264 and October when precipitation was more frequent, and the watershed began to exhibit traits of
265 hydrologic recovery. One indication of increased water availability was an increase soil moisture
266 at 5 cm and 35 cm depths and more groundwater recharge in October.

267 Rainfall events recorded at a nearby long-term research station between June to October from
268 1997-2008 represented approximately 30.1% of annual precipitation (Winkler et al.,
269 2021). Over the 2021 study period, there was 147.8 mm of rainfall, while the mean summer
270 rainfall from 1997 to 2008 was 232.5 mm, and most of the rainfall occurred in the early
271 growing season. SPI and SPEI were significantly lower in 2021 than the mean historical range
272 (Figure 2). Although there was precipitation and the beginning of hydraulic recovery in
273 October, drought conditions persisted. Drought conditions of the study site reflected the
274 drought conditions of the region as reported by the Agriculture and Agri-Food Canada from June to August 2021 in moving from
275 severe (level 2 drought) to exceptional (level 4) before recovering in September (Canada, 2014:
276
277
278
279
280
281
282
283
284
285
286
287
288

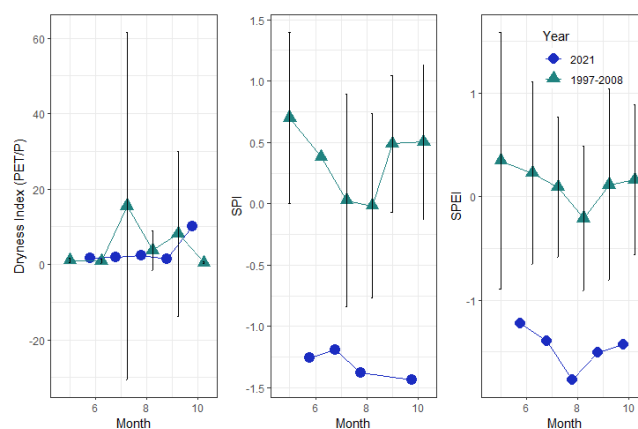


Figure 2 From left to right: dryness index (monthly PET using the Thornthwaite method divided by mean monthly precipitation), standard precipitation index (SPI) with a 3-month period, and standardized precipitation evapotranspiration index (SPEI) with a 3-month period.

289 [https://agriculture.canada.ca/en/agricultural-production/weather/canadian-drought-](https://agriculture.canada.ca/en/agricultural-production/weather/canadian-drought-monitor/drought-analysis)
290 [monitor/drought-analysis](https://agriculture.canada.ca/en/agricultural-production/weather/canadian-drought-monitor/drought-analysis)).

291

292 3.2. Water Stable Isotopes

293 The biplot of sample isotopic composition shows the distribution and effect of fractionation on
294 source water isotope ratios where the meteoric water line of samples collected during the 2021
295 field season produced a slope and intercept of 5.79 and -28.64 ($R^2=0.89$), respectively; the slope
296 was less steep than the one reported by Wassenaar et al. (2011) (OMWL) while the intercept was
297 slightly more negative (Figure 3). Precipitation samples collected during the field season fell
298 along the OMWL (Wassenaar et al., 2011). The $\delta^2\text{H}$ and $\delta^{18}\text{O}$ of the June 11th rainfall event were
299 -127.5‰ and -13.03‰, respectively. The September rainfall event was much more enriched with
300 a $\delta^2\text{H}$ of -38.4‰ and $\delta^{18}\text{O}$ of -2.89 (Figure 3). The snowfall collected on October 7th more
301 closely resembled the lighter, colder, June precipitation event.

302

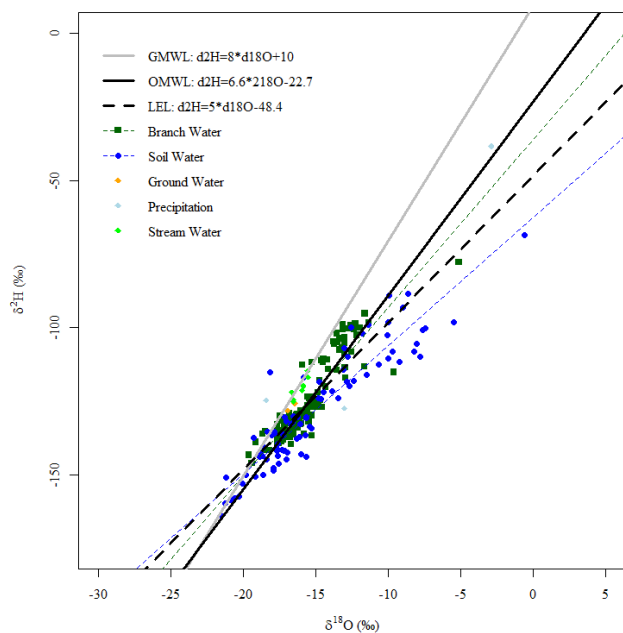


Figure 3 Isoscape biplot of $\delta^{18}\text{O}$ and $\delta^2\text{H}$ including precipitation, xylem, soil, stream, and groundwater from the 241-creek watershed thinning treatments during the 2021 growing season compared to the global meteoric waterline (GMWL), and local meteoric waterline for the Okanagan (OMWL) produced by Wassenaar et al. (2011).

303 3.2.1. Soil Moisture and Seasonal Water Composition



304 Soil moisture probes and percent soil water content from samples collected for isotopic analysis
305 were compared between treatments and deployment depths. Water content of soil samples was
306 highest in June (21.5% at 5 cm and 21.6% at 35 cm) because of high snow melt and early spring
307 precipitation, while soils were driest in September (6.32% at 5 cm and 6.19% at 35 cm).
308 Continuous soil moisture measurements showed that soil water began to increase in mid-
309 September as precipitation became more frequent, daily solar radiation decreased, and water
310 percolated into deeper soil layers. There were significant differences in the continuously
311 measured soil moisture by depths, treatments, and month, respectively (5-35 cm) (Depth: F-
312 value=3545.9, $p < 2e-16^{***}$) (Treatment: F-value = 1883.3, $p < 2e-16^{***}$) (Month: F-
313 value=3359.8, $p < 2e-16^{***}$), but soil water content of samples for isotopic analysis only varied
314 significantly by month (August – October) (F-value = 22, $p < 5.4e-9^{***}$).

