An experimental assessment of the impact of drought and fire on western larch injury, mortality, and recovery

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Manuscripts

1 **Title:** An experimental assessment of the impact of drought and fire on western larch injury,

2 mortality, and recovery

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4 **Short title:** Drought and fire effects on larch mortality

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14 **Abstract**

15 Climate change is increasing drought and fire activity in many fire-prone regions including the

16 western U.S. and circumpolar boreal forest. These changes highlight the need for improved

17 understanding of how multiple disturbances impact trees in these regions. Recent studies linking

18 fire behavior to plant ecophysiology have improved understanding of how fire impacts tree

19 function and mortality but have not investigated interactions between drought stress and fire. In

20 this study, *Larix occidentalis* saplings were subjected to different levels of water stress, followed

21 by low-intensity surface fires in a controlled laboratory setting. Post-fire mortality, recovery and

22 growth were monitored for up to a year post-fire. Generally, increased pre-fire water stress

23 resulted in decreased post-fire stem diameter (up to 5% lower) and height (up to 19% lower)

24   growth. However, severely water stressed saplings whose foliage had senesced prior to the fires

25   had lower one-year mortality (14%) and significantly greater post-fire bud densities than

26   moderately stressed saplings that did not senesce (86% mortality). The mortality patterns suggest

27   that water-stressed western larch saplings exposed to low-intensity wildfires, or prescribed fires

28   conducted as part of forest management activities, may exhibit lower mortality rates if stress-

29   induced foliar senescence has occurred.

30

31   **Table of contents summary:** Through a controlled nursery and combustion laboratory

32   experiment, we show that increased pre-fire water stress decreased post-fire growth in surviving

33   saplings. However, low mortality and high bud density of severely stressed saplings suggests that

34   pre-fire foliar senescence can improve post-fire survival and recovery.

35

36   **Keywords:** Trees: conifers, fire severity, post-fire impacts, carbon cycling, tree growth, sapling,

37   deciduous

38

39   **Introduction**

40   Drought stress has produced widespread tree mortality and decreased growth in circumpolar

41   boreal forests, including those dominated by deciduous conifers in Eurasia and evergreen-

42   dominated forests in North America (Dulamsuren *et al.* 2010; Beck *et al.* 2011; Peng *et al.*

43   2011). *Larix*, a genus composed of deciduous needle-leaf gymnosperms, is a common

44   component of many fire-prone ecosystems in these regions and plays a significant role in

45   regional carbon cycle dynamics and surface albedo (Gower and Richards 1990; Shuman *et al.*

46   2011). In western North America, western larch (*Larix occidentalis* Nutt.) is a highly valued

47 timber species, in part due to its high growth rate (Schmidt *et al.* 1976; Rehfeldt and Jaquish

48 2010). Along with other regions, climate change is predicted to increase frequency and severity

49 of droughts and fires in North America (Kharuk *et al.* 2008; Dai 2013; De Groot *et al.* 2013;

50 Young *et al.* 2016), which could alter the biological range of productive conifer species such as

51 western larch (Rehfeldt and Jaquish 2010; Coops and Waring 2011; Smith *et al.* 2014), yielding

52 younger forest age class distributions (Bonan 2008) and land cover type conversions (Shuman *et*

53 *al.* 2011; Millar and Stephenson 2015). However, the impacts and interaction of multiple

54 disturbances, such as drought and fire, on tree function, mortality, and post-fire recovery are

55 poorly understood (Millar and Stephenson 2015).

56   Independently, drought-induced water stress and fire can substantially affect tree

57 physiology, growth, and mortality. Water-stressed trees may close stomata for extended periods

58 to reduce cavitation in xylem tissues, leading to decreased photosynthesis and increased reliance

59 on nonstructural carbohydrate stores (NSC) (McDowell *et al.* 2011). If stomata remain closed,

60 trees utilize NSCs for maintenance respiration, as well as osmotic and defense needs (McDowell

61 *et al.* 2011; Adams *et al.* 2017). Under severe stress, deciduous trees can undergo leaf

62 senescence to conserve nutrients (Silla and Escudero 2006; Marchin *et al.* 2010). Because water

63 stress can decrease pools of NSCs, drought can potentially increase fire-induced mortality by

64 limiting carbon (C) available for post-fire recovery.

65   Fires can damage trees via multiple mechanisms involving the transfer of heat to the roots,

66 bole, and crown (Michaletz and Johnson 2007). Cell death (necrosis) or deformation in tree

67 tissues can severely impair C sequestration and vegetative bud regeneration (Michaletz and

68 Johnson 2006, 2008). Severe crown damage (~80% crown scorch) reduces photosynthesis in

69 remaining live foliage (Smith *et al.* 2016a, 2017) and is linked to decreased nitrogen uptake and

70   total NSCs in roots (Guo *et al.* 2004). Likewise, cell death or deformation in tree xylem and

71   phloem can impair movement of water, nutrients, and C (Bär *et al.* 2018). Several studies have

72   observed heat-induced cavitation in xylem conduits of cut plant segments (Michaletz *et al.* 2012;

73   West *et al.* 2016), and non-functioning xylem in tree cross-sections after wildfires (Balfour and

74   Midgley 2006; Smith *et al.* 2016b), leading to the hypothesis that reduced xylem conductivity is

75   an important mechanism of fire-caused injury and mortality (Balfour and Midgley 2006;

76   Kavanagh *et al.* 2010).

77   Interactions and feedbacks between water stress and fire on tree physiology are not well

78   understood. Pre-fire climatic stress can increase the probability that trees will die from fire-

79   induced damage in temperate (van Mantgem *et al.* 2013) and tropical forests (Van Nieuwstadt

80   and Sheil 2005; Brando *et al.* 2014). Yet, van Mantgem et al. (2016) observed lower post-fire

81   mortality probability for some temperate conifers during a subsequent severe drought compared

82   to unburned trees, which they attributed to lower stand densities and reduced competition for

83   resources in burned areas. In semi-controlled nursery experiments, exposure to fire did not affect

84   fine root growth of water-stressed *Quercus* spp. saplings (Chiatante *et al.* 2005; Di Iorio *et al.*

85   2011). Although these studies provide probabilistic evidence of interactions between drought and

86   fire effects, mechanistic research is needed to support accurate predictions of ecosystem

87   function.

88   Toxicological dose-response experiments provide a potential framework to study

89   interactions of water stress and fire on trees. Previous fire dose-response studies have used well-

90   watered saplings (Smith *et al.* 2016a, 2017; Sparks *et al.* 2016) or low-intensity prescribed fires

91   that did not result in tree mortality (Sparks *et al.* 2017). In this study, western larch saplings were

92   subjected to water stress doses followed by a low-intensity surface fire that in a prior study only

93   caused limited mortality in well-watered individuals (Sparks *et al.* 2016). Sapling is defined as

94   the growth stage following seedlings, where seedlings are plants dependent on stored seed

95   reserves. We tested the hypothesis presented in Smith *et al.* (2017) that pre-fire stress leads to

96   increased mortality in fire-affected saplings (Figure 1). We further sought to test whether the

97   degree of pre-fire water stress amplifies the dose-response relationship; i.e. trees with greater

98   pre-fire water stress would exhibit decreased growth, physiological function, and survival post-

99   fire.

100

101   **Methods**

102   *Larix saplings and growing conditions*

103   Western larch (*Larix occidentalis* Nutt.) saplings ($N = 28$) were grown in a climate-

104   controlled greenhouse in Moscow, Idaho, USA, through two growing seasons under natural light

105   conditions. The total number of saplings used in this experiment was limited due to the logistical

106   limitations (nursery space and cost) of growing and conditioning these trees to multiple levels of

107   water stress in a controlled nursery environment for this amount of time. Average (±SE) sapling

108   height was 96.1 ± 0.6 cm, with a height to crown base of 36.3 ± 0.3 cm. Average diameter at root

109   collar was 12.9 ± 0.4 mm. Over this period, nutrient solutions (N-P-K) of Peters Professional

110   (The Scotts Co, Marysville, OH) fertilizer were applied during the early (10-30-20), mid (20-7-

111   19), and late (4-25-35) growing season each year. Prior to the water stress and burn treatments,

112   saplings were repotted in a soil media mix consisting of 50% perlite, 22.5% sphagnum peat

113   moss, 22.5% vermiculite, and 5% fine bark chips in 9.5 L pots and allowed to acclimate for 2.5

114   months. During this time saplings were watered to field capacity daily to minimize water stress.

