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Vapor-pressure deficit and extreme climatic variables limit tree growth

3   *Running head:* Vapor-pressure deficit limits tree growth

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24
25   Abstract

26   Assessing the effect of global warming on forest growth requires a better understanding

27   of species-specific responses to climate change conditions. Norway spruce and European

28   beech are among the dominant tree species in Europe and are largely used by the timber

29   industry. Their sensitivity to changes in climate and extreme climatic events, however,

30   endangers their future sustainability. Identifying the key climatic factors limiting their

31   growth and survival is therefore crucial for assessing the responses of these two species

32   to ongoing climate change. We studied the vulnerability of beech and spruce to warmer

33   and drier conditions by transplanting saplings from the top to the bottom of an elevational

34   gradient in the Jura Mountains in Switzerland. We (1) demonstrated that a longer growing

35   season due to warming could not fully account for the positive growth responses, and the

36   positive effect on sapling productivity was species-dependent, (2) demonstrated that the

37   contrasting growth responses of beech and spruce were mainly due to different

38   sensitivities to elevated vapor-pressure deficits, (3) determined the species specific limits

39   to vapor-pressure deficit above which growth rate began to decline and (4) demonstrated

40   that models incorporating extreme climatic events could account for the response of

growth to warming better than models using only average values. This results support that the sustainability of forest trees in the coming decades will depend on how extreme climatic events will change, irrespective of the overall warming trend.

1. Introduction

Climate change is currently escalating so rapidly that many trees may not be able to adapt (Rogers, Jantz, & Goetz, 2017). In addition to the gradual global warming, the frequency and severity of extreme events such as heat waves, heavy precipitation, summer droughts and cold spells are expected to increase in the coming decades (IPCC, 2013; Schar et al., 2004) , which may ultimately determine future tree distributions (Zimmermann et al., 2009). Extreme events can have strong impacts on tree growth and survival, due to typically stronger responses and shorter response times than for normal climatic events (Hanson, Palutikof, Dlugolecki, & Giannakopoulos, 2006; Kreyling, Jentsch, & Beierkuhnlein, 2011). Forest researchers must estimate the resilience of forests to expected climate change and extreme climatic events to guide sustainable forest management (Lindner et al., 2014). An increasing number of studies are therefore testing the impact of extreme events on forest growth (Ciais et al., 2005; Teskey et al., 2015), some under controlled conditions (Lendzion & Leuschner, 2008). Experiments are often conducted *ex situ* (e.g. in climate-controlled chambers), which is valuable for understanding the impact of a single factor on tree physiology but does not represent real *in situ* conditions that involve many abiotic and biotic interactions that determine tree growth (De Boeck, Dreesen, Janssens, & Nijs, 2010; Körner et al., 2016; Vicca et al., 2016; Zimmermann et al., 2009).

Increased tree growth has been correlated with warmer temperatures (Way & Oren, 2010) and longer growing seasons (Keenan, 2015; Menzel & Fabian, 1999; Piao, Friedlingstein, Ciais, Viovy, & Demarty, 2007; Signarbieux et al., 2017).However, divergent responses to warming among co-existing tree species have been also widely reported (C. Allen et al., 2010; Carnicer, Barbeta, Sperlich, Coll, & Penuelas, 2013), reflecting different

physiological needs and growth strategies. A change in environmental conditions due to altitude is one of the factors leading to this divergence. For instance, tree growth during the extremely hot and dry summer in 2003 in the Swiss Alps increased at high altitudes but decreased at low altitudes (Jolly, Dobbertin, Zimmermann, & Reichstein, 2005). This contrasting growth response was explained by the differences in resource, temperature and water limitations between lower and higher elevations.

Shifts in the onset of spring phenology, due to increasing temperatures, generally are related to an increase in growing season length (Keenan, 2015). It has been reported that leaf unfolding of European woody species has advanced by about 13 days during the period 1982-2011 in Europe, which together with delayed autumn phenology has contributed to extend the growing vegetative period (Fu et al., 2014) by 24 days during the same period (Kolářová, Nekovář, & Adamík, 2014). Moreover, it has been hypothesized that the length of the growing season affects productivity to a larger extent in angiosperms than in conifers (Carnicer et al., 2013). However, Körner (2017) argued that longer growing seasons may contribute to higher annual tree growth, but only to a certain limit, which is not yet clearly identified (Delpierre, Guillemot, Dufrêne, Cecchini, & Nicolas, 2017).

The stomatal response of trees to changing environmental conditions is complex and it is a process which is still not well understood (Damour et al., 2010). The closure of stomata at midday is regulated by the water available in the soil, leaf and atmosphere, and it is highly species-specific (Bond & Kavanagh, 1999). Stomatal responses to increasing evaporative demand of the air seem to be another explanation for the contrasting growth responses between functional groups. Carnicer et al. (2013) reviewed various hypotheses that could account for the contrasting responses of growth to temperature in Mediterranean angiosperm and coniferous trees. They included a hypothesis involving the effect of eco-physiological and hydraulic traits on tree growth. More specifically, they suggested that different sensitivities of stomatal conductance to vapor-pressure deficit (VPD) lead to different growth responses. Several studies have been performed in order to understand the mechanisms triggering stomatal closure in response to vapor pressure deficit (Sellin, 2001; Brodribb & McAdam, 2011; Mott & Peak, 2013) and agree that stomata typically close at high VPD and open at low VPD (McAdam & Brodribb, 2015). The sensitivity of VPD to changes in air temperature differs among plant functional groups (Ogaya & Peñuelas, 2007; Way & Oren, 2010) and underlies the strategies

106 optimizing carbon uptake with reduced water loss (Franks & Farquhar, 1999). For

107 instance, the positive response of growth to increased temperature in angiosperms could

108 be due to a narrower hydraulic safety margin and a higher capacity to reverse embolisms

109 (Carnicer et al., 2013). The higher hydraulic safety margin in conifers implies an earlier

110 response of stomatal closure before cavitation (Carnicer et al., 2013), at a cost of reducing

111 carbon uptake. Therefore, vapor-pressure deficit (VPD) can limit tree growth (C. D.

112 Allen, Breshears, & McDowell, 2015), but its importance has not been fully recognized

113 (Lendzion & Leuschner, 2008). Leaf-to-air VPD is expected to increase with the

114 predicted increase in air temperature (Novick et al., 2016), with subsequent impacts on

115 plant transpiration and photosynthesis. Reciprocal common garden experiments along

116 altitudinal transects have been suggested to be a powerful tool for testing ecological

117 responses to changes in environmental conditions (Carnicer et al., 2013; Christian Körner,

118 2007), such as increasing temperature and evaporative demand of the air. This type of

119 experiment is based on the variation of environmental conditions (temperature,

120 atmospheric pressure, etc.) with elevation, simulating climate change conditions without

121 needing to wait decades to observe an impact and therefore predict responses and adapt

122 forest managements. Most studies of the impacts of climate change on vegetation are

123 based on changes in the averages of climatic variables (Miyamoto, Griesbauer, & Scott

124 Green, 2010), such as the mean annual or summer temperature. Extreme climatic events

125 can have a large effect on tree growth but have been rarely studied (Lendzion &

126 Leuschner, 2008; Teskey et al., 2015) and there is no accurate definition related to the

127 existence of an "extreme" (Stephenson, 2008). In this study, we defined "extreme"

128 according to IPCC (Murray & Ebi, 2012), i.e. we quantified climate extremes by

129 determining specific thresholds above which tree growth could be largely affected. We

130 thus analysed the effects of changes in climatic factors on the growth of beech and spruce

131 saplings and compared the variances of the data for averages vs. extremes. Specifically,

132 our main questions were: 1) how does species-specific growth respond to warmer and

133 drier conditions, 2) to what extent does a longer growing season increase tree growth, 3)

134 how does an elevated VPD affect tree growth and 4) what benefit does the study of

135 "extreme conditions" have on a mechanistic understanding of the responses of tree growth

136 under various environmental conditions? The novelty in this study is that we used a

137 'natural warming experiment' to assess how trees adapted to cold and wet environments

138 respond to warmer and drier conditions by a translocation experiment along a transect

139 across an altitudinal gradient. Generally, altitudinal gradient experiments compare

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populations of a same species but growing at different elevations, or use climate chambers to control climatic variables, without taking account the effects of extreme climatic variables. In our approach, we transplanted beech and spruce saplings from a donor site at a high altitude to three recipient sites at lower altitudes to assess the effects of warmer and drier conditions on growth of individuals adapted to cold and wet environments. We focused on the saplings of the two dominant sylvopastoral species of the Jura Mountains, Norway spruce and European common beech. A good understanding of regeneration and its consequences under conditions of climate change are crucial for both species conservation and the sustainable and adaptive management of landscapes (Buttler 2014). These two species are also among the dominant trees in central Europe and are key to the timber industry, so forest managers need to know whether they will be sustainable in the coming decades.

