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3 Elevated temperature differently affects growth, photosynthetic capacity, nutrient

4 absorption and leaf ultrastructure of *Abies faxoniana* and *Picea purpurea*

5 under intra- and interspecific competition

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22 **Head title:** Warming affects plant-plant competition

Abstract The impact of global warming on plant-plant competition is yet to be fully understood. Resolving this knowledge gap is important for predicting the potential influence of global warming on forests, particularly on high-altitude trees, which are more sensitive to warming. In this study, we investigated intra- and interspecific competition in *Abies faxoniana* and *Picea purpurea* seedlings under control (ambient temperature) and elevated temperature (ET, 2 °C above ambient temperature) conditions for 2 years. We found that *A. faxoniana* and *P. purpurea* grown under intra- and interspecific competition showed significant differences in dry matter accumulation, photosynthetic capacity, nutrient absorption, non-structural carbohydrate (NSC) contents and leaf ultrastructure under ET conditions. ET significantly increased leaf, stem and root dry matter accumulation (DMA) of both conifers under both competition patterns. Moreover, under ET, *P. purpurea* possessed a better performance and had higher organ (leaf, stem and root) and total DMA, height growth rate, net photosynthetic rate, specific leaf area (SLA), water use efficiency (δ^{13}C), leaf and root N and NSC contents, and more plasticity in N uptake forms compared to *A. faxoniana* under interspecific competition. Thus, the growth of *P. purpurea* benefitted from the presence of *A. faxoniana* under ET. Our results demonstrated that ET significantly affects competition patterns among conifer species in a subalpine region. It follows that global warming may alter plant-plant competition, thus influencing the composition, structure and functioning of subalpine coniferous forests.

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Introduction

According to the IPCC report (IPCC 2013), the mean global surface temperature is forecasted to rise by 1.4 °C to 5.8 °C between 1990 and 2100, and the temperature increase will be most significant in high altitude and latitude ecosystems. Therefore, it is crucial to be able to predict how tree growth will respond to a warmer future environment, particularly in high-altitude regions. Many studies have demonstrated that warming can induce increased height and growth performance and biomass accumulation in tree seedlings, which are currently growing below their thermal optimum (Way and Oren 2010, Dieleman et al. 2012, Reich et al. 2018, Yuan et al. 2018). On the other hand, heat stress may reduce plant growth (Berry and Björkman 1980, Bauweraerts et al. 2014, Schippers et al. 2015).

Changed biomass allocation may be a way to improve plants' responses to climate change (Huang et al. 2015). For example, a meta-analysis conducted by Yuan et al. (2018) showed that warming has no effect on biomass allocation between roots and shoots, while Wertin et al. (2011) and Duan et al. (2018) reported that warming induces increased or decreased allocation to roots. In addition, warming normally increases total chlorophyll concentrations of trees (Wang et al. 2012, Zhao et al. 2012, Yuan et al. 2018). Similarly, warming can lead to increased leaf nitrogen (N) concentrations in conifers (Tingey et al. 2003, Luomala et al. 2005, Xu et al. 2012), and enhance nutrient cycling and increase nutrient availability (Rustad et al. 2001,

89 Melillo et al. 2011). Warming can also alter the storage of non-structural

90 carbohydrates (NSC, i.e. starch and soluble sugars), which act as a carbon buffer

91 when carbon assimilation cannot meet the demand (Sala et al. 2012, Pokhilko et al.

92 2014). In many species, elevated temperature has been found to reduce NSC

93 concentrations (Tingey et al. 2003, Way and Sage 2008, Duan et al. 2013).

94 Furthermore, tree seedlings are relatively sensitive to environmental stressors, and

95 they are typically exposed to competition with neighbors, rarely growing in isolation

96 in nature.

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98 Plant-plant competition is a biotic factor that can affect plants' growth, species

99 abundance and distribution, and community composition (Michalet 2006, Raynaud et

100 al. 2008, Novoplansky 2009, Pierik et al. 2013). Adjustments in morphological and

101 physiological characteristics are fundamental ways for plants to cope with changes in

102 the resource availability and composition of neighboring plants, which, in turn, may

103 increase plants' competitive ability and fitness (Callaway et al. 2003, Anten et al.

104 2005). Abiotic factors, such as resource availability, often interact with plant-plant

105 competition (Niinemets 2010, Chen et al. 2014, 2015). Yu et al. (2017) have observed

106 that *Abies fabri* has a better performance and displays a higher net photosynthesis rate

107 and water use efficiency, and also a better N acquisition capability under interspecific

108 competition with *Picea brachytyla* when compared to intraspecific competition under

109 phosphorus fertilization. Duan et al. (2014) have discovered that under elevated

110 temperature, *Abies faxoniana* can change its nitrogen uptake and benefit from *Betula*

albo-sinensis under interspecific competition. Yet, there are still many uncertainties in the mechanisms of morphological and physiological responses of plants (e.g. subalpine conifers) to intra- and interspecific competition and warming climate.

Subalpine coniferous forests form the second greatest biome in China. *Abies faxoniana* and *Picea purpurea* occur widely in these regions and contribute to the maintenance of the ecological stability and succession of regional ecosystems (Wang 2004, Taylor et al. 2006). The most important limiting factors controlling the performance of subalpine plants are generally considered to be a low temperature, low nutrient availability and short growing season (Wang 2004, Hyvönen et al. 2007). Previous studies investigating subalpine coniferous species have found that warming shows a positive effect on plant growth and significantly increases photosynthesis and biomass accumulation (Ran et al. 2013, Wang et al. 2013, Yin et al. 2013). For example, a 6-year warming period significantly increased the leaf stem, root and total biomass, specific leaf area and total chlorophyll concentration in *Abies faxoniana* seedlings (Wang et al. 2012). However, previous studies have largely neglected the interactions between plant-plant competition and warming, especially concerning subalpine conifers, which are more sensitive to climate warming.

In the present study, we investigated the morphological and physiological responses of *A. faxoniana* and *P. purpurea* to elevated temperature and intra- and interspecific competition. Physiological and functional traits, such as growth traits, net

133   photosynthetic rate (P_n), chlorophyll fluorescence, leaf carbon isotope composition

134   (δ^{13}C), C, N and non-structural carbohydrate concentrations, and leaf ultrastructure

135   were analyzed to discover the competitive ability of *A. faxoniana* and *P. purpurea*

136   under elevated temperature and intra- and interspecific competition. Furthermore,

137   different forms of ^{15}N-labeled (^{15}NH$_4$NO$_3$ and NH$_4$^{15}NO$_3$) were used to determine,

138   whether there are differences in the N absorption of *A. faxoniana* and *P. purpurea*

139   under elevated temperature and intra- and interspecific competition. The aim was to

140   answer the following questions: (1) How does elevated temperature affect

141   physiological and functional traits of *A. faxoniana* and *P. purpurea* under intra- and

142   interspecific competition? (2) Do *A. faxoniana* and *P. purpurea* express different

143   competitive strategies when exposed elevated temperature and interspecific

144   competition? (3) Does elevated temperature change asymmetric competition

145   outcomes in these two conifers?

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Materials and methods

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Study site, plant material and experimental design

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This study was performed in the experimental area (2600 m above sea level) in the Wanglang National Nature Reserve (32°49'-33°02'N, 103°55'-104°10'E, altitude range 2,300-4,980 m), which is situated in the Pingwu County, western Sichuan Province, Southwest China. The details of climate, temperature and precipitation were described in Ran et al. (2013). In the Reserve, at elevations between 2800 and 3500 m, *A. faxoniana* and *P. purpurea* dominate on lower side slopes and alluvial bottomlands, whereas other *Abies* and *Picea*, *Betula* sp., and *Sabina saltuaria* grow on upper slope sites (Taylor et al. 2006). In addition, the life history of *P. purpurea* is characterized by longevity and high survivorship, which prevents the replacement by *A. faxoniana* (Wang 2004, Taylor et al. 2006). A total of 180 uniform-sized seedlings with a height of about 30 cm, 90 seedlings of *A. faxoniana* and 90 seedlings of *P. purpurea*, were selected from a nursery close to the station. At the end of September 2014, healthy *A. faxoniana* and *P. purpurea* seedlings were planted into plastic pots (two seedlings in each pot) with homogenized soil, which was obtained from the natural habitat of the two conifers. After adaptation to the environment for seven months, all seedlings were grown in growth chambers with a controlled environment from early May 2015 to the end of August 2016, and plants were harvested on 30 August 2016.