115

116   *Water Stress and Fire Treatments*

117   We randomly divided the saplings into four groups ($n = 7$) and applied different treatments

118   to each group. Each group was conditioned to different predawn water potentials ($\Psi_{predawn}$):

119   control (no water stress or fire), low water stress ($\Psi_{predawn}$: 0 to -0.75 MPa), moderate water stress

120   ($\Psi_{predawn}$: -1 to -1.75 MPa) and severe water stress ($\Psi_{predawn}$: -2 to -2.75 MPa). The low-water-

121   stress $\Psi_{predawn}$ range was chosen to match $\Psi_{predawn}$ in well-watered *Larix* of similar size and age

122   in prior studies (Sparks *et al.* 2016; Smith *et al.* 2017). The severe-water-stress $\Psi_{predawn}$ range

123   was chosen to match values of $\Psi_{predawn}$ in water-stressed *Larix* in prior studies where net

124   photosynthesis and stomatal conductance approached zero (Higgins *et al.* 1987), a common

125   indicator of severe drought stress (Rodriguez-Dominguez *et al.* 2016; Martin-StPaul *et al.* 2017).

126   This $\Psi_{predawn}$ range also encompassed measurements of *Larix* saplings in a central Idaho forest

127   during a severe drought year ($\Psi_{predawn}$ = -2.2 MPa) (K.V. Baker and D.M. Johnson, unpubl. data)

128   and coincided with stress-induced leaf senescence for the severe-water-stress *Larix* in this study.

129   The moderate-water-stress $\Psi_{predawn}$ range was in between the low and severe ranges. Water was

130   withheld from each water stress group until the desired shoot $\Psi_{predawn}$ range was reached. During

131   the water stress treatment period, fertilizer was also withheld from all saplings to avoid

132   confounding effects of the treatments. Low-water-stress *Larix* were watered daily to keep

133    $\Psi_{predawn}$ above -0.75 MPa.

134   At the end of the water stress treatment period, each non-control *Larix* group was subjected

135   to a surface fire of the same intensity. Following Smith *et al.* (2017) and Sparks *et al.* (2016), we

136   determined the fuel load (kg m^{-2}) of dry (~0% fuel moisture content) *Pinus monticola* needles

137   needed to produce a fire radiative energy (FRE) "dose" of ~0.4 MJ m^{-2}. This dose was chosen as

138   Sparks *et al.* (2016) demonstrated that >66% of well-watered *Larix* of similar age and size

139 survived for a year at this intensity level. Saplings in the same water stress group were burned

140 individually on the same day; low and moderate stress groups were burned six days after the

141 severe stress group. Post-burn, all saplings were immediately returned to the greenhouse and

142 watered to field capacity daily until foliar senescence (~60 days post-fire). Temperature and

143 relative humidity were recorded in the greenhouse facility every 30 min throughout the course of

144 the study using a model EL-21CFR-2-LCD temperature and humidity sensor (LASCAR

145 electronics, Erie, PA, USA) and used to calculate the vapor pressure deficit (VPD: kPa).

146

147 *Sapling Physiology, Growth, and Mortality*

148   Shoot water potential was measured at predawn every two days starting at the beginning of

149 each water stress treatment using a Model 1505D Pressure Chamber (PMS Instruments

150 Company, Albany, OR, USA). Additionally, $\Psi_{predawn}$ was measured on burn day (pre-burn) and

151 at 1, 4, 14, 30 days post-fire; midday water potential (Ψ_{midday}) was also acquired on burn day and

152 at the same post-fire intervals. Shoots of ~10 cm in length were used for $\Psi_{predawn}$ and Ψ_{midday}

153 measurements. Due to the limited number of shoots on these small saplings and the destructive

154 nature of these measurements, three saplings from each group were randomly selected for water

155 potential measurement per sampling interval. As other studies have shown that removal of large

156 proportions of leaf area does not substantially affect subsequent leaf water potential (Reich *et al.*

157 1993; Pataki *et al.* 1998), we assumed that excising shoots did not significantly change sapling

158 water stress.

159   Light-saturated (1,500 μmol m^{-2} s^{-1} PPFD) gas exchange measurements were performed on

160 the same days as $\Psi_{predawn}$ using a LI-6400XT and 6400–05 LED light source and broadleaf

161 chamber (LI-COR, Inc., Lincoln, NE) on five randomly-selected plants in each water stress

162 group. Five needles from each sapling were used per measurement. Needle area for each sample

163 was measured with a LI-COR LI-3100C leaf area meter and used to calculate net photosynthesis

164 (A) and stomatal conductance (g_s) on leaf area basis. Height and diameter-at-root-collar (DRC)

165 were measured at the same intervals as gas exchange. Relative growth measures (% deviation

166 from pre-treatment) for DRC and height were calculated as: [(Growth – Growth$_{avgPreTreatment}$) /

167 Growth$_{avgPreTreatment}$)]. Crown scorch was visually estimated for each sapling following Sparks *et*

168 *al.* (2016). Bud emergence date, density (number of buds per sapling), and general condition for

169 each *Larix* sapling were also recorded. We defined "immediate mortality" as tree death occurring

170 from 1 to 60 (date of needle senescence) days post-fire, while "delayed mortality" was defined as

171 tree death between 160 (date of needle emergence) and 365 days post-fire. Mortality was defined

172 as the death of all foliage and inability to regenerate shoots.

173

174 *Data Analysis*

175   Arithmetic mean ± SE is given throughout the paper. Physiologic and growth differences

176 between treatment groups were compared with ANOVA, and if significant (α=0.05), a Tukey's

177 Honest Significant Difference test.

178

179 **Results**

180 *Impacts of water stress on pre-burn physiology and growth*

181      $\Psi_{predawn}$ did not significantly differ (p > 0.05) between low-water-stress and control *Larix* at

182 any point during the study (Figure 2). Likewise, pre-fire physiology (Figure 3a,b) and growth

183 (Figure 3c,d) of the low-water-stress *Larix* was not different (p > 0.05) from the control *Larix*.

184 Moderate-water-stress *Larix* took seven days to reach the desired $\Psi_{predawn}$ range (Figure 2).

185 During these seven days, $\Psi_{predawn}$, A, and g_s decreased by an average of 65% from pre-water

186 stress levels (Figures 2 and 3a,b). On burn day, moderate-water-stress *Larix* $\Psi_{predawn}$ was more

187 negative (p = 0.005) than both the control and low-water-stress groups. Height and DRC

188 continued to increase in the moderate water stress group and did not differ (p > 0.05) from the

189 control. Severe-water-stress *Larix* took 12 days to reach the desired $\Psi_{predawn}$ range. On burn day,

190 $\Psi_{predawn}$ was more negative (p = 0.005) than all other groups. Like the moderate-water-stress

191 larch, $\Psi_{predawn}$, A, and g_s decreased by an average of 60% from pre-water stress levels (Figures 2

192 and 3a,b). During the last 4-5 days of the water stress period, foliage senesced sequentially in the

193 severe-water-stress treatment, with older green foliage on each sapling turning yellow before

194 younger foliage. Height and DRC growth were less than all other groups during this time but

195 were not significantly different (p > 0.05) than the control.

196

197 *Impacts of water stress and fire on physiology, growth, and mortality*

198 All burns had approximately the same duration (186 ± 0.6 seconds). Mean flame height (18

199 cm; measured using still-frame video data) was nearly half of the average height-to-crown (36.3

200 cm), resulting in minimal live foliage combustion (<5% of crown) across all water stress groups.

