1 **Water limitations on forest carbon cycling and conifer traits along a steep climatic gradient**
2 **in the Cascade Mountains, Oregon**

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4 *Logan T. Berner and Beverly E. Law*

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6 Department of Forest Ecosystems and Society, Oregon State University, Corvallis, Oregon

7 Correspondence to: L.T. Berner (logan.berner@oregonstate.edu)

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1   Introduction

Droughts in the western United States had severe impacts on human and natural systems during the past century (Allen et al., 2010; Schwalm et al., 2012; Williams et al., 2012; Woodhouse and Overpeck, 1998) and sustained climatic warming due to human greenhouse gas emissions will likely exacerbate drought impacts over the coming century (Collins et al., 2013; Dai, 2013; Williams et al., 2012). Mean annual air temperatures in the western United States increased 0.8-1.1°C from 1895 to 2011 (Kunkel et al., 2013; Mote et al., 2014) and could rise an additional 5.4°C by the end of the 21st century (Walsh et al., 2014). Rising temperatures resulted in substantial reductions (up to 80%) in spring snowpack across most mountain ranges in the region since observations became widespread in the 1950s (Mote et al., 2014; Mote et al., 2005) and during April 2015 snowpack was less than 25% of the 30-yr average across the Cascade and Sierra Mountain Ranges (USDA Natural Resources Conservation Service, 2015).

Tree-ring based reconstructions indicate that very persistent, severe, and extensive droughts ('mega-droughts') occurred over the past 1200 years in the western United States, especially during an abnormally warm period from around AD 900 to 1300 (Cook et al., 2004; Woodhouse et al., 2010), and suggest an increase in the area annually affected by drought over the 20th century (Cook et al. 2004). The most severe drought over the past 800 years occurred in 2000-2004 (Schwalm et al., 2012) and continued regional warming over the 21st century is expected to produce droughts that are much more severe and persistent than the documented historical mega-droughts (Collins et al., 2013; Dai, 2013; Schwalm et al., 2012; Williams et al., 2012), with widespread ecological and socioeconomic consequences (Diffenbaugh and Field, 2013; Jiang et al., 2013; Mote et al., 2014).

46   Water availability varies widely across the western United States and shapes the

47   distribution and composition of forests, as well as forest carbon cycling. Mean annual

48   precipitation (1971-2000) ranged from <100 mm yr^{-1} in parts of the Southwest to >5000 mm yr^{-1}

49   in parts of the Pacific Northwest, with spatial patterns largely governed by proximity to the

50   ocean and the distribution of mountain ranges (Daly et al., 2008). Strong spatial gradients in

51   water availability across this region play an important role in shaping the distribution of tree

52   species and plant communities (Franklin and Dyrness, 1988; Mathys et al., 2014). For instance,

53   drought-tolerant western juniper (*Juniperus occidentalis*) form open woodlands in the dry

54   foothills of the eastern Cascade Mountains, Oregon, while increased rainfall at higher elevations

55   leads to a sequence of forest zones dominated by species with progressively lower drought

56   tolerance, such as ponderosa pine (*Pinus ponderosa*), grand fir (*Abies grandis* Dougl.) and

57   western hemlock (*Tsuga heterophylla*; Franklin & Dyrness 1988), and progressively higher leaf

58   area, productivity and biomass (Gholz, 1982; Grier and Running, 1977). Warming-induced

59   drought-stress contributed to increased tree mortality rates (Allen, 2009; Peng et al., 2011; van

60   Mantgem et al., 2009) and wildfire activity (Dennison et al., 2014; Westerling et al., 2006) in

61   parts of western North America over the 20th century and the rapid velocity of climate change

62   projected for the 21st century (Loarie et al., 2009) is expected to drive pronounced, though

63   relatively uncertain changes in forest distribution (Coops and Waring, 2011; Jiang et al., 2013;

64   Rehfeldt et al., 2006) and biogeochemical cycling (Hudiburg et al., 2011; Jiang et al., 2013;

65   Kang et al., 2014), with impacts dependent in part on species' morphological and physiological

66   adaptions to drought stress (Law, 2014; McDowell and Allen, 2015).

67   Plants have evolved numerous adaptations to prevent hydraulic dysfunction, yet

68   adaptations that allow plants to withstand very arid conditions often reduce their ability to

69   compete in wetter, more productive environments. Water is used for myriad physiological

70   processes (e.g., photosynthesis, heat dissipation, osmotic regulation; Kozlowski et al., 1991) and

71   ascends from the soil into vascular plant canopies through xylem conduits, driven by tension

72   imparted on the water column from molecules being evaporated from leaf substomatal chambers

73   (Sperry, 2011; Tyree, 1997). Plants have adaptations to maintain xylem water potentials (Ψ)

74   within physiologically operable ranges so as to prevent runaway cavitation of the water column

75   and subsequent hydraulic and photosynthetic impairment (Pockman et al., 1995; Sperry and

76   Tyree, 1988) caused by low soil Ψ and high atmospheric vapor pressure deficit (VPD;

77   Whitehead et al., 1984). The xylem Ψ required for substantial hydraulic impairment [e.g. 50%

78   loss of hydraulic conductance (P50)] varies both within (Domec et al., 2009) and among species

79   (Anderegg, 2015; Choat et al., 2012; Willson et al., 2008), depending in part on the mechanical

80   strength of the xylem conduits, which tends to increase with wood density (Chave et al., 2009;

81   Hacke et al., 2001; Jacobsen et al., 2007). When conditions are dry, some plants reduce stomatal

82   conductance to help maintain xylem Ψ within an operable range, yet this simultaneously reduces

83   carbon assimilation and can lead to carbon starvation and mortality if sustained (McDowell,

84   2011). Plants can also manage xylem Ψ by shedding leaves or, more gradually, by increasing

85   investment in sapwood (Maherali and DeLucia, 2001; Mencuccini and Grace, 1995), either of

86   which lowers the leaf:sapwood area ratio (LA:SA). Holding other factors constant, taller trees

87   experience lower (i.e. more negative) xylem Ψ at the top of the canopy due to increased

88   gravitational pull and cumulative path-length resistance (Koch et al., 2004; Whitehead et al.,

89   1984), which is potentially a key factor limiting maximum tree height in a given environment

90   (Koch et al., 2004; Ryan and Yoder, 1997) and can predispose taller trees to drought-induced

91   mortality (McDowell and Allen, 2015). Adaptations that enable plants to endure harsh abiotic

92   stress (e.g. drought) often come at a competitive cost in more productive environments due to

93   lower rates of resource acquisition and processing (Grime, 2001; Grime, 1974; Reich, 2014).

94   Given the potential socioeconomic and ecologic impacts it is imperative that we better

95   understand how forest ecosystems in the western United States respond to spatial and temporal

96   variations in water availability. Our objective in this study was to investigate how forest carbon

97   cycling and conifer morphological traits responded to variation in water availability across a

98   network of field sites in the eastern Cascade Mountains, Oregon, which included forests

99   dominated by western juniper, ponderosa pine, and grand fir. We used the average growing-year

100   climate moisture index ($CMI_{\overline{gy}}$; 1964-2013) as an indicator of water availability (Berner et al.,

101   2013; Hogg and Hurdle, 1995), calculated as the difference between monthly precipitation (*PPT*)

102   and reference evapotranspiration (ET_0) from October of year *t-1* through September of year *t* (see

103   Table S1 for a key of abbreviations). The Cascade Mountains exhibit one of the steepest $CMI_{\overline{gy}}$

104   gradients in North America (Fig. 1a), making it an excellent natural laboratory for studying plant

105   adaptation and ecosystem response to water stress (e.g., Gholz, 1982; Law and Waring, 1994).

106   We used a combination of stand survey, tree ring, and morphological measurements to test the

107   following three hypotheses:

108   I.   Long-term water availability limits forest carbon cycling at low- to mid-elevations in the

109   eastern Cascade Mountains. Building on prior analyses in the region (Gholz, 1982; Grier

110   and Running, 1977; Law and Waring, 1994), we predicted that forest leaf area index

111   (LAI), annual aboveground net primary productivity (ANPP), and aboveground live

112   biomass (AGB) would increase with $CMI_{\overline{gy}}$.