2. Materials and methods

2.1 Study sites and elevational gradient

The conditions of climate change were simulated using an elevational gradient along a south-facing slope of the Jura Mountains in Switzerland. This space-for-time substitution (Körner, 2003) simulated a climatic gradient, i.e. an increase in temperature and a decrease in precipitation towards lower altitudes. A detailed description of the site selection is given by Gavazov *et al.* (2014). Briefly, the donor site was at Combe des Amburnex (N46°54′, E6°23′; 1350 m a.s.l.), with an oceanic climate, a mean annual temperature and precipitation of 4.5°C and 1750 mm, respectively, and a permanent snow cover from November to may (K. S. Gavazov, Peringer, Buttler, Gillet, & Spiegelberger, 2013). The three recipient sites were at St.-George at 1010 m a.s.l. (N46°52′, E6°26′), Arboretum d'Aubonne at 570 m a.s.l. (N46°51′, E6°37′) and Les Bois Chamblard at 395 m a.s.l. (N46°47′, E6°41′). Combe des Amburnex was the control site with native climatic conditions, so this climatic gradient covered three possible warming scenarios of the Intergovernmental Panel on Climate Change (K. S. Gavazov et al., 2013; K. Gavazov et al., 2014): moderate at 1010 m a.s.l. (on average + 2°C and 20 % rainfall reduction), intermediate at 570 m a.s.l. (+ 4°C and 40 % rainfall reduction) and extreme at 395 m a.s.l. (+ 5°C and 50 % rainfall reduction).

In this study we mainly focused on the impact of changes in air temperature and precipitation in the tree growth of saplings. However, we acknowledge that there is a decrease in total atmospheric pressure and partial pressure of gases with altitude, as well as an increase in radiation under cloudless sky due to a decrease in atmospheric turbidity (Körner, 2007). Sanginés et al. (2017) showed that temperature gradients had a major effect on the morphological changes of leaves as compared to changes in partial pressure. Regarding solar radiation, the actual dose received by a plant will also depend on scattering elements such as clouds, which generally increase with altitude in mountain regions (Körner, 2007). Therefore, we assume that the increase in solar radiation at high elevations during the growing season is, to some extent, compensated with the associated increase in cloudiness. To support this assumption, we visually inspected the data of solar radiation recorded by meteo-stations placed at our study sites and observed similar July solar radiation averages and same trends along the spatial-temporal gradient (data not shown).

2.2 Experimental design and species

Saplings of beech (*Fagus sylvatica* L.) and spruce (*Picea abies* (L.) H.Karst.) were collected at the donor site (1350 m) immediately before the budburst of the 2012 growing season. The surface of collection was assumed to be reduced enough to ensure the same provenance of saplings. The saplings had similar sizes (average height of 33 cm for beech and 31 cm for spruce) and were excavated with intact root systems and soil. They were then transplanted to 20-L pots and randomly reallocated in four plots, one at each altitude, in open spaces and far enough from the forest to avoid shade from surroundings adult trees. Half of the saplings were transplanted a second time to 40-45-L pots in autumn 2014, two years after the first transplantation, due to the potential limitation of growth by the initial pots. The other half was harvested for analysis. The soil of the harvested plants was used for the transplantation of the remaining individuals to maintain the same soil characteristics for each species and site.

The experimental design was a generalized block with repeated measures (2013, 2014 and 2015). The four blocks were considered as fixed and corresponded to the four sites at altitudes of 1350, 1010, 570 and 395 m. Ten replicate saplings per species (beech and spruce) and treatment (non-irrigated and irrigated) were randomly allocated within each block. The experimental unit was a pot with one sapling, which was randomly placed on a grid with a spacing of 0.3×0.9 m to avoid light competition. The pots were recessed

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204 belowground, and a geotextile cap was placed at the top and bottom of the pots to reduce

205 both the evaporation of soil water and the penetration of roots into the soil of the site. All

206 sites were equipped with wireless meteorological stations (Sensorscope, Climaps.

207 available at: https://www.climaps.com/) that continuously recorded climatic parameters

208 (precipitation and air temperature), enabling us to add water weekly during the growing

209 season to ensure equal amounts of precipitation at the recipient and donor sites for the

210 irrigated treatment. The saplings in the non-irrigated treatment were subjected to the local

211 environmental conditions of each site. The purpose of the irrigation treatment was to

212 identify the effect of rainfall for studying the responses of the saplings to temperature

213 alone.

214 *2.3 Biomass estimation*

215   *2.3.1.* In situ *measurements of growth rate*

216 Growth was monitored twice (before budburst and after senescence) for all saplings for

217 three consecutive growth periods (2013, 2014 and 2015) to evaluate the effects of the

218 changes in environmental conditions on aboveground biomass. Overall growth was

219 estimated by dasometric measurements of the stem and four main branches. The four

220 longest branches for each sapling were identified and tagged to allow continuous

221 monitoring. Stem and branch diameters (basal and apical) were measured using an

222 electronic caliper with an accuracy of 0.01 mm. The basal diameter *(Sb)* of the stem was

223 an average of two perpendicular measurements approximately 1-2 cm from the base of

224 the root collar. The basal diameter of a branch *Bb* was recorded at the base. The apical

225 diameter of the branches *(Ba)* and the stem *(Sa)* were measured below a dormant bud.

226 Stem length *(H)* and branch length *(l)* were measured with a ruler from the base to below

227 a winter bud (accuracy of 0.1 cm).

228   *2.3.2. Biomass models*

229   *2.3.2.1. Sampling and independent variables*

230 We expressed tree growth as total aboveground woody biomass using an allometric

231 equation. This equation estimated the aboveground woody biomass from non-destructive

232 measurements of easily measured variables (e.g. basal diameter). This model was

233 constructed using a total of 95 additional saplings per species collected from the donor

234 site and harvested. The allometric equation based on these additional saplings served to

235 estimate the biomass of the saplings included in the study in a non-destructive way. Tree

components (stem, four longest branches, remaining branches and roots) were separated

in the laboratory and placed in paper bags. *Sa, Sb, H, Ba, Bb* and *l* were measured on the

stems and main branches, which were then oven-dried at 65 °C to constant weights. These

independent variables and their combinations (e.g. stem diameter and height) were then

correlated with the total dry weight (g) using linear regressions to obtain the most

parsimonious model.

2.3.2.2. Model construction and validation

Several criteria were followed for selecting the optimal allometric equation for each

species: (1) the highest adjusted coefficient of determination *(R²*adj), (2) the lowest root-

mean-square error RMSE, (3) $F < 0.05$, (4) the regression model with the best biomass

estimates for both species and (5) and the practicality of the model (cost of measuring the

independent variables).

The selected model indirectly estimated the aboveground biomass using the total volume

of the stem and the four main branches (Eq. 1). This method was the best for quantifying

and comparing the aboveground biomass of the two species with different growth patterns

(i.e. beech growing in height and spruce producing more branches). The model developed

was:

$$Ln(B) = c + aLn(V) \quad Eq. (1)$$

where B is the aboveground woody biomass (g), V is the total volume of the four main

branches and stem (cm^3) and c is the intercept and a is the slope coefficient of the

regression line. The allometric equation for beech was B = exp ^ (1.012535 * (Ln(V))-

0.585528), with an *R²*adj of 0.995 and $P < 0.0001$. The model for spruce was B =

exp^1.00926 * (LnV), with an *R²*adj of 0.997 and $P < 0.0001$. The model selected for

each species was then validated with half of the saplings used in the study harvested in

autumn 2014 during the transplantation to larger pots.

We used these models to calculate the initial and final biomasses of each sapling for each

growing season. The difference between the final and initial biomasses was divided by

the initial biomass to normalize for sapling size, allowing the removal of any possible

effect of sapling size.

2.4. Definition of length of the growing season

2.4.1. Onset of the vegetative period

267 Phenological variables were observed along the elevational gradient during the entire

268 study period. Leaf emergence was monitored in spring every 2-3 days by the same

269 observer. The developmental stages that were chosen were based on Vitasse (2009). The

270 stages for beech were: (0) dormant buds, (1) swollen and/or elongated buds, (2) budburst

271 and (3) at least one fully unfolded leaf. The stages for spruce were: (0) dormant buds, (1)

272 expanded buds with new green visible behind the transparent cupule and (2) unfolded

273 needles. The date of leaf unfolding was defined as the date when 50% of the buds had

274 reached this stage.