315 Soil isotopic results were broken into two datasets to analyze the variation in isotopic
316 composition over time and between treatments, and then a profile of isotopic variance with depth
317 was constructed. Soil water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ varied significantly by depth ($\delta^2\text{H}$: $p = 2.57e-6^{***}$;
318 $\delta^{18}\text{O}$: $p = 2.45e-7^{***}$). $\delta^2\text{H}$ significantly varied monthly except between July and September and
319 September to October. $\delta^{18}\text{O}$ also had significant change in water stable isotope composition by
320 month except when directly comparing July to October and September to October, then there
321 was no significant change in soil isotopic
322 composition. Despite variability in
323 continuous soil moisture by the treatments,
324 there were no statistically significant
325 distinctions in the isotopic composition $\delta^2\text{H}$
326 or $\delta^{18}\text{O}$ of soil water at either depth. Soil
327 $\delta^{18}\text{O}$ in June was $-16.8 \pm 2.57\%$, and $\delta^2\text{H}$
328 was $-136.7 \pm 13.6\%$ at 5 cm; at 35 cm depth,
329 $\delta^{18}\text{O}$ was $-19.2 \pm 1.52\%$, and $\delta^2\text{H}$ was -
330 $149.2 \pm 9.6\%$. Both $\delta^{18}\text{O}$ and $\delta^2\text{H}$ increased
331 more during the growing season at 5 cm
332 depth and with more variability (Figure 4).
333 In October, $\delta^{18}\text{O}$ at the 5 cm depth
334 decreased to $-11.4 \pm 2.58\%$, but $\delta^{18}\text{O}$ at 35
335 cm as well as $\delta^2\text{H}$ at 5 and 35 cm remained
336 enriched at $-15.8 \pm 2.02\%$, $-101.1 \pm 12.4\%$,
337 and $-129.4 \pm 18.8\%$, respectively. These
338 results suggest that soil isotopic
339 composition follows trends in precipitation
340 samples, being most enriched in
341 September, while the precipitation samples
342 collected in June and October were much
343 more depleted. Shallow soil water (depth
344 5cm) varied more throughout the study than
345 deeper soil water. In October, $\delta^{18}\text{O}$ in shallow
346 soils began decreasing again, indicating the
347 addition of less enrichment as water
348 availability began to increase.

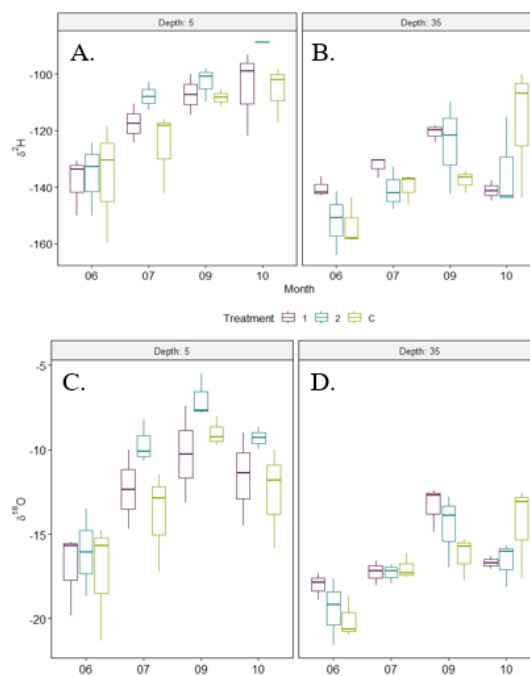


Figure 4 Soil water $\delta^2\text{H}$ (top) and $\delta^{18}\text{O}$ (bottom) at 5 (left) and 35 cm (right) depths collected repeatedly over the growing season from each treatment and block.



349 Both $\delta^2\text{H}$ and $\delta^{18}\text{O}$ were higher in the shallow soils than deeper in the profile (Figure 4A and
 350 4C). While there were significant differences in the $\delta^2\text{H}$ and $\delta^{18}\text{O}$ of soil water by month ($\delta^2\text{H}$:
 351 $p=2.72e-5^{**}$; $\delta^{18}\text{O}$: $p=1.5e-5^{**}$), there was no significant difference between treatments.

352

353 *Table 1 Depth profile of moisture content, $\delta^{18}\text{O}$, and $\delta^2\text{H}$ including the mean and standard deviation across C, T1,*
 354 *and T2 in Block 2 as well as groundwater (GW) samples collected at the end of the growing season.*

Depth	Treatment	Mean $\delta^{18}\text{O}$	Mean $\delta^2\text{H}$	SMC (%)
5	C	-17.23	-141.9	6.89
	T1	-10	-110.5	12.16
	T2	-9.66	-107.84	11.25
20	C	-0.61	-68.7	7.95
	T1	-17.96	-148.55	4.96
	T2	-16.24	-130.5	13.12
40	C	-16.62	-132.1	9.35
	T1	-18.7	-144.53	4.84
	T2	-18.15	-141.5	6.41
60	C	-18.36	-137.5	3
	T1	-17.04	-131.8	7.25
	T2	-20.32	-157.33	6.94
80	C	-19.31	-137.5	4.48
	T1	-17.89	-135.45	4.44
	T2	-20.11	-153.1	5.3
100	C	-19.31	-151.1	2.91
	T1	-17.64	-139.5	4.56
	T2	-18.66	-141.45	5.08
Groundwater		-16.8	-127.3	



355

356 From the isotopic soil profile, there
357 were three significant groupings of
358 isotopic composition ($p < 0.05$):
359 shallow soil water (5-20cm), deep
360 soil water (35-100cm), and
361 groundwater. Mean groundwater
362 collected at the end of the growing
363 season most closely resembled
364 spring and fall snowfall events. The
365 mean $\delta^{18}\text{O}$ of groundwater was $-16.82 \pm 0.34\text{‰}$ which resembles that
366 in the soil profile but mean $\delta^2\text{H}$ was
367 slightly more depleted than soil water
368 (n=4) (Table 1). This fractionation
369 may be due to interactions with

370 bound soil water and soils as the water infiltrates through the vadose zone. One extreme outlier
371 of B1C at the 20 cm depth was removed; the high $\delta^2\text{H}$ and $\delta^{18}\text{O}$ values were likely due to
372 contamination or incomplete cryogenic distillation. The more negative values for both $\delta^{18}\text{O}$ and
373 $\delta^2\text{H}$ with soil depth indicate that snow melt is the main source of water to the deep unsaturated
374 zone and that enriched summer precipitation is not infiltrating deeper soil layers (Figure 5).
375

376 3.2.2. Isotopic Variability in Branch Xylem Water

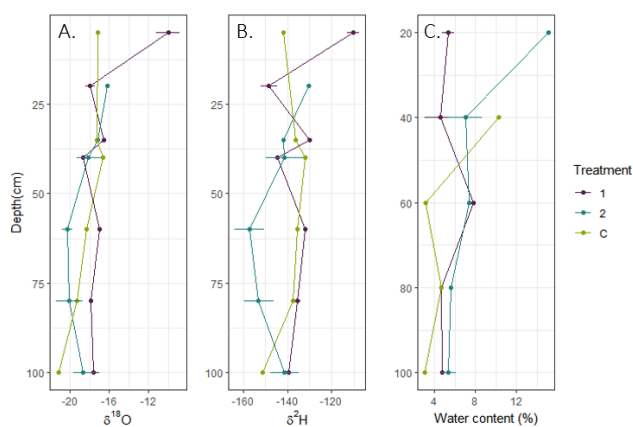


Figure 5 Vertical isotopic profiles and soil water content from treatments in Block 2 and samples collected in mid-July.