113   II.   Interannual fluctuations in water availability exert a stronger influence on tree growth in

114   dry, low-elevation forests than in wet, mid-elevation forests. We anticipated the

115   proportion of trees exhibiting a significant positive correlation between annual tree ring-

116   width indices (RWI) and *CMI* over the past 50 years ($F_{RWI\text{-}CMI}$) would be highest among

117   western juniper, followed by ponderosa pine and then grand fir. Furthermore, we

118   predicted that the site-average strength of the RWI-*CMI* correlation ($\bar{r}_{RWI\text{-}CMI}$) across

119   years would decrease with increasing $CMI_{\overline{gy}}$ across sites

120 III.   Trees respond to increased long-term water availability (i.e., reduced hydraulic stress) by

121   increasing investment of resources to competition for light. We anticipated that average

122   stem wood density ($\overline{WD}$) would decrease with increased $CMI_{\overline{gy}}$, whereas maximum tree

123   height (H_{max}) and LA:SA would increase with $CMI_{\overline{gy}}$.

124

2   Materials and methods

2.1   Study design

127 We employed a gradient analysis that included 12 sites evenly distributed among three forest

128 types (western juniper, ponderosa pine, and grand fir) along the eastern slopes of the Cascade

129 Mountains, Oregon, which ranged in elevation from 929 to 1560 m above sea level (Fig. 1a,b).

130 Guided by maps of forest type (Kagan et al., 2006), historical wildfires (Eidenshink et al., 2007),

131 and land ownership we selected sites in areas with mature (>80 years), publicly-owned forest

132 that showed minimal evidence of recent natural (e.g. fire, insect) or human disturbance (e.g.

133 thinning). Furthermore, sites were situated within 100 m of a road to facilitate access. We

134 included the long-term AmeriFlux Metolius Mature Pine (US-Me2) eddy covariance flux tower

135 (Law et al., 2004) as one of our ponderosa pine sites. Additionally, we collected samples at three

136 relatively young stands, one for each species, which included the Metolius Young Pine Burn flux

137   tower site (US-Me6). These data are present in Table S2, though were not included in our

138   analysis given that the mean cambial age at breast height was 17 to 38 years, depending on site.

139   At each new site we established a randomly located 1-ha plot, as per the Global

140   Terrestrial Observing System (GTOS) protocol (Law et al., 2008), though used pre-existing plots

141   at US-Me2 and US-Me6. The plot design, similar to that used by the USDA Forest Service

142   Forest Inventory and Analysis program, included one central subplot and three subplots arranged

143   in a circular pattern around the center and offset from the center by 35 m. Subplot radii were held

144   consistent within a site, but varied among sites from 10-17 m for trees and from 5-17 m for

145   saplings, depending on stem density. Stems with a diameter at breast height (DBH; 1.4 m)

146   greater than 10 cm were considered trees, while those with DBH from 1-10 cm were considered

147   saplings. We tagged every tree (n=730) and sapling (n=39) in the study with a unique identifier.

148   Seedlings (DBH < 1 cm) were not sampled.

149

2.2   Field sampling

151   Field activities included stem survey measurements, collection of tree core and foliage samples,

152   and optical measurements of leaf area, as per the GTOS protocol (Law et al., 2008). We

153   measured DBH and total height (H) of every tagged stem and then, within each subplot,

154   randomly selected a subset of trees for intensive measurement. Tree H was measured using a

155   laser rangefinder (Laser Technology Inc., Centennial, USA).We cored five trees of the dominant

156   species per subplot (20 trees per plot) for growth measurements. Tree cores were extracted near

157   breast height using a 5.15 mm increment borer and, if necessary, oriented perpendicular to the

158   slope. We then randomly selected two or three of the five trees per subplot (10 trees total per

159   plot) and collected an additional core from each tree for wood density and sapwood area

160   measurements. For each of the 10 intensively measured trees we also excised mid-canopy, south-

161   facing branches and collected foliage for measurements of leaf longevity (LL), specific leaf area

162   (SLA), and foliar carbon (C) and nitrogen (N). For ponderosa pine and grand fir we estimated LL

163   on the excised branches using the "counting cohorts" method (Pérez-Harguindeguy et al., 2013).

164   Since western juniper do not form distinct cohorts we calculated LL based on estimates of

165   foliage biomass and annual leaf litter fall from a near-by site (Runyon et al., 1994). Foliage was

166   then stored following standard protocols prior to laboratory analysis (Pérez-Harguindeguy et al.,

167   2013). We collected additional tree cores and foliage samples when non-dominant tree species

168   were present in the subplots. The number of additional trees varied from one to six depending on

169   the diversity and relative abundance of additional species. Lastly, we measured canopy gap

170   fraction on each subplot using an optical LI-2200 Plant Canopy Analyzer for conifers (LI-COR,

171   Lincoln, USA).

172

173   **2.3   Sample processing**

174   **2.3.1   Tree cores: radial growth, sapwood area, and stem wood density**

175   We measured annual radial growth using 256 tree cores, focusing principally on the 50-year

176   period from 1964 to 2013, and estimated tree age on cores that included the pith. The tree cores

177   were processed using standard procedures (Pilcher, 1990). We measured annual ring-widths

178   using a desktop scanner and WinDendro software (89% of cores) or a stereoscopic microscope,

179   Velmex sliding stage, and MeasureJ2X software if the growth-rings were very tight (11% of

180   cores). We cross-dated the cores visually (Yamaguchi, 1991) and then statistically in R (R Core

181   Team, 2015; version 3.2.0) using the Dendrochronology Program Library in R package (dplR;

182   Bunn, 2010).

183   We estimated sapwood area and basic stem wood density initially using the same set of

184   tree cores (n=144). Sapwood width was measured using calipers. Sapwood area at breast height

185   was calculated for each sampled tree as the difference between stem basal area (excluding bark)

186   and stem heartwood area, assuming a circular trunk. For each species DBH was a strong

187   predictor of sapwood area (r^2=0.85-0.93; Table S3) and therefore we used these relationships to

188   predict sapwood basal area for trees that were not sampled.

189   We estimated basic stem wood density following published guidelines (Williamson and

190   Wiemann, 2010), which involved removing the bark, cutting each core into multiple segments

191   and then measuring segment cross-sectional diameter and length using calipers. The core

192   segments were oven-dried at 101-105°C for 72 hours and then immediately weighed. We

193   calculated basic stem wood density (WD; g cm^{-3}) for each core segment by dividing oven dry

194   mass (g) by the green volume (cm^3). Since each segment represented a different portion of the

195   total trunk cross-sectional area, we calculated an area-weighted mean WD across segments to

196   account for potential variation in WD between the cambium and the pith (Muller-Landau, 2004).

197   Williamson and Wiemann (2010) recommended estimating WD from tree cores only when the

198   core include the pith. Since 25% of our tree cores (n=43) did not include the pith, we tested, for

199   each species, whether WD estimates differed significantly depending on whether the tree had

200   been or had not been pithed. For fir and pine, the WD estimates did not differ significantly (t-

201   tests, P>0.05) between samples with or without the pith; however, for juniper, the WD estimates

202   were significantly lower for samples that did not include the pith (P<0.05). We therefore chose to

203   exclude samples from 14 juniper that did not include the pith, yet retained all samples from fir

204   and pine irrespective of whether the sample included the pith. In total, we analyzed samples from

205   120 trees.

206

207   **2.3.2   Foliage samples: specific leaf area and chemistry**

208   We measured SLA [one-half total leaf (i.e., hemisurface area) area per gram of carbon] and leaf

209   chemistry (C and N) using samples collected from 186 trees during the middle of the growing

210   season. Mid-growing season leaf characteristics tend to be representative of species average

211   conditions (e.g., Nippert and Marshall, 2003). We carefully trimmed the needles from each

212   sample (usually about 0.5 g dry weight), measured the cumulative projected surface area using a

213   LI-3100C Area Meter (LI-COR, Lincoln, USA), dried each sample at 70°C for at least 72 hours,

214   and then immediately weighed each sample (Pérez-Harguindeguy et al., 2013). Samples were

215   then finely ground and sent to Central Analytical Laboratory at Oregon State University for

216   analysis of C and N content using a Leco CNS-2000 Macro Analyzer. We calculated SLA (cm^2

217   leaf g^{-1} C) as

218     $$SLA = \frac{A \times \beta}{M \times C} \qquad (1)$$

219   where A was the projected surface area (cm^2); β was a species-specific conversion coefficient

220   drawn from the literature that related A to one-half total surface area (Table 1); M was oven dry

221   mass (g); and C was the species-average carbon content of leaf dry matter (%).