275 2.4.2. *End of the vegetative period*

276 Leaf colouring and/or leaf fall in autumn were the criteria used to assess the senescence

277 of beech leaves and therefore the end of the vegetative period. Senescence was defined

278 as the time when 50% of the leaves of a sapling were no longer functional, i.e. either

279 coloured or fallen, using the equation (Vitasse, 2009):

280 $$x_t = \frac{a_t \times (100 - \beta_t)}{100} + \beta_t \quad \text{Eq. (2)}$$

281 where x_t is the percentage of coloured or fallen leaves for a sapling at time t, α_t is the

282 percentage of coloured leaves at time t and β_t is the percentage of missing leaves at time

283 t.

284 Norway spruce is an evergreen coniferous tree, so determining the exact end of the

285 vegetative period is challenging. We therefore also monitored budset for both species

286 three times per week from August to October in 2014 and 2015. The stages recorded

287 were: (0) ongoing leaf development, (1) newly formed green and soft buds, (2) small and

288 brown buds and (3) elongated (> 1 cm) and brown buds. The time of budset was recorded

289 when 50 % of the buds of a sapling had reached stage 3. The two proxies used for the

290 definition of the cessation of primary growth were compared for beech to further

291 understand bud formation and hardening before winter.

292 *2.4.3. Length of the growing season*

293 We defined the length of the beech growing season as the number of days between the

294 date of leaf unfolding and the date of leaf senescence. We assumed that spruce ended its

295 primary growth at beech senescence at the latest (see Results). The mean dates of beech

296 senescence were thus calculated per site and year and assigned to the corresponding site

and year of the spruce saplings. The length of the spruce growing season was consequently defined as the number of days between needle unfolding and the corresponding mean date of beech senescence.

2.5 Defining mean climatic variables

We took into consideration three mean climatic variables to explain the tree growth observed: mean air temperature during the growing season (Tmean), the precipitation rate per day (Rain mm/day) and the soil moisture by measurements of volumetric water content in the soil (VWC, m3/m3). For the last we used sensors 5TM (Decagon S.A) placed at 20cm soil depth. Even though soil moisture was continuously measured, due to technical problems with the sensors we were obliged to limit the data used for the model to the period between the months of May and July of each year. Nevertheless we had sufficient information about the soil moisture during the period where tree growth fundamentally takes place (i.e. the 2-3 first months after bud break). To support this, we observed in our study that primary growth was mainly suppressed at the end of the summer (August) when the winter bud formation takes place (Fig 1).

2.6 Defining climatic extremes

There is no accurate definition related to the existence of an "extreme" (Stephenson, 2008). An established definition would be "an episode or occurrence in which a statistically rare or unusual climatic period alters ecosystem structure and/or function well outside the bounds of what is considered typical or normal variability" (Smith, 2011). A special report of IPCC (Murray & Ebi, 2012) defined an "extreme climate or weather event" or "climate extreme" as "the occurrence of a value of a weather of climate variable above (or below) a threshold value near the upper (or lower) ends of the range of observed values of the variable". They clarify definition by stating that it includes absolute thresholds as extreme events and give the example of specific critical temperatures for health impacts.

In this study, we defined "extreme" as done by IPCC (Murray & Ebi, 2012) in a special report about managing the risks of extreme events. Therefore, we established impact-related thresholds in beech and spruce performance for saplings growing in the Swiss Jura. The thresholds were based in thermal-hydric requirements of each species. Vapor pressure deficit (VPD) is a measure of the difference between the pressure exerted by the

328   moisture currently in the air and the pressure at saturation. We calculated the VPD, as a

329   measure of the drying power of the air, as follows:

330                  $VPD = (1 - (RH/100)*SVP$ Eq. (3)

331   where RH is the relative humidity and SVP is the saturated vapor pressure for a given

332   temperature.

333   A VPD threshold of 1.5 kPa was chosen to represent the approximate value above which

334   stomata close in both species (Kurjak et al., 2012; Lendzion & Leuschner, 2008; Zweifel,

335   Bohm, & Hasler, 2002). We used this VPD to represent the extremely dry air during an

336   extended summer drought. Heat waves and cold spells were represented by two

337   predefined temperature thresholds: above 25°C and below 5°C. The superior threshold (

338   25°C during the vegetative period), was based on the thermal requirements of the two

339   species (Gelete, 2010). Additionally, photosynthesis temperature-response curve

340   performed in saplings growing at the extremes sites revealed that from 25°C the net

341   photosynthesis starts to decline for both species. The lower limit was established at 5°C

342   as it appears to be the limit for higher plant tissue growth (Körner, 2008). We thus

343   calculated i) the accumulation of hours over threshold 25°C (AOT25) during the growing

344   season and ii) the accumulation of hours below threshold 5°C (ABT5) We also calculated

345   the number of events with thirty consecutive days without rain during the growing season

346   at each site (P30).

347   *2.7 Statistical analysis*

348   General additive mixed effects models (GAMMs) were used to explore the response of

349   aboveground tree biomass to changing climate over time. Briefly, GAMMs allow the

350   change in mean biomassto follow any smooth curve, not just a linear form or a sequence

351   of unrelated estimates. The form of the predictor function is the principal difference

352   between the classical generalized mixed-effects models and GAMMs. All models were

353   fitted according to a Gaussian distribution. We assessed five fixed effects (mean climate

354   and extreme events) and one random effect (site nested into date) to take into account the

355   inflation of the residual degrees of freedom that would occur if we were using repeated

356   measurements within sites as true replicates. Several combinations of models were tested

357   to find the most parsimonious model that would best explain the biomass response. We

358   used Akaike's Information Criterion (AIC) (Akaike, 1973), R^2adj and the normality of

359   residuals to compare the different models. As explanatory variables, we included soil

360   moisture (m³/m³) along with the other "average" variables Tmean (°C), Rain (mm/day)

361   and the defined "extreme" temperature variables AOVPD1.5 (hours) and ABT5 (hours).

362   According to Dormann's et al. review (2013), correlation coefficients between variables

363   of |r|>0.7 is an appropriate indicator for when collinearity begins to severely distort model

364   estimation. Therefore, we ensured that none of the two explanatory variables had a

365   Pearson's correlation coefficient higher than 0.7 which gives us relatively good

366   confidence that collinearity among predictors is not affecting our inference. Using effect

367   size (Eq.4) allowed to quantify the impact of changing environmental conditions on the

368   growth of the transplanted saplings. All statistical analyses were performed in R 3.1.2

369   using the *mgcv* package.

370
$$Effsize[i] = \frac{x[i] - \overline{x_c}}{\sigma x_c} \quad \text{Eq. (4)}$$

371   where x is the variable considered for each observation [i], $\bar{x}_c$ and σx_c are the mean and

372   standard deviation of the control population.

373   We measured the interannual climatic variability along the elevational gradient to identify

374   the factors influencing tree growth (Table 1). The wireless meteorological stations

375   continuously recorded the climatic parameters needed for calculating the duration of

376   extreme events. Data from nearby stations were used when necessary to complete the data

377   set (Agroscope, 2016). The climatic variables were calculated individually for each

378   sapling as a function of the growing season.

379

380   **3. Results**

381   **3.1 Interannual climatic variability**

382   The elevational gradient provided a distinct climatic gradient, with warmer and drier

383   conditions towards the lower sites (Table 1). The mean annual temperature increased by

384   an average of 5.5°C between the highest and lowest sites during the study period.

385   Precipitation was 20 to 47% (data not shown) lower at the two lower sites compared to

386   the donor site. The number of cold days (ATB5) was generally considerably higher at

387   1350 and 1010 m than at 570 and 395 m, and the number of warm days (ATO25) had the

388   opposite trend. The lower altitudes had warmer conditions, but precipitation was not

389   linear along the elevational gradient. Precipitation varied widely between years, and the

390 saplings received considerable rainwater during spring and summer, despite the lower

391 rainfall at the lower altitudes (especially in 2015).

392 Higher mean temperatures during the 2015 growing season led to a higher evaporative

393 demand compared to the two previous years. For example, the accumulation of hours of

394 VPD > 1.5 kPa (AOVPD1.5) in the growing season 2015, were 107, 220, 444 and 366,

395 respectively at 1350, 1010, 570 and 395 m, but were 41, 33, 65 and 92 h, respectively, at

396 the same sites in the previous year (Table 1). Mean temperature, however, was not always

397 a good indicator of the dryness of the air. The mean temperatures at the lowest site during

398 the 2013 and 2014 beech growing seasons were 16.5 and 16.1°C, respectively, but

399 AOVPD1.5 was 2.5-fold higher in 2013 than 2014. Similarly, the mean temperatures at

400 570 m during the 2013 and 2015 beech growing seasons were 17.6 and 17.2°C, and the

401 corresponding AOVPD1.5 were 160 and 444 h, respectively.

