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Vapor-pressure deficit and extreme climatic variables limit tree growth

Running head: Vapor-pressure deficit limits tree growth

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Abstract

Assessing the effect of global warming on forest growth requires a better understanding of species-specific responses to climate change conditions. Norway spruce and European beech are among the dominant tree species in Europe and are largely used by the timber industry. Their sensitivity to changes in climate and extreme climatic events, however, endangers their future sustainability. Identifying the key climatic factors limiting their growth and survival is therefore crucial for assessing the responses of these two species to ongoing climate change. We studied the vulnerability of beech and spruce to warmer and drier conditions by transplanting saplings from the top to the bottom of an elevational gradient in the Jura Mountains in Switzerland. We (1) demonstrated that a longer growing season due to warming could not fully account for the positive growth responses, and the positive effect on sapling productivity was species-dependent, (2) demonstrated that the contrasting growth responses of beech and spruce were mainly due to different sensitivities to elevated vapor-pressure deficits, (3) determined the species specific limits to vapor-pressure deficit above which growth rate began to decline and (4) demonstrated that models incorporating extreme climatic events could account for the response of

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

44

45 **Keywords**

46 Tree growth, spruce, beech, climate change, vapor-pressure deficit, extreme events,
47 wooded pastures

48

49 **1. Introduction**

50 Climate change is currently escalating so rapidly that many trees may not be able to adapt
51 (Rogers, Jantz, & Goetz, 2017). In addition to the gradual global warming, the frequency
52 and severity of extreme events such as heat waves, heavy precipitation, summer droughts
53 and cold spells are expected to increase in the coming decades (IPCC, 2013; Schar et al.,
54 2004) , which may ultimately determine future tree distributions (Zimmermann et al.,
55 2009). Extreme events can have strong impacts on tree growth and survival, due to
56 typically stronger responses and shorter response times than for normal climatic events
57 (Hanson, Palutikof, Dlugolecki, & Giannakopoulos, 2006; Kreyling, Jentsch, &
58 Beierkuhnlein, 2011). Forest researchers must estimate the resilience of forests to
59 expected climate change and extreme climatic events to guide sustainable forest
60 management (Lindner et al., 2014). An increasing number of studies are therefore testing
61 the impact of extreme events on forest growth (Ciais et al., 2005; Teskey et al., 2015),
62 some under controlled conditions (Lendzion & Leuschner, 2008). Experiments are often
63 conducted *ex situ* (e.g. in climate-controlled chambers), which is valuable for
64 understanding the impact of a single factor on tree physiology but does not represent real
65 *in situ* conditions that involve many abiotic and biotic interactions that determine tree
66 growth (De Boeck, Dreesen, Janssens, & Nijs, 2010; Körner et al., 2016; Vicca et al.,
67 2016; Zimmermann et al., 2009).

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

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

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

90 The stomatal response of trees to changing environmental conditions is complex and it is
91 a process which is still not well understood (Damour et al., 2010). The closure of stomata
92 at midday is regulated by the water available in the soil, leaf and atmosphere, and it is
93 highly species-specific (Bond & Kavanagh, 1999). Stomatal responses to increasing
94 evaporative demand of the air seem to be another explanation for the contrasting growth
95 responses between functional groups. Carnicer et al. (2013) reviewed various hypotheses
96 that could account for the contrasting responses of growth to temperature in
97 Mediterranean angiosperm and coniferous trees. They included a hypothesis involving
98 the effect of eco-physiological and hydraulic traits on tree growth. More specifically, they
99 suggested that different sensitivities of stomatal conductance to vapor-pressure deficit
100 (VPD) lead to different growth responses. Several studies have been performed in order
101 to understand the mechanisms triggering stomatal closure in response to vapor pressure
102 deficit (Sellin, 2001; Brodribb & McAdam, 2011; Mott & Peak, 2013) and agree that
103 stomata typically close at high VPD and open at low VPD (McAdam & Brodribb, 2015).
104 The sensitivity of VPD to changes in air temperature differs among plant functional
105 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