222

223   **2.4   Forest leaf area, biomass, and productivity**

224   **2.4.1.   Forest leaf area**

225   We estimated LAI [one half surface area of needles (m^2) per square meter of ground] at 35-45

226   random points on each subplot based on optical measurements. We used the FV2200 software

227   (LI-COR, Lincoln, USA) to calculate effective leaf area (L_e) from field measurements of canopy

228   gap fraction, which implemented a foliage scattering and transmittance correction that permits

229   measurements to be made during periods of direct sunlight (Kobayashi et al., 2013). The LAI

230   measurements were subsequently corrected for foliage (γ) and canopy clumping (Ω), as well as

231   for light interception by branches and stems (Chen, 1996; Law et al., 2008). We computed LAI

232   as

233    $$LAI = L_e\left(\frac{\gamma}{\Omega}\right) - W \qquad (2)$$

234   where species-specific γ were derived from the literature (Frazer et al., 2000; Law et al., 2001)

235   and Ω was derived directly from the LI-2200. We calculated wood area index (W) from stand

236   basal area (BA; m^2 ha^{-1}) as

237    $$W = 2.061 \times (1 - e^{(-0.006 \times BA)}) \qquad (3)$$

238   based on the strong relationship (r^2=0.90) observed between W and BA across 96 sites in Oregon

239   (Law, unpublished data). For mixed species subplots we calculated a biomass-weighted mean γ.

240

241   **2.4.2   Forest biomass**

242   We estimated forest AGB (kg C m^{-2}) for each subplot as the total mass of bole, branch, bark, and

243   leaf carbon of all trees and saplings, divided by the areal extent of each plot. Tree component

244   biomass was computed using species-specific allometric equations based on tree DBH and H,

245   while sapling biomass was calculated from height alone (Gholz et al., 1979; Means et al., 1994;

246   Wenzel, 1977). Bole volume estimates were converted to dry matter using species-average WD

247   measurements from our study sites. Bole, branch, and bark dry matter were assumed to be 51%

248   carbon (Law et al. 2001). Leaf mass was computed by dividing LAI by ecosystem-averaged

249   SLA, with ecosystem-average SLA calculated based on the relative biomass of each species

250   present.

251

252 **2.4.3   Forest productivity**

253 We estimated forest ANPP (kg C m^{-2} yr^{-1}) biometrically for each site by calculating the change

254 in forest AGB (excluding leaf mass) between 2005 and 2014, divided by the number of

255 intervening years, plus annual leaf turnover (e.g., Hudiburg et al., 2009; Van Tuyl et al., 2005).

256 This necessitated hindcasting DBH and H for each tree using radial growth measurements and

257 allometric models to predict H from DBH. We did not collect cores from every tree and therefore

258 we divided the trees at each site into three equal sized, species-specific groups based on DBH.

259 We then took the available ring-width measurements within each size class and calculated the

260 average diameter increment over the preceding 10-years, which was then subtracted from the

261 DBH$_{2014}$ of each tree in the size class to yield an estimate of DBH$_{2005}$. For each species we

262 developed a nonlinear Weibull-type model (Yang et al., 1978) to predict H from DBH (r^2 = 0.66-

263 0.87; RMSE = 1.55-3.21 m; Table S4). We estimated H$_{2005}$ from DBH$_{2005}$ for each tree and

264 subsequently calculated forest AGB in 2005 (excluding leaf mass) for each subplot. Forest

265 ANPP was then estimated for each subplot by differencing woody AGB between 2014 and 2005,

266 divided by the ten intervening years, plus annual leaf turnover computed by dividing leaf mass in

267 2014 by ecosystem-average leaf longevity measured at our sites.

268

269 **2.5   Climate data and derivation of climate moisture index**

270 We derived monthly estimates of *CMI* (Hogg, 1997) for each site as the difference between *PPT*

271 and *ET$_0$* using gridded climate data from 1964 to 2013. The climate data were produced by the

272 Parameter-elevation Relationships on Independent Slopes Model (PRISM;

273 http://www.prism.oregonstate.edu/; Daly et al., 2008) based on climate station observations and

274 spatial modeling at 4 km resolution. We calculated monthly ET$_0$ (mm month^{-1}) using a version of

275   the Hargreaves equation (Hargreaves and Samani, 1985) modified by Droogers and Allen

276   (2002):

277    $$ET_0 = 0.0013 \times 0.408R\left(T_{avg} + 17.0\right)\left(T_{rng} - 0.0123PPT\right)^{0.76} \qquad (4)$$

278   which is based average daily extraterrestrial radiation (R; MJ m^{-2} d^{-1}), average daily temperature

279   (T_{avg}; °C), daily temperature range (T_{rng}; °C), and precipitation (PPT; mm month^{-1}). Estimates of

280   R were derived based on equations provided by Allen et al. (1998). Modeled monthly ET$_0$ and

281   PPT agreed relatively well with meteorological measurements at the US-Me2 flux tower site

282   from 2002 to 2012 (r^2=0.57-0.64, P<0.01) and at the US-Me6 flux tower from 2010 to 2013

283   (r^2=0.58-0.65, P<0.01). For each site we then summarized climate conditions over the growing-

284   year (gy; October in year t-1 through September of year t), which involved calculating average

285   T_{avg}, as well as cumulative PPT, ET_0, and CMI (e.g. denoted CMI_{gy}). Lastly, we averaged

286   growing-year climate conditions from 1964 to 2013 to produce 50-year climatologies for each

287   variable (e.g. $CMI_{\overline{gy}}$).

288

289   **2.6   Analyses**

290   **2.6.1   Constraints of long-term water availability on forest carbon cycling**

291   For each site we computed the average and standard error (SE) of LAI, ANPP, and AGB among

292   subplots and then examined the relationship between each of the variables and $CMI_{\overline{gy}}$ across

293   sites. Scatter plots revealed nonlinear relationships between each variable and $CMI_{\overline{gy}}$, which

294   could be described using power functions (Y = aX^b). Power function models were fit using the

295   nonlinear least squares (*nls*) function in R (version 3.2.0) and model residuals were visually

296   examined. For each model we calculated the root mean squared error (RMSE) and the coefficient

297   of determination (r^2), which was computed based on the proportion of the total sum of squares

298   explained by the model. We also examined the relationships among forest LAI, ANPP, and AGB

299   using least-squares linear regression.

300

301   **2.6.2   Influence of interannual fluctuations in water availability on tree radial growth**

302   We derived standardized tree ring-width indices (RWI) for each mature tree using functions in

303   dlpR (Bunn, 2010) and then quantified the association between each RWI series and monthly

304   *CMI* aggregated over the preceding 1- to 36-months. For each tree at least 70 years old (n=216)

305   we subset measurements from 1964 to 2013, detrended the series using a flexible spline and then

306   standardized the series by dividing the ring-width in year *t* by the value predicted for year *t* by

307   the fitted function (Fritts, 2001). Splines were fit with the *detrend* function in dplR using a 30-

308   year window and frequency response of 0.5. Next, we removed lag-1 autocorrelation (i.e. pre-

309   whitened) from each RWI series by taking the residuals of an ordinary least squares regression

310   that related the RWI from each year against that of the prior year. We then computed Pearson's

311   correlations between each RWI series and monthly pre-whitened and linearly-detrended *CMI*

312   aggregated from 1- to 36-months. This approach resulted in 432 correlations per tree (12 months

313   x 36 lags). For each tree we calculated the overall strength of the RWI-*CMI* correlation as the

314   average of the 95% quantile of all computed correlations. We then summarized these responses

315   by both species and site. For each of the three species we calculated the percent of trees that

316   exhibited a significant ($P < 0.05$) positive RWI-*CMI* correlation at each month x lag combination.

317   Next, we computed an ecosystem-average RWI-*CMI* correlation ($\bar{r}$ RWI-*CMI*) for each site, based

318   on the relative biomass of each species, and then examined how $\bar{r}$ RWI-*CMI* changed with $CMI_{\overline{gy}}$.