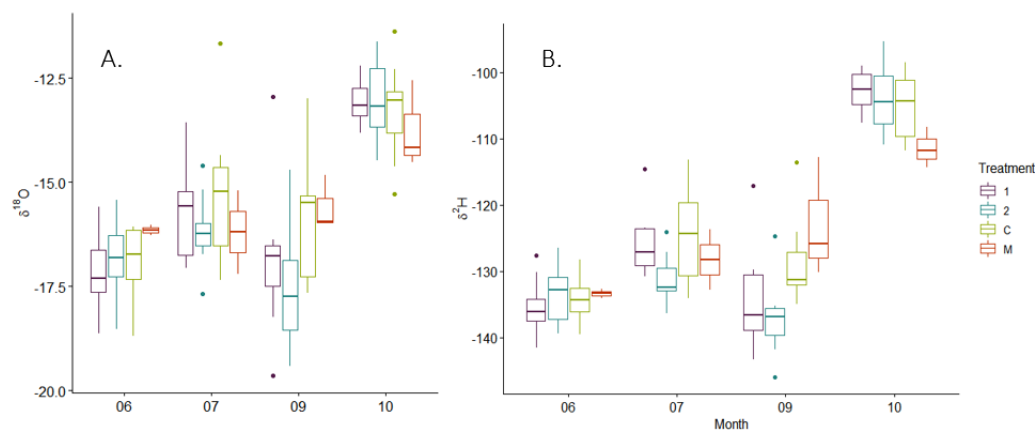


Figure 6 Branch A. $\delta^{18}\text{O}$ and B. $\delta^2\text{H}$ by month and treatment

377 There were no significant differences in both $\delta^{18}\text{O}$ and $\delta^2\text{H}$ of xylem water across blocks and
378 thinning treatments; there was, however, significant variation over time ($\delta^{18}\text{O}$: $F=24.8^*$; $\delta^2\text{H}$: $F =$
379 146.6^*). More specifically, $\delta^{18}\text{O}$ and $\delta^2\text{H}$ of xylem water varied by month for all months
380 collected except for between June and September and July and September (Figure 6). Because
381 the isotopic composition of xylem water showed significant change over the growing season but



382 did not follow the same seasonal trends as soil water, the trees were likely changing their
383 primary water source within the soil profile.

384 3.3. Partitioning xylem source water and seasonal fluxes using MixSIAR

385 With a “normal” runtime (chain
386 length: 100,000; burn: 50,000;
387 thin: 50; chains: 3), scenarios 1,
388 2 and 6 approached the
389 Gelman-Rubin diagnostic,
390 which indicates convergence
391 when the variable is less than
392 1.05 (Table S2). Scenarios 4
393 and 6 were rerun with the run
394 time set to “long” (chain length:
395 300,000; burn: 200,000; thin:
396 100; chains: 3). The Gelman-
397 Rubin diagnostic variable for
398 scenario 4 was 120, and
399 scenario 6 was 17, meaning
400 scenario 6 was closer to
401 convergence (>1.05). Results of
402 scenario 6 indicate that, in June,
403 trees in each treatment acquired
404 the most water from the 5 cm
405 depth (C: 76%; T1: 77%; T2:
406 79%) (Figure 7). In July,
407 shallow soil water was still the
408 primary source for T1 and T2 at
409 47% and 61%, but C had 55%

410 water from 45-100 cm deep and only 33% from 5 cm below the surface. By September, all
411 treatments acquired less than 15% of tree water from shallow soil. Lodgepole pine water use in
412 treatments 1 and 2 was composed of approximately 48% and 54% from around 35 cm, and 72%
413 of water in control stand trees was from 35-100 cm. By October, although SPEI results indicate
414 more moisture and less evaporative demand, scenario six indicated that all three treatments had
415 most water uptake from below 45 cm in the soil profile (Figure 7). Results of the MixSIAR
416 model support findings of branch water stable isotope trends over the growing season where the
417 branch water started with a mean $\delta^{18}\text{O}$ and $\delta^2\text{H}$ of $-16.9\pm 0.89\%$ and $-134.37\pm 3.8\%$ in June and
418 was slightly more enriched in July. There was a shift to a more depleted source in September.
419 And, Lodgepole pine water was the most enriched with heavy isotopes in October, like shallow
420 soil water, with a mean $\delta^{18}\text{O}$ and $\delta^2\text{H}$ of $-12.9\pm 1.76\%$ and $-103.77\pm 7.0\%$, respectively.

421

422 4. Discussion

423 4.1. Seasonal variability in soil water

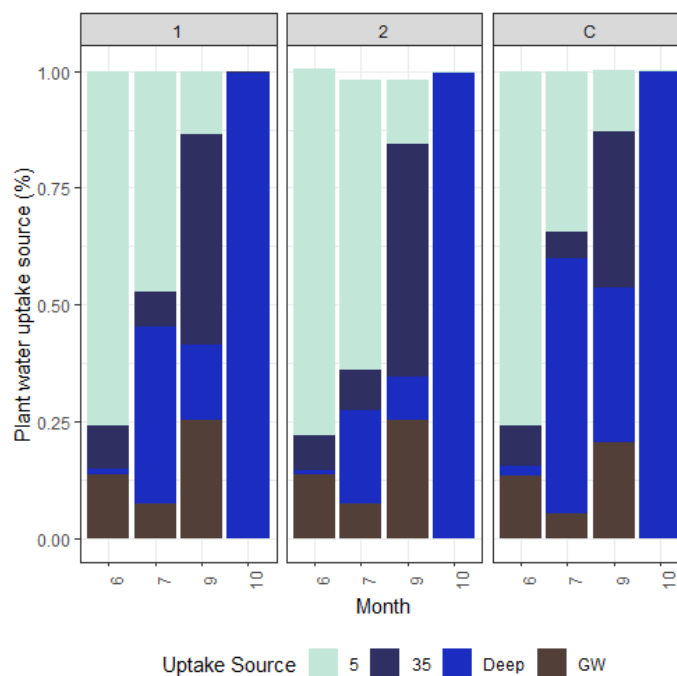


Figure 7 Partitioned relative contribution of different sources of water in the soil profile by the MixSIAR model of scenario 6 with long runtime.



424 Soil water showed mixed gradient of older, more depleted, water molecules deeper in the profile
425 indicating that deep soil water mainly originates from spring snowmelt and that low intensity and
426 less frequent summer precipitation events are evaporated out of the shallow soil layers before
427 they can recharge the unsaturated zone. The muted enrichment of $\delta^{18}\text{O}$ around 35 cm depth in the
428 soil indicates a mixing of the left-over enriched summer precipitation with older and lighter
429 water. Our results did not indicate that differences in soil exposure canopy coverage were
430 effective enough to significantly change the isotopic composition of soil water across treatments.