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178 The chambers were almost cylindrical with 11 walls, the height of 3.45 m and the

179 internal ground size of 13.45 m^2. The chambers were made of hollow tempered glass

180 walls with a hollow polycarbonate top transmitting more than 85% of

181 photosynthetically active radiation (PAR). The natural photoperiod was 12 h

182 (0800-2000 h). The controlled environment was composed of air-conditioning,

183 automatic controlling, CO_2 injection mechanism and monitoring equipment for

184 environmental factors (e.g. total solar radiation, PAR, UV-B, and temperature). The

185 computer-controlled heating and cooling system, together with CO_2 sensors

186 (LT/WSK-PLC; Copeland and Vaisala, Beijing, China), can automatically adjust the

187 temperature and CO_2 concentration in the chambers to ensure a rise in temperature or

188 an ambient condition. The CO_2 level was kept at a similar level with the ambient

189 condition. Additionally, a water supply equipment with a monitor was used to control

190 air humidity.

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192 The experimental design was randomized with three factors (species, competition and

193 temperature) and included two species (*A. faxoniana* and *P. purpurea*), two levels of

194 temperature (ambient temperature and 2 °C above ambient temperature) and three

195 competition setups, i.e., two intraspecific (*A. faxoniana* + *A. faxoniana* and *P.*

196 *purpurea* + *P. purpurea*) and one interspecific competition treatment (*A. faxoniana* + *P.*

197 *purpurea*). There were fifteen replicates per treatment. There were three control

198 chambers (ambient temperature) and three elevated temperature chambers (2 °C

199　above ambient temperature), each chamber including 15 pots (diameter of 36 cm,

200　height of 40 cm). All pots were watered regularly to maintain non-limiting soil

201　moisture throughout the experimental period. Furthermore, labeled $^{15}NH_4NO_3$ and

202　$NH_4{}^{15}NO_3$ solutions were injected into the soil (5 cm depth) round the rhizosphere (30

203　mg/plant) in each treatment in the ^{15}N tracer experiment. Then, 72 h after the ^{15}N

204　solution was applied, we harvested the plants and measured the ^{15}N values of leaves.

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206　*Determination of dry matter accumulation*

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208　We monitored the height and stem diameter of plants every week during the

209　experimental period. The height and diameter growth rates (HGR, cm day^{-1}; DGR,

210　mm day^{-1}) were calculated as (example for height) HGR = (height$_2$ – height$_1$) / (t_2 –

211　t_1), in which the denominator is the period between the first and last measurements.

212　Five seedlings were selected randomly from each treatment to determine the dry

213　matter accumulation (DMA) at the end of the growth experiment. All harvested plants

214　were separated into leaves, stems, coarse roots (>2 mm) and fine roots (<2 mm), then

215　dried at the temperature of 70 °C for 72 h to, and the biomass was weighed. The

216　root/shoot ratio (R/S) was determined as the ratio between total root DMA and

217　aboveground DMA (the sum of leaf DMA and stem DMA). The leaf area was

218　measured utilizing a scanner (Cannon Scanner 5600F, Chengdu, China) with 600 dpi

219　resolution and imaging software (Image J; National Institutes of Health, Maryland,

220　USA). The specific leaf area (SLA) was calculated as leaf area per dry mass.

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Determination of gas exchange and chlorophyll fluorescence

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The portable LI-COR 6400 photosynthesis measuring device (LI-COR, Lincoln, NE, USA) was employed to measure the light-saturated net photosynthetic rate (P_n) in healthy current-year leaves between 08:00 a.m. and 11:30 a.m. in the middle of August 2016. We illuminated the target leaves with saturating irradiance (1000 μmol m^{-2} s^{-1} PPFD) for about 5–20 min to gain complete photosynthetic induction before starting the measurements. Conifer type chambers (PLC-broad, PP Systems) were utilized under standard measurement conditions, as described by Song et al. (2017). The mass-based photosynthetic N use efficiency (PNUE) was determined as the mass-based photosynthetic rate (P_n) per the N content of leaves.

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The portable fluorometer PAM-2100 (Walz, Effeltrich, Germany) was used to determine the chlorophyll fluorescence of neighboring leaves in gas exchange measurements according to the protocol of Schreiber et al. (1986). Additional details were described in Chen et al. (2015).

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Neighboring leaves used for P_n estimation were randomly sampled for chlorophyll concentration determinations. The spectrophotometer UV-330 (Unicam, Cambridge, UK) was employed to measure chlorophyll concentrations following the protocol of Lichtenthaler (1987). The total chlorophyll concentration (*TChl*) was the sum of the

243   concentrations of chlorophyll *a* and *b*.

244

245   *Determination of C and N concentrations*

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247   Plant samples (leaves, stems and roots) were collected from five randomly chosen

248   individuals from each treatment and ground into fine powder for C and N

249   determinations using the rapid dichromate oxidation method (Nelson and Sommers

250   1982) and the semi-micro Kjeldahl technique (Mitchell 1998), respectively.

251

252   *Determination of non-structural carbohydrates*

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254   Plant samples (leaves, stems and roots) for non-structural carbohydrate analyses were

255   collected from five individuals chosen randomly from each experiment between 10:30

256   a.m. and 11:30 a.m. at the end of study (Chen et al. 2015). Around 50 mg of dry

257   powdered samples (leaves, stems and roots) were transferred into 10-ml centrifuge

258   tubes, followed by 30-min incubation in 80% (v/v) ethanol at 80 °C and centrifugation

259   at 5000 g for 10 min. The extraction was utilized for soluble sugar determination, and

260   the residue for starch determination. To prepare the residue for starch determination,

261   tubes with residue were left uncovered under the fume hood over the night to

262   evaporate the residual ethanol (Landhäusser et al. 2018). Glucose equivalents were

263   used to assay starch and soluble sugar concentrations by the anthrone-sulfuric acid

264   method (Yemm and Willis 1954). Methodological details were described in Chen et al.

265   (2015) and Song et al. (2017).

266

267   *Determination of C and N isotope composition*

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269   DELTA V Advantage Isotope Ratio Mass Spectrometer (Thermo Fisher Scientific,

270   Inc., Waltham, Massachusetts, USA) was employed to measure the C and N isotope

271   compositions. The same leaves used for P_n estimation were sampled for the C isotope

272   composition ($\delta^{13}C$) determination. The C isotope content was shown as $\delta^{13}C$ values.

273

274   In the ^{15}N tracer experiment, $^{15}NH_4NO_3$ and $NH_4^{15}NO_3$ were used to reveal nitrogen

275   uptake under different treatments, and the N isotope composition was expressed as

276    $\delta^{15}N$. In each treatment, healthy leaves were sampled from the same upper position of

277   the seedlings 72 h after the application of ^{15}N. Additional details concerning the C and

278   N isotope analyses are given in Chen et al. (2014) and Song et al. (2017).

279

280   *Transmission electron microscopy*

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282   Transmission electron microscopy (TEM) was performed using H-600IV TEM

283   (Hitachi, Tokyo, Japan) for sections (2 mm in length) of healthy leaves neighboring

284   those exposed to gas exchange measurements. The methodology followed Zhang et al.

285   (2014).

286

287   *Statistical analyses*

288

289   Before performing statistical analyses, the data were examined for normality and the

290   homogeneity of variances and, when needed, log-transformed to correct for deviations

291   from the assumptions. Tukey's HSD tests along with one-way ANOVA were utilized

292   to compare individual differences among means at the significance level $P < 0.05$.

293   Differences between the temperature treatments were determined by

294   independent-samples t-test. The effects of species, temperature and competition, and

295   their interactions were determined by three-way ANOVAs. To gain deeper insight into

296   intra- and interspecific competition, elevated temperature effects, and differences in

297   physiological and functional traits, a principal component analysis (PCA) was

298   conducted. Canoco 5.0 (Microcomputer Power, USA) was used for the PCA analysis.