319   We also tested whether the percent of trees at each site that exhibited a significant RWI-*CMI*

320   correlation ($F_{RWI-CMI}$) differed among the three forest types using a nonparametric Kruskal-

321   Wallis rank sum test (Kruskal and Wallis, 1952), which assess the null hypothesis that all

322   samples come from the same distribution. Lastly, we examined the relationship between RWI

323   and other climate variables, including T_{avg}, T_{min}, T_{max}, *VPD*, number of freeze days, the

324   standardized precipitation-evaporation index (SPEI; Vicente-Serrano et al., 2010) and the

325   climatic water deficit (i.e., monthly ET in excess of PPT), yet focused on *CMI* because trees

326   were generally most sensitive to this climate variable. For completeness, we provide summaries

327   of these additional growth-climate relationships in Figure S1 and Table S6.

328

329   2.6.3   Constraints of long-term water availability on tree morphological traits

330   To explore long-term hydraulic constraints on forest morphology we compared LA:SA (m^2 leaf

331   cm^{-2} sapwood), H_{max} (m), and $\overline{WD}$ (g cm^{-3}) against $CMI_{\overline{gy}}$. For each subplot we calculated

332   LA:SA as the ratio between LAI and sapwood basal area, H_{max} as the height of the tallest tree,

333   and $\overline{WD}$ as the biomass-weighted average WD of each species present. We then computed the

334   average and SE of each characteristic for each plot. Next, we modeled each trait as a function of

335    $CMI_{\overline{gy}}$ using either linear or nonlinear regression.

336

337   3   Results

338   3.1   Climate conditions

339   Summary statistics in this section are for 1964 to 2013 and represent cross-site averages (± 1 SD)

340   within each of the three forest types (site-level summaries are given in Table S5). Average

341    $T_{\overline{gy}}$ decreased from 8.32±0.80 °C at the juniper sites to 6.26±0.72 °C at the fir sites, while

342    $CMI_{\overline{gy}}$ increased from -1250±120 mm yr^{-1} to -280±250 mm yr^{-1} (Table 2). Across forest types

343   July was the climatically driest month, while December, conversely, was the climatically wettest

344   month. At juniper sites, *CMI* tended to be negative (i.e. *ET* exceeded *PPT*) for nine consecutive

345   months each year (February-October), whereas *CMI* was generally negative at pine and fir sites

346   for eight (March-October) and seven (April-October) consecutive months, respectively.

347   Large interannual fluctuation in CMI_{gy} occurred between 1964 and 2013 (Fig. 2a,b,c). For

348   instance, 1982 and 1997 were abnormally wet, whereas 1977 and 1994 were abnormally dry. At

349   the juniper sites, CMI_{gy} during these wet years was around 300-400 mm greater than during the

350   dry years. At the fir sites the difference in CMI_{gy} between these abnormally wet and dry years

351   was more pronounced, exceeding 1000 mm. Other notable dry years included 1973, 1992, 2001

352   and 2003. Conditions were consistently drier than normal from 1985 to 1994, with $CMI_{gy} <$

353     $CMI_{\overline{gy}}$ for eight or nine years, depending on forest type (Fig. S2).

354

355   **3.2   Constraints of long-term water availability on forest carbon cycling**

356   The 12 sites spanned a gradient in $CMI_{\overline{gy}}$ from -1240±120 mm yr^{-1} to 50±290 mm yr^{-1} and

357   across this gradient forest LAI, ANPP, and AGB increased significantly (P<0.05) and non-

358   linearly with $CMI_{\overline{gy}}$, which explained 67-88% of the variability in these stand characteristics

359   (Fig. 3; Table 3, S2, S5). After accounting for wood interception and clumping, LAI ranged from

360   0.09±0.03 to 6.15±1.12 across sites, with average (± 1 SD) LAI in each forest type increasing

361   progressively from the open-canopy juniper sites (0.26±0.13) into the pine (1.92±0.51) and then

362   closed-canopy fir sites (4.54±1.49; Fig. 3a; Table 4). Annual productivity along this gradient

363   increased from 11±2 to 311±60 g C m^{-2} yr^{-1} and averaged 17±4, 185±62, and 238±54 g C m^{-2} yr^{-1}

364   at the juniper, pine and fir sites, respectively (Fig. 3b). Aboveground biomass also tended to be

365   quite low at the juniper sites (2.6±0.4 kg C m^{-2}), yet reached higher levels at sites dominated by

366   pine (10.6±4.1 kg C m^{-2}) and fir (14.4±5.9 kg C m^{-2}). Across sites there was a significant (P <

367   0.01) positive linear relationship between LAI and ANPP (r^2 = 0.75). Furthermore, AGB was

368   positively associated with both LAI (r^2=0.57) and ANPP (r^2=0.68; Table 3).

369

370   **3.3   Influence of interannual fluctuations in water availability on tree radial growth**

371   Annual radial growth varied considerable from 1964 to 2013 (Fig. 2d,e,f) and tracked *CMI* more

372   closely at the chronically dry juniper sites than at the wetter pine and fir sites (Figs. 4, 5). Growth

373   reductions in response to single-year drought events (e.g. 1977, 1994, and 2001) were evident at

374   the juniper sites, whereas reductions were more modest at the pine and fir sites (Fig. 2d,e,f). For

375   instance, the 1977 drought led to a 73% reduction in average radial growth among juniper in

376   comparison to growth during 1976 (0.66±0.05 mm vs. 0.18±0.03 mm). In contrast, this drought

377   drove a 35% reduction in average growth among pine (1.74±0.14 mm vs. 1.08±0.10 mm) and a

378   7% reduction among fir (1.87±0.14 mm vs. 1.74±0.14 mm).

379   The vast majority of juniper (91±3%) exhibited a significant positive RWI-*CMI*

380   correlation ($\bar{r}$ $_{RWI-CMI}$ = 0.52±0.02) and responded most strongly to *CMI* over the 6 to 12 months

381   leading up to late spring and summer (Fig. 4a; Table S6). Around 51±6% of pine ($\bar{r}$ $_{RWI-CMI}$ =

382   0.27±0.02) and 12±4% of fir ($\bar{r}$ $_{RWI-CMI}$ = 0.11±0.02) also exhibited a significant positive

383   correlation with *CMI,* yet the influence of *CMI* seasonality and time scale were less distinct than

384   for juniper (Fig. 4b,c). The proportion of trees exhibiting a significant RWI-*CMI* association

385   differed significantly among the three forest types (Kruskal-Wallis, X^2=8.77, P=0.01) and among

386   sites there was a significant negative relationship between $\bar{r}$ $_{RWI-CMI}$ and $CMI_{\overline{gy}}$ (r^2=0.53,

387   P<0.05), with $\bar{r}$ $_{RWI-CMI}$ decreasing from 0.57±0.14 to -0.02±0.07 as conditions became wetter

388   (Fig. 5). There was a very strong linear relationship between $\bar{r}$ $_{RWI-CMI}$ and F$_{RWI-CMI}$ across sites

389   (r^2=0.92, P<0.001). Significant proportions of western juniper and, to a lesser extent, ponderosa

390   pine also showed negative correlations between growth and *VPD, T_{max}*, climatic water deficit, as

391   well as positive correlations with *SPEI*, while grand fir were largely unresponsive to any of the

392   climate variables that we examined (Fig. S1; Table S6).

393   Each species showed relatively high growth around 1980 to 1984, followed by a general

394   decline from c. 1985 to 1994 (Fig. 2 right panel) that corresponded with a period of relatively

395   *sustained*, below-average CMI_{gy} (Fig. 2 left panel) and, as discussed below, a widespread western

396   spruce budworm (*Choristoneura freeman*) outbreak. The growth decline was particularly severe

397   among fir; average radial growth in 1993 (0.55±0.04 mm) and 1994 (1.00±0.09 mm) were 73%

398   and 52% lower, respectively, than in 1985 (2.07±0.14 mm). In contrast, pine growth was 38%

399   lower (1.23±0.09 mm vs. 1.83±0.12 mm) and juniper growth 42% lower (0.38±0.03 mm vs.

400   0.66±0.03 mm) in 1994 than in 1985. Since disturbances can obscure RWI-climate relationship,

401   we reevaluated the correlations using measurements from 1994 to 2013 and found that the

402   correlations changed little in comparison to those computed from1964 to 2013 (Table S6).