431 4.2. Seasonal lodgepole pine water use

432 Literature utilizing stable water isotopic analysis to determine plant preferential water uptake in
433 arid regions indicates that vegetation can utilize precipitation despite the temporal origin
434 (Andrews et al., 2012; Brinkmann et al., 2019; Ehleringer et al., 1991). Seasonal water
435 availability depends on precipitation, soil water holding capacity and drainage, and evaporative
436 loss (Gibson & Edwards, 2002; Kleine et al., 2020; Stumpp et al., 2018). Based on the seasonal
437 shift in the isotopic composition of soil water 5 cm below the surface showed more enrichment
438 over the growing season than around 35 cm below the surface due to more evaporative
439 fractionation of the soil surface and a lack of heavy rainfall to drive precipitation deeper into the
440 soil profile. However, variability in branch isotopic composition did not follow the same trends.
441 Our results indicate that lodgepole pines access water from multiple depths in the soil profile.
442 Regardless of depth and forest density, spring snowmelt is the main source for lodgepole pines as
443 it infiltrates through the vadose zone.

444 The MixSIAR isotopic partitioning model results from each of the six scenarios also indicated a
445 seasonal shift in uptake source. At the beginning of the growing season, when snow meltwater is
446 more available at shallow depths and beginning to infiltrate through the soils, lodgepole pines
447 obtain most of their water likely from snow melt in shallow soils with small contributions from
448 other potential sources (< 25% of June water uptake in all treatments). The mean $\delta^{18}\text{O}$ and $\delta^2\text{H}$ of
449 branch water from each treatment in September was more depleted than in July and a larger
450 proportion of tree water was from 35-100 cm deep in the soil profile as shallow soils were dry
451 from a lack of rainfall and surface soil evaporation. Local monitoring close to the study site
452 indicated that the depth to groundwater stayed 6.5 m below the surface from August through the
453 end of the study period. The continued use of deep soil water even during rewetting in late
454 September and October suggests that the drought conditions may have led to fine root mortality
455 or some other mechanistic restriction in the use of shallow soil water late in the growing season.

456 Our results indicate that lodgepole pine, like other pine species in arid regions, is flexible in its
457 ability to access deep soil water and can change its depth to water uptake over time (Brinkmann
458 et al., 2018; Grossiord et al., 2017; Kerhoulas et al., 2013; Kleine et al., 2020; Moreno-Gutiérrez
459 et al., 2011; Simonin et al., 2006; Sohn et al., 2014; Wang et al., 2021). Our results of depth to
460 water uptake by lodgepole pine support the reports of lodgepole pine's seasonal shift in depth to
461 water uptake in Alberta (Andrews et al., 2012). Tree species native to arid regions exhibit a
462 variety of adaptations to long-term drought stress and decreased water availability in the soil
463 profile such as deep tap roots, access to the water table, utilizing bound and mobile soil water,
464 fine root mortality, and hydraulic redistribution in ecosystems with low water holding capacity
465 (Amin et al., 2020; Brinkmann et al., 2018; Grossiord et al., 2017; Kerhoulas et al., 2013; Kleine



466 et al., 2020; Langs et al., 2020; Meinzer et al., 2007b; Prieto et al., 2012; Sohn et al., 2016; J.
467 Wang et al., 2017, p. 201).

468 However, the literature is inconsistent across different biogeoclimatic regions and species
469 regarding the effects of thinning on inter-tree competition or altered depth to water uptake with
470 tree density (Kerhoulas et al., 2013; Moreno-Gutiérrez et al., 2011; Sohn et al., 2016; Wang et
471 al., 2021). Our findings that there is no significant impact of forest thinning on depth to water
472 uptake. Despite stem density, seasonal shifts in depth to water uptake support results of a study
473 on the impacts of thinning intensity on 60-year-old *Pinus halepensis* Mill. in a semi-arid region
474 of Spain which concluded that forest thinning reduced competition for water resources but did
475 not alter water uptake patterns (Moreno-Gutiérrez et al., 2011). Another study on the impact of
476 thinning *Pinus ponderosa* Dougl. on depth to water uptake concluded that water was consistently
477 more isotopically enriched in low-density stands potentially due to prolonged evaporative
478 fractionation in the soil profile, or that understory vegetation utilized more shallow water sources
479 (Kerhoulas et al., 2013). The impact of forest thinning on stand and understory water use is
480 highly variable and dependent on understory growth, canopy structure, water availability, when
481 forest thinning is implemented, and the time since stem removal (Kerhoulas et al., 2013;
482 Moreno-Gutiérrez et al., 2011; Sohn et al., 2016). More research is needed to discern if lodgepole
483 pine relies more on mobile or bound soil water, the extent of lodgepole pine rooting zones, what
484 biogeochemical factors cause seasonal shifts in water uptake, and if severe seasonal drought has
485 a lasting effect on water uptake strategies during hydrologic recovery (Simonin et al., 2007;
486 Vargas et al., 2017).

487 4.3. Impacts of the drought and implications for future climate conditions

488 The 2021 growing season was an abnormally hot and dry period for the interior of British
489 Columbia with severe to exceptional drought conditions. Wang et al. (2019) found that thinning
490 improved water-use efficiency, drought tolerance, and drought recovery by decreasing stand
491 density and improving carbon storage. Our results support the finding that lodgepole pine trees
492 can adjust to prolonged water scarcity, and that over-populated stands may be more resilient than
493 the literature initially indicated. In fact, drought conditions over the study period likely
494 intensified the change in xylem water isotopic composition over the growing season. However,
495 the scope of this study did not include pre-drought seasonal water use patterns nor the impact of
496 forest density on depth to water uptake during drought recovery. Because lodgepole pine depth
497 to water uptake changes during prolonged dry growing season conditions, the trees are more
498 reliant on winter snowpack and spring infiltration to recharge deeper source water below the
499 evaporative front. One experiment on juniper (*Juniperus monosperma* (Engelm.) Sarg.) and
500 piñon pine (*Pinus edulis* Engelm.) investigated the simultaneous stress of increased heat and
501 decreased precipitation on depth to water uptake and found that extreme temperatures and
502 decreased precipitation lead to less reversible embolism and more root death in surface soil
503 levels preventing trees from accessing shallow water sources if precipitation becomes more
504 available late in the growing season (Grossiord et al., 2017). It is becoming more imperative to
505 understand the climatic drivers of lodgepole pine water use and access as mean annual
506 temperatures continue to rise, the seasonal frequency and intensity of precipitation change, and
507 drought conditions become more severe. This study indicates that severe seasonal dryness pushes
508 lodgepole pines to rely more on snowmelt while losing function in shallow roots. Decreased



509 winter snowpack could lead to water scarcity in the late growing season if lodgepole pines are
510 unable to access water during the rewetting period post-summer drought.