402 **3.1.2** Comparison of soil moisture along the gradient

403 Globally, we observed a soil moisture gradient between the higher sites (1350 m and 1010

404 m) and the lowest site (395 m and 570 m) (Table 1, see also supplementary Fig S1). This

405 gradient was notable during the growing season 2015.

406 Table 1: Interannual climatic variability along the elevational gradient during the study period. Mean annual air temperature and mean growing season length
407 (GSL) was calculated for each species (F.s., beech; P.a., spruce), site, altitude and year. Soil moisture is presented by the average volumetric water content in
408 the soil (VWC, m^3/m^3), measured at hour resolution by sensors 5TM (Decagon S.A) placed at 20cm soil depth, during the period from May to July. For each
409 length of growing season (GSL, days), we calculated the corresponding precipitation rate, number of hours with vapor-pressure deficit above 1.5 kPa (VPD >
410 1.5), number of hours of temperature below 5°C (T < 5°C), number of hours of temperature above 25°C (T > 25°C), number of hours of temperature below or
411 equal to 0°C (T ≤ 0°C), and the number of events with more than 30 consecutive days without rainfall (P ≥ 30).

412

Altitude (m)	Year	Mean annual temp. (°C)	GSL (d)		May-July Soil VWC (m³/m³)		Growing season													
							Mean temp. (°C)		Precipitation rate (mm/d)		VPD >1.5 kPa (h)		T < 5°C (h)		T > 25°C (h)		T ≤ 0°C (h)		P ≥ 30 (# events)	
			F.s.	P.a.	F.s.	P.a.	F.s	P.a.	F.s.	P.a.	F.s.	P.a.	F.s.	P.a.	F.s.	P.a.	F.s.	P.a.	F.s.	P.a.
	2013	5.0	98	93	0.38	0.31	12.7	12.5	4.4	4.6	28	16	204	204	23	17	3	3	0	0
1350	2014	5.9	133	125	0.40	0.32	11.3	11.5	4.2	4.3	41	41	189	148	6	6	0	0	0	0
	2015	6.1	113	120	0.36	0.36	12.8	12.9	3.0	2.9	107	41	244	148	83	6	15	0	0	0
	2013	5.2	142	141	0.44	0.39	10.9	11.0	4.7	4.5	48	48	209	196	86	86	2	2	0	0
1010	2014	7.7	158	159	0.54	0.22	12.8	12.8	4.8	4.8	33	33	95	95	34	34	0	0	0	0
	2015	7.9	159	147	0.15	0.18	14.1	14.3	4.0	3.9	220	208	124	95	195	195	0	0	0	0
	2013	9.8	152	148	0.20	0.20	17.6	17.7	1.9	2.0	160	160	35	35	186	186	0	0	1	1
570	2014	10.9	166	164	0.17	0.20	15.7	15.9	3.3	3.2	65	65	15	15	115	115	0	0	0	0
	2015	10.6	174	166	0.10	0.17	17.2	17.5	3.8	3.2	444	441	10	6	447	447	0	0	0	0
	2013	10.1	171	157	0.16	0.20	16.5	16.8	3.9	3.9	228	228	20	13	284	284	0	0	0	0
395	2014	11.4	182	169	0.14	0.16	16.1	16.5	3.1	3.2	92	92	23	1	77	77	0	0	0	0
	2015	11.5	182	163	0.07	0.20	17.4	17.9	1.8	1.1	366	365	12	11	466	466	0	0	1	1

413

3.2 Phenological responses to the simulated conditions of climate change

Spring phenology shifted along the elevational gradient for both species (Fig. 1). Budburst was delayed towards the higher altitudes by averages of ~4.8 d 100 m^{-1} ($\pm$ 0.16) and 4.0 d 100 m^{-1} ($\pm$ 0.42) for beech and spruce, respectively. Autumn phenology, i.e. budset and leaf senescence, tended to occur later at the lower altitudes, but the pattern was more variable and less pronounced than for budburst. Overall, a decrease in elevation extended the growing season. The growing season length (GSL) at 1350 and 395 m over the three years averaged 115 $\pm$ 10 d (mean $\pm$ 1 SE) and 179 $\pm$ 3 d for beech and 113 $\pm$ 10 and 165 $\pm$ 3 d for spruce, respectively. Interestingly, the interannual variation of GSL was higher at the donor than the lowest site for both species, at $\pm$ 10 and $\pm$ 3 at 1350 and 395 m, respectively.

The time lag between budset and senescence varied between years. For example, budset for both species in 2014 was very advanced compared to beech senescence, but budset and senescence in 2015 occurred at nearly the same time.
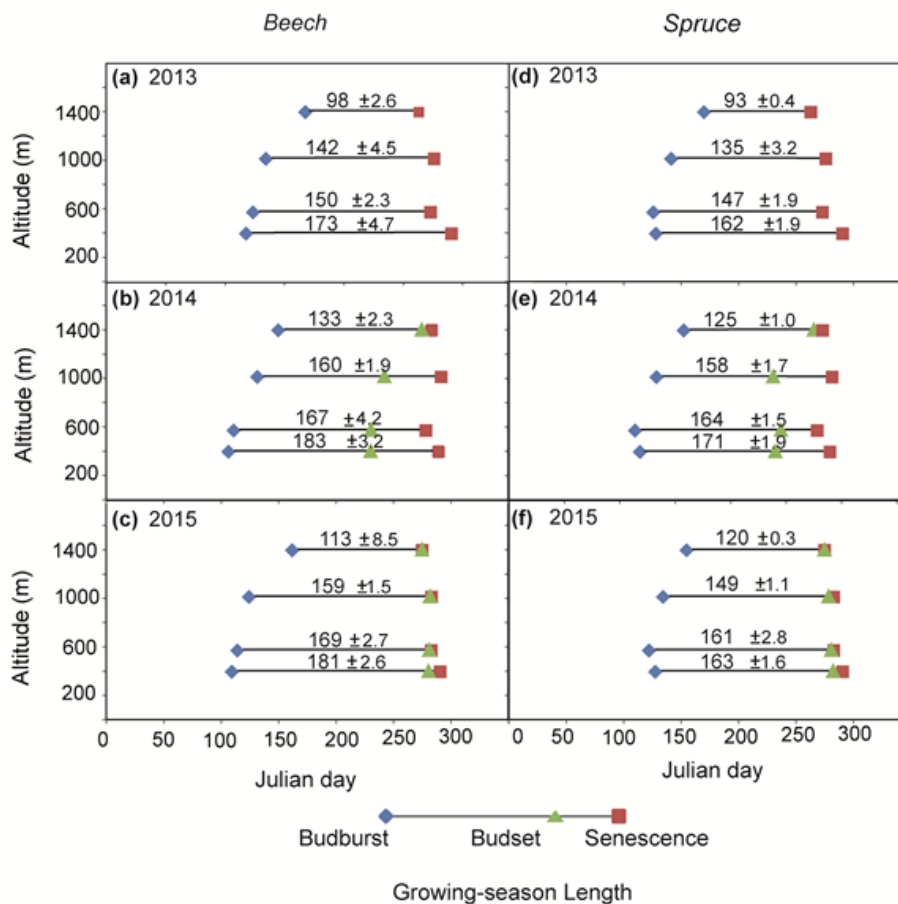
429 Fig. 1. Time of budburst, budset and leaf senescence for the beech and spruce saplings along the
430 elevational gradient in 2013, 2014 and 2015. The length of the growing season was defined as the
431 time between the dates of budburst and senescence, represented by the numbers above the black
432 lines (mean ± 1 SE). We pooled the treatments (irrigated and non-irrigated), because irrigation
433 did not have a significant effect on the phenological dates. The number of replicates for each
434 species and altitude were thus 20 in 2013 and 2014 and 10 in 2015.

435

3. 3. Growth responses to the simulated conditions of climate change

437 Exposure to the warmer and drier conditions at the lower altitudes for three years had

438 contrasting effects on beech and spruce saplings from 1350 m (Fig. 2). The growth of the

439 spruce saplings did not differ significantly along the elevational gradient, but beech

440 growth increased significantly between the donor and lower altitudes (Fig. 2a). Growth

441 increased more for spruce than beech at 1350 m but more for beech than spruce at 395 m.