403

404   **3.4   Constraints of long-term water availability on tree morphological traits**

405   Notable changes in morphological traits were evident along the water availability gradient (Fig.

406   6a,b,c; Tables 3, 4, S1). In general, ecosystem-average stem wood density, $\overline{WD}$, decreased with

407   increased $CMI_{\overline{gy}}$ (r^2=0.36, Fig. 6a). Correspondingly, species-average stem WD of juniper

408   (0.47±0.02 g cm^{-3}) was 4% higher than pine (0.45±0.02 g cm^{-3}) and 18% higher than fir

409   (0.40±0.03 g cm^{-3}). Maximum tree height increased non-linearly by 220% with $CMI_{\overline{gy}}$ (r^2=0.69),

410   from average H_{max} of 10.54±0.53 m at the juniper sites to 33.54±5.56 m at the fir-dominated sites

411   (Fig. 6b). Many of the tallest trees at the fir-dominated sites were actually old pine, the tallest of

18

412   which reached 41.2 m. Forest LA:SA also increased with $CMI_{\overline{gy}}$ (r^2=0.76; Fig. 6c), ranging from

413   0.02±0.01 to 0.19±0.02 m^2 cm^{-2}. Average LA:SA was quite low at the juniper sites (0.04±0.02

414   m^2 cm^{-2}), and 75% to 300% higher at the pine (0.07±0.02 m^2 cm^{-2}) and fir sites (0.16±0.02 m^2

415   cm^{-2}), respectively. Lastly, there were significant relationships among H$_{max}$, $\overline{WD}$, and LA:SA

416   across sites (r^2=0.35-0.55, P<0.05; Table 3).

417

418   **4   Discussion and conclusions**

419   **4.1   Constraints of long-term water availability on forest carbon cycling**

420   Consistent with predictions from our first hypothesis, forest ecosystem LAI, ANPP, and AGB

421   increased with $CMI_{\overline{gy}}$, yet residual variance in the regression models implies the characteristics

422   were influenced by additional bioclimatic or disturbance-related factors. Our results, along with

423   those of several prior field studies (Gholz, 1982; Grier and Running, 1977), indicate that water

424   availability is the dominant constraint on forest leaf area of mature stands in the eastern

425   Cascades. The constraint of water availability on forest leaf area in this environment is driven by

426   the need to maximize carbon assimilation while simultaneously minimizing water loss. Net

427   carbon uptake by trees (i.e., photosynthesis - respiration) occurs within the limits of the hydraulic

428   system (Ruehr et al., 2014), minimizing the risk of embolism when evaporative demand exceeds

429   supply (Meinzer et al., 2010). While $CMI_{\overline{gy}}$ explained 68% of the observed variance in LAI,

430   differences among sites in soil nitrogen, stand age, and disturbance history (e.g., windthrow,

431   insect outbreaks) might account for some of the residual variance (Gholz, 1982; Law et al.,

432   2003). For instance, we observed low-level leaf herbivory at several of the grand fir sites,

433   possibly due to western spruce budworm, which affected large areas of forest in this region over

434   the past three decades (Meigs et al., 2015; Willamette National Forest, 1995). Defoliation could

435   have temporarily reduced leaf area without killing the trees, drawing-down stored carbohydrates

436   during refoliation. Additionally, there is uncertainty in both destructive and nondestructive

437   estimates of forest leaf area (Law et al., 2001; Runyon et al., 1994) that could have further

438   obscured the relationship with long-term climate. For example, summer maximum LAI at the

439   Metolius Mature Pine flux site averaged about 2.5 over the past eight years, starting around 2.1

440   in 1997 (Law et al., 2001), and our estimate for 2014 was about 2.0. The substantial increase in

441   forest leaf area from the dry western juniper woodlands to the more mesic grand fir forests

442   highlights the importance of long-term water availability in controlling light harvesting potential

443   and subsequent carbon accumulation.

444   Forest productivity is highly dependent on leaf area (Gholz, 1982; Waring, 1983; Waring

445   et al., 2014) and therefore the observed increase in forest ANPP with $CMI_{\overline{gy}}$ can be largely

446   explained by the concomitant increase in leaf area. Forest leaf area and $CMI_{\overline{gy}}$ respectively

447   explained 75% and 88% of the variation in ANPP across sites. Forest leaf area largely

448   determines interception of photosynthetically active radiation (IPAR; Runyon et al., 1994), while

449   subsequent utilization of IPAR for photosynthesis depends on physiological constraints imposed

450   by environmental conditions (Landsberg and Waring, 1997; Runyon et al., 1994; Tezara et al.,

451   1999). For instance, Runyon et al. (1994) found at seven sites in Oregon that annual IPAR

452   increased linearly with LAI (r^2=0.95), while subsequent ANPP depended on utilized IPAR

453   (r^2=0.99), which was calculated by reducing IPAR based on constraints imposed due to low soil

454   moisture, high VPD, and duration of sub-freezing temperatures. Differences in biotic and abiotic

455   constraints among our sites could explain some of the remaining variance in the ANPP-CMI_{gy}

456   relationship (e.g. summer VPD, extent of freezing days each year, soil fertility and ratio of

457   above- to belowground C allocation; Schwarz et al., 2004).

458   Our estimates of ANPP for ponderosa pine over the past 10 years (125-262 g C m^{-2} yr^{-1})

459   were within the range reported by Law et al. (2003) for six mature to old stands (103-473 g C m^{-2}

460   yr^{-1}) in the region and agreed to within 14% at the Mature Pine flux tower site (210±23 vs.

461   242±57 g C m^{-2} yr^{-1}). Productivity at our four ponderosa pine sites was about 20-60% higher

462   than at sites examined by Gholz (1982; ≈110 g C m^{-2} yr^{-1}) and Runyon et al. (1994; ≈95 g C m^{-2}

463   yr^{-1}), whereas ANPP at our western juniper sites (11-21 g C m^{-2} yr^{-1}) was considerably lower

464   than at sites examined by either Gholz (1982; ≈60 g C m^{-2} yr^{-1}) or Runyon et al. (1994; ≈80 g C

465   m^{-2} yr^{-1}). Spatial differences in soil water holding capacity in the rocky volcanic soils (Peterman

466   et al., 2013) could account for some of the discrepancy in productivity, as could differences in

467   stand density or age. Western juniper at our sites were generally quite old and had accumulated

468   considerably higher overall AGB (2-3 kg C m^{-2} vs. ≈0.5 kg C m^{-2}). Overall, forest ANPP

469   increased with long-term average water availability, largely owing to the increased leaf area, but

470   potentially also due to reductions in abiotic constraints on carbon assimilation.

471   Forest AGB reflects the long-term integration of ANPP minus carbon loss (e.g. litterfall,

472   herbivory, tree mortality) and therefore higher biomass observed at wetter sites was likely driven

473   by higher rates of ANPP sustained over centennial time scales. Forest AGB increased with

474    $CMI_{\overline{gy}}$ (r^2=0.67) and achieved a carbon density, when averaged across the grand fir sites, that

475   was 6% greater than the average AGB estimated for temperate forests worldwide (≈13.5 kg C m^{-2}

476   ; Houghton et al. 2009). We found that $CMI_{\overline{gy}}$ explained less of the variance in forest AGB than

477   ANPP (r^2=0.88), potentially as a result of differences among sites in tree mortality rates. For

478   instance, there was little sign of recent tree mortality at the western juniper or ponderosa pine

479   sites, yet there were several large, freshly wind-thrown trees at two of the grand fir sites (GF-1

480   and GF-4) that could somewhat account for lower AGB at these sites (8.8-10.4 kg C m^{-2})

21

481 compared with the other two grand fir sites (16.9-21.6 kg C m^{-2}). Additionally, differences

482 among sites in growth impairment and mortality from periodic, historic outbreaks of spruce

483 budworm and mountain pine beetle (*Dendroctonus ponderosae*; Meigs et al. 2015) could account

484 for some of the unexplained variance in the AGB-$CMI_{\overline{gy}}$ regression model. Our findings, and

485 those of prior field (Franklin and Dyrness, 1988; Gholz, 1982; Grier and Running, 1977) and

486 modeling (Kang et al., 2014; Runyon et al., 1994) analyses, demonstrate that steep gradients in

487 water availability are a key factor shaping forest distribution and carbon cycling in the Pacific

488 Northwest, with regional forests further molded by disturbances such as timber harvest, wildfire,

489 and insect outbreaks (Law et al., 2004; Law and Waring, 2015; Meigs et al., 2015).