299   All data were analyzed with the Statistical Package for the Social Sciences (SPSS,

300   Chicago, Illinois, USA), version 18.0.

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309 **Results**

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311 *Effects of competition and elevated temperature on plant growth traits*

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313 Elevated temperature (ET) significantly increased leaf, stem, root and total dry matter

314 accumulation (DMA) of both conifers under both competition patterns (Figure 1 a-e).

315 Moreover, under ET condition, *P. purpurea* possessed higher organ (leaves, stems and

316 roots) and total DMA than *A. faxoniana* under interspecific competition. Thus, the

317 growth of *P. purpurea* benefitted from the interspecific competition under ET. In

318 addition, the R/S ratio showed no significant difference among different treatments.

319 The statistical analysis showed that the interaction of species × competition ×

320 temperature significantly affected stem, total root and total DMA, indicating that

321 under ET, stem, total root and total DMA of *P. purpurea* had a greater increase under

322 interspecific competition.

323

324 ET significantly increased HGR and DGR (height and diameter growth rate) of both

325 conifers under both competition patterns (Figure 2). In addition, *P. purpurea*

326 possessed higher HGR than *A. faxoniana* under ET and interspecific competition

327 conditions. The statistical analysis showed that the interaction of species ×

328 competition × temperature significantly influenced HGR, indicating that under ET

329 HGR of *P. purpurea* significantly increased under interspecific competition.

330

Effects of competition and elevated temperature on gas exchange and leaf

332 *ultrastructure*

333

334 Under ET conditions, P_n, $TChl$, F_v/F_m and SLA of both conifers increased, and P_n,

335 F_v/F_m, SLA and $\delta^{13}C$ of *P. purpurea* were significantly higher than those parameters

336 in *A. faxoniana* under interspecific competition (Figure 3). In addition, ET had no

337 effect of PNUE in either conifer species. The statistical analysis showed that the

338 interaction of species × competition × temperature significantly affected $TChl$ and

339 SLA, indicating that under ET, $TChl$ and SLA of *P. purpurea* increased more under

340 interspecific competition.

341

342 The TEM observations of mesophyll cells showed that *A. faxoniana* and *P. purpurea*

343 exhibited specific features under different competition and temperature treatments.

344 Under control conditions, both conifers showed fewer chloroplasts and more starch

345 accumulation. Under ET, *A. faxoniana* and *P. purpurea* exhibited smooth and

346 continuous cell membranes and a typical chloroplast structure. Moreover, *P. purpurea*

347 was characterized by bigger chloroplasts when compared to *A. faxoniana* under

348 interspecific competition and ET conditions (Figure 4).

349

350 *Effects of competition and elevated temperature on concentrations of C, N and*

351 *non-structural carbohydrates*

352

353 C concentrations of organs (leaves, stems and roots) changed slightly among different

354 treatments, and ET significantly influenced the root C concentration. ET increased N

355 concentrations but decreased C/N in all organs of both conifers. Moreover, *P.*

356 *purpurea* showed a higher leaf N concentration than *A. faxoniana* under ET and

357 interspecific competition conditions (Table 1). The statistical analysis showed that the

358 interaction of species × competition × temperature significantly affected N

359 concentrations of organs (leaves, stems and roots) and C/N ratios in stems and roots.

360

361 ET significantly decreased leaf starch and NSC concentrations of both conifers (Table

362 2). Under ET and interspecific competition conditions, *P. purpurea* possessed

363 significantly higher concentrations of leaf and root starch and NSC than *A. faxoniana*

364 (Table 2). The statistical analysis showed that the interactive effects of species ×

365 competition and competition × temperature significantly influenced NSC

366 concentrations in organs, except for soluble sugars in stems.

367

368 *Effects of competition and elevated temperature on $\delta^{15}NH_4{}^+$-N and $\delta^{15}NO_3{}^-$-N*

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370 Under interspecific competition and ET conditions, both conifers showed significantly

371 higher $\delta^{15}NH_4{}^+$-N, and this was also significantly higher than $\delta^{15}NO_3{}^-$-N. Moreover, *P.*

372 *purpurea* had the greatest $\delta^{15}NH_4{}^+$-N level under interspecific competition and ET

373 (Figure 5). In addition, under ET treatment, interspecific competition decreased

374 $\delta^{15}NO_3{}^-$-N of *A. faxoniana* more than intraspecific competition, while *P. purpurea*

375 expressed no differences between the competition patterns (Figure 5b).

376

377 *Relationships among studied traits under different competition patterns and elevated*

378 *temperature*

379

380 The two components of the principal component analysis (PCA) explained 82.2% of

381 the total variance of studied traits in *A. faxoniana* and *P. purpurea* in response to

382 different competition patterns and temperature treatments (Figure 6). Control and

383 elevated temperature experiments were separated along the second PCA axis. Under

384 elevated temperature, the competition treatments of both conifers were clearly

385 separated. Furthermore, *A. faxoniana* and *P. purpurea* were separated by the first PCA

386 axis (Figure 6). PC1 was greatly affected by root starch, NSC and TS, leaf and stem

387 TS, stem and root C and N, leaf C, stem N, HGR, DGR, PNUE, F_v/F_m and *TChl*. PC2

388 was strongly affected by leaf, stem, root and total DMA, SLA, P_n, leaf N, leaf and

389 stem starch, NSC, and C/N. In addition, SLA and leaf N showed positive correlations

390 with leaf, stem, root and total DMA and P_n.

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Discussion

Competition and elevated temperature affect plant growth traits

Lavorel and Garnier (2002) and Fynn et al. (2005) have reported that growth and physiological traits can be used as indicators of plants' responses to competition and environmental factors. We found species-specific responses to elevated temperature (ET) and competition, particularly the interaction effects of ET and interspecific competition on the growth traits of *A. faxoniana* and *P. purpurea* were considerable. Under control conditions, there were no differences in stem, root and total dry matter accumulation (DMA) between intra- and interspecific competition in either conifer, while under ET conditions, leaf, stem, root and total DMA of *A. faxoniana* and *P. purpurea* significantly increased, as observed previously in conifers (Wang et al. 2012, 2013, Yin et al. 2013, Reich et al. 2018). Furthermore, *P. purpurea* possessed higher organ and total DMA than *A. faxoniana* under ET and interspecific competition (Figure 1 a-e). These findings indicated that under ET, the growth of *P. purpurea* benefited from the presence of *A. faxoniana*, whereas *A. faxoniana* seemed to be slightly inhibited under interspecific competition. This result was further supported by the significant interaction effect of species × competition × temperature on total DMA (Figure 1), which indicated that under ET, total DMA of *P. purpurea* increased more under interspecific competition. These interactive effects demonstrated that species-specific responses in DMA rise along environmental gradients (e.g.

419   temperature), but the results also indicated that the two conifers utilize different

420   growth strategies under climate warming.

421

422   Gedroc et al. (1996) and Lewis and Tanner (2000) have proposed that the

423   morphological and physiological plasticity of plants can change their allocation to

424   roots and shoots to cope with different environments. In this study, the R/S ratio of

425   neither conifer showed significant differences among different temperature treatments

426   (Figure 1f), which indicated that elevated temperature did not affect biomass

427   allocation between roots and shoots (as also in Yuan et al. 2018), or above- and

428   below-ground growth. In addition, *P. purpurea* possessed higher fine root and total

429   root DMA than *A. faxoniana* under ET and interspecific competition (Figure 1d). The

430   size of the root system plays an important role in the belowground competition (Lewis

431   and Tanner 2000, Rajaniemi 2002), as increased fine roots improve the capacity of

432   nutrient uptake and water and carbohydrate transportation (Fitter et al. 1998). The

433   relatively higher fine root and total root DMA of *P. purpurea* may play a key role in

434   contributing to the relatively higher N demand of continuously accelerated

435   photosynthesis under ET and interspecific competition. In addition, ET increased

436   HGR and DGR of both conifers (Figure 2), indicating that ET promotes tree height

437   and stem diameter growth (Xu et al. 2012, Wang et al. 2013, Fu et al. 2015), and

438   induces greater resource allocation to above-ground biomass, which also implies that

439   above-ground competition for resources (e.g. light) is important in trees (Suding et al.