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

152

153 **2. Materials and methods**

154 *2.1 Study sites and elevational gradient*

155 The conditions of climate change were simulated using an elevational gradient along a
156 south-facing slope of the Jura Mountains in Switzerland. This space-for-time substitution
157 (Körner, 2003) simulated a climatic gradient, i.e. an increase in temperature and a
158 decrease in precipitation towards lower altitudes. A detailed description of the site
159 selection is given by Gavazov *et al.* (2014). Briefly, the donor site was at Combe des
160 Amburnex (N46°54', E6°23'; 1350 m a.s.l.), with an oceanic climate, a mean annual
161 temperature and precipitation of 4.5°C and 1750 mm, respectively, and a permanent snow
162 cover from November to may (K. S. Gavazov, Peringer, Buttler, Gillet, & Spiegelberger,
163 2013). The three recipient sites were at St.-George at 1010 m a.s.l. (N46°52', E6°26'),
164 Arboretum d'Aubonne at 570 m a.s.l. (N46°51', E6°37') and Les Bois Chamblard at 395
165 m a.s.l. (N46°47', E6°41'). Combe des Amburnex was the control site with native climatic
166 conditions, so this climatic gradient covered three possible warming scenarios of the
167 Intergovernmental Panel on Climate Change (K. S. Gavazov *et al.*, 2013; K. Gavazov *et al.*,
168 2014): moderate at 1010 m a.s.l. (on average + 2°C and 20 % rainfall reduction),
169 intermediate at 570 m a.s.l. (+ 4°C and 40 % rainfall reduction) and extreme at 395 m
170 a.s.l. (+ 5°C and 50 % rainfall reduction).

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

185 2.2 *Experimental design and species*

186 Saplings of beech (*Fagus sylvatica* L.) and spruce (*Picea abies* (L.) H.Karst.) were
187 collected at the donor site (1350 m) immediately before the budburst of the 2012 growing
188 season. The surface of collection was assumed to be reduced enough to ensure the same
189 provenance of saplings. The saplings had similar sizes (average height of 33 cm for beech
190 and 31 cm for spruce) and were excavated with intact root systems and soil. They were
191 then transplanted to 20-L pots and randomly reallocated in four plots, one at each altitude,
192 in open spaces and far enough from the forest to avoid shade from surroundings adult
193 trees. Half of the saplings were transplanted a second time to 40-45-L pots in autumn
194 2014, two years after the first transplantation, due to the potential limitation of growth by
195 the initial pots. The other half was harvested for analysis. The soil of the harvested plants
196 was used for the transplantation of the remaining individuals to maintain the same soil
197 characteristics for each species and site.

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

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

236 components (stem, four longest branches, remaining branches and roots) were separated
237 in the laboratory and placed in paper bags. *Sa*, *Sb*, *H*, *Ba*, *Bb* and *l* were measured on the
238 stems and main branches, which were then oven-dried at 65 °C to constant weights. These
239 independent variables and their combinations (e.g. stem diameter and height) were then
240 correlated with the total dry weight (g) using linear regressions to obtain the most
241 parsimonious model.

242 *2.3.2.2. Model construction and validation*

243 Several criteria were followed for selecting the optimal allometric equation for each
244 species: (1) the highest adjusted coefficient of determination (R^2_{adj}), (2) the lowest root-
245 mean-square error RMSE, (3) $F < 0.05$, (4) the regression model with the best biomass
246 estimates for both species and (5) and the practicality of the model (cost of measuring the
247 independent variables).