511

512 5.1 Conclusions

513 Lodgepole pine, across all treatments, was able to shift from shallow soil water at the beginning
514 of the growing season to deeper soil water as drought conditions progressed. The quick draining
515 and sun-exposed soils do not retain small summer precipitation events, and as a result, either due
516 to changes in water availability or limitations in rooting function, lodgepole pines shift to a more
517 readily available source in the soil profile (Aranda et al., 2012; Prieto et al., 2012). Our findings
518 support the literature that lodgepole pines are a drought-tolerant species with dimorphic rooting
519 systems making them more advantageous in their ability access water from varying depths in the
520 soil layer depending on water availability (Andrews et al., 2012; Liu et al., 2011). Despite the
521 ecological plasticity under extreme heat and low summer precipitation conditions, there was no
522 significant difference in depth to water use between the over-populated plots and thinned ones.
523 Future climate projections indicate hotter growing seasons and less precipitation (Allen et al.,
524 2010). Further investigation is needed to discern how lodgepole pines, under different stand
525 densities, use water during prolonged drought and drought recovery periods (Grossiord et al.,
526 2017; Navarro-Cerrillo et al., 2019; Simonin et al., 2007; Sohn et al., 2016). However, from our
527 findings, during prolonged growing season, stand density does not alter tree depth to water
528 uptake, nor seasonal shifts in water sources. Lodgepole pines indicate a strong level of drought
529 tolerance and ability to access water under extreme heat conditions. If summer precipitation
530 decreases, lodgepole pines have alternative strategies to access deeper soil water from spring
531 snowmelt in the interior of British Columbia. However, if snowpack and spring snowmelt begin
532 to decrease, lodgepole pines will need to acclimate to these hydrological shifts.

533

534 *Code and Data Availability:*

535 The codes of the data analysis and plotting are available at <https://github.com/emory->
536 [ce/LodgepolePineWaterUseStrategies2021](https://github.com/emory-ce/LodgepolePineWaterUseStrategies2021) and are available upon request (ece58@nau.edu)

537

538 *Author Contributions:*

539 EE conceived the idea as a part of their Master's research with AW, and performed the
540 extractions with RG. Analysis was primarily conducted by EE with guidance from AW and RG.
541 All authors contributed to the manuscript.

542

543 *Competing Interests:*

544 None of the authors have competing interests.

545



546 *Acknowledgements:*

547 This study was funded by the Ministry of Forests, Lands, Natural Resource Operations and Rural
548 Development. Field work was done with the assistance of Fiona Moodie. Cryogenic distillation
549 was conducted at the University of British Columbia. Samples were sent to the Stable Isotope
550 Facility at University of California, Davis.

551

552 *Financial Support:*

553 This research was funded by the Ministry of Forests, Lands, Natural resource Operations and
554 rural Development (grant number: RE21NOR-029)



555 References

- 556 Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M.,
557 Kitzberger, T., Rigling, A., Breshears, D. D., Hogg, E. H. (Ted), Gonzalez, P., Fensham,
558 R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S. W., Semerci,
559 A., & Cobb, N. (2010). A global overview of drought and heat-induced tree mortality
560 reveals emerging climate change risks for forests. *Forest Ecology and Management*,
561 259(4), 660–684. <https://doi.org/10.1016/j.foreco.2009.09.001>
- 562 Amin, A., Zuecco, G., Geris, J., Schwendenmann, L., McDonnell, J. J., Borga, M., & Penna, D.
563 (2020). Depth distribution of soil water sourced by plants at the global scale: A new
564 direct inference approach. *Ecohydrology*, 13(2), e2177. <https://doi.org/10.1002/eco.2177>
- 565 Andrews, S. F., Flanagan, L. B., Sharp, E. J., & Cai, T. (2012). Variation in water potential,
566 hydraulic characteristics and water source use in montane Douglas-fir and lodgepole pine
567 trees in southwestern Alberta and consequences for seasonal changes in photosynthetic
568 capacity. *Tree Physiology*, 32(2), 146–160. <https://doi.org/10.1093/treephys/tpr136>
- 569 Andrews, S. F., & Science, U. of L. F. of A. and. (2009). *Tracing changes in uptake of*
570 *precipitation and groundwater and associated consequences for physiology of Douglas-*
571 *fir and lodgepole pine trees in montane forests of SW Alberta* [Thesis, Lethbridge, Alta. :
572 University of Lethbridge, Dept. of Biological Sciences, c2009].
573 <https://opus.uleth.ca/handle/10133/2482>
- 574 Aranda, I., Forner, A., Cuesta, B., & Valladares, F. (2012). Species-specific water use by forest
575 tree species: From the tree to the stand. *Agricultural Water Management*, 114, 67–77.
576 <https://doi.org/10.1016/j.agwat.2012.06.024>



- 577 Beguería, S., Vicente-Serrano, S. M., Reig, F., & Latorre, B. (2014). Standardized precipitation
578 evapotranspiration index (SPEI) revisited: Parameter fitting, evapotranspiration models,
579 tools, datasets and drought monitoring. *International Journal of Climatology*, 34(10),
580 3001–3023. <https://doi.org/10.1002/joc.3887>
- 581 Belmonte, A., Ts. Sankey, T., Biederman, J., Bradford, J. B., & Kolb, T. (2022). Soil moisture
582 response to seasonal drought conditions and post-thinning forest structure. *Ecohydrology*,
583 15(5), e2406. <https://doi.org/10.1002/eco.2406>
- 584 Brinkmann, N., Eugster, W., Buchmann, N., & Kahmen, A. (2019). Species-specific differences
585 in water uptake depth of mature temperate trees vary with water availability in the soil.
586 *Plant Biology*, 21(1), 71–81. <https://doi.org/10.1111/plb.12907>
- 587 Brinkmann, N., Seeger, S., Weiler, M., Buchmann, N., Eugster, W., & Kahmen, A. (2018).
588 Employing stable isotopes to determine the residence times of soil water and the temporal
589 origin of water taken up by *Fagus sylvatica* and *Picea abies* in a temperate forest. *The*
590 *New Phytologist*, 219(4), 1300–1313.
- 591 Canada, A. and A.-F. (2014, December 4). *Canadian Drought Monitor* [Search interface].
592 [https://agriculture.canada.ca/en/agricultural-production/weather/canadian-drought-](https://agriculture.canada.ca/en/agricultural-production/weather/canadian-drought-monitor/drought-analysis)
593 [monitor/drought-analysis](https://agriculture.canada.ca/en/agricultural-production/weather/canadian-drought-monitor/drought-analysis)
- 594 Chillakuru, D. R. (2009). *Towards locating and quantifying rrepiration in the soil and in the*
595 *plant using a novel 18-oxygen labelling technique* [MSc Thesis]. University of British
596 Columbia.
- 597 Coupe, R., Steward, A. C., & Wikeem, B. M. (1991). *Engelmann Spruce—Subalpine Fir Zone*.
598 Creed, I. F., Spargo, A. T., Jones, J. A., Buttle, J. M., Adams, M. B., Beall, F. D., Booth, E. G.,
599 Campbell, J. L., Clow, D., Elder, K., Green, M. B., Grimm, N. B., Miniati, C., Ramlal, P.,