440   2005) under global warming.

Competition and elevated temperature affect photosynthetic capacity and

non-structural carbohydrates

In the present study, ET significantly increased the net photosynthesis rate (P_n), total

chlorophyll ab (*Tchl*), F_v/F_m and SLA of both conifers (Figure 3), indicating that ET

had a positive influence on the photosynthetic capacity and growth (see also Xu et al.

2008, Fu et al. 2015, Huang et al. 2015, Reich et al. 2018, Yuan et al. 2018). This was

further supported by the mesophyll cell structure of leaves that showed that both

conifers exhibited smooth and continuous cell membranes and a typical chloroplast

structure under ET. This was ascribed to the more optimal temperature conditions for

gas exchange, as induced by warming (Wang et al. 1995). The photosynthetic N use

efficiency (PNUE) is an important functional trait of species closely related to their

leaf economics strategy (Hikosaka 2004). However, in the present study, ET showed

no effect on PNUE of *A. faxoniana* and *P. purpurea* (Figure 3d). This result is partly

similar to that of Duan et al. (2014), who found that ET decreased PNUE of *Betula*

albosinensis but had no effect on PNUE of *A. faxoniana*. In addition, previous studies

have showed that the N concentration of leaves is positively related to plants'

photosynthetic capacity across all biomes (Kattge et al. 2009, Xu et al. 2012), because

the N concentration of leaves is correlated with the Rubisco content (Field and

Mooney 1986). Our study showed that under interspecific competition and ET

treatment, *P. purpurea* possessed higher P_n, F_v/F_m and leaf N than *A. faxoniana*

463   (Figure 3ac, Table 1). The greater N acquisition capacity and lower long-term water

464   use efficiency (Figure 3f; Farquhar et al. 1989 and Livingston et al. 1999 have

465   discussed the interpretation of $\delta^{13}C$) could be highly important for the superior

466   photosynthetic performance of *P. purpurea* exposed to interspecific competition and

467   ET.

468

469   Reich et al. (1999) and Westoby et al. (2002) have demonstrated that plants with a

470   relatively high SLA are normally associated with high growth rates and a better

471   absorption of aboveground resources. In line with those studies, we found that *P.*

472   *purpurea* had a higher growth rate and SLA than *A. faxoniana* under interspecific

473   competition and ET (Figures 2a, 3e). The greater leaf area (leaf mass by SLA)

474   observed in *P. purpurea* demonstrates that a better capacity to enhance photosynthetic

475   productivity was the reason for its greater leaf, stem, root and total DMA relative to *A.*

476   *faxoniana* under interspecific competition and ET. There were positive correlations

477   among leaf, stem, root and total DMA, leaf N concentration, SLA and P_n according to

478   the PCA analysis (Figure 6). Moreover, under ET, the competition experiments of both

479   conifers were clearly separated from each other; *A. faxoniana* and *P. purpurea* were

480   separated by the first PCA axis (Figure 6). These results indicated that ET caused

481   species-specific responses under different competition treatments, as also supported

482   by the significant interaction effect of species × competition × temperature on many

483   studied parameters (total DMA, HGR, *TChl*, SLA, and N concentrations, etc).

484

485   Non-structural carbohydrates (NSC) can mobilize in plants, and their storage can

486   serve as a buffer of energy in face of higher demands for growth or other

487   physiological processes (Niinemets 2010, Wiley et al. 2013, Martínez-Vilalta et al.

488   2016). In this study, ET significantly decreased leaf starch and NSC concentrations of

489   both conifers (Table 2), which is consistent with the observed leaf mesophyll structure:

490   the presence of greater starch granules in both conifers under control conditions than

491   under ET (Figure 4). This result matches previous studies, which showed that ET

492   decreases the NSC concentration (Zha et al. 2001, Tingey et al. 2003, Zhao et al. 2012,

493   Duan et al. 2013). One explanation for such decline in the NSC concentration is that

494   ET increases the leaf respiration rate, which will lead to an increased consumption of

495   assimilation compounds (e.g. soluble sugars and starch) (Tingey et al. 2003). In

496   addition, *P. purpurea* exhibited higher concentrations of leaf and root starch and NSC

497   when compared to *A. faxoniana* under interspecific competition and ET treatment

498   (Table 2), indicating that *P. purpurea* has a better carbohydrate storage ability. The

499   greater amounts of carbon storage reserves are important means for the responses of

500   plants to environmental stress, such as drought and shading (Lawlor and Cornic 2002,

501   Wiley et al. 2017). Furthermore, Kobe et al. (2010) and Pokhilko et al. (2014) have

502   demonstrated that high root NSC may provide assimilation energy for nutrient

503   absorption. Thus, the higher root N concentration might be due to the increase in the

504   root NSC content of *P. purpurea* under ET and interspecific competition (Table 1),

505   and the better ability of nutrient absorption might play an important role in the higher

506   competitiveness of *P. purpurea* exposed to ET and interspecific competition.

507

508   *Competition and elevated temperature affect nutrient absorption*

509

510   In this study, ET did not increase leaf and stem C concentrations of either conifer

511   (Table 1), the reason possibly being the diluting effect of an increased growth. It has

512   been reported that leaf N concentrations of conifers increase under ET (Lewis et al.

513   2004, Luomala et al. 2005, Xu et al. 2012). As consistent with previous studies, we

514   found that ET significantly increased leaf N concentrations of both conifers (Table 1).

515   D'Orangeville et al. (2014) found that an elevated temperature increases the

516   mineralization of the forest floor and the N availability in soil, which consequently

517   leads to higher N concentrations in leaves (Bai et al. 2013). In this study, the C

518   concentration changed slightly and the N concentration increased significantly, thus

519   inducing a C/N decrease in all organs (leaves, stems and roots) of both conifers under

520   ET condition (Table 1). Opposite to our findings, Olszyk et al. (2003) and Wang et al.

521   (2012) claimed that warming increases the needle C/N ratio and decreases the needle

522   N concentration. In addition, under interspecific competition and ET, *P. purpurea* had

523   a significantly greater leaf N concentration than *A. faxoniana* (Table 1), indicating that

524   the former had a better capability to absorb N sources. Previous studies have

525   demonstrated that nutrient availability plays an important role in plants' competitive

526   ability and species composition (Portsmuth and Niinemets 2007, Boer et al. 2016).

527   For instance, N supply levels regulate carbon balance and affect the competitive

528   ability of *Larix*; *L. kaempferi* performs better than *L. olgensis* under N fertilization

529   (Guo et al. 2016). Evidently, a better ability for N absorption in *P. purpurea* can

530   enhance its competitive ability under interspecific competition and ET conditions.

531

532   ^{15}N isotope tracing was utilized to determine differences in N uptake forms between *A.*

533   *faxoniana* and *P. purpurea* under different competition patterns and temperature

534   treatments. We observed that under interspecific competition and ET, both conifers

535   had significantly higher $\delta^{15}NH_4^+$-N than in control treatments, and they showed

536   significantly higher $\delta^{15}NH_4^+$-N than $\delta^{15}NO_3^-$-N (Figure 5a, b). This result

537   demonstrated that under interspecific competition and ET, $\delta^{15}NH_4^+$-N is the main N

538   resource for *A. faxoniana* and *P. purpurea*. Moreover, under interspecific competition

539   and ET, *P. purpurea* had the highest $\delta^{15}NH_4^+$-N, which may be the key factor for its

540   higher leaf N concentration, and better growth performance and dry matter

541   accumulation. Earlier studies have reported that neighboring plants can influence the

542   absorption of different N forms (Miller et al. 2007, Ouyang et al. 2016). In this study

543   under ET, *A. faxoniana* had significantly lower $\delta^{15}NO_3^-$-N under interspecific

544   competition compared to intraspecific competition, while *P. purpurea* showed no

545   difference in $\delta^{15}NO_3^-$-N between the two competition patterns (Figure 5b). These

546   results indicated that *P. purpurea* has a greater plasticity concerning N uptake forms

547   under interspecific competition and ET treatment, as indicated by significantly higher

548    $\delta^{15}NH_4^+$-N and no changes in $\delta^{15}NO_3^-$-N, whereas *A. faxoniana* showed significantly

549   lower $\delta^{15}NH_4^+$-N and declining $\delta^{15}NO_3^-$-N under interspecific competition and ET.