201 There were no significant differences (p = 0.337) in crown scorch between low (85 ± 3%),

202 moderate (87 ± 5%), and severe (82 ± 9%) water stress groups. For all water-stress groups,

203 $\Psi_{predawn}$ recovered to pre-fire levels immediately after re-watering (within 1 day) and did not

204 differ (p > 0.05) from the control until all saplings started to senesce (~30-40 days post-fire)

205 (Figure 2). At 30 days post-fire, $\Psi_{predawn}$ was more negative in the moderate-water-stress *Larix* (p

206 = 0.028) than in the control or severe-water-stress groups. Likewise, Ψ_{midday} for all water stress

207 groups recovered to pre-fire levels immediately after re-watering (Figure S1) and remained less

208   negative ($p < 0.05$) than control saplings until all saplings started to senesce around early

209   October. Minimum observed A for all water stress groups occurred one day post-fire. A and g_s

210   recovered to control levels within 14 days post-fire in the severe and low-water-stress groups,

211   but A recovery took 30 days in the moderate-stress group (Figure 3a,b).

212   Post-fire DRC and height growth decreased with increasing water stress, although groups

213   did not differ significantly ($p > 0.05$) (Figure 3c,d). Generally, post-fire DRC and height growth

214   decreased or remained the same for the duration of the experiment (Figure 3c,d). Post-fire bud

215   density was consistently higher ($p < 0.0001$) in the severe-water-stress group than the low- and

216   moderate-stress-groups (Figure 4), with nearly a 3x difference at the end of the growing season.

217   Immediate mortality (<60 days post-fire) was greater in the moderate-stress group (43%)

218   than the severe-stress (14%) and low-stress (0%) groups (Figure 4). Likewise, delayed mortality

219   (160 to 365 days post-fire) was also greater in the moderate-stress group (86%) than the severe-

220   stress (14%) and low-stress (14%) groups. No control trees died during the experiment.

221

Discussion

223   This study supports previous experiments of the same fire intensity (0.4 MJ m^{-2}) with

224   similarly-sized *Larix occidentalis* where saplings experiencing minimal water stress ($\Psi_{predawn} > -$

225   0.4 MPa and $\Psi_{midday} > -1.5$ MPa) had low mortality rates (<33%) up to 1 year post-fire (Sparks *et*

226   *al.* 2016). Likewise, observed patterns of post-fire growth reductions with increasing water stress

227   agree with other studies where drought and fire treatments significantly reduced above- and

228   below-ground growth in *Quercus* spp. seedlings compared to control and drought-only seedlings

229   (Chiatante *et al.* 2015).

230   The unexpected mortality patterns observed among the different water stress groups indicate

231   more complex dose-response relationships between water stress, fire, and physiology than

232   expected (Figure 1). We hypothesize that the severe-water-stress group displayed lower mortality

233   than the moderate-water-stress group because the severe-water-stress group were able to use

234   nutrients and C translocated from foliage to other tree tissues during the pre-fire water stress-

235   induced foliar senescence. Nutrient resorption during drought-induced senescence can increase

236   survival among deciduous plants (Munne-Bosch and Alegre 2004) and deciduous trees benefit

237   from nutrient resorption even under extreme drought conditions (Silla and Escudero 2006;

238   Marchin *et al.* 2010). As all treatment groups experienced a similar amount of crown scorch

239   (Figure 5), the severely water-stressed trees may have had more resources available to survive

240   and produce buds post-fire. *Larix* spp. are very efficient at translocating nutrients from senescing

241   needles to other tree tissues (Carlyle and Malcolm 1986; Gower and Richards 1990). During

242   foliar senescence in autumn, *Larix occidentalis* has been observed to translocate ~87% of

243   nitrogen and ~66% of phosphorus from foliage (Gower *et al.* 1989). *Larix* spp. have also been

244   observed to have high resorption of NSC from senescing needles (Kagawa *et al.* 2006). This

245   hypothesis is supported by the observed bud densities for the three water stress groups. Despite

246   similar post-fire crown loss (~85%) across all water stress groups, severe-water-stress *Larix* had

247   nearly triple the density of buds 30 and 60 days post-fire compared to the low and moderate

248   *Larix* (Figure 4). Stored carbohydrates are the C source for new needle formation in deciduous

249   trees such as *Larix* (Kagawa *et al.* 2006), and the bud density observations suggest that the

250   severe-water-stress *Larix* had greater C reserves to regenerate foliage.

251   In addition to regenerating foliage, C is a critical input for refilling embolized xylem

252   conduits (Salleo *et al.* 2009; Zwieniecki and Holbrook 2009; Nardini *et al.* 2011). Repeated

253   embolism formation and repair, such as that likely experienced by the moderate- and severe-

254   water-stress groups pre-fire, could have depleted C stores (McDowell *et al.* 2008) and decreased

255   cavitation resistance (e.g. cavitation fatigue - Hacke *et al.* 2001). As drying soil can limit

256   refilling of embolisms (McDowell *et al.* 2011), it is likely that the moderate- and severe-water-

257   stress *Larix* had higher proportions of non-refilled conduits than the low-water-stress *Larix* that

258   were watered pre-fire. It is possible that the fire exacerbated xylem cavitation in the saplings

259   with higher proportions of functioning, non-senesced crown (low- and moderate-water-stress

260   *Larix*). Several studies have indicated that elevated vapor pressure deficit in the super-heated

261   plume that rises above the surface flames may be sufficient to induce cavitation in tree canopy

262   branches and foliage (Kavanagh *et al.* 2010; West *et al.* 2016). However, translocation of

263   nutrients and C, either during senescence or during embolism repair, requires functioning phloem

264   (Nardini *et al.* 2011; Hartmann *et al.* 2013). Translocation of nutrients and C under severe water

265   stress conditions can be significantly impaired by decreased phloem transport (Sala *et al.* 2010).

266   For example, Hartmann *et al.* (2013) observed that water-stressed Norway spruce (*Picea abies*)

267   saplings had higher NSC concentrations in all tissues than non-water stressed saplings at

268   mortality, indicating that reduced hydraulic function impaired mobilization of NSC. Thus, while

269   drought-induced senescence provides a mechanism that preserves nutrients and C for survival

270   and post-disturbance bud growth, severe drought can also constrain mobilization and utilization

271   of these resources.

272   We acknowledge that because our experiment lacked unburned water-stress treatment

273   groups, we are assuming the observed physiological, growth, and mortality differences between

274   the drought-stress treatments were created by the fire treatments. However, previous studies

275   provide clues to help decouple the effects of water stress and fire. Vance and Running (1985)

276 subjected smaller *Larix occidentalis* (~15 cm in height) to water stress treatments and found that

277 *Larix* with $\Psi_{predawn}$ of -1.5 MPa were able to survive the drought treatment. The presence of

278 stress-induced leaf senescence was not noted. This finding suggests that the high mortality

279 observed in the moderate-water-stress *Larix* in this study ($\Psi_{predawn}$: -1 to -1.75 MPa) was the

280 result of the combined effects of the drought and fire treatments.

281

282 *Future research needs*

283   Our observations suggest an intriguing possibility where *Larix* that senesce and translocate

284 resources pre-fire may experience lower mortality in a subsequent low-intensity fire. Testing this

285 hypothesis would require measuring translocation to assess whether senescing foliage supplies

286 sufficient nutrients (NSC, N, P) for bud growth; xylem conductivity measurements to quantify

287 whether heat-induced cavitation and cell deformation observed in water bath studies (e.g.

288 Michaletz *et al.* 2012; West *et al.* 2016; Bär *et al.* 2018) occurs under natural fire conditions; and

289 gas exchange measurements to gauge stomatal activity for green and senesced needles at the time

290 of burning.