248 The selected model indirectly estimated the aboveground biomass using the total volume
249 of the stem and the four main branches (Eq. 1). This method was the best for quantifying
250 and comparing the aboveground biomass of the two species with different growth patterns
251 (i.e. beech growing in height and spruce producing more branches). The model developed
252 was:

$$253 \quad \text{Ln}(B) = c + a\text{Ln}(V) \quad \text{Eq. (1)}$$

254 where *B* is the aboveground woody biomass (g), *V* is the total volume of the four main
255 branches and stem (cm³) and *c* is the intercept and *a* is the slope coefficient of the
256 regression line. The allometric equation for beech was $B = \exp^{(1.012535 * (\text{Ln}(V)) - 0.585528)}$,
257 with an R^2_{adj} of 0.995 and $P < 0.0001$. The model for spruce was $B = \exp^{1.00926 * (\text{Ln}V)}$,
258 with an R^2_{adj} of 0.997 and $P < 0.0001$. The model selected for
259 each species was then validated with half of the saplings used in the study harvested in
260 autumn 2014 during the transplantation to larger pots.

261 We used these models to calculate the initial and final biomasses of each sapling for each
262 growing season. The difference between the final and initial biomasses was divided by
263 the initial biomass to normalize for sapling size, allowing the removal of any possible
264 effect of sapling size.

265 *2.4. Definition of length of the growing season*

266 *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
$$x_t = \frac{\alpha_t \times (100 - \beta_t)}{100} + \beta_t \quad \text{Eq. (2)}$$

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

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

300 *2.5 Defining mean climatic variables*

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

312 *2.6 Defining climatic extremes*

313 There is no accurate definition related to the existence of an “extreme” (Stephenson,
314 2008). An established definition would be “an episode or occurrence in which a
315 statistically rare or unusual climatic period alters ecosystem structure and/or function well
316 outside the bounds of what is considered typical or normal variability” (Smith, 2011). A
317 special report of IPCC (Murray & Ebi, 2012) defined an “extreme climate or weather
318 event” or “climate extreme” as “the occurrence of a value of a weather or climate variable
319 above (or below) a threshold value near the upper (or lower) ends of the range of observed
320 values of the variable”. They clarify definition by stating that it includes absolute
321 thresholds as extreme events and give the example of specific critical temperatures for
322 health impacts.

323 In this study, we defined “extreme” as done by IPCC (Murray & Ebi, 2012) in a special
324 report about managing the risks of extreme events. Therefore, we established impact-
325 related thresholds in beech and spruce performance for saplings growing in the Swiss
326 Jura. The thresholds were based in thermal-hydric requirements of each species. Vapor
327 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
$$\text{VPD} = (1 - (\text{RH}/100)) * \text{SVP} \text{ Eq. (3)}$$

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 biomass to 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^2_{adj} and the normality of
359 residuals to compare the different models. As explanatory variables, we included soil

360 moisture (m^3/m^3) along with the other “average” variables Tmean ($^{\circ}\text{C}$), 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
$$Effsize[i] = \frac{x[i]-\bar{x}_c}{\sigma x_c} \text{ Eq. (4)}$$

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, m³/m³), 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