550   Thus, the greater plasticity of N uptake forms in *P. purpurea* under interspecific

551 competition and ET condition will probably enhance its competitive ability and fitness

552 (see also Ashton et al. 2010, Duan et al. 2014).

553

554 Despite extensive research on plant-plant competition, little is known about the

555 interactions of warming climate and plant-plant competition on growth and

556 physiological traits in high-altitude plants. Duan et al. (2014) found that *Abies*

557 *faxoniana* was a superior competitor when compared to *Betula albo-sinensis* under

558 interspecific competition and warming conditions. In the present study, we showed

559 that intra- and interspecific competition and ET significantly influence dry matter

560 accumulation, nutrient absorption, photosynthetic capacity, non-structural

561 carbohydrates and leaf ultrastructure in *A. faxoniana* and *P. purpurea*, and ET alters

562 the competitive outcomes between the two conifers. Moreover, under interspecific

563 competition and ET condition, *P. purpurea* possesses a better growth performance and

564 competitive advantage. A better ability for resource storage (e.g., higher root N and

565 non-structural carbohydrates) and for the maintenance of carbon balance (e.g., higher

566 P_n, F_v/F_m and water use efficiency), as well as better plasticity concerning N uptake

567 forms make *P. purpurea* trees better competitors when grown with *A. faxoniana* under

568 ET.

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571

572 **Conclusions**

573

574 The present study showed that elevated temperature (ET) can alter the competitive

575 relationship between *A. faxoniana* and *P. purpurea*, thus influencing the composition,

576 structure and functioning of subalpine coniferous forests. In nature, species generally

577 interact with others and their surroundings. It is expected that *P. purpurea* first

578 benefits from the presence of *A. faxoniana* and grows better under ET condition.

579 However, invasive species are likely to be well adapted to global warming (Whutney

580 and Gabler 2008). Furthermore, ET may have indirect effects on natural systems by

581 affecting soil moisture (Brzostek et al. 2012) and the length of the growing season (Fu

582 et al. 2014) as well as by altering plant phenology (Norby et al. 2003, Menzel et al.

583 2006). The complexity of natural systems constrains our capacity to predict the

584 responses of plant-plant competition to ET in natural systems. Thus, a long-term field

585 experiment is needed to investigate the natural systems under future global warming.

586 Therefore, plant-plant competition should be considered in climate warming

587 experiments and models predicting the potential responses of high-altitude plants to

588 global climate warming.

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595   Hangzhou Normal University (2016QDL020).

596

597   **Author contributions** Lei Yu had the main responsibility for data collection, analysis

598   and writing, Mengya Song and Zhichao Xia had a significant contribution to data

599   analysis, Helena Korpelainen and Ülo Niinemets had a significant contribution to the

600   interpretation of data and manuscript preparation, and Chunyang Li (the

601   corresponding author) had the overall responsibility for experimental design and

602   project management.

603

604   **Conflict of interest** The authors declare that they have no conflict of interest.

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Table 1. C and N concentrations and C/N ratios of leaves, stems and roots (mean ± SE) of *A. faxoniana* and *P.purpurea* under different competition and temperature (control versus +2 °C) treatments.

	Competition treatment	Leaf C (mg g^{-1})	Leaf N (mg g^{-1})	Leaf C/N	Stem C (mg g^{-1})	Stem N (mg g^{-1})	Stem C/N	Root C (mg g^{-1})	Root N (mg g^{-1})	Root C/N
Control	A/AA	506.36(1.70)a	10.57(0.24)c	47.99(1.08)a	472.54(1.49)a	6.61(0.03)b	71.50(0.53)a	413.20(3.08)a	8.34(0.03)a	49.54(0.46)a
	P/PP	498.70(2.01)bc	12.10(0.31)ab	41.33(1.14)bc	475.79(1.51)a	7.04(0.06)a	67.57(0.70)b	403.30(3.00)ab	8.34(0.11)a	48.40(0.83)a
	A/AP	504.59(1.24)ab	11.32(0.21)bc	44.61(0.81)ab	474.31(2.13)a	6.41(0.05)b	74.03(0.26)a	399.40(3.10)b	8.16(0.06)a	48.98(0.68)a
	P/AP	496.72(1.79)c	12.43 (0.19)a	40.01(0.72)c	476.09(1.57)a	6.49 (0.09)b	73.43(1.14)a	403.55(3.05)ab	8.35 (0.06)a	48.33(0.59)a
Elevated temperature	A/AA	506.18(1.95)^{AB}	12.86(0.13)^{C***}	39.37(0.28)^{A***}	471.17(1.76)^{A}	7.58(0.15)^{A***}	62.26(1.29)^{A***}	409.39(3.29)^{A*}	9.15(0.05)^{A***}	44.77(0.56)^{B**}
	P/PP	498.90(2.09)^{B}	14.76(0.23)^{B***}	33.84(0.56)^{B***}	474.47(1.11)^{A}	7.19(0.07)^{A***}	66.03(0.59)^{A***}	410.05(1.89)^{A*}	8.86(0.03)^{B***}	46.29(0.25)^{B**}
	A/AP	508.14(2.33)^{B}	13.17(0.26)^{C***}	38.65(0.83)^{A***}	472.89(1.99)^{A}	7.21(0.13)^{A***}	65.65(0.93)^{A***}	410.17(2.57)^{A*}	8.22(0.04)^{C***}	49.93(0.39)^{A**}
	P/AP	500.09(1.62)^{B}	16.00(0.11)^{A***}	31.26(0.28)^{C***}	475.85(1.99)^{A}	7.51(0.10)^{A***}	63.36(0.84)^{A***}	411.02(1.41)^{A*}	8.81(0.13)^{B***}	46.68(0.68)^{B**}
	$P:F_S$	0.000	0.000	0.000	0.028	0.109	0.214	0.590	0.019	0.041
	$P:F_C$	0.910	0.000	0.001	0.303	0.004	0.001	0.139	0.000	0.005
	$P:F_T$	0.198	0.000	0.000	0.388	0.000	0.000	0.010	0.000	0.000
	$P:F_{S\times C}$	0.855	0.410	0.941	0.699	0.195	0.265	0.076	0.000	0.014
	$P:F_{S\times T}$	0.970	0.002	0.465	0.789	0.026	0.017	0.357	0.572	0.971
	$P:F_{C\times T}$	0.201	0.450	0.534	0.822	0.009	0.003	0.058	0.000	0.001
	$P:F_{S\times C\times T}$	0.913	0.037	0.084	0.806	0.000	0.000	0.084	0.002	0.003

A/AA, *A. faxoniana* individuals from intraspecific competition; P/PP, *P. purpurea* individuals from intraspecific competition; A/AP, *A. faxoniana* individuals from interspecific competition; P/AP, *P. purpurea* individuals from interspecific competition.

Different lowercase letters indicate significant differences among the competition treatments within the control treatment and different uppercase letters within the elevated temperature treatment according to Tukey's tests ($P < 0.05$). The asterisks demonstrate statistically significant differences according to independent samples *t*-test between the temperature treatments within each competition treatment (* $0.01 < P < 0.05$; ** $0.001 < P \leq 0.01$; *** $P \leq 0.001$.).

Three-way analyses of variance (ANOVA) were applied to evaluate the effects of different factors and their interactions. F_S, species effect; F_C, competition effect; F_T, temperature effect; $F_{S \times C}$, the interactive effect of species and competition treatment; $F_{S \times T}$, the interactive effect of species and temperature treatment; $F_{C \times T}$, the interactive effect of competition and temperature treatment; $F_{S \times C \times T}$, the interactive effect of species, competition and temperature treatment.

Table 2. Soluble sugar, starch and NSC concentrations of leaves, stems and roots (mean ± SE) of *A. faxoniana* and *P.purpurea* under different competition and temperature (control versus +2 °C) treatments.