442 Standardizing the growth data by the growing season length produced similar patterns,

443 which varied with altitude and species (Fig. 2b).
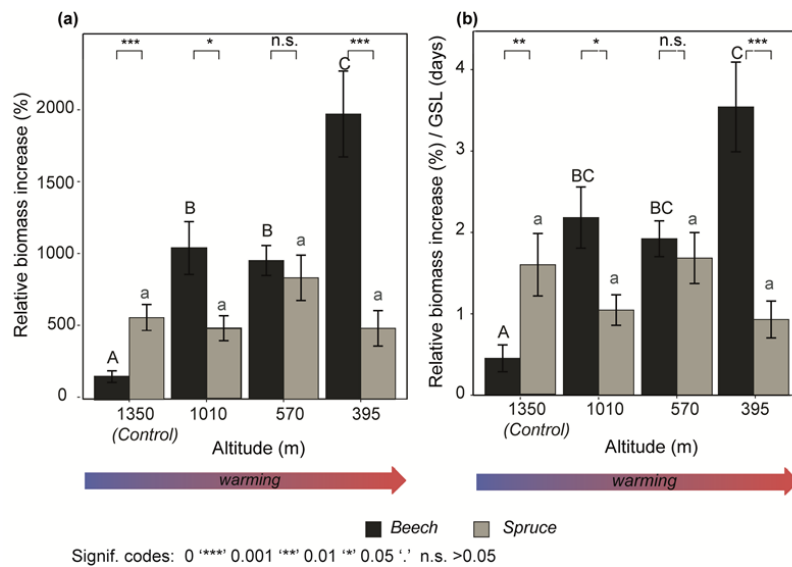
444

445 Fig. 2. Relative increase in biomass after three growing seasons (2013-2015) at the control site
446 (1350 m) and the three recipient sites. (a) Relative biomass increase and (b) relative biomass
447 increase standardized by the length of the growing season, which varied along the gradient and
448 for each species. The data for the irrigated and non-irrigated treatments were pooled because
449 irrigation did not have a significant effect ($P < 0.05$) on the increase in biomass during this period.
450 Different letters represent significant differences within a species, uppercase for beech and
451 lowercase for spruce, along the gradient identified by an ANOVA. The asterisks represent
452 significant differences between the means (± 1 SE) for each species at an altitude (n = 5) identified
453 by a Tukey's post hoc test.

454 **3.4 Effect size for tree growth under warmer and drier conditions**

16

The transplantation to warmer and drier conditions generally had a positive impact on beech growth and a negative impact on spruce growth. The growth of the beech saplings from 1350 m differed significantly between 2013 and 2015 (Fig. 3a), but the tree effect size was similar along the gradient in 2014, with an overall very positive effect relative to the donor site. We also observed a species-specific effect size at the same altitude. The effect size was mostly positive for beech but was negative for spruce (except in 2014). The irrigation treatment significantly mitigated the lower soil moisture, thus negative impact of warming on spruce growth in 2015 ($p = 0.001$).
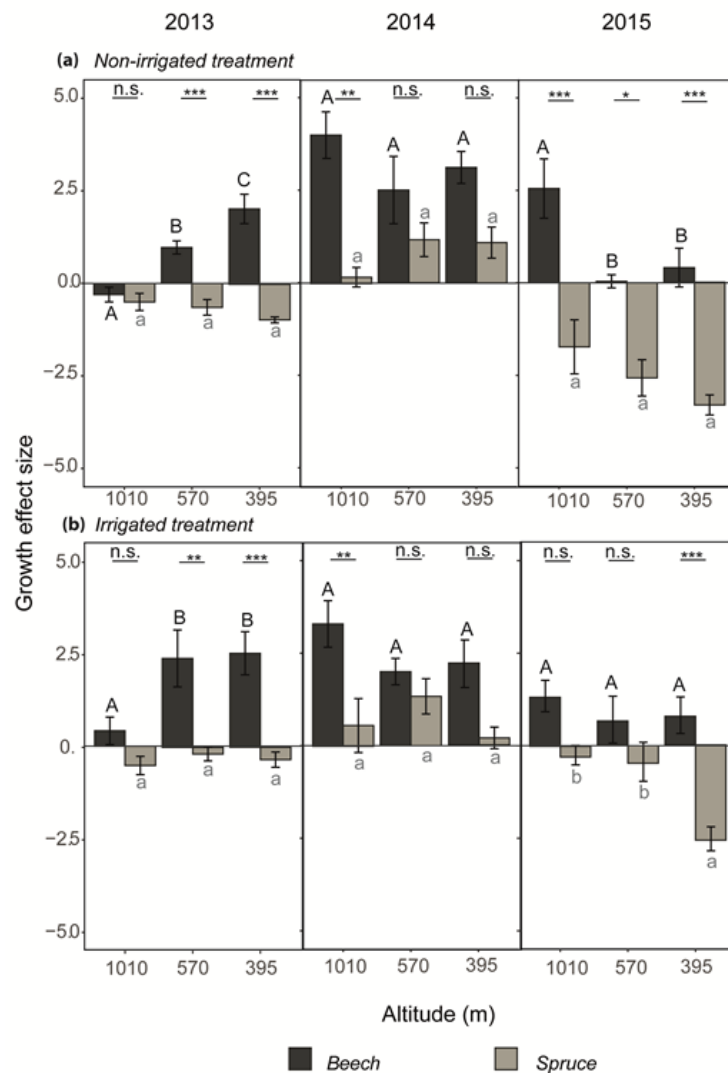

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' n.s. >0.05

Fig. 3. The effect size (1350 m as the control site) of the biomass increase along the gradient and throughout the three years for both species and for the non-irrigated (a) and irrigated (b) treatments. The larger the absolute value, the higher the impact of the local conditions on the relative biomass increase (standardized by GSL). Different upper- and lowercase letters represent significant differences within a species and year, respectively, identified by Tukey's post hoc tests.

469 Significant differences between the species at each altitude are indicated by asterisks above each

470 graph. The biomass annual increase (Δ % d^{-1}) was calculated for each sapling.

3.5 Impacts of the extreme climatic conditions on sapling growth

472 The relationship between effect size for growth and the measured extreme conditions

473 identified a distinct interannual climatic variability (Fig. 4). The AOVPD1.5 was lowest

474 in 2014, whereas 2015 had the longest period of dry air during the growing season, with

475 more than 400 h of AOVPD1.5. The effect size was negative beyond 300 h of AOVPD1.5

476 for beech and beyond 100 h for spruce. The effect size for cold days was negative for

477 beech in 2013, with growth decreasing as the number of cold days increased. In contrast,

478 the effect size for spruce had no clear pattern, suggesting that other variables limited its

479 growth. The irrigation treatment mitigated the negative effect of increasing VPD,

480 especially for spruce during the dry 2015 growing season.
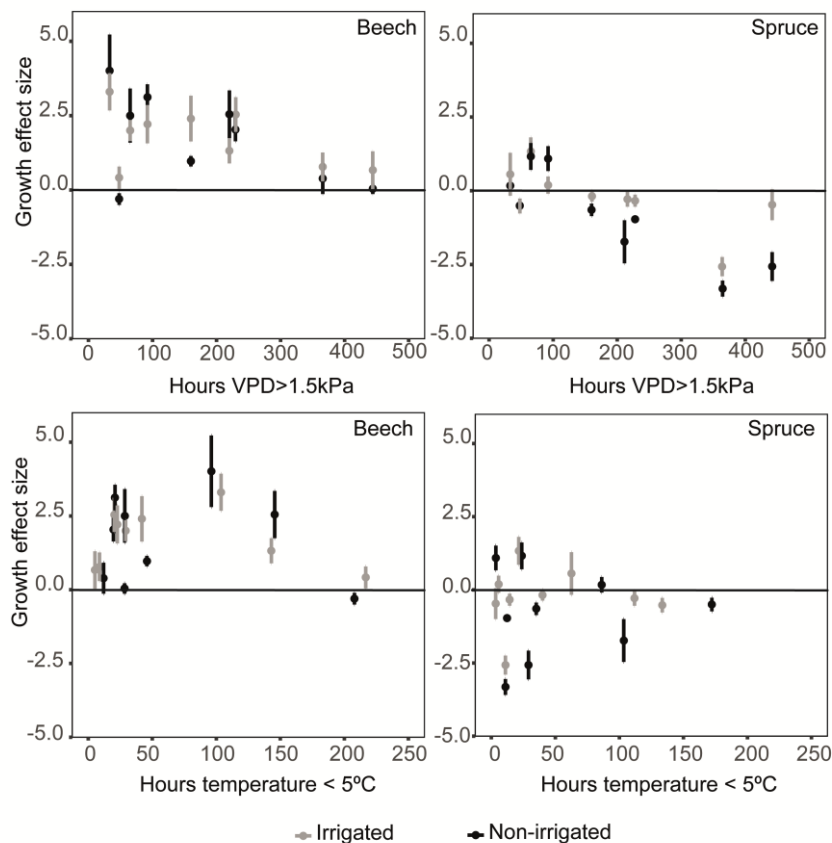
481

482 Fig. 4 Effect size (1350 m as the control) for biomass increase compared to the number of hours
483 of VPD > 1.5 kPa and the number of hours with T < 5°C for both species and treatments. The
484 larger the absolute value, the larger the impact of the extreme on the increase in biomass
485 (standardized by GSL and initial biomass). Each dot is the mean at a site ± 1 SE, with n = 10 for
486 2013 and 2014 and n = 5 for 2015.