291   It is important to note that the mortality hypothesis presented in this study may not translate

292 to larger trees. For example, drought-induced crown dieback in larger trees often occurs at the

293 periphery of the tree crown (Rood *et al.* 2000; Sperry *et al.* 2002; Zhang *et al.* 2017), rather than

294 sequential senescence observed in this study, where older leaves senesce first to supply nutrients

295 to younger leaves and shoots (Munne-Bosch and Alegre 2004). As low-intensity fires typically

296 scorch tree crowns from the bottom-up, senescing foliage at the periphery of a large tree crown

297 may not provide the post-fire recovery advantage hypothesized for saplings. In fact, there is

298 evidence from temperate (van Mantgem *et al.* 2013) and tropical forests (Van Nieuwstadt and

299 Sheil 2005; Brando *et al.* 2014) that large trees with greater pre-fire water stress are more

300 susceptible to fire-induced mortality. Current hypotheses for fire-induced mortality of larger

301 trees, such as xylem dysfunction (Michaletz 2018), have been demonstrated on excised branches

302 in laboratory water bath experiments (Michaletz *et al.* 2012; West *et al.* 2016; Bär *et al.* 2018).

303 In terms of natural forest fires, there is evidence that fires impair large tree xylem hydraulics

304 (Smith 2015; Smith *et al.* 2016b; Bär *et al.* 2018) and evidence that fires do not affect xylem

305 hydraulics (Battipaglia *et al.* 2016; Thompson *et al.* 2017). Experiments that incorporate a range

306 of tree sizes and tree-scale treatments (Sparks *et al.* 2017) and physiology measurements are

307 needed for an improved understanding of size-dependent mortality (McDowell *et al.* 2018).

308

309 **Conclusions**

310 We observed that western larch under greater pre-fire water stress exhibit decreased growth

311 after a low-intensity surface fire. However, the unexpected bud density and mortality patterns

312 observed among the different water stress groups indicates that interactions between water stress,

313 fire, and deciduous tree physiology are more complex than a linear dose-response relationship.

314 The mortality patterns observed in this study suggest that water-stressed western larch saplings

315 exposed to low-intensity wildfires, or prescribed fires conducted as part of forest management

316 activities, may exhibit lower mortality rates if stress-induced foliar senescence has occurred.

317 While this research improves understanding of drought-fire interaction impacts on saplings, more

318 research is needed to assess whether mortality patterns change with increasing tree size.

319

320 **Conflicts of interest**

321 The authors declare no conflicts of interest.

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References

Adams HD, Zeppel MJB, Anderegg WRL, Hartmann H, Landhäusser SM, Tissue DT, Huxman TE, Hudson PJ, Franz TE, Allen CD, Anderegg LDL, Barron-Gafford GA, Beerling DJ, Breshears DD, Brodribb TJ, Bugmann H, Cobb RC, Collins AD, Dickman LT, Duan H, Ewers BE, Galiano L, Galvez DA, Garcia-Forner N, Gaylord ML, Germino MJ, Gessler A, Hacke UG, Hakamada R, Hector A, Jenkins MW, Kane JM, Kolb TE, Law DJ, Lewis JD, Limousin J-M, Love DM, Macalady AK, Martínez-Vilalta J, Mencuccini M, Mitchell PJ, Muss JD, O'Brien MJ, O'Grady AP, Pangle RE, Pinkard EA, Piper FI, Plaut JA, Pockman WT, Quirk J, Reinhardt K, Ripullone F, Ryan MG, Sala A, Sevanto S, Sperry JS, Vargas R, Vennetier M, Way DA, Xu C, Yepez EA, McDowell NG (2017) A multi-species synthesis of physiological mechanisms in drought-induced tree mortality. *Nature Ecology &*

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345 *Evolution* **1**, 1285–1291. doi:10.1038/s41559-017-0248-x.

346 Balfour DA, Midgley JJ (2006) Fire induced stem death in an African acacia is not caused by

347 canopy scorching. *Austral Ecology* **31**, 892-896. doi:10.1111/j.1442-9993.2006.01656.x.

348 Bär A, Nardini A, Mayr S (2018) Post-fire effects in xylem hydraulics of Picea abies, Pinus

349 sylvestris and Fagus sylvatica. *New Phytologist* **217**, 1484-1493. doi:10.1111/nph.14916.

350 Battipaglia G, Savi T, Ascoli D, Castagneri D, Esposito A, Mayr S, Nardini A (2016) Effects of

351 prescribed burning on ecophysiological, anatomical and stem hydraulic properties in Pinus

352 pinea L. *Tree Physiology* **36**, 1019-1031. doi:10.1093/treephys/tpw034.Beck PSA, Juday

353 GP, Alix C, Barber VA, Winslow SE, Sousa EE, Heiser P, Herriges JD, Goetz SJ (2011)

354 Changes in forest productivity across Alaska consistent with biome shift. *Ecology Letters*

355 **14**, 373–379. doi:10.1111/j.1461-0248.2011.01598.x.Bonan GB (2008) Forests and Climate

356 Change: Forcings, Feedbacks, and the Climate Benefits of Forests. *Science* **320**, 1444–1449.

357 doi:10.1126/science.1155121.

358 Brando PM, Balch JK, Nepstad DC, Morton DC, Putz FE, Coe MT, Silverio D, Macedo MN,

359 Davidson EA, Nobrega CC, Alencar A, Soares-Filho BS (2014) Abrupt increases in

360 Amazonian tree mortality due to drought-fire interactions. *Proceedings of the National*

361 *Academy of Sciences* **111**, 6347–6352. doi:10.1073/pnas.1305499111.

362 Carlyle JC, Malcolm DC (1986) Larch litter and nitrogen availability in mixed larch–spruce

363 stands. I. Nutrient withdrawal, redistribution, and leaching loss from larch foliage at

364 senescence. *Canadian Journal of Forest Research* **16**, 321–326. doi:10.1139/x86-054.

365 Chiatante D, Di Iorio A, Scippa GS (2005) Root responses of Quercus ilex L. seedlings to

366 drought and fire. *Plant Biosystems* **139**, 198–208. doi:10.1080/11263500500160591.

367 Chiatante D, Tognetti R, Scippa GS, Congiu T, Baesso B, Terzaghi M, Montagnoli A (2015)

368   Interspecific variation in functional traits of oak seedlings (Quercus ilex, Quercus trojana,

369   Quercus virgiliana) grown under artificial drought and fire conditions. *Journal of Plant*

370   *Research* **128**, 595–611. doi:10.1007/s10265-015-0729-4.

371 Coops NC, Waring RH (2011) Estimating the vulnerability of fifteen tree species under changing

372   climate in Northwest North America. *Ecological Modelling* **222**, 2119-2129.

373   doi.org/10.1016/j.ecolmodel.2011.03.033.

374 Dai AG (2013) Increasing drought under global warming in observations and models. *Nature*

375   *Climate Change* **3**, 52–58. doi:10.1038/nclimate1633.

376 De Groot WJ, Flannigan MD, Cantin AS (2013) Climate change impacts on future boreal fire

377   regimes. *Forest Ecology and Management* **294**, 35–44. doi:10.1016/j.foreco.2012.09.027.

378 Di Iorio A, Montagnoli A, Scippa GS, Chiatante D (2011) Fine root growth of Quercus

379   pubescens seedlings after drought stress and fire disturbance. *Environmental and*

380   *Experimental Botany* **74**, 272–279. doi:10.1016/j.envexpbot.2011.06.009.

381 Dulamsuren C, Hauck M, Leuschner C (2010) Recent drought stress leads to growth reductions

382   in Larix sibirica in the western Khentey, Mongolia. *Global Change Biology* **16**, 3024–3035.

383   doi:10.1111/j.1365-2486.2009.02147.x.

384 Gower ST, Grier CC, Vogt KA (1989) Aboveground production and N and P use by Larix

385   occidentalis and Pinus contorta in the Washington Cascades, USA. *Tree physiology* **5**, 1–11.

386   http://www.ncbi.nlm.nih.gov/pubmed/14972994.

387 Gower ST, Richards JH (1990) Larches: Deciduous Conifers in an Evergreen World. *BioScience*

388   **40**, 818–826. doi:10.2307/1311484.

389 Guo DL, Mitchell RJ, Hendricks JJ (2004) Fine root branch orders respond differentially to

390   carbon source-sink manipulations in a longleaf pine forest. *Oecologia* **140**, 450–457.