	Competition treatment	Leaf soluble sugar (mg g^{-1})	Leaf starch (mg g^{-1})	Leaf NSC (mg g^{-1})	Stem soluble sugar (mg g^{-1})	Stem starch (mg g^{-1})	Stem NSC (mg g^{-1})	Root soluble sugar (mg g^{-1})	Root starch (mg g^{-1})	Root NSC (mg g^{-1})
Control	A/AA	75.23(2.25)c	114.19(3.89)b	189.42(4.69)b	31.65(0.77)a	83.81(1.41)c	115.45(2.13)c	30.29(1.06)b	47.38(1.69)b	77.67(1.70)b
	P/PP	104.09(2.51)a	72.21(3.89)c	176.30(2.52)c	35.38(1.41)a	100.06(3.84)b	135.44(4.62)b	12.47(0.39)c	12.89(0.43)c	25.36(0.40)c
	A/AP	90.54(0.53)b	108.36(2.83)b	198.90(2.75)b	34.16(1.84)a	111.11(2.05)a	145.26(1.46)ab	40.76(1.93)a	56.25(1.67)a	97.02(2.02)a
	P/AP	92.67(1.24)b	176.74 (2.78)a	269.42(2.19)a	31.71(0.71)a	120.33(1.10)a	152.04(1.49)a	26.10(1.02)b	51.64(1.38)ab	77.74(1.92)b
Elevated temperature	A/AA	90.18(1.56)^{AB}	80.89(2.13)^{B**}	171.07(2.72)^{B**}	34.51(1.54)^{BC*}	85.05(1.53)^{BC}	119.56(2.46)^{C}	29.27(0.54)^{B}	38.58(1.02)^{C}	67.85(1.12)^{C}
	P/PP	94.79(1.43)^{A}	80.63(2.17)^{B**}	175.41(2.51)^{B**}	40.92(0.97)^{A*}	126.36(2.19)^{A}	167.28(2.55)^{A}	37.06(1.59)^{A}	55.72(1.63)^{B}	92.78(1.56)^{B}
	A/AP	82.44(3.15)^{B}	58.95(3.06)^{C**}	141.40(4.29)^{C**}	31.40(1.31)^{C*}	84.31(1.38)^{C}	115.71(1.05)^{C}	24.67(0.45)^{B}	30.32(0.75)^{C}	54.98(0.81)^{D}
	P/AP	90.64(2.07)^{AB}	120.54(3.82)^{A**}	211.19(4.07)^{A**}	38.65(0.96)^{AB*}	94.40(3.40)^{B}	133.05(3.03)^{B}	42.38(2.04)^{A}	72.82(4.61)^{A}	115.21(5.89)^{A}
	$P:F_S$	0.000	0.000	0.000	0.000	0.000	0.000	0.064	0.001	0.064
	$P:F_C$	0.166	0.000	0.002	0.073	0.032	0.262	0.000	0.000	0.000
	$P:F_T$	0.433	0.000	0.000	0.001	0.001	0.094	0.000	0.000	0.000
	$P:F_{S \times C}$	0.000	0.000	0.000	0.140	0.000	0.000	0.001	0.000	0.000
	$P:F_{S \times T}$	0.003	0.000	0.086	0.001	0.000	0.000	0.000	0.000	0.000
	$P:F_{C \times T}$	0.009	0.000	0.000	0.240	0.000	0.000	0.000	0.000	0.000
	$P:F_{S \times C \times T}$	0.000	0.000	0.063	0.055	0.001	0.025	0.071	0.440	0.750

Treatment codes and statistical analyses as in Table 1.

Figure legends

Figure 1. Dry matter accumulation and partitioning of *Abies faxoniana* and *Picea purpurea* under different competition and temperature (control versus +2 °C) treatments. (a) leaf dry matter accumulation, (b) stem dry matter accumulation, (c) total root dry matter accumulation, (d) total dry matter accumulation, (e) fine root dry matter accumulation and (f) root to shoot (R/S) ratio. Each value is the mean ± SE (n = 5). Different lowercase letters indicate significant differences among the competition treatments within the control treatment and different uppercase letters within the elevated temperature treatment according to Tukey's tests ($P < 0.05$). The asterisks demonstrate statistically significant differences according to independent samples t-test between the temperature treatments within each competition treatment (***$P \leq 0.001$). Three-way analyses of variance (ANOVA) were applied to evaluate the effects of different factors and their interactions. S, species effect; C, competition effect; T, temperature effect; S × C, the interactive effect of species and competition treatment; S × T, the interactive effect of species and temperature treatment; C × T, the interactive effect of competition and temperature treatment; S × C × T, the interactive effect of species, competition and temperature treatment. A/AA, *A. faxoniana* individuals from intraspecific competition; P/PP, *P. purpurea* individuals from intraspecific competition; A/AP, *A. faxoniana* individuals from interspecific competition; P/AP, *P. purpurea* individuals from interspecific competition.

Figure 2. (a) Height growth rate (HGR) and (b) diameter growth rate (DGR) of *Abies faxoniana* and *Picea purpurea* grown under different competition and temperature (control versus +2 °C) treatments. Each value is the mean ± SE ($n = 5$). Treatment codes and statistical analyses as in Figure 1.

Figure 3. (a) Net photosynthetic rate (P_n), (b) total chlorophyll content, (c) the dark-adapted quantum yield of PSII (F_v/F_m), (d) photosynthetic nitrogen use efficiency (PNUE), (e) specific leaf area (SLA) and (f) carbon isotope composition ($\delta^{13}C$) of *Abies faxoniana* and *Picea purpurea* grown under different competition and temperature (control versus +2 °C) treatments. Each value is the mean ± SE ($n = 5$). Treatment codes and statistical analyses as in Figure 1.

Figure 4. Ultrastructure of mesophyll cells in *Abies faxoniana* and *Picea purpurea* grown under different competition and temperature (control versus +2 °C) treatments according to transmission electron microscopy (TEM). (a-d) control treatments: (a) A/AA, (b) P/PP, (c) A/AP, (d) P/AP. (e-h) elevated temperature treatments: (e) A/AA, (f) P/PP, (g) A/AP, (h) P/AP. The bar indicates 2 um (a). C, chloroplast; CW, cell wall; S, starch granule. Treatment codes as in Figure 1.

Figure 5. (a) $\delta^{15}NH_4^+$-N and (b) $\delta^{15}NO_3^-$-N of *Abies faxoniana* and *Picea purpurea* grown under different competition and temperature (control versus +2 °C) treatments. Each value is the mean ± SE ($n = 5$). Treatment codes and statistical analyses as in

Figure 1.