487 The results from GAMM models of beech (Table 2) showed that the model including

488 only mean variables (i.e. Rain, Tmean and SoilVWC) was the less accurate for explaining

489 beech saplings' growth. However, when including the extreme variables (i.e. ABT5 and

490 AOVPD1.5) we observe an important increase in the explanation of beech biomass with

491 a R^2>0.75. Specifically, the model including ABT5, AOVPD1.5 and Rain, best explained

492 the growth response of beech with a R^2 of 0.94. Models explained in lesser extent the

493 growth patterns of spruce than those of beech, and none of the models presented a

494 significant effect of the soil moisture (Table 2).

495 Table 2: Results from GAMM models.. Biomass was the response variable explained by the
496 climatic variables Rain (amount of precipitation per day during the growing season), AOVPD1.5
497 (n° of hours during the growing season with VPD > 1.5 kPa), ABT5 (n° of hours during the
498 growing season with temperatures < 5°C), T_{mean} (mean temperature during the growing season),
499 P30 (n° of events of > 30 consecutive days without rainfall) and Soil VWC (may-July). All
500 explanatory variables were measured during the growing season. The model selection was based
501 on the Bayesian information criterion (BIC), the Akaike information criterion (AIC) and log
502 likelihood (logLik).

Beech

Model	Response variable	Explanatory variable	Signif var.	R-sq(adj)	df	AIC	BIC	logLik
1	sqrt (Biomass)	Rain	n.s.	0.17	10	140.9	152.7	-60.5
		Tmean	*					
		SoilVWC	n.s.					
2	sqrt (Biomass)	ABT5	***	0.79	10	114.3	126.1	-47.1
		AOVPD1.5	***					
		SoilVWC	n.s.					
3	sqrt (Biomass)	Rain	***	0.94	10	103.6	115.4	-41.8
		ABT5	***					
		AOVPD1.5	***					
4	sqrt (Biomass)	ABT5	***	0.77	8	110.9	120.3	-47.5
		AOVPD1.5	***					

Spruce

Model	Response variable	Explanatory variable	Signif var.	R-sq(adj)	df	AIC	BIC	logLik
5	Biomass	Rain	n.s.	0.47	10	254.5	265.9	-117.2
		Tmean	**					
		SoilVWC	n.s.					
6	Biomass	ABT5	***	0.47	10	245.6	257.0	-112.8
		AOVPD1.5	***					
		SoilVWC	n.s.					
7	Biomass	AOVPD1.5	***	0.6	10	243.5	254.8	-111.7
		ABT5	***					

		Rain	.					
8	Biomass	ABT5	***	0.48	8	242.1	251.2	-113.1
		AOVPD1.5	***					

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

503

Discussion

505 Transplanting saplings to lower elevation provides crucial insights on how trees in their
506 juvenile life stage will face climate change. The analysis of growth response over
507 contrasted climatic conditions from year to year allowed us to differentiate responses due
508 to mean over extreme climatic conditions. Here, focusing on growth performances, we
509 showed that beech saplings may benefit to warmer conditions and even drier conditions,
510 whereas spruce seems already constrained by water limitation and air dryness (VPD) at
511 low elevations of the Jura mountains. The higher sensitivity of spruce to increasing VPD,
512 compared to beech, likely explain its limited growth at the lower elevations. This study
513 highlights the importance to account for the effects of extreme climatic events when
514 assessing the impact of climate warming on tree performance because these events are
515 likely to deviate from the overall expected growth response to change in the mean climatic
516 conditions.

Contrasting growth responses of beech and spruce saplings exposed to simulated climate change

519 Beech and spruce saplings' growth was differently affected when transplanted towards
520 lower elevations during the three monitored years. In these drier and warmer conditions,
521 beech growth was significantly enhanced, whereas spruce growth was similar to the
522 growth at the native higher elevation site. The extension of the growing season may
523 explain such tendencies. Our phenological observations showed a lengthening of the
524 growing season towards the lower altitudes for both species, regardless of the proxy used
525 for the end of the growing season (budset or beech senescence). The time lag between
526 budset and senescence varied between years. For example, budset for both species was
527 substantially advanced in 2014 compared to beech senescence, but budset and senescence
528 occurred at nearly the same time in 2015, likely influencing the effective period of
529 nutrient mobilization. The growing season was nonetheless consistently longer at the
530 lower altitudes, which may partly account for the increase in beech biomass at the lower

531   altitudes, as also suggested by Lenz *et al.* (2014), but does not account for the patterns of

532   spruce growth. However, we found similar responses to warming when standardizing the

533   growth data by the length of the growing season. Increasing the length of the growing

534   season thus had a positive effect on tree growth only to a certain limit, which was species-

535   dependent. This suggests that additional factors (e.g. air temperature, VPD, nutrient

536   turnover) than phenological variations promoted beech growth while limiting spruce

537   growth at lower elevations.

538   The continuum of soil-plant-atmosphere is critical for tree growth and their respective

539   impacts in tree growth are very difficult to disentangle. However, depending on the site

540   conditions there is always one factor being more limiting than the others. In this study,

541   we aimed to find which factors explained best tree growth variation during years with

542   contrasted climate and at different elevations. Because the two species are known to be

543   sensitive to drought, one may expect that the transplantation of saplings to lower

544   elevations with warmer and drier conditions would expose them to water deficits and

545   limit their growth. However, we found that saplings were not water limited at the lower

546   sites during the growing seasons 2013 and 2014, which was also supported by the

547   ecophysiological measurements of leaf water potential (see supplementary table S1).

548   : "To answer the question as to whether it is VPD and not soil moisture that best explains

549   beech growth responses, we compared models 2 and 4 by test anova. This test revealed

550   that both models did not significantly differ in the degree of biomass explanation.

551   Therefore, by including the soil moisture variable (model 2) we did not add any valuable

552   information to the model (p-value= 0.73). We also observed that including the rain

553   variable (model 3) it increased significantly the explanation of beech biomass (p-value

554   =0.003). This means that by adding the rain term we did add more information in the

555   explanation of biomass variance. To sum up, model 3, which includes ABT5, AOVPD1.5

556   and Rain, best explained the growth response of beech with a R^2 of 0.94. All explanatory

557   variables were significant; the residuals of the model followed a normal distribution, and

558   AIC and BIC were the lowest compared to the other models, revealing that there is a good

559   balance between the fitness of the model and the number of explanatory variables. For

560   spruce, none of the models presented a significant effect of the soil moisture. Models

561   explained in lesser extent the growth patterns of spruce than those of beech, suggesting

562   that other factors, not taken into account in this study, may explain part of spruce's

563   biomass variance. Following the same logical procedure than beech we found that model

564 7, including the variable rain and the extremes, had a higher R² adj coefficient (0.6). In

565 conclusion, GAMM models showed that soil moisture was not a significant factor

566 explaining tree growth in this humid area of study. Interestingly, the "extreme" climatic

567 variables, ABT5 and AOVPD1.5, significantly explained tree growth and even more than

568 the models integrating exclusively "average" variables, such as mean temperature.

569 Growth rates between years revealed an interannual variability within species (Fig S2).

570 The growth patterns of beech showed that in 2013 and 2014 tree growth was higher at the

571 lowest elevation compared to the control site. In the growing season 2015, beech saplings

572 grew at the same rate along the gradient except at 1010 m. In contrast, spruce showed a

573 decrease in growth rate at lower altitudes compared to the control site, for years 2013 and

574 2015. Yet, interestingly higher growth rates were observed at lower altitudes (Fig S2 blue

575 rectangle) during the growing season 2014, in spite of the lower soil moisture and lower

576 amount of precipitation recorded during this year. Regarding atmospheric conditions,

577 average temperatures during the growing season hardly differed in 2013 and 2014, but

578 significantly differed in the amount of hours during which saplings were exposed to

579 elevated VPD. It has been hypothesized that VPD may trigger stomatal closure to avoid

580 an excess of water loss due to high evaporative demand of the air (Carnicer et al., 2013).