490

491 **4.2.   Influence of interannual fluctuations in water availability on tree radial growth**

492 We found evidence to support the hypothesis that interannual fluctuation in water availability

493 exerted less influence over tree growth as conditions became wetter; however, we unexpectedly

494 observed a pronounced growth decline across species from c. 1985 to 1994 that was particularly

495 severe among grand fir and potentially associated with relatively sustained, dry conditions over

496 that decade. We observed that as $CMI_{\overline{gy}}$ increased there was a decline in the proportion of trees

497 at each site that showed a significant correlation with between radial growth and *CMI*, as well as

498 a decline in the magnitude of that correlation. This suggests that, on an annual basis, water tends

499 to limit growth of western juniper to a greater extent than either ponderosa pine or grand fir; a

500 finding consistent with results from a modeling study that showed drought imposed greater

501 physiological reductions on the utilization of annual IPAR by western juniper than by ponderosa

502 pine or other conifers at higher elevations in the eastern Cascade Mountains (Runyon et al.,

503 1994). Western juniper occupy sites with chronically low rainfall, high summer *VPD* and *ET*,

504   and often thin, rocky soils, leading to generally low soil moisture that is highly dependent on

505   annual recharge. Thus, annual photosynthesis and subsequent stem wood production of western

506   juniper track the annual water balance to a greater extent than ponderosa pine or grand fir, which

507   occupy sites with not only higher rainfall, but reduced summer *VPD* and *ET*. Furthermore, soils

508   in the ponderosa pine and grand fir zones tend to be deeper and have greater water storage

509   capacity than in the western juniper zone (Kern, 1995). Soil depth averaged about 0.5 m at a

510   nearby juniper site (Anthoni et al., 1999) and about 2 m at the Metolius Mature Pine site (Law,

511   unpublished data). Our analysis focused on changes in tree growth-climate relations over tens of

512   kilometers, yet evidence from tree-ring and remote sensing analyses at regional (Huang et al.,

513   2015; Littell et al., 2008; Wilmking and Juday, 2005), hemispheric (Vicente-Serrano et al., 2014)

514   and global scales (Vicente-Serrano et al., 2013) suggest that as landscapes become wetter, annual

515   tree growth generally becomes increasingly decoupled from interannual fluctuations in water

516   availability, yet trees in characteristically wet landscapes can still be vulnerable to drought-

517   induced mortality (Allen et al., 2010).

518   What factor, or complex of factors, were responsible for the notable cross-species decline

519   in tree radial growth from c. 1985 to 1994, and why was the decline most severe in grand fir?

520   Ponderosa pine at low and high elevations in southern Oregon also experienced reduced growth

521   during these years (Knutson and Pyke, 2008). This ten-year period was characterized by nine

522   years where CMI_{gy} was at or below the 50-year average and punctuated by very dry conditions in

523   1994, the second most severe single-year drought over the record examined. This period

524   corresponded with the most extensive mountain pine beetle and western spruce budworm

525   outbreaks to have occurred in the eastern Cascades since 1970 (Meigs et al., 2015). Inspection of

526   aerial survey data collected annually since the 1940s by federal and state agencies (available

527   online: http://www.fs.usda.gov/detail/r6/forest-grasslandhealth/) revealed that from 1985 to 1994

528   our grand fir sites showed signs of western spruce budworm defoliation for between two to eight

529   years, depending on site. Western spruce budworm defoliation was also detected at three of our

530   four ponderosa pine sites in 1986. Our woodland western juniper sites were not surveyed. We

531   speculate that a multi-year drawdown of soil moisture due to insufficient recharge could have

532   triggered the growth declines; which, in the case of grand fir and, to a lesser extent, ponderosa

533   pine, were further exacerbated by insect attack. We suspect that grand fir growth is buffered

534   against single-year meteorological droughts by ample soil water storage and recharge during wet

535   years, yet potentially vulnerable to soil water draw down due to sustained, multi-year periods of

536   below average recharge. Soil moisture buffering might explain the lack of significant RWI-*CMI*

537   correlations among grand fir. Although beyond the scope of this study, additional lines of

538   evidence to support or refute this hypothesis could be drawn from tree-ring isotopes, remote

539   sensing observations, and detailed hydraulic and ecological modeling. This presents an intriguing

540   possibility that although annual growth tends to become decoupled from interannual fluctuations

541   in water as conditions become wetter, forests occupying generally wet zones could experience

542   greater impact from infrequent, multi-year periods of below-normal soil water recharge due to

543   increased biotic pressure (e.g. insects) and morphological investment in competition for light

544   over water.

545   Dendroecological analyses often involve sampling trees at multiple sites and then

546   producing a mean ring-width chronology, at the site- or regional-level, that is used to reconstruct

547   paleoclimatic conditions (e.g., Fritts, 2001) or assess spatial variability in historic forest growth

548   (Berner et al., 2011; Bunn et al., 2013); however, growth and climate sensitivity of neighboring

549   trees can vary widely (Berner et al., 2013; Bunn et al., 2005; Lloyd et al., 2010) and additional

550   ecological information can be gained by examining growth-climate relations on an

551   individualistic basis (Carrer, 2011). Our study demonstrates that not all trees within a site

552   responded uniformly to drought, particularly at the ponderosa pine and grand fir sites. We did

553   not explore the underlying mechanisms responsible for differences in drought response among

554   individual trees within a site; however, factors such as age, genotype, competition, and

555   microclimate could have contributed to these differences (Bunn et al., 2011; Bunn et al., 2005;

556   Hultine et al., 2013; Loranty et al., 2010) and warrant further investigation. The substantial intra-

557   and inter-specific variation in drought sensitivity that we observed highlights the need for fine

558   spatial and taxonomical resolution when modeling potential climate change impacts on mixed-

559   species forests in mountainous terrain.

560

561   **4.3   Constraints of long-term water availability on tree morphological traits**

562   As conditions became wetter, forest $\overline{WD}$ declined, while H_{max} and LA:SA increased, suggesting

563   that trees responded to reduced hydraulic stress by increasing investment in competition for light

564   to the extent that xylem tensions were maintained within an operable range. These morphological

565   changes, together with the observed differences in forest productivity and growth-climate

566   relations across our network of sites, highlight trade-offs associated with investment in stress

567   tolerance versus competitive ability (Grime, 2001; Reich, 2014). Since cavitation resistance (e.g.

568   P50) tends to increase with WD (Chave et al., 2009; Hacke et al., 2001; Jacobsen et al., 2007),

569   the decline in stem $\overline{WD}$ that we observed between the juniper and fir communities is generally

570   congruent with prior research showing that small western juniper branches are more resistant to

571   drought-induced cavitation (P50=-9.0 MPa; Willson et al., 2008) than those of ponderosa pine

572   (P50=-4.5 to -4.8; Domec et al., 2009) or grand fir (P50=-3.6 to -6.1 MPa; Cochard, 2006;

573   McCulloh et al., 2011) and, furthermore, that ponderosa pine stems are more cavitation-resistant

574   (P50=-2.5 to -4.1; Domec et al., 2009) than those of grand fir (P50=-1.1 to -1.0; McCulloh et al.,

575   2011). Several previous syntheses similarly found general declines in WD (Swenson and

576   Enquist, 2007; Wiemann and Williamson, 2002) and increases in P50 (Choat et al., 2012;

577   Maherali et al., 2004) as conditions become wetter, yet these relationships tend to be quite weak

578   since trees have evolved a variety of strategies to maintain hydraulic integrity, which depends on

579   a suite of traits integrated at the organism level (e.g. stomatal regulation, xylem capacitance,

580   embolism repair, LA:SA plasticity; Meinzer et al., 2010; Whitehead et al., 1984). High WD

581   helps enable trees to endure hydraulic and mechanical stress, yet could come at a competitive

582   cost in productive environments since dense wood is carbon-intensive to construct (Chave et al.,

583   2009), generally has low hydraulic conductivity (Hacke et al., 2009; Reich, 2014), and limits the

584   maximum height that a tree can obtain before buckling under its own weight (Swenson and

585   Enquist, 2007).

586   Canopy height plays an important role in competition for light among plants (Hartmann,

587   2011; King, 1990) and, in trees, might ultimately be constrained by low leaf water potential

588   inhibiting cell expansion and growth (Koch et al., 2004; Sala and Hoch, 2009) and/or

589   photosynthesis (Koch et al., 2004; Ryan and Yoder, 1997) at the top of the canopy. In the juniper

590   woodlands, low stem density (99-157 trees ha^{-1}) and high water stress would place little premium

591   on height growth, whereas ponderosa pine (127-334 trees ha^{-1}) and grand fir (205-645 trees ha^{-1})

592   formed progressively denser stands where greater canopy height would be more competitively

593   beneficial and hydraulically feasible, which potentially explains the nearly three-fold increase in

594   H_{max} that occurred among these forest communities. While taller trees can compete more

595   effectively for light, the additional height causes them to experience lower xylem Ψ (Whitehead

596   et al., 1984) and could render these trees more vulnerable to drought impacts if conditions

597   become increasingly arid (Hartmann, 2011; McDowell and Allen, 2015).