391   doi:10.1007/s00442-004-1596-1.

392 Hacke UG, Stiller V, Sperry JS, Pittermann J, McCulloh KA (2001) Cavitation fatigue.

393   Embolism and refilling cycles can weaken the cavitation resistance of xylem. *Plant*

394   *Physiology* **125**, 779-786. doi.org/10.1104/pp.125.2.779.

395 Hartmann H, Ziegler W, Kolle O, Trumbore S (2013) Thirst beats hunger - declining hydration

396   during drought prevents carbon starvation in Norway spruce saplings. *New Phytologist* **200**,

397   340–349. doi:10.1111/nph.12331.

398 Higgins SS, Black RA, Radamaker GK, Bidlake WR (1987) Gas exchange characteristics and

399   water relations of larix occidentalis. *Can J For Res* **17**, 1364–1370.

400 Kagawa A, Sugimoto A, Maximov TC (2006) Seasonal course of translocation, storage and

401   remobilization of 13C pulse-labeled photoassimilate in naturally growing Larix gmelinii

402   saplings. *New Phytologist* **171**, 793–804. doi:10.1111/j.1469-8137.2006.01780.x.

403 Kavanagh KL, Dickinson MB, Bova AS (2010) A way forward for fire-caused tree mortality

404   prediction: Modeling a physiological consequence of fire. *Fire Ecology* **6**, 80–94.

405   doi:10.4996/fireecology.0601080.

406 Kharuk VI, Ranson KJ, Dvinskaya ML (2008) Wildfires dynamic in the larch dominance zone.

407   *Geophysical Research Letters* **35**, 1–6. doi:10.1029/2007GL032291.

408 Marchin R, Zeng H, Hoffmann W (2010) Drought-deciduous behavior reduces nutrient losses

409   from temperate deciduous trees under severe drought. *Oecologia* **163**, 845–854.

410   doi:10.1007/s00442-010-1614-4.

411 Martin-StPaul N, Delzon S, Cochard H (2017) Plant resistance to drought depends on timely

412   stomatal closure. *Ecology Letters* **20**, 1437-1447. doi.org/10.1111/ele.12851.

413 McDowell N, Pockman WT, Allen CD, Breshears DD, Cobb N, Kolb T, Plaut J, Sperry J, West

414   A, Williams DG, Yepez EA (2008) Mechanisms of plant survival and mortality during

415   drought: why do some plants survive while others succumb to drought? *New Phytologist*

416   **178**, 719-739. doi:10.1111/j.1469-8137.2008.02436.x.

417   McDowell NG, Beerling DJ, Breshears DD, Fisher RA, Raffa KF, Stitt M (2011) The

418   interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends in*

419   *Ecology and Evolution* **26**, 523–532. doi:10.1016/j.tree.2011.06.003.

420   McDowell NG, Michaletz ST, Bennett KE, Solander KC, Xu C, Maxwell RM, Allen CD,

421   Middleton RS (2018) Predicting chronic climate-driven disturbances and their mitigation.

422   *Trends in Ecology & Evolution* **33**, 15-27. doi.org/10.1016/j.tree.2017.10.002 15.

423   Michaletz ST, Johnson EA (2006) A heat transfer model of crown scorch in forest fires.

424   *Canadian Journal of Forest Research* **36**, 2839–2851. doi:10.1139/x06-158.

425   Michaletz ST, Johnson EA (2007) How forest fires kill trees: A review of the fundamental

426   biophysical processes. *Scandinavian Journal of Forest Research* **22**, 500–515.

427   doi:10.1080/02827580701803544.

428   Michaletz ST, Johnson EA (2008) A biophysical process model of tree mortality in surface fires.

429   *Canadian Journal of Forest Research* **38**, 2013–2029. doi:10.1139/X08-024.

430   Michaletz ST, Johnson EA, Tyree MT (2012) Moving beyond the cambium necrosis hypothesis

431   of post-fire tree mortality: Cavitation and deformation of xylem in forest fires. *New*

432   *Phytologist* **194**, 254–263. doi:10.1111/j.1469-8137.2011.04021.x.

433   Michaletz ST (2018) Xylem dysfunction in fires: towards a hydraulic theory of plant responses

434   to multiple disturbance stressors. *New Phytologist* **217**, 1391-1393. doi:10.1111/nph.15013.

435   Millar CI, Stephenson NL (2015) Temperate forest health in an era of emerging

436   megadisturbance. *Science* **349**, 823–826. doi:10.1126/science.aaa9933.

437   Munné-Bosch S, Alegre L (2004) Die and let live: leaf senescence contributes to plant survival

438   under drought stress. *Functional Plant Biology* **31**, 203-216. doi:10.1071/FP03236.

439   Nardini A, Lo Gullo MA, Salleo S (2011) Refilling embolized xylem conduits: is it a matter of

440   phloem unloading? *Plant Science* **180**, 604–611. doi:10.1016/j.plantsci.2010.12.011.

441   Pataki DE, Oren R, Phillips N (1998) Responses of sap flux and stomatal conductance of *Pinus*

442   *taeda* L. trees to stepwise reductions in leaf area. *Journal of Experimental Botany* **49**, 871-

443   878. doi.org/10.1093/jxb/49.322.871.

444   Peng C, Ma Z, Lei X, Zhu Q, Chen H, Wang W, Liu S, Li W, Fang X, Zhou X (2011) A

445   drought-induced pervasive increase in tree mortality across Canada's boreal forests. *Nature*

446   *Climate Change* **1**, 467–471. doi:10.1038/nclimate1293.

447   Rehfeldt GE, Jaquish BC (2010) Ecological impacts and management strategies for western

448   larch in the face of climate-change. *Mitigation and Adaptation Strategies for Global*

449   *Change* **15**, 283-306. doi:10.1007/s11027-010-9217-2.

450   Reich PB, Walters MB, Krause SC, Vanderklein DW, Raffs KF, Tabone T (1993) Growth,

451   nutrition and gas exchange of Pinus resinosa following artificial defoliation. *Trees* **7**, 67-77.

452   doi.org/10.1007/BF00225472.

453   Rodriguez-Dominguez CM, Buckley TN, Egea G, Cires A, Hernandez-Santana V, Martorell S,

454   Diaz-Espejo A (2016) Most stomatal closure in woody species under moderate drought can

455   be explained by stomatal responses to leaf turgor. *Plant, Cell & Environment* **39**, 2014-

456   2026. https://doi.org/10.1111/pce.12774.

457   Rood SB, Patiño S, Coombs K, Tyree MT (2000) Branch sacrifice: cavitation-associated drought

458   adaptation of riparian cottonwoods. *Trees* **14**, 248-257. doi.org/10.1007/s004680050010.

459   Sala, A.; Piper, F.; Hoch G (2010) Physiological mechanisms of drought induced tree mortality

460   are far from being resolved. *New Phytologist* **186**, 274–281. doi:10.1111/nph.12154.

461   Salleo S, Trifilò P, Esposito S, Nardini A, Gullo MAL (2009) Starch-to-sugar conversion in

462   wood parenchyma of field-growing Laurus nobilis plants: a component of the signal

463   pathway for embolism repair? *Functional Plant Biology* **36**, 815-825.

464   doi.org/10.1071/FP09103.

465   Schmidt WC, Shearer RC, Roe AL (1976) Ecology and silviculture of wester larch forests.

466   United States Department of Agriculture, Techinical Bulletin 1520.

467   Shuman JK, Shugart HH, O'Halloran TL (2011) Sensitivity of Siberian larch forests to climate

468   change. *Global Change Biology* **17**, 2370–2384. doi:10.1111/j.1365-2486.2011.02417.x.

469   Silla F, Escudero A (2006) Coupling N cycling and N productivity in relation to seasonal stress

470   in Quercus pyrenaica Willd. saplings. *Plant and Soil* **282**, 301–311. doi:10.1007/s11104-

471   006-6249-1.