581 The degree of sensitivity of stomatal closure to elevated VPD is highly species-specific.

582 Two main hydraulic functional groups have been distinguished in the literature depending

583 on their strategies to cope with higher evaporative demand (Bond & Kavanagh, 1999;

584 Carnicer et al., 2013). Isohydric trees (e.g. spruce) avoid drought-induced hydraulic

585 failure via stomatal closure, reducing the carbon assimilation (McDowell et al., 2008;

586 Carnicer et al., 2013). This greater stomatal control maintains a relatively constant day-

587 time leaf water potential (see supplementary table S1). This allows them to prevent leaf

588 water potential from falling below a threshold associated with cavitation (McDowell et

589 al., 2008; Pangle et al., 2015) Typically, anisohydric tree species are associated with a

590 higher ability to reverse embolisms leading to this narrower hydraulic safety margins

591 compared to isohydric species (Carnicer et al., 2013). Therefore, the difference in amount

592 of hours with elevated VPD to which saplings were exposed in this study may cause

593 important physiological responses and cannot be disregarded.

594 Our findings show that beech and spruce respond differently to high VPD. Meanwhile,

595 the measurements of leaf water potential of these species also revealed us different

596 patterns of regulating water transpiration (see supplementary Table S1). It is known from

597   literature that species may exhibit intraspecific variation in degree of anisohydricity or
598   isohydricity (Cocozza et al., 2016) meaning that no species is strictly anisohydric or
599   isohydric. However, in our study beech did present a more anisohydric behaviour than
600   spruce (see supplementary Table S1). Therefore, we suggest that the different responses
601   to elevated VPD could be linked to a difference in isohydric behavior. Our results show
602   that increasing VPD limits tree growth even before soil moisture starts to be limiting.
603   Moreover, tree growth is even more limited when both VPD and soil moisture reach
604   limiting thresholds. The key finding of this paper is the demonstration of the different
605   degree of sensitivity of these species to increasing VPD, and suggesting that this
606   sensitivity is linked to the degree of isohydricity of these two species.

607   Many other authors have also hypothesized that contrasting growth responses between
608   angiosperms and gymnosperms is due to species different sensitivities of stomatal
609   conductance to vapor pressure deficit leads to contrasting growth responses (Martínez-
610   Ferri et al., 2000; Brodersen et al., 2010; Carnicer et al., 2013; Coll et al., 2013; Meinzer
611   et al., 2013). In the contrast, Martínez-Vilalta and Garcia-Forner (2017) have recently
612   argued that water potential regulation and stomatal behavior are decoupled across
613   species, so it remains today as an open debate whether isohydric and anisohydric trees
614   lead to different responses to VPD. Further research in this topic is encouraged.

615   **The use of means and extremes for analysing the impact of interannual climatic**
616   **variability on the growth responses of the saplings**

617   Growth responses are commonly correlated with mean temperatures (Bowman,
618   Williamson, Keenan, & Prior, 2014; Jump, Hunt, & Peñuelas, 2006; Lévesque, Rigling,
619   Bugmann, Weber, & Brang, 2014; Miyamoto et al., 2010; Way & Oren, 2010). Mean
620   annual temperature in our study differed by ca. 5.5°C between the native and lowest sites.
621   Growth of saplings inhabiting high elevation (1350 m) are likely to be limited by
622   temperature and we expect warmer temperatures to elicit positive effects on growth, in
623   the absence of water stress (Way & Oren, 2010). Yet, growth was not enhanced for spruce
624   when transplanted towards lower elevations in contrast to beech. This difference or
625   response may root in different sensitivity of the two species to extreme climatic
626   conditions, in particular to high VPD, which can be observed by analysing growth
627   response of the two species to interannual climatic variations.

628 For instance, cold spells at the beginning of the season were about twice as long in 2013

629 as in the other two years. Important precipitation deficits were further observed in the two

630 lowest sites for more than 30 consecutive days (at 570 m in 2013 and at 395 m in 2015)

631 compared to the native site. Thus, the mean interannual climatic variability of 2°C did not

632 fully explain tree growth pattern because it hides substantial variations in the extreme

633 climatic values and their frequency. The mean temperature during the growing season at

634 the lowest site (395 m) was similar in 2013 and 2014, with 16.5 and 16.1°C, respectively,

635 which was 3.8 - 4.8°C higher than at the donor site. The quantification of the effect size,

636 however, identified contrasting growth responses for spruce between these two years: the

637 effect size was negative in spruce's growth response to warming in 2013 whilst a positive

638 effect size was found in 2014. Spruce saplings were subjected to 228 hours of AOVPD1.5

639 at the lowest site in 2013, which is more than twice as much as in 2014 (92 hours). An

640 exceedance in VPD above the threshold of 1.5kPa can stimulate the closure of stomata in

641 spruce (Kurjak et al., 2012; Zweifel et al., 2002). Assuming that there is a reduction in

642 carbon up take, or even suppression depending on the degree of stomatal closure, these

643 results suggest that spruce growth was limited by a large amount of VPD hours above 1.5

644 kPa in 2013 but not in 2014. Spruce is more sensitive to VPD increases than beech as it

645 closes rapidly its stomata to reduce hydraulic conductivity before substantial cavitation

646 occurs. By contrast, stomatal conductance in beech, an angiosperm, can remain high even

647 at very high evaporative demands due to its higher capacity to reverse embolisms

648 (Carnicer et al., 2013).

649 Saplings' growth transplanted at 1010 m were likely constrained by temperature (Koch,

650 1958; Modrzyński & Eriksson, 2002).There was a strong contrasting growth response for

651 beech between 2013 and 2014 at this site associated to the 2°C difference in mean

652 temperature during the two growing seasons, i.e. warmer temperature during summer

653 2014 may have contributed to enhance beech growth. Conversely, the growth of the

654 saplings at the lowest sites was likely strongly limited by water in 2015. Rainfall was

655 47% lower at 395 m, accompanied by an increase in AOVPD1.5 of 259 h compared to

656 the donor site. A water deficit also occurred at the treatment level; irrigation had a lower

657 negative impact on the growth response, i.e. the impact of a water deficit in 2015 for

658 spruce was mitigated by the irrigation treatment ($P = 0.001$).

659 **Difference in species sensitivities to extreme conditions due to different tolerance**

660 **thresholds**

The quantitative assessment of the impacts of an increase in the AOVPD1.5 and ABT5 on tree growth provided new insights for assessing climate-growth relationships. The higher sensitivity of spruce than beech to increasing VPD could account for the limited growth of spruce at the lower altitudes. We used a scatterplot of VPD vs. growth effect size to determine the approximate upper limit threshold for each species. The lower tolerance limit of spruce (~100 h) compared to beech (~300 h) partly could account for the contrasting growth responses between these species. The negative impacts of extreme conditions also depended on the conditions of the site, i.e. the impact on growth was not the same at 1010 and 395 m for the same duration of increased VPD, mainly due to the differences in the limitation of tree growth at higher and lower altitudes (temperature vs. water deficit). The absence of a clear response of spruce to the length of cold spells during the growing season suggested that spruce growth was limited by other variables. In contrast, beech growth was negatively affected by an ABT5 above 200 h during the growing season. The large range of responses of both species under this threshold of 200 h indicated that lower temperatures were not the main limitation to growth at the recipient sites. Our results suggest that both spruce and beech are limited by increasing air dryness but present different degrees of tolerance. The final GAMMs identified VPD as the main explanatory variables of the increases in biomass for both species. As second main explanatory variable the precipitation rate during the growing season (mm/day GS) was determinant factor for beech while the number consecutive days without precipitation during the growing season was for spruce. This leads to a differentiation between the main factor which is common for both species (VPD) and more species-dependent factors related to precipitation and consecutive days without rain.

We conclude that elevated vapor deficit limits tree growth. Our results showed that (i) a longer growing season due to induced-elevation warming (downward shift) could not fully account for the species-specific positive growth responses; (ii) the contrasting species growth responses were linked to different sensitivities to elevated vapor-pressure deficits; (iii) models could better account for the growth response to warming after incorporating extreme climatic events and their effects. On the top of that, for the first time we determined the threshold above which tree growth starts to decline for each species when soil moisture was not limiting. It is however likely that if soil moisture would have been lower during these high VPD conditions saplings growth would have been further reduced. Finally, the inclusion of climate extremes will likely improve

models predicting species distribution under future climatic conditions (Zimmermann et

695 al., 2009). The potential extrapolation of this approach and results, through further

696 research on adult trees, will be crucial for a better understanding of forest response to

697 climate change and for adapting forest management to the predicted increase in duration

698 and in frequency of extreme climate conditions.