598   As with H_{max}, forest LA:SA increased nearly three-fold between the western juniper and

599   grand fir stands, demonstrating that trees responded to increased water availability by increasing

600   investment in light absorption relative to water transport. In a review of conifer LA:SA, Waring

601   et al. (1982) reported that LA:SA varied from 0.14 to 0.75 m^2 cm^{-2} across 14 conifer species and

602   noted qualitatively that taxa with low LA:SA occurred in desiccating environments (e.g. *J.*

603   *occidentalis*), whereas taxa with high LA:SA occupied mild climates (e.g. *A. lasiocarpa*). Our

604   results provide quantitative support for this earlier observation. Several studies have additionally

605   shown that pine inhabiting sites with contrasting climatic conditions can adjust LA:SA to

606   maintain xylem Ψ within a narrow range that prevents cavitation (Maherali and DeLucia, 2001;

607   Mencuccini and Grace, 1995). Low LA:SA enables trees to maintain higher leaf specific

608   hydraulic conductance, which helps regulate leaf Ψ (Maherali and DeLucia, 2001; Mencuccini

609   and Grace, 1995), and is likely an important adaptation allowing western juniper to inhabit such

610   arid sites. While low LA:SA helps ease leaf Ψ, this must be balanced against the increase in stem

611   respiration resulting from greater investment in sapwood, given that stem respiration increases

612   with both sapwood volume and temperature (Ryan et al., 1995). Relative to western juniper, the

613   high LA:SA observed at the grand fir stands likely enables greater light absorption and

614   photosynthate production, yet reduced water transport capabilities that could render these trees

615   more susceptible to significant changes in water availability. Our findings demonstrate several

616   adaptive responses to shifts in water availability, highlighting trade-offs between hydraulic

617   stress-tolerance and competition for light, and suggesting potential changes in forest community

618   morphological characteristics that could result from future changes in water availability due to

619   sustained regional warming. Investigating the extent and causes of variation in traits across

620   species and regions is a critical step towards understanding and modeling ecosystem properties

621   and their responses to environmental change (Anderegg, 2015; Law, 2014; Westoby and Wright,

622   2006).

623

624   **4.4   Limitations**

625   We note several limitations associated with using an observational study to elicit the response of

626   plant form and function to variation in climate, as well as with using *CMI* as an indicator of

627   water availability. The observational approach makes it very challenging to separate the effect of

628   a single environmental factor on plant form or function given that it is not possible to control the

629   suite of environmental factors that can influence plant processes. For instance, although we

630   focused on *CMI* as a dominant driver of carbon cycling and trait characteristics, there were

631   additional differences among sites in climate (e.g. *VPD,* frost frequency, snow pack), soil, and

632   disturbance history that independently, or interactively, could affect the processes of interest.

633   Observational studies can elucidate existing spatial and temporal variation in plant response to

634   climate or other controlling factors, yet are strengthened when coupled with experimental and

635   modeling studies focused on the underlying mechanisms of response.

636   We used the *CMI* as an indicator of plant water availability and acknowledge that while

637   useful, it is a rather simple index with several shortcomings. The index is easy to calculate from

638   gridded climate data and serves as the water balance calculation underpinning the *SPEI* (Vicente-

639   Serrano et al., 2010), which together have been used to examine hydroclimatic controls over

640   forest distribution (Hogg, 1997), productivity (Berner et al., 2013; Vicente-Serrano et al., 2014;

641   Vicente-Serrano et al., 2013), and wildfire (Williams et al., 2014). The *CMI* is sensitive to

642   changes in temperature and integrates both atmospheric inputs and withdrawals; however, it does

643   not account for spatial variation in soil depth, soil water holding capacity, or snowpack that,

644   along with rooting depth and architecture, further determine plant water availability.

645   Additionally, we estimated CMI at each site using gridded PRISM climate data and an empirical

646   equation for calculating ET_0 from T, PPT, and R. Different climate datasets, or means of

647   estimating ET_0, could affect the statistical relationships that we observed, yet it is the overall

648   tendencies, rather than the absolute statistical parameters, that we are most interested in

649   capturing.

650

651   **4.5   Implications and future efforts**

652   Forests ecosystems in the Pacific Northwest are a critical element of the regional economy,

653   culture, biodiversity and biophysics, yet future changes in water availability due to sustained

654   regional warming could have significant adverse impacts on these unique and valuable

655   ecosystems. Uncertainty in forest physiologic, demographic and disturbance-related responses to

656   changing environmental settings hinder projections of future forest conditions (Fisher et al.,

657   2010; Hudiburg et al., 2013a; Law, 2014; van der Molen et al., 2011) and thus our adaptation and

658   mitigation capabilities. For instance, CO_2 fertilization might ameliorate some impacts of reduced

659   water availability by increasing plant water-use efficiency (WUE), yet the potential magnitude of

660   this response is unclear. Ecological simulations suggest that warming and increased WUE could

661   lead to a ~20% increase in plant NPP by 2100 (Hudiburg et al., 2013b; Kang et al., 2014), or,

662   conversely, that conifer forest NPP, carbon storage, and extent could decline substantially over

663   this period due to reduced water availability and increased heat stress, despite increased WUE

664   (Jiang et al., 2013). These divergent projections underscore the need to further reduce uncertainty

665   in ecological models, which will necessitate investment in high-performance computing,

666   experiments to elucidate physiologic mechanisms driving intra- and inter-specific differences in

667   drought and heat sensitivity, regional field studies (such as ours) to provide physiological

668   measurements for model parameterization, and a combination of remote sensing and eddy

669   covariance flux tower measurements to hone and validate model predictions. By understanding

670   current climatic controls over forest ecosystem function and refining prognostic models of

671   ecosystem processes, we can better anticipate the potential impacts of climate change and thus

672   improve our mitigation and adaptation capabilities.

673

674   **Author contributions**

675   LB and BL designed the experiment. LB performed data collection, processing, and analysis, and

676   led the manuscript, with contributions form BL.

677

678   **Data availability**

679   In addition to providing species- and site-level summaries for each carbon cycling and trait

680   variable, we include both the underlying datasets and code as a supplemental so as to help enable

681   future data syntheses, increase transparency, and prevent long-term data loss. The datasets

682   include measurements of tree stem characteristics (e.g. DBH, height, bark thickness, wood

683   density, sapwood area), tree ring-width time series, leaf traits (e.g. carbon, nitrogen, specific leaf

684   area, leaf longevity), and leaf area index. The leaf trait and site-level carbon cycling

685   measurements were recently combined into a regional database with similar measurements made

686   as part of other NASA-, DOE-, and EPA-funded projects at over 200 sites across the Pacific

687 Northwest. The North American Carbon Program Terrestrial Ecosystem Research and Regional

688 Analysis Pacific Northwest (NACP TERRA-PNW) Forest Plant Traits, NPP, Biomass, and Soil

689 Properties (1999-2014) dataset (Law and Berner, forthcoming) is being publicly archived with

690 the Oak Ridge National Laboratory Distributed Active Archive Center (ORNL DAAC).

691 Furthermore, our tree ring-width measurements will be made publicly available through the

692 NOAA International Tree Ring Data Bank (NOAA ITRDB). In addition to archiving the

693 datasets, we provide a set of R scripts that were written for data preprocessing, analysis, and

694 visualization. We make these datasets and code freely available for non-commercial community

695 use. Following the AmeriFlux Fair Use Policy (http://bwc.berkeley.edu/Amflux/fairuse.htm), we

696 request to be (1) informed of how these data are used prior to publication and (2) either

697 acknowledged via citation as the data source or, if the dataset constitutes a significant

698 contribution, offered participation as authors.

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1061 **Tables**

1062 Table 1. Species conversion coefficients (*β*) relating leaf projected surface area to one-half total
1063 surface area.