- 600 Saha, A., Sebestyen, S., Spittlehouse, D., Sterling, S., Williams, M. W., ... Yao, H.
601 (2014). Changing forest water yields in response to climate warming: Results from long-
602 term experimental watershed sites across North America. *Global Change Biology*,
603 20(10), 3191–3208. <https://doi.org/10.1111/gcb.12615>
- 604 Dawson, T. E., & Pate, J. S. (1996). Seasonal water uptake and movement in root systems of
605 Australian phraeatophytic plants of dimorphic root morphology: A stable isotope
606 investigation. *Oecologia*, 107(1), 13–20. <https://doi.org/10.1007/BF00582230>
- 607 Ehleringer, J. R., Phillips, S. L., Schuster, W. S. F., & Sandquist, D. R. (1991). Differential
608 utilization of summer rains by desert plants. *Oecologia*, 88(3), 430–434.
609 <https://doi.org/10.1007/BF00317589>
- 610 Evaristo, J., Jasechko, S., & McDonnell, J. J. (2015). Global separation of plant transpiration
611 from groundwater and streamflow. *Nature*, 525(7567), Article 7567.
612 <https://doi.org/10.1038/nature14983>
- 613 Fahey, T. J., & Knight, D. H. (1986). Lodgepole Pine Ecosystems. *BioScience*, 36(9), 610–617.
614 <https://doi.org/10.2307/1310196>
- 615 Fernandes, T. J. G., Del Campo, A. D., Herrera, R., & Molina, A. J. (2016). Simultaneous
616 assessment, through sap flow and stable isotopes, of water use efficiency (WUE) in
617 thinned pines shows improvement in growth, tree-climate sensitivity and WUE, but not in
618 WUEi. *Forest Ecology and Management*, 361, 298–308.
619 <https://doi.org/10.1016/j.foreco.2015.11.029>
- 620 Flanagan, L. B., & Ehleringer, J. R. (1991). Stable Isotope Composition of Stem and Leaf Water:
621 Applications to the Study of Plant Water Use. *Functional Ecology*, 5(2), 270–277.
622 <https://doi.org/10.2307/2389264>



- 623 Flint, A. L., & Childs, S. W. (1991). Use of the Priestley-Taylor evaporation equation for soil
624 water limited conditions in a small forest clearcut. *Agricultural and Forest Meteorology*,
625 56(3), 247–260. [https://doi.org/10.1016/0168-1923\(91\)90094-7](https://doi.org/10.1016/0168-1923(91)90094-7)
- 626 Gibson, J. J., & Edwards, T. W. D. (2002). Regional water balance trends and evaporation-
627 transpiration partitioning from a stable isotope survey of lakes in northern Canada.
628 *Global Biogeochemical Cycles*, 16(2), 10-1-10–14.
629 <https://doi.org/10.1029/2001GB001839>
- 630 Giles-Hansen, K., Wei, X., & Hou, Y. (2021). Dramatic increase in water use efficiency with
631 cumulative forest disturbance at the large forested watershed scale. *Carbon Balance and*
632 *Management*, 16(1), 6. <https://doi.org/10.1186/s13021-021-00169-4>
- 633 Giuggiola, A., Ogée, J., Rigling, A., Gessler, A., Bugmann, H., & Treydte, K. (2016).
634 Improvement of water and light availability after thinning at a xeric site: Which matters
635 more? A dual isotope approach. *New Phytologist*, 210(1), 108–121.
636 <https://doi.org/10.1111/nph.13748>
- 637 Grossiord, C., Sevanto, S., Dawson, T. E., Adams, H. D., Collins, A. D., Dickman, L. T.,
638 Newman, B. D., Stockton, E. A., & McDowell, N. G. (2017). Warming combined with
639 more extreme precipitation regimes modifies the water sources used by trees. *The New*
640 *Phytologist*, 213(2), 584–596.
- 641 Halter, M. R., & Chanway, C. P. (1993). Growth and root morphology of planted and naturally-
642 regenerated Douglas fir and Lodgepole pine. *Annales Des Sciences Forestières*, 50(1),
643 71–77. <https://doi.org/10.1051/forest:19930105>



- 644 Hope, G. D. (2011). Clearcut harvesting effects on soil and creek inorganic nitrogen in high
645 elevation forests of southern interior British Columbia. *Canadian Journal of Soil Science*.
646 <https://doi.org/10.4141/CJSS06032>
- 647 Kerhoulas, L. P., Koch, G. W., & Kolb, T. E. (2013). Tree size, stand density, and the source of
648 water used across seasons by ponderosa pine in northern Arizona. *Forest Ecology and*
649 *Management*, 289, 425–433.
650 <http://dx.doi.org.ezproxy.library.ubc.ca/10.1016/j.foreco.2012.10.036>
- 651 Kleine, L., Tetzlaff, D., Smith, A., Wang, H., & Soulsby, C. (2020). Using water stable isotopes
652 to understand evaporation, moisture stress, and re-wetting in catchment forest and
653 grassland soils of the summer drought of 2018. *Hydrology and Earth System Sciences*,
654 24(7), 3737–3752. <https://doi.org/10.5194/hess-24-3737-2020>
- 655 Langs, L. E., Petrone, R. M., & Pomeroy, J. W. (2020). A $\delta^{18}\text{O}$ and $\delta^2\text{H}$ stable water isotope
656 analysis of subalpine forest water sources under seasonal and hydrological stress in the
657 Canadian Rocky Mountains. *Hydrological Processes*, 34(26), 5642–5658.
658 <https://doi.org/10.1002/hyp.13986>
- 659 Lin, G., & da S. L. Sternberg, L. (1993). 31—Hydrogen Isotopic Fractionation by Plant Roots
660 during Water Uptake in Coastal Wetland Plants. In J. R. Ehleringer, A. E. Hall, & G. D.
661 Farquhar (Eds.), *Stable Isotopes and Plant Carbon-water Relations* (pp. 497–510).
662 Academic Press. <https://doi.org/10.1016/B978-0-08-091801-3.50041-6>
- 663 Liu, S., Chen, Y., Chen, Y., Friedman, J. M., Hati, J. H. A., & Fang, G. (2015). Use of ^2H and
664 ^{18}O stable isotopes to investigate water sources for different ages of *Populus euphratica*
665 along the lower Heihe River. *Ecological Research*, 30(4), 581–587.
666 <https://doi.org/10.1007/s11284-015-1270-6>