472   Smith AMS, Kolden CA, Tinkham W, Talhelm A, Marshall J, Hudak A, Boschetti L, Falkowski

473   M, Greenberg J, Anderson J, Kliskey A, Alessa L, Keefe R, Gosz J (2014) Remote sensing

474   the vulnerability of vegetation in natural terrestrial ecosystems. *Remote Sensing of*

475   *Environment* **154**, 322-337. doi.org/10.1016/j.rse.2014.03.038 0034-4257.

476   Smith AMS, Sparks AM, Kolden CA, Abatzoglou JT, Talhelm AF, Johnson DM, Boschetti L,

477   Lutz JA, Apostol KG, Yedinak KM, Tinkham WT, Kremens RJ (2016a) Towards a new

478   paradigm in fire severity research using dose – response experiments. *International Journal*

479   *of Wildland Fire* **25**, 158–166. doi:10.1071/WF15130.

480   Smith AMS, Talhelm AF, Johnson DM, Sparks AM, Kolden CA, Yedinak KM, Apostol KG,

481   Tinkham WT, Abatzoglou JT, Lutz JA, Davis AS, Pregitzer KS, Adams HD, Kremens RL

482   (2017) Effects of fire radiative energy density dose on Pinus contorta and Larix occidentalis

483   seedling physiology and mortality. *International Journal of Wildland Fire* **26**, 82–94.

484   doi:10.1071/WF16077.

485   Smith KT (2015) Compartmentalization, resource allocation, and wood quality. *Current Forestry*

486   *Reports* **1**, 8-15. doi.org/10.1007/s40725-014-0002-4.

487   Smith KT, Arbellay E, Falk DA, Sutherland EK (2016b) Macroanatomy and

488   compartmentalization of recent fire scars in three North American conifers. *Canadian*

489   *Journal of Forest Research* **46**, 535-542. doi.org/10.1139/cjfr-2015-0377.

490   Sparks AM, Kolden CA, Talhelm AF, Smith AMS, Apostol K, Johnson DM, Boschetti L (2016)

491   Spectral Indices Accurately Quantify Changes in Seedling Physiology Following Fire:

492   Towards Mechanistic Assessments of Post-Fire Carbon Cycling. *Remote Sensing* **8**, 572.

493   doi:10.3390/rs8070572.

494   Sparks AM, Smith AMS, Talhelm AF, Kolden CA, Yedinak KM, Johnson DM (2017) Impacts

495   of fire radiative flux on mature Pinus ponderosa growth and vulnerability to secondary

496   mortality agents. *International Journal of Wildland Fire* **26**, 95–106.

497   doi:10.1071/WF16139.

498   Sperry JS, Hacke UG, Oren R., Comstock JP (2002) Water deficits and hydraulic limits to leaf

499   water supply. *Plant, Cell & Environment* **25**, 251-263. https://doi.org/10.1046/j.0016-

500   8025.2001.00799.x.

501   Thompson MT, Koyama A, Kavanagh KL (2017) Wildfire effects on physiological properties in

502   conifers of central Idaho forests, USA. *Trees* **31**, 545-555. doi:10.1007/s00468-016-1489-z.

503   Van Mantgem PJ, Nesmith JCB, Keifer M, Knapp EE, Flint A, Flint L (2013) Climatic stress

504   increases forest fire severity across the western United States. *Ecology Letters* **16**, 1151–

505   1156. doi:10.1111/ele.12151.

506   Van Mantgem PJ, Caprio AC, Stephenson NL, Das AJ (2016) Does prescribed fire promote

507   resistance to drought in low elevation forests of the Sierra Nevada, California, USA? *Fire*

508   *Ecology* **12**, 13–25. doi:10.4996/fireecology.1201013.

509   Van Nieuwstadt MGL, Sheil D (2005) Drought, fire and tree survival in a Borneo rain forest,

510   East Kalimantan, Indonesia. *Journal of Ecology* **93**, 191–201. doi:10.1111/j.1365-

511   2745.2005.00954.x.

512   Vance NC, Running SW (1985) Light reduction and moisture stress: effects on growth and water

513   relations of western larch seedlings. *Canadian Journal of Forest Research* **15**, 72–77.

514   doi:10.1139/x85-013.West AG, Nel JA, Bond WJ, Midgley JJ (2016) Experimental

515   evidence for heat plume-induced cavitation and xylem deformation as a mechanism of rapid

516   post-fire tree mortality. *New Phytologist* **211**, 828–838. doi:10.1111/nph.13979.

517   Young AM, Higuera PE, Duffy PA, Hu FS (2016) Climatic thresholds shape northern high-

518   latitude fire regimes and imply vulnerability to future climate change. *Ecography* **40**, 1–12.

519   doi:10.1111/ecog.02205.

520   Zhang SB, Zhang JL, Cao KF (2017) Divergent Hydraulic Safety Strategies in Three Co-

521   occurring Anacardiaceae Tree Species in a Chinese Savanna. *Frontiers in Plant Science* **7**,

522   2075. doi.org/10.3389/fpls.2016.02075

523   Zwieniecki MA, Holbrook NM (2009) Confronting Maxwell's demon: biophysics of xylem

524   embolism repair. *Trends in Plant Science* **14**, 530-534.

525   doi.org/10.1016/j.tplants.2009.07.002.

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529   **Figures**
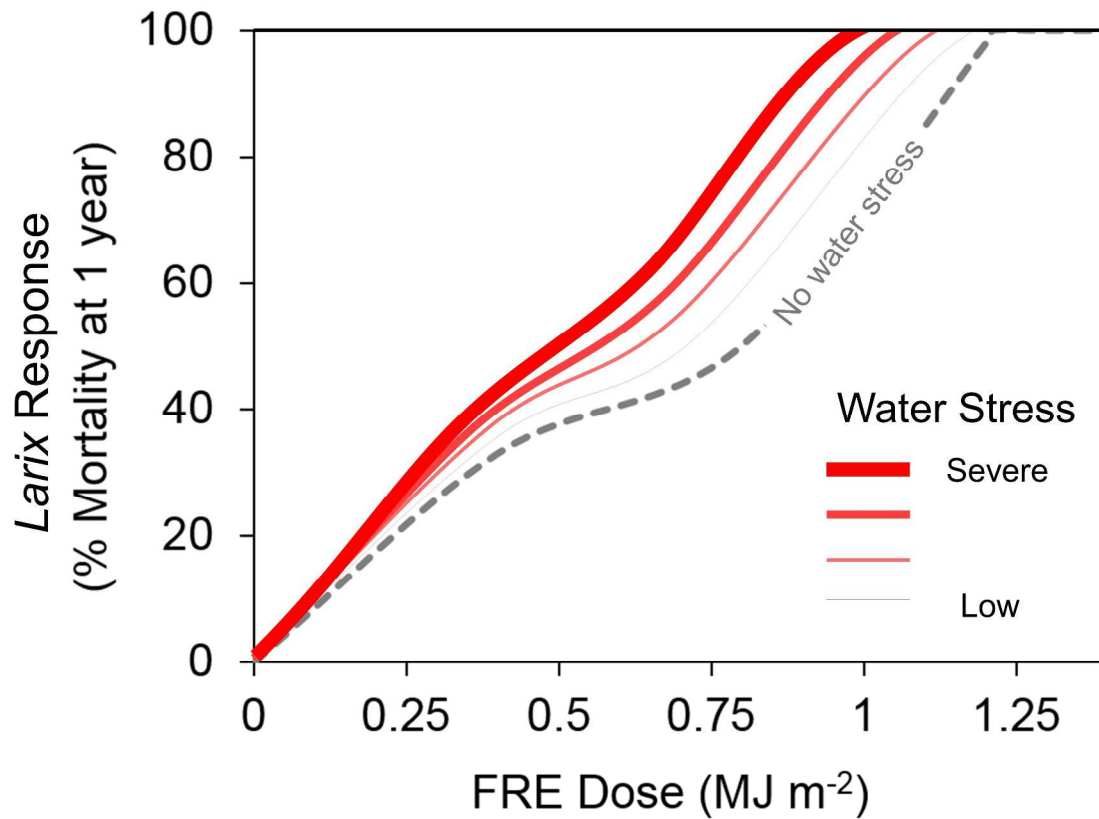
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531   **Figure 1.** Hypothesized shift of relationship between *Larix* mortality and Fire Radiative Energy

532   (FRE) (dose-response curve) as tree water stress increases (adapted from Smith et al. 2017).