Species	*β*	Source	Notes
western juniper	1.57	Hicks and Dugas (1998)	
lodgepole pine	1.28	Barclay (1998)	
ponderosa pine	1.20	Cregg (1994)	average of values in table 4
incense cedar	1.14	Barclay and Goodman (2000)	coefficient for western red cedar
grand fir	1.09	Barclay and Goodman (2000)	also used for noble fir

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1077   Table 2. Average (± 1 SD) growing-year climate conditions from 1964 to 2013 for sites

1078   dominated by western juniper, ponderosa pine, and grand fir in the eastern Cascade Mountains,

1079   Oregon. The growing-year extended from October of year *t-1* through September of year *t*.

1080   Climate variables include average daily temperature (T_{gy}), precipitation (PPT_{gy}), reference

1081   evapotranspiration (ET_{0gy}) and climate moisture index ($CMI_{gy} = PPT_{gy} - ET_{0gy}$) calculated from

1082   monthly PRISM climate data (Daly et al. 2008). We averaged the climate time series for each of

1083   the four sites in a given forest type prior to calculating summary statistics.

Forest type	T_{gy} (° C)	PPT_{gy} (mm yr^{-1})	ET_{0gy} (mm yr^{-1})	CMI_{gy} (mm yr^{-1})
western juniper	8.32 ± 0.80	290 ± 70	1540 ± 70	-1250 ± 120
ponderosa pine	6.90 ± 0.72	610 ± 150	1365 ± 70	-750 ± 190
grand fir	6.26 ± 0.72	950 ± 210	1230 ± 70	-280 ± 250

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1098 Table 3. Regression equations relating forest community carbon cycling, morphological

1099 characteristics, and long-term (1964-2013) mean growing-year climate moisture index ($CMI_{\overline{gy}}$;

1100 mm yr^{-1}) across 12 sites in the eastern Cascade Mountains, Oregon. Forest characteristics include

1101 leaf area index (LAI; half-total surface area; m^2 leaf m^{-2} ground), annual aboveground net

1102 primary productivity (ANPP; g C m^{-2} yr^{-1}), aboveground live biomass (AGB; kg C m^{-2}),

1103 leaf:sapwood area ratio (LA:SA; m^2 leaf cm^{-2} sapwood), maximum tree height (H$_{max}$; m), and

1104 average stem wood density ($\overline{WD}$; g cm^{-3}). Also included are the community-average correlation

1105 between tree ring-width indices (RWI) and *CMI* from 1964 to 2013 ($\bar{r}$ RWI-CMI; unitless) and the

1106 fraction of individual trees in the community that exhibited a significant (P<0.05) positive RWI-

1107 *CMI* correlation (F$_{RWI-CMI}$; %). Equations are either power form (Y = aX^b) or linear (Y = a + bX),

1108 where *a* and *b* are fitted coefficients, with X and Y in units provided above.

Explanatory	Response	Form	a	a [se]	b	b [se]	r^2	P	RMSE
$CMI_{\overline{gy}}$	LAI	power	0.02	0.03	0.79	0.30	0.68	0.025	1.08
	ANPP	power	2.47	2.23	0.66	0.13	0.88	0.001	35.7
	AGB	power	0.24	0.33	0.59	0.20	0.67	0.014	3.52
	$\bar{r}$ RWI-CMI	linear	0.02	0.07	-0.00037	0.00008	0.65	0.001	0.11
	F$_{RWI-CMI}$	linear	4.90	13.10	-0.07	0.02	0.63	0.001	20.32
	LA:SA	linear	0.29	0.03	0.00018	0.00003	0.76	0.001	0.05
	H$_{max}$	power	4.25	2.25	0.30	0.08	0.69	0.004	5.61
	$\overline{WD}$	linear	0.41	0.01	-0.00005	0.00002	0.36	0.002	0.02
LAI	ANPP	linear	42.05	23.97	46.82	8.11	0.75	0.002	49.51
	AGB	linear	3.66	1.85	2.48	0.63	0.57	0.003	3.83
ANPP	AGB	linear	1.84	1.81	0.05	0.01	0.68	0.001	3.23
$\bar{r}$ RWI-CMI	F$_{RWI-CMI}$	linear	2.08	5.53	174.97	15.29	0.92	<0.001	9.34
$\overline{WD}$	LA:SA	linear	0.67	0.15	-1.32	0.35	0.55	0.003	0.03
	H$_{max}$	linear	118.14	36.20	-214.39	82.23	0.35	0.026	8.12
H$_{max}$	LA:SA	linear	-0.001	0.027	0.0038	0.0010	0.54	0.004	0.03

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1112 Table 4. Summary of carbon cycling, growth-climate, morphological, and chemical

1113 characteristics for three conifer species in the eastern Cascade Mountains, Oregon. Both stand-

1114 and tree-level characteristics are included. Excluding specific leaf area (SLA), the full name of

1115 each characteristic is given in Table 2. The stand-level characteristics provided for grand fir

1116 actually represent an average mixture of 2/3 grand fir and 1/3 ponderosa pine. The mean,

1117 standard deviation, and sample size are provided for each characteristic.

Characteristic	Level	Units	Species		
			Western juniper	Ponderosa pine	Grand fir
LAI	Stand	$m^2\ m^{-2}$	0.26±0.13 (4)	1.92±0.51 (4)	4.54±1.49 (4)
ANPP	Stand	$g\ C\ m^{-2}\ yr^{-1}$	17±4 (4)	185±62 (4)	238±54 (4)
AGB	Stand	$kg\ C\ m^{-2}$	2.6±0.4 (4)	10.6±4.1 (4)	14.4±5.9 (4)
$\bar{r}_{RWI-CMI}$	Stand	unitless	0.52±0.18 (72)	0.27±0.21 (82)	0.11±0.13 (62)
$F_{RWI-CMI}$	Stand	%	91±3 (72)	51±6 (82)	12±4 (62)
LA:SA	Stand	$cm^2\ m^{-2}$	0.08±0.03 (4)	0.12±0.03 (4)	0.28±0.03 (4)
H_{max}	Stand	m	10.5±0.5 (4)	27.9±5.3 (4)	33.5±5.6 (4)
WD	Tree	$g\ cm^{-3}$	0.47±0.02 (32)	0.45±0.02 (52)	0.40±0.03 (36)
SLA	Tree	$cm^2\ HSA\ g^{-1}\ C$	63±6 (40)	91±11 (47)	100±16 (42)
Leaf longevity	Tree	years	5.6[b]	4.3±1.0 (59)	9.2±2.1 (50)
Leaf C	Tree	%	48.2±0.8 (40)	48.3±0.5 (47)	47.8±0.5 (42)
Leaf N	Tree	%	0.89±0.13 (40)	1.14±0.12 (47)	0.83±0.13 (42)
Leaf C:N	Tree	unitless	55±9 (40)	43±4 (47)	59±10 (42)

1118 [b] Western juniper leaf longevity was calculated as the ratio of foliage biomass to annual leaf fall using
1119 measurements from Runyon et al. (1994).

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1149   the growing-year values from 1964 to 2013. Each point represents the mean (± 1 SE) of four

1150   subplots. Regression coefficients are given in Table 3.

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1152   Figure 4. Correlations between annual tree radial growth and the climate moisture index ($CMI =$

1153 $PPT - ET_0$) from 1964 to 2013 for three tree species in the eastern Cascades, Oregon. Depicted is

1154   the proportion of trees with a significant positive correlation between annual ring-width indices

1155   (RWI) and CMI calculated for each month at time lags extending from 1 to 36 months. See Fig.

1156   S1 and Table S6 for correlations between RWI and additional climate variables.

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1158   Figure 5. Mean ecosystem-weighted correlation ($\bar{r}$ RWI-CMI) between annual tree ring-width

1159   indices (RWI) and the climate moisture index ($CMI = PPT - ET_0$) plotted against the 50-year

1160   mean (±1 SE) growing year CMI. The dashed horizontal line denotes statistical significance at

1161 $\alpha=0.05$. The 12 sites were located in the eastern Cascade Mountains and represented forest types

1162   dominated by western juniper, ponderosa pine and grand fir. Regression coefficients are given in

1163   Table 3.

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1165   Figure 6. Forest ecosystem (a) average stem wood density, (b) maximum tree height, and (c)

1166   leaf:sapwood area ratio plotted against the average growing-year climate moisture index from

1167   1964 to 2013 ($CMI_{\overline{gy}}$). Each point represents the mean (± 1 SE) of four subplots sampled at each

1168   site. Regression coefficients are given in Table 3.