- 667 Liu, X., Silins, U., Lieffers, V. J., & Man, R. (2011a). Stem hydraulic properties and growth in
668 lodgepole pine stands following thinning and sway treatment. *Canadian Journal of*
669 *Forest Research*. <https://doi.org/10.1139/x03-061>
- 670 Liu, X., Silins, U., Lieffers, V. J., & Man, R. (2011b). Stem hydraulic properties and growth in
671 lodgepole pine stands following thinning and sway treatment. *Canadian Journal of*
672 *Forest Research*. <https://doi.org/10.1139/x03-061>
- 673 Maier, C. A., Burley, J., Cook, R., Ghezehei, S. B., Hazel, D. W., & Nichols, E. G. (2019). Tree
674 water use, water use efficiency, and carbon isotope discrimination in relation to growth
675 potential in *Populus deltoides* and hybrids under field conditions. *Forests*, *10*(11), Article
676 11. <https://doi.org/10.3390/f10110993>
- 677 Manrique-Alba, À., Beguería, S., Molina, A. J., González-Sanchis, M., Tomàs-Burguera, M., del
678 Campo, A. D., Colangelo, M., & Camarero, J. J. (2020). Long-term thinning effects on
679 tree growth, drought response and water use efficiency at two Aleppo pine plantations in
680 Spain. *Science of The Total Environment*, *728*, 138536.
681 <https://doi.org/10.1016/j.scitotenv.2020.138536>
- 682 Meinzer, F. C., Clearwater, M. J., & Goldstein, G. (2001). Water transport in trees: Current
683 perspectives, new insights and some controversies. *Environmental and Experimental*
684 *Botany*, *45*(3), 239–262. [https://doi.org/10.1016/S0098-8472\(01\)00074-0](https://doi.org/10.1016/S0098-8472(01)00074-0)
- 685 Meinzer, F. C., Warren, J. M., & Brooks, J. R. (2007a). Species-specific partitioning of soil
686 water resources in an old-growth Douglas-fir–western hemlock forest. *Tree Physiology*,
687 *27*(6), 871–880. <https://doi.org/10.1093/treephys/27.6.871>



- 688 Meinzer, F. C., Warren, J. M., & Brooks, J. R. (2007b). Species-specific partitioning of soil
689 water resources in an old-growth Douglas-fir–western hemlock forest. *Tree Physiology*,
690 27(6), 871–880. <https://doi.org/10.1093/treephys/27.6.871>
- 691 Meinzer, F. C., Woodruff, D. R., Eissenstat, D. M., Lin, H. S., Adams, T. S., & McCulloh, K. A.
692 (2013). Above- and belowground controls on water use by trees of different wood types
693 in an eastern US deciduous forest. *Tree Physiology*, 33(4), 345–356.
694 <https://doi.org/10.1093/treephys/tpt012>
- 695 Molina, A. J., & del Campo, A. D. (2012). The effects of experimental thinning on throughfall
696 and stemflow: A contribution towards hydrology-oriented silviculture in Aleppo pine
697 plantations. *Forest Ecology and Management*, 269, 206–213.
698 <https://doi.org/10.1016/j.foreco.2011.12.037>
- 699 Moore, R. D., Allen, D. M., McKenzie, L. M., Spittlehouse, D. L., & Winkler, R. D. (2021).
700 *Upper Penticton Creek Watershed Experiment—Data Repository* [Data set]. Zenodo.
701 <https://doi.org/10.5281/zenodo.5520109>
- 702 Moore, R. D., & Wondzell, S. M. (2005). Physical Hydrology and the Effects of Forest
703 Harvesting in the Pacific Northwest: A Review1. *JAWRA Journal of the American Water*
704 *Resources Association*, 41(4), 763–784. [https://doi.org/10.1111/j.1752-](https://doi.org/10.1111/j.1752-1688.2005.tb03770.x)
705 [1688.2005.tb03770.x](https://doi.org/10.1111/j.1752-1688.2005.tb03770.x)
- 706 Moreno-Gutiérrez, C., Barberá, G. G., Nicolás, E., De Luis, M., Castillo, V. M., Martínez-
707 Fernández, F., & Querejeta, J. I. (2011). Leaf $\delta^{18}\text{O}$ of remaining trees is affected by
708 thinning intensity in a semiarid pine forest. *Plant, Cell & Environment*, 34(6), 1009–
709 1019. <https://doi.org/10.1111/j.1365-3040.2011.02300.x>



- 710 Navarro-Cerrillo, R. M., Sánchez-Salguero, R., Rodríguez, C., Duque Lazo, J., Moreno-Rojas, J.
711 M., Palacios-Rodríguez, G., & Camarero, J. J. (2019). Is thinning an alternative when
712 trees could die in response to drought? The case of planted *Pinus nigra* and *P. Sylvestris*
713 stands in southern Spain. *Forest Ecology and Management*, 433, 313–324.
714 <https://doi.org/10.1016/j.foreco.2018.11.006>
- 715 Ogle, K., Tucker, C., & Cable, J. M. (2014). Beyond simple linear mixing models: Process-based
716 isotope partitioning of ecological processes. *Ecological Applications*, 24(1), 181–195.
717 <https://doi.org/10.1890/12-1970.1>
- 718 Orłowski, N., Frede, H.-G., Brüggemann, N., & Breuer, L. (2013). Validation and application of
719 a cryogenic vacuum extraction system for soil and plant water extraction for isotope
720 analysis. *Journal of Sensors and Sensor Systems*, 2(2), 179–193.
721 <https://doi.org/10.5194/jsss-2-179-2013>
- 722 Park, J., Kim, T., Moon, M., Cho, S., Ryu, D., & Seok Kim, H. (2018). Effects of thinning
723 intensities on tree water use, growth, and resultant water use efficiency of 50-year-old
724 *Pinus koraiensis* forest over four years. *Forest Ecology and Management*, 408, 121–128.
725 <https://doi.org/10.1016/j.foreco.2017.09.031>
- 726 Pearcy, R. W., Ehleringer, J. R., Mooney, H., & Rundel, P. W. (2012). *Plant Physiological*
727 *Ecology: Field methods and instrumentation*. Springer Science & Business Media.
- 728 Prieto, I., Armas, C., & Pugnaire, F. I. (2012). Water release through plant roots: New insights
729 into its consequences at the plant and ecosystem level. *The New Phytologist*, 193(4), 830–
730 841.
- 731 RStudio Team. (2020). *R Studio: Integrated Development Environment for R* (1.3.1073).
732 RStudio, PBC.