699

700 **Supplementary information**

701

702 Supplementary Fig. S1 Variation of the volumetric water content (VWC %) measured weekly
703 (years 2013 and 2014) by means of TDR at 20 cm depth along the elevation gradient. The specific
704 dates correspond to ecophysiological measurements (i.e. stomatal conductance, predawn and
705 midday leaf water potential) performed under same environmental conditions (see supplementary
706 Table S1). Considering that at 1350 m trees are more temperature limited than water limited, we
707 fixed 20 % of VWC at 20 cm as the minimum soil moisture observed in the control site (red line).
708 We observed that beech saplings growing at the two lower altitudes experience values of VWC
709 under this threshold no matter the treatment (either irrigated or non-irrigated), while for spruce
710 the saplings irrigated at the lowest elevation experienced the lowest values of VWC

711

712
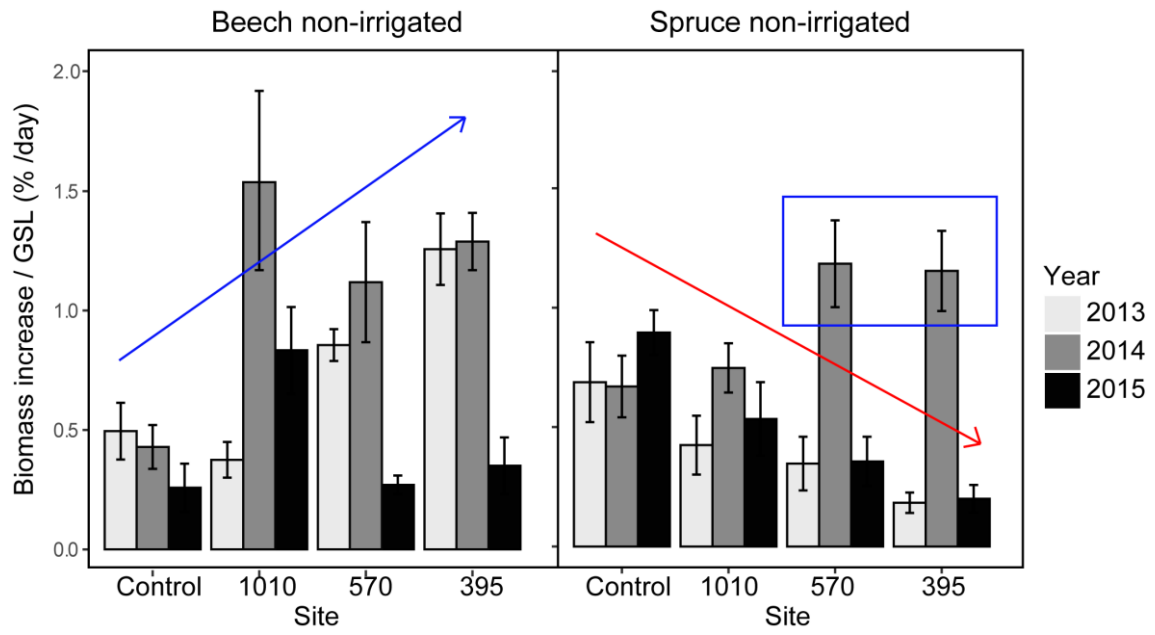
Supplementary Fig. S2: Temporal and spatial trends of biomass increase standardized by the growing season

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715

716

Supplementary Table S1 Ecophysiological measurements in leaves performed twice during the growing seasons 2013 and 2014 at each elevation (m). The mean values of predawn leaf water potential Ψ_p (MPa), midday leaf water potential Ψ_m (MPa) and leaf stomatal conductance (mmol g^{-1} s^{-1}) $\pm$ the standard error (SE) for both treatments non-irrigated (NI) and irrigated (I)

Elevation	Species	Leaf trait	Year 2013								Year 2014							
			1.7.2013				29.8.2013				16.7.2014				27.8.2014			
			NI	SE	I	SE	NI	SE	I	SE	NI	SE	I	SE	NI	SE	I	SE
1350	Beech	Ψ_p	-0.1	± 0.02			-0.2	± 0.09			-0.1	± 0.01			-0.2	± 0.03		
		Ψ_m	-1.5	± 0.00			-2.4	± 0.41			-1.9	± 0.13			-1.4	± 0.22		
		Gs	0.8	± 0.74			4.1	± 0.70			1.7	± 0.30			2.9	± 0.33		
	Spruce	Ψ_p	-0.3	± 0.03			-0.5	± 0.08			-0.3	± 0.04			-0.5	± 0.04		
		Ψ_m	-1.2	± 0.09			-1.6	± 0.18			-1.4	± 0.05			-1.1	± 0.20		
		Gs	0.9	± 0.12			1.1	± 0.30			1.5	± 0.22			1.8	± 0.18		
1010	Beech	Ψ_p	-0.3	± 0.05	-0.1	± 0.01	-0.1	± 0.03	-0.2	± 0.02	-0.1	± 0.00	-0.1	± 0.03	-0.2	± 0.05	-0.2	± 0.03
		Ψ_m	-1.2	± 0.27	-1.8	± 0.32	-2.4	± 0.07	-2.6	± 0.20	-2.3	± 0.15	-2.2	± 0.12	-1.4	± 0.46	-2.1	± 0.09
		Gs	3.2	± 0.40	3.9	± 0.25	6.7	± 0.57	5.8	± 1.13	2.5	± 1.02	3.7	± 0.90	7.0	± 0.78	6.6	± 1.79
	Spruce	Ψ_p	-0.3	± 0.05	-0.2	± 0.04	-0.5	± 0.08	-0.5	± 0.03	-0.2	± 0.04	-0.4	± 0.15	-0.4	± 0.08	-0.5	± 0.04
		Ψ_m	-1.1	± 0.09	-1.3	± 0.10	-1.8	± 0.06	-1.8	± 0.12	-1.7	± 0.09	-1.7	± 0.23	-1.3	± 0.03	-1.0	± 0.17
		Gs	1.1	± 0.13	1.3	± 0.09	1.2	± 0.23	1.4	± 0.16	1.7	± 0.44	1.9	± 0.15	1.0	± 0.44	1.4	± 0.26
570	Beech	Ψ_p	-0.1	± 0.06	-0.1	± 0.08	-0.7	± 0.16	-0.8	± 0.30	-0.1	± 0.01	-0.1	± 0.00	-0.2	± 0.02	-0.2	± 0.03
		Ψ_m	-2.1	± 0.13	-1.9	± 0.12	-2.8	± 0.12	-2.9	± 0.05	-2.3	± 0.01	-2.5	± 0.24	-1.5	± 0.20	-1.9	± 0.22
		Gs	3.8	± 1.06	3.0	± 0.22	1.6	± 0.35	3.2	± 1.20	2.5	± 0.16	3.1	± 0.94	3.9	± 0.44	3.6	± 0.38
	Spruce	Ψ_p	-0.2	± 0.09	-0.4	± 0.09	-0.4	± 0.05	-0.4	± 0.05	-0.2	± 0.03	-0.1	± 0.16	-0.4	± 0.01	-0.4	± 0.10
		Ψ_m	-1.5	± 0.19	-1.3	± 0.12	-1.9	± 0.13	-1.6	± 0.22	-1.7	± 0.18	-1.5	± 0.28	-1.1	± 0.16	-1.0	± 0.08
		Gs	1.0	± 0.10	0.9	± 0.06	0.6	± 0.09	0.6	± 0.19	1.2	± 0.19	1.2	± 0.42	1.1	± 0.17	1.2	± 0.16
395	Beech	Ψ_p	-0.3	± 0.10	-0.2	± 0.06	-0.5	± 0.37	-0.7	± 0.38	-0.1	± 0.01	-0.1	± 0.01	-0.2	± 0.04	-0.2	± 0.02
		Ψ_m	-1.9	± 0.09	-1.8	± 0.12	-3.0	± 0.31	-2.2	± 0.22	-2.5	± 0.18	-2.4	± 0.12	-2.5	± 0.17	-2.0	± 0.24
		Gs	3.4	± 0.65	3.5	± 0.73	2.5	± 0.67	2.9	± 0.64	4.3	± 0.45	1.8	± 0.18	5.2	± 0.30	4.8	± 1.03
	Spruce	Ψ_p	-0.2	± 0.09	-0.2	± 0.04	-0.6	± 0.00	-0.6	± 0.11	-0.2	± 0.04	-0.2	± 0.02	-0.4	± 0.07	-0.3	± 0.03
		Ψ_m	-1.2	± 0.03	-1.2	± 0.12	-1.7	± 0.25	-2.2	± 0.18	-1.6	± 0.03	-1.4	± 0.24	-0.9	± 0.14	-0.9	± 0.17
		Gs	1.2	± 0.28	1.3	± 0.12	0.6	± 0.15	0.6	± 0.31	1.1	± 0.46	0.9	± 0.44	1.3	± 0.38	1.1	± 0.20

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