Figure 6. Principal component analysis (PCA) based on eco-physiological traits of *Abies faxoniana* and *Picea purpurea* under different competition and temperature (control versus +2 °C) treatments. The white circle, triangle, square and diamond indicate A/AA, P/PP, A/AP and P/AP under control conditions, respectively. The black circle, triangle, square and diamond indicate A/AA, P/PP, A/AP and P/AP under elevated temperature conditions, respectively. P_n, net photosynthetic rate; *TChl*, total chlorophyll content; F_v/F_m, the dark-adapted quantum yield of PSII; PNUE, photosynthetic nitrogen use efficiency; SLA, specific leaf area; Leaf TS, leaf total sugar concentration; Stem TS, stem total sugar concentration; Root TS, root total sugar concentration; HGR, height growth rate; DGR, diameter growth rate. Treatment codes as in Figure 1.
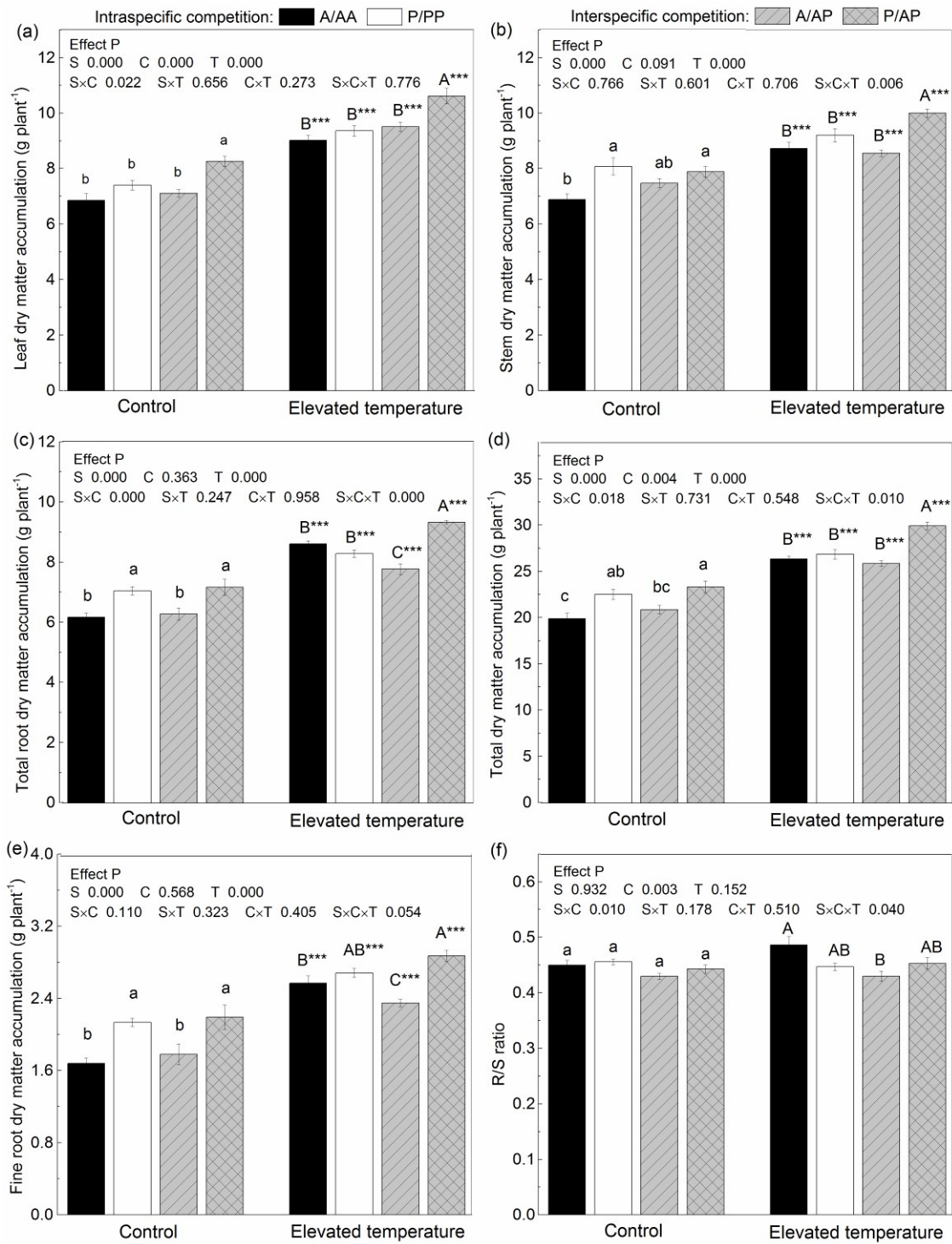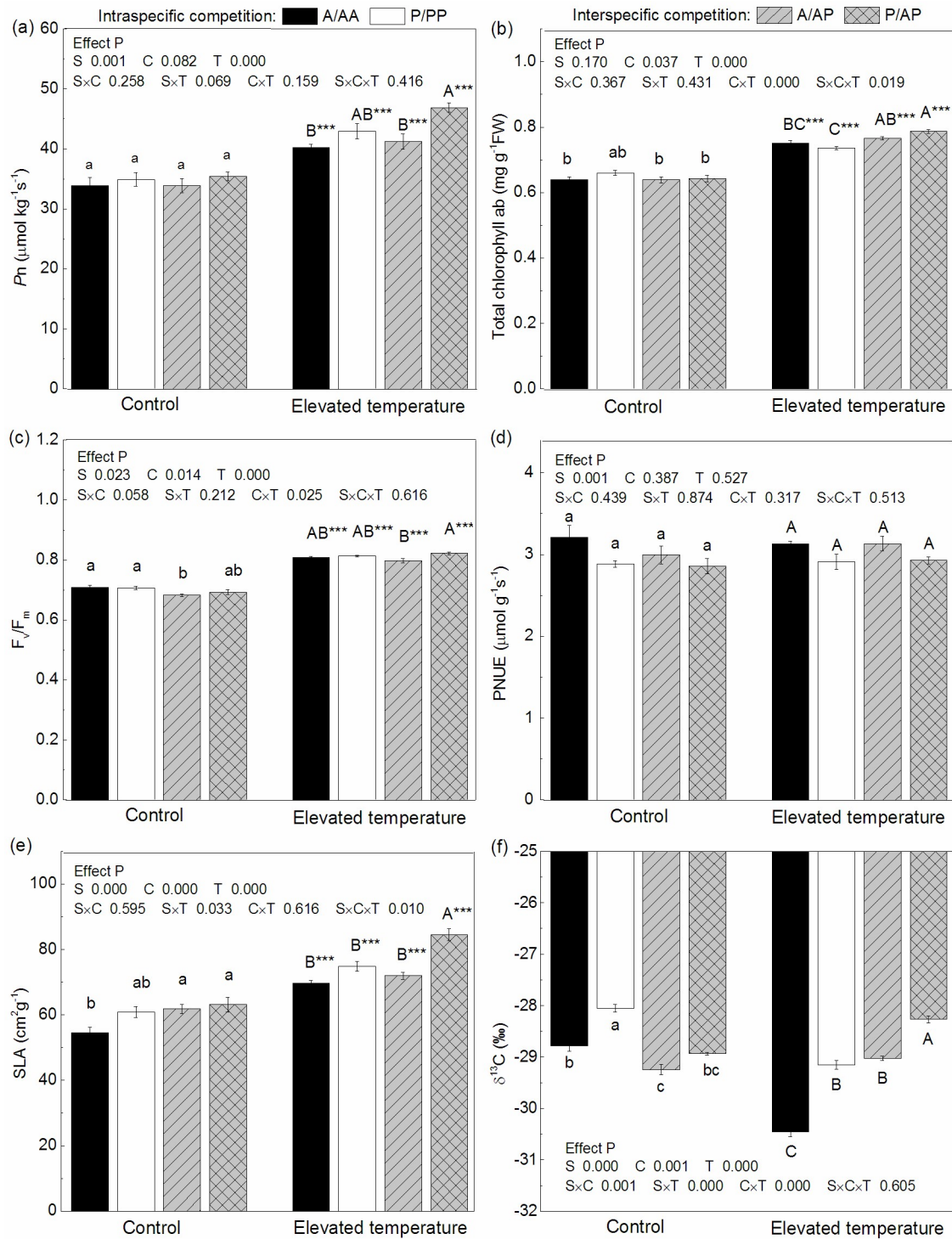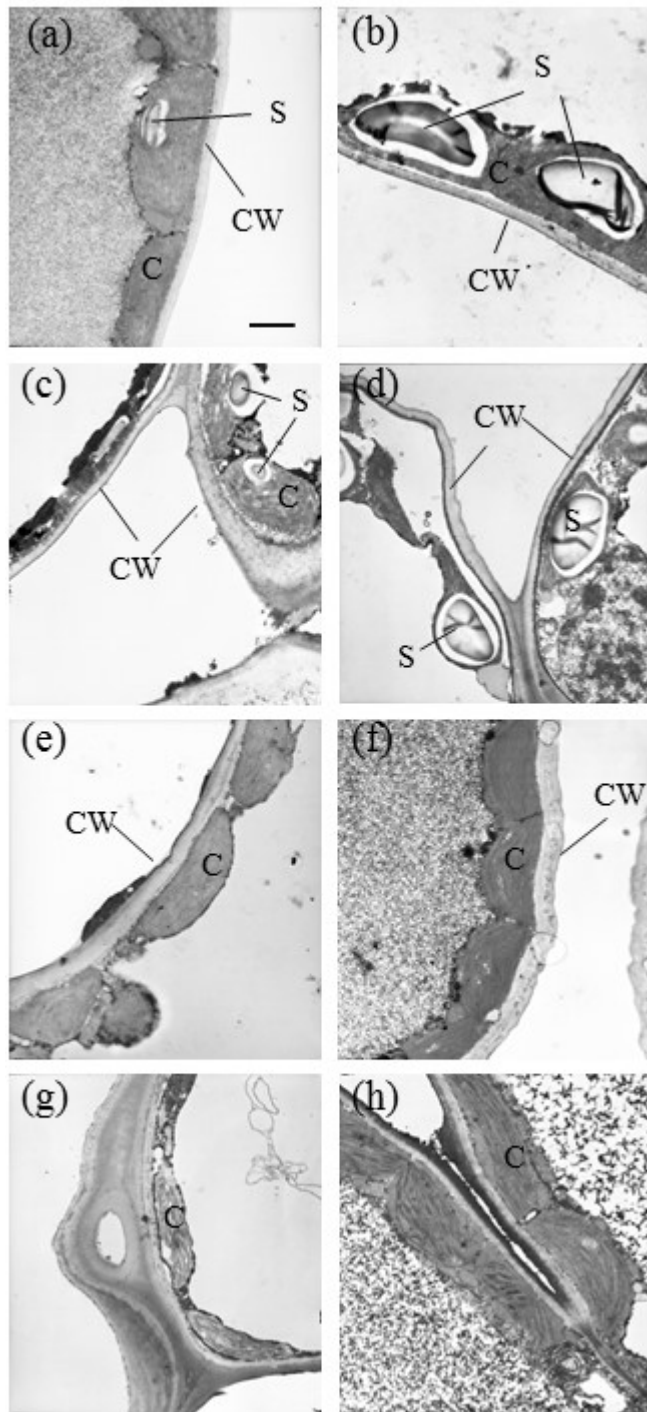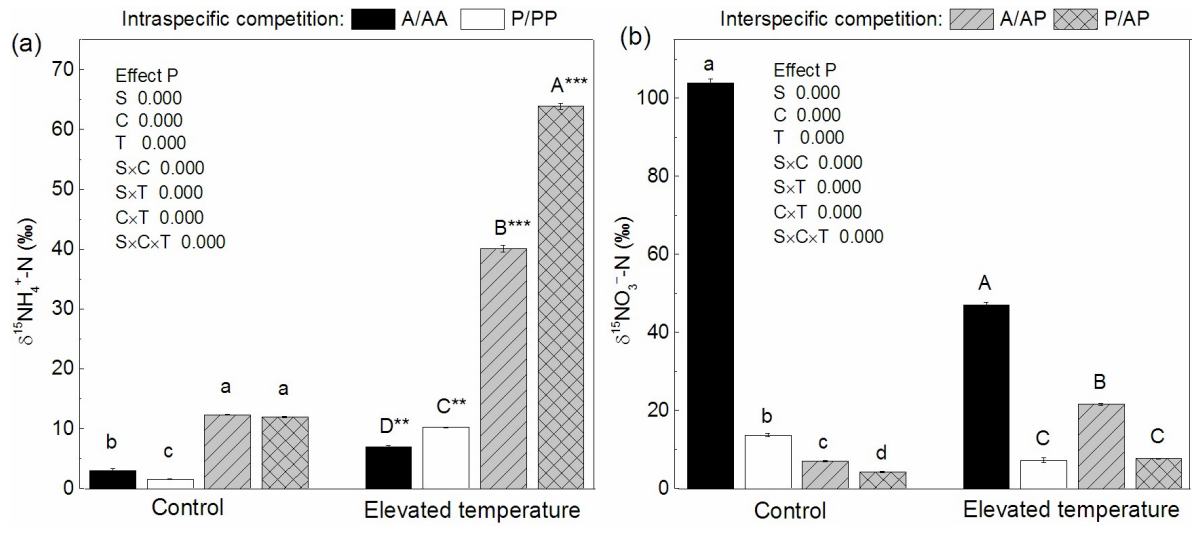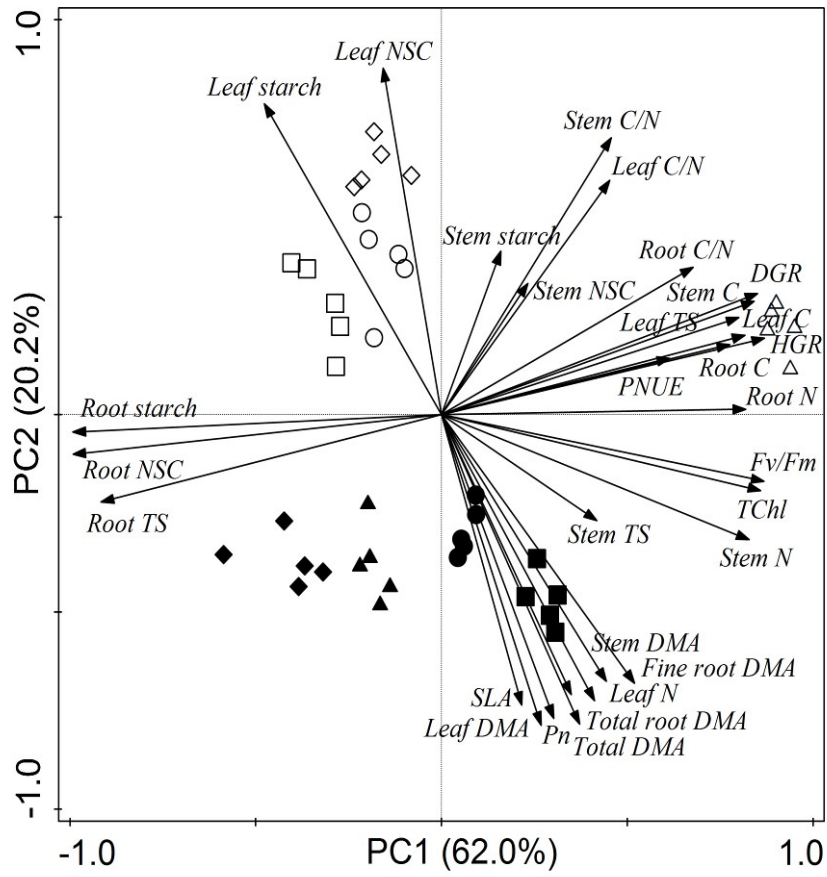
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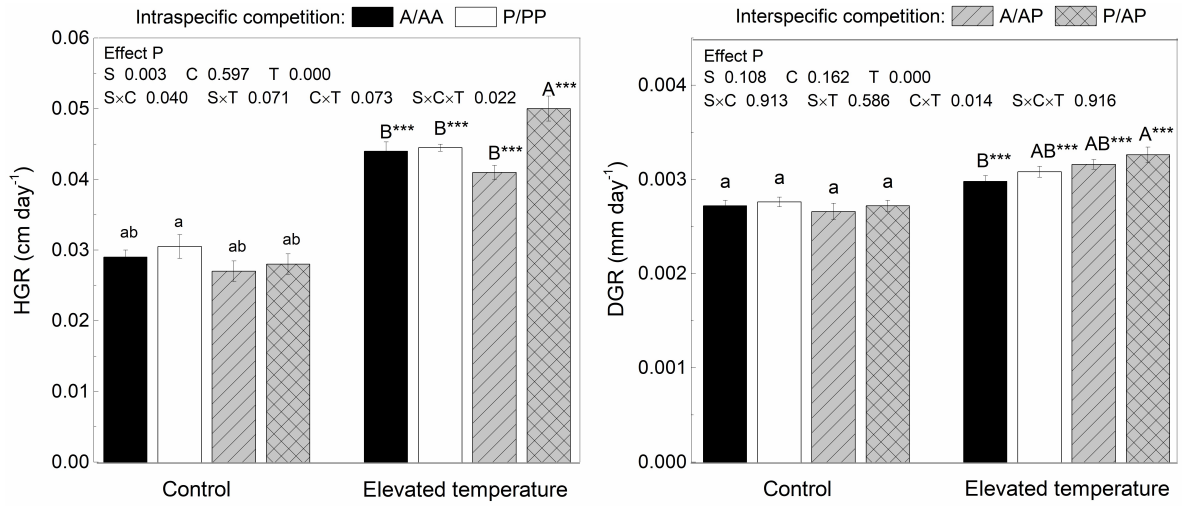
Figure 2

Figure 3

Figure 4

Figure 5

Figure 6