533   Grey line indicates observed *Larix* mortality in Smith et al. (2017).
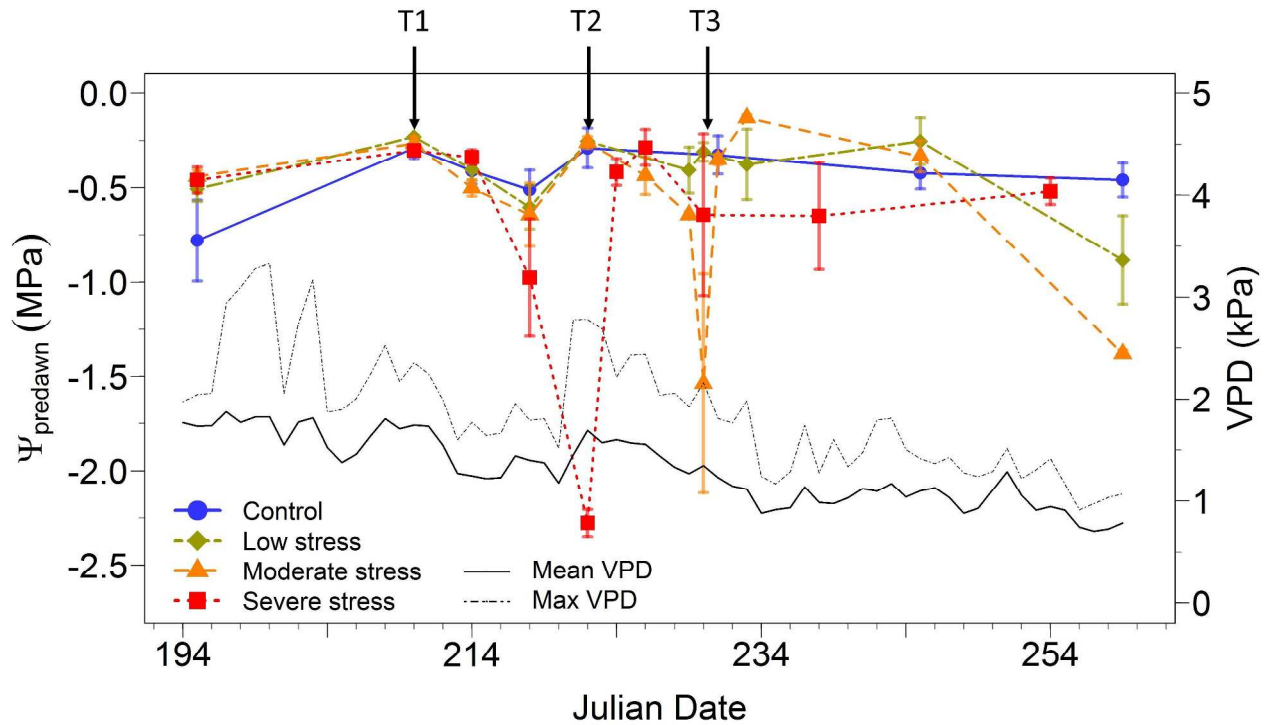
Figure 2. Predawn water potential ($\Psi_{predawn}$, units: MPa) of *Larix* groups throughout the study period with annotations marking significant timepoints (T1-3). Timepoints are as follows: T1 – Severe-water-stress *Larix* treatment start; T2 – severe-water-stress *Larix* are subjected to fire treatment, moderate-water-stress *Larix* treatment start; T3 – low and moderate-water-stress *Larix* are subjected to fire treatment. Error bars represent standard error ($n = 3$). Mean vapor pressure deficit (VPD, units: kPa) (solid black line) and max VPD (dotted black line) are also shown.
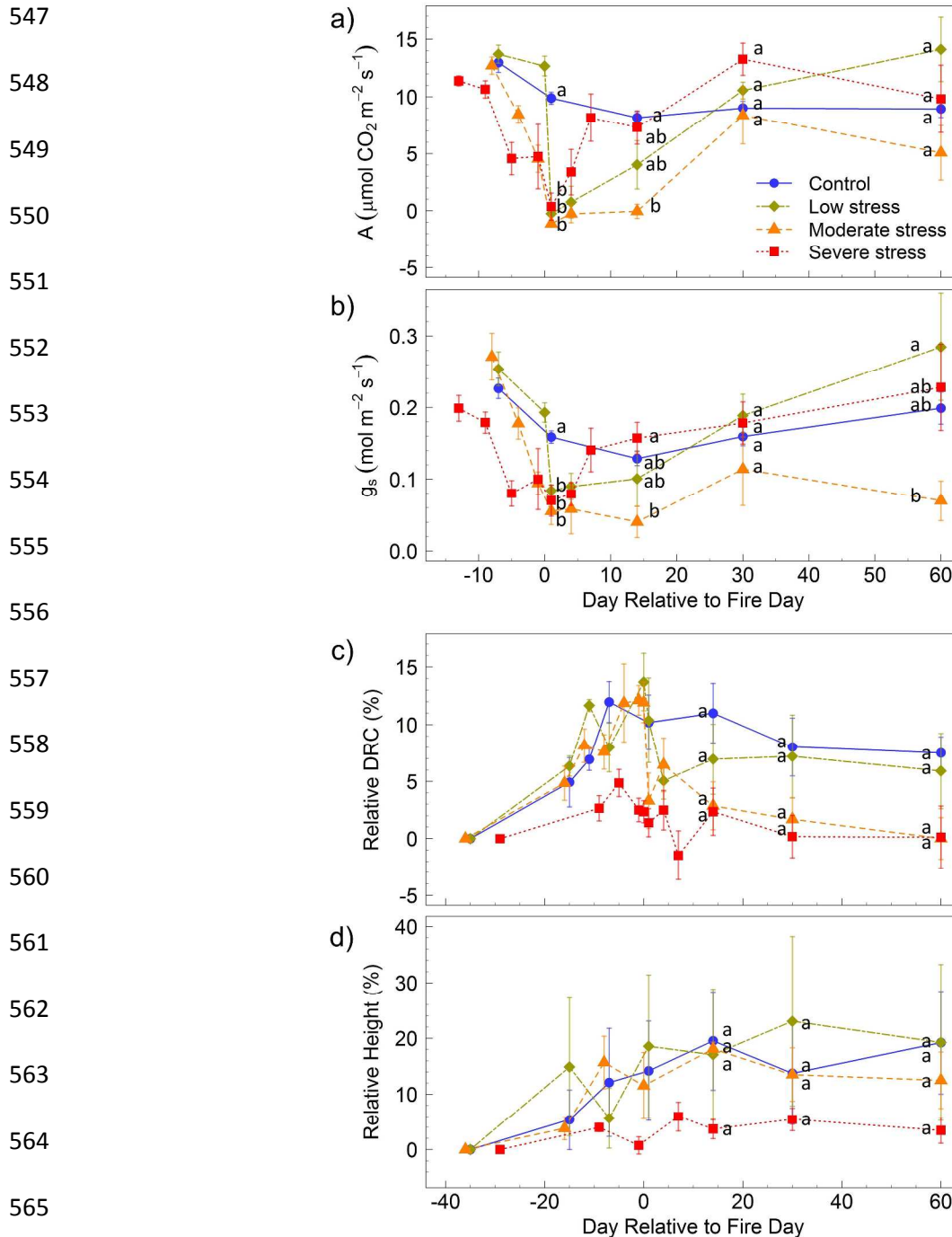
Figure 3. *Larix* physiology and growth changes from pre- to post-fire by water stress group. Data are displayed for a) net photosynthesis (*A*), b) stomatal conductance (g_s), c) relative diameter at root collar (DRC), and d) relative height. Mean values sharing the same letter are not significantly different (p < 0.05). Error bars represent standard error (*n* = 5).