- 733 Russell, H. W. (1960). *Estimating Potential Evapotranspiration*. Massachusetts Institute of
734 Technology.
- 735 Sánchez-Pérez, J. M., Lucot, E., Bariac, T., & Trémoières, M. (2008). Water uptake by trees in a
736 riparian hardwood forest (Rhine floodplain, France). *Hydrological Processes*, 22(3),
737 366–375. <https://doi.org/10.1002/hyp.6604>
- 738 Simonin, K., Kolb, T. E., Montes-Helu, M., & Koch, G. W. (2006). Restoration thinning and
739 influence of tree size and leaf area to sapwood area ratio on water relations of *Pinus*
740 *ponderosa*. *Tree Physiology*, 26(4), 493–503. <https://doi.org/10.1093/treephys/26.4.493>
- 741 Simonin, K., Kolb, T. E., Montes-Helu, M., & Koch, G. W. (2007). The influence of thinning on
742 components of stand water balance in a ponderosa pine forest stand during and after
743 extreme drought. *Agricultural and Forest Meteorology*, 143(3), 266–276.
744 <https://doi.org/10.1016/j.agrformet.2007.01.003>
- 745 Sohn, J. A., Brooks, J. R., Bauhus, J., Kohler, M., Kolb, T. E., & McDowell, N. G. (2014).
746 Unthinned slow-growing ponderosa pine (*Pinus ponderosa*) trees contain muted isotopic
747 signals in tree rings as compared to thinned trees. *Trees - Structure and Function*, 28(4),
748 1035–1051. <https://doi.org/10.1007/s00468-014-1016-z>
- 749 Sohn, J. A., Kohler, M., Gessler, A., & Bauhus, J. (2012). Interactions of thinning and stem
750 height on the drought response of radial stem growth and isotopic composition of
751 Norway spruce (*Picea abies*). *Tree Physiology*, 32(10), 1199–1213.
752 <https://doi.org/10.1093/treephys/tps077>
- 753 Sohn, J. A., Saha, S., & Bauhus, J. (2016). Potential of forest thinning to mitigate drought stress:
754 A meta-analysis. *Forest Ecology and Management*, 380, 261–273.
755 <https://doi.org/10.1016/j.foreco.2016.07.046>



- 756 Sprenger, M., Tetzlaff, D., & Soulsby, C. (2017). Soil water stable isotopes reveal evaporation
757 dynamics at the soil–plant–atmosphere interface of the critical zone. *Hydrology and*
758 *Earth System Sciences*, 21(7), 3839–3858. <https://doi.org/10.5194/hess-21-3839-2017>
- 759 Stage, J. H., Tallaksen, L. M., Xu, C. Y., & Lanen, H. A. J. V. (2014). *Standardized*
760 *precipitation-evapotranspiration index (SPEI): Sensitivity to potential evapotranspiration*
761 *model and parameters*. 363, 367–373. <https://library.wur.nl/WebQuery/wurpubs/558281>
- 762 Stock, B. (2022). *MixSIAR* [R]. <https://github.com/brianstock/MixSIAR> (Original work
763 published 2013)
- 764 Stock, B. C., Jackson, A. L., Ward, E. J., Parnell, A. C., Phillips, D. L., & Semmens, B. X.
765 (2018). Analyzing mixing systems using a new generation of Bayesian tracer mixing
766 models. *PeerJ*, 6, e5096. <https://doi.org/10.7717/peerj.5096>
- 767 Streck, N. A. (2003). Stomatal Response to water vapor pressure deficit: An unsolved issue.
768 *Current Agricultural Science and Technology*, 9(4).
769 <https://doi.org/10.18539/cast.v9i4.649>
- 770 Stumpp, C., Brüggemann, N., & Wingate, L. (2018). Stable Isotope Approaches in Vadose Zone
771 Research. *Vadose Zone Journal*, 17(1), 180096. <https://doi.org/10.2136/vzj2018.05.0096>
- 772 Szymczak, S., Barth, J., Bendix, J., Huneau, F., Garel, E., Häusser, M., Juhlke, T., Knerr, I.,
773 Santoni, S., Mayr, C., Trachte, K., van Geldern, R., & Bräuning, A. (2020). First
774 indications of seasonal and spatial variations of water sources in pine trees along an
775 elevation gradient in a Mediterranean ecosystem derived from $\delta^{18}\text{O}$. *Chemical Geology*,
776 549, 119695. <https://doi.org/10.1016/j.chemgeo.2020.119695>



- 777 Tsuruta, K., Yamamoto, H., Katsuyama, M., Kosugi, Y., Okumura, M., & Matsuo, N. (2019).
778 Effects of cryogenic vacuum distillation on the stable isotope ratios of soil water.
779 *Hydrological Research Letters*, 13(1), 1–6. <https://doi.org/10.3178/hrl.13.1>
- 780 Vargas, A. I., Schaffer, B., Yuhong, L., & Sternberg, L. da S. L. (2017). Testing plant use of
781 mobile vs immobile soil water sources using stable isotope experiments. *The New*
782 *Phytologist*, 215(2), 582–594.
- 783 Wang, J., Fu, B., Lu, N., & Zhang, L. (2017). Seasonal variation in water uptake patterns of three
784 plant species based on stable isotopes in the semi-arid Loess Plateau. *Science of The*
785 *Total Environment*, 609, 27–37. <https://doi.org/10.1016/j.scitotenv.2017.07.133>
- 786 Wang, T., Xu, Q., Gao, D., Zhang, B., Zuo, H., & Jiang, J. (2021). Effects of thinning and
787 understory removal on the soil water-holding capacity in *Pinus massoniana* plantations.
788 *Scientific Reports*, 11(1), Article 1. <https://doi.org/10.1038/s41598-021-92423-5>
- 789 Wang, Y., Wei, X., del Campo, A. D., Winkler, R., Wu, J., Li, Q., & Liu, W. (2019). Juvenile
790 thinning can effectively mitigate the effects of drought on tree growth and water
791 consumption in a young *Pinus contorta* stand in the interior of British Columbia, Canada.
792 *Forest Ecology and Management*, 454, 117667.
793 <https://doi.org/10.1016/j.foreco.2019.117667>
- 794 Warren, J. M., Meinzer, F. C., Brooks, J. R., & Domec, J. C. (2005). Vertical stratification of soil
795 water storage and release dynamics in Pacific Northwest coniferous forests. *Agricultural*
796 *and Forest Meteorology*, 130(1), 39–58. <https://doi.org/10.1016/j.agrformet.2005.01.004>
- 797 Wassenaar, L. I., Athanasopoulos, P., & Hendry, M. J. (2011). Isotope hydrology of
798 precipitation, surface and ground waters in the Okanagan Valley, British Columbia,



- 799 Canada. *Journal of Hydrology*, 411(1), 37–48.
800 <https://doi.org/10.1016/j.jhydrol.2011.09.032>
- 801 West, A. G., Patrickson, S. J., & Ehleringer, J. R. (2006). Water extraction times for plant and
802 soil materials used in stable isotope analysis. *Rapid Communications in Mass*
803 *Spectrometry*, 20(8), 1317–1321. <https://doi.org/10.1002/rcm.2456>
- 804 Winkler, R. D., & Moore, R. D. (2006). Variability in snow accumulation patterns within forest
805 stands on the interior plateau of British Columbia, Canada. *Hydrological Processes*,
806 20(17), 3683–3695. <https://doi.org/10.1002/hyp.6382>
- 807 Winkler, R., Diana, A., Giles, T., Heise, B., Moore, R. D., Redding, T., Spittlehouse, D., & Wei,
808 X. (2021). *Approaching four decades of Forest Watershed research at Upper Penticton*
809 *Creek, British Columbia: A Synthesis*.
- 810 Wu, H., Hayes, M. J., Wilhite, D. A., & Svoboda, M. D. (2005). The effect of the length of
811 record on the standardized precipitation index calculation. *International Journal of*
812 *Climatology*, 25(4), 505–520. <https://doi.org/10.1002/joc.1142>
- 813
814
815