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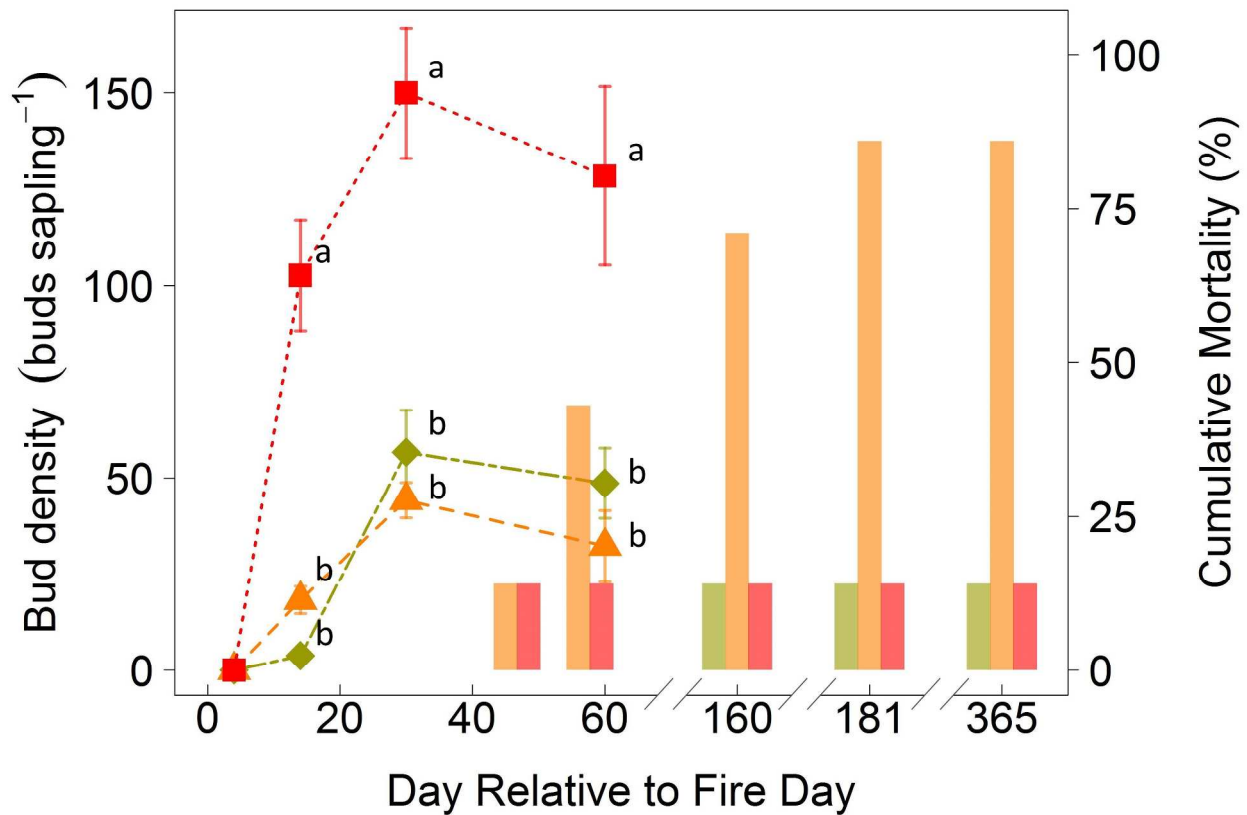
Figure 4. Bud density (buds sapling^{-1}) from 1 to 60 days post-fire. Cumulative mortality (%) is also shown (bar graph) from 1 to 365 days post-fire. Green diamonds and bars represent low-water-stress *Larix*, orange triangles and bars represent moderate-water-stress *Larix*, and red squares and bars represent severe-water-stress *Larix*. Mean values sharing the same letter are not significantly different (p < 0.05). Error bars for bud density represent standard error (*n* = 5).

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Figure 5. Pre- and post-fire condition of representative low (top row), moderate (middle row), and severe-water-stress *Larix* (bottom row). Average predawn water potential for each group is denoted as $\Psi_{predawn}$. Yellow, senescing needles are clearly visible in the severe-water-stress photo on burn day (bottom row, '0' day) as well as differences in bud density between the groups at 30 and 60 days post-fire.

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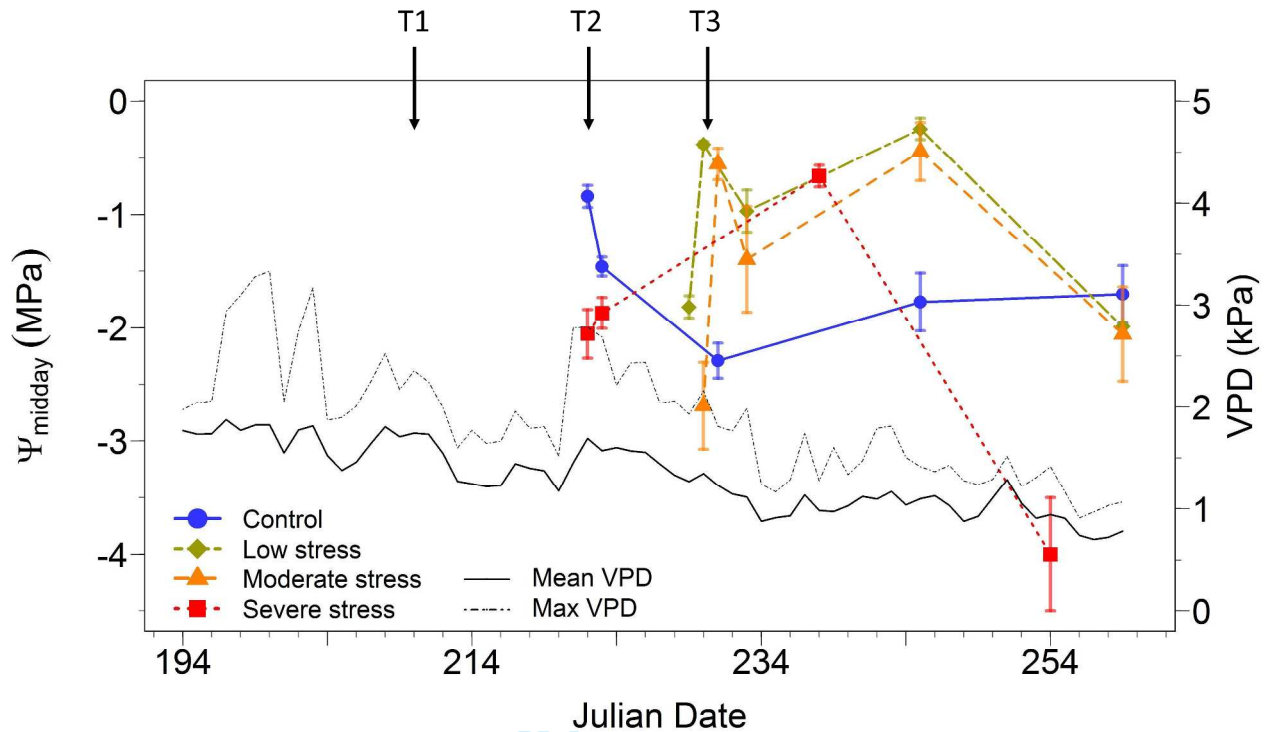
Figure S1. Midday water potential (Ψ_{midday}, units: MPa) of *Larix* groups post-fire treatment, with

annotations marking significant timepoints (T1-3). Timepoints are as follows: T1 – Severe-

water-stress *Larix* treatment start; T2 – severe-water-stress *Larix* are subjected to fire treatment,

moderate-water-stress *Larix* treatment start; T3 – low and moderate-water-stress *Larix* are

subjected to fire treatment. Error bars represent standard error ($n = 3$). Mean vapor pressure

deficit (VPD, units: kPa) (solid black line) and max VPD (dotted black line) are also shown.

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