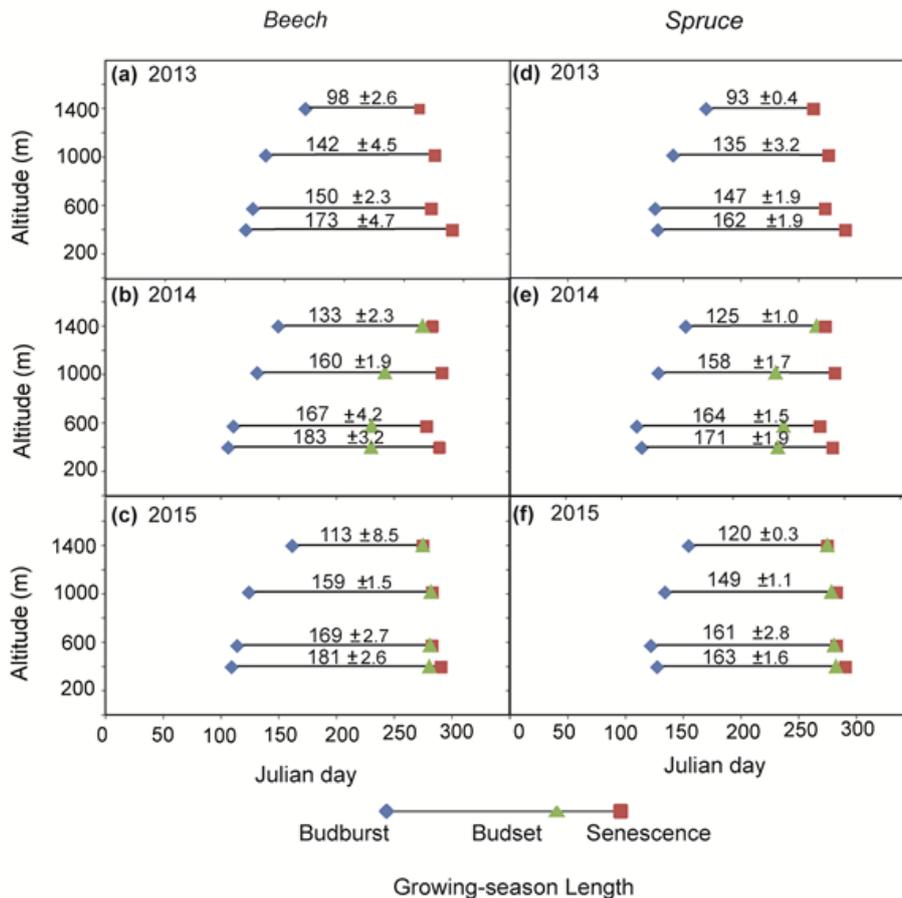
Altitude (m)	Year	Mean annual temp. (°C)	GSL (d)		May-July		Growing season													
					Soil VWC (m ³ /m ³)		Mean temp. (°C)		Precipitation rate (mm/d)		VPD >1.5 kPa (h)		T < 5°C (h)		T > 25°C (h)		T ≤ 0°C (h)		P ≥ 30 (# events)	
			F.s.	P.a.	F.s.	P.a.	F.s.	P.a.	F.s.	P.a.	F.s.	P.a.	F.s.	P.a.	F.s.	P.a.	F.s.	P.a.	F.s.	P.a.
1350	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
	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
1010	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
	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
570	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
	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
395	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
	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

414 **3.2 Phenological responses to the simulated conditions of climate change**

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

425 The time lag between budset and senescence varied between years. For example, budset
 426 for both species in 2014 was very advanced compared to beech senescence, but budset
 427 and senescence in 2015 occurred at nearly the same time.



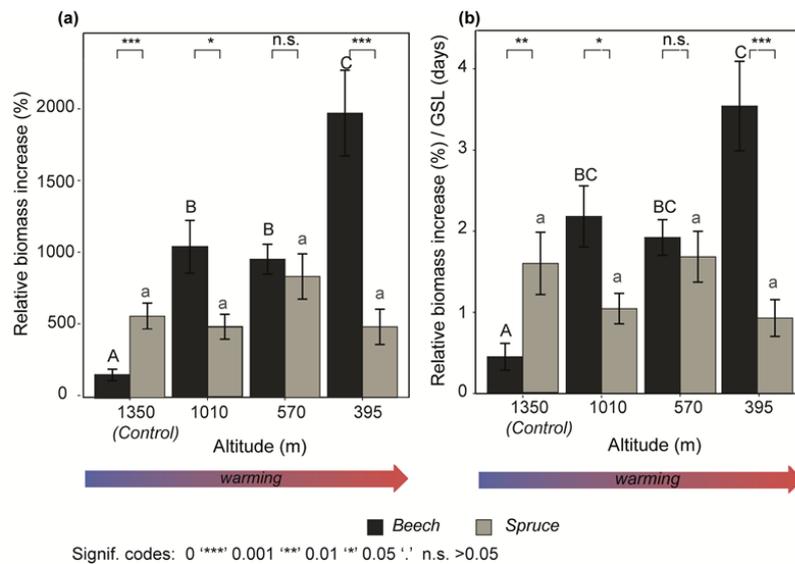
428

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 \pm 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

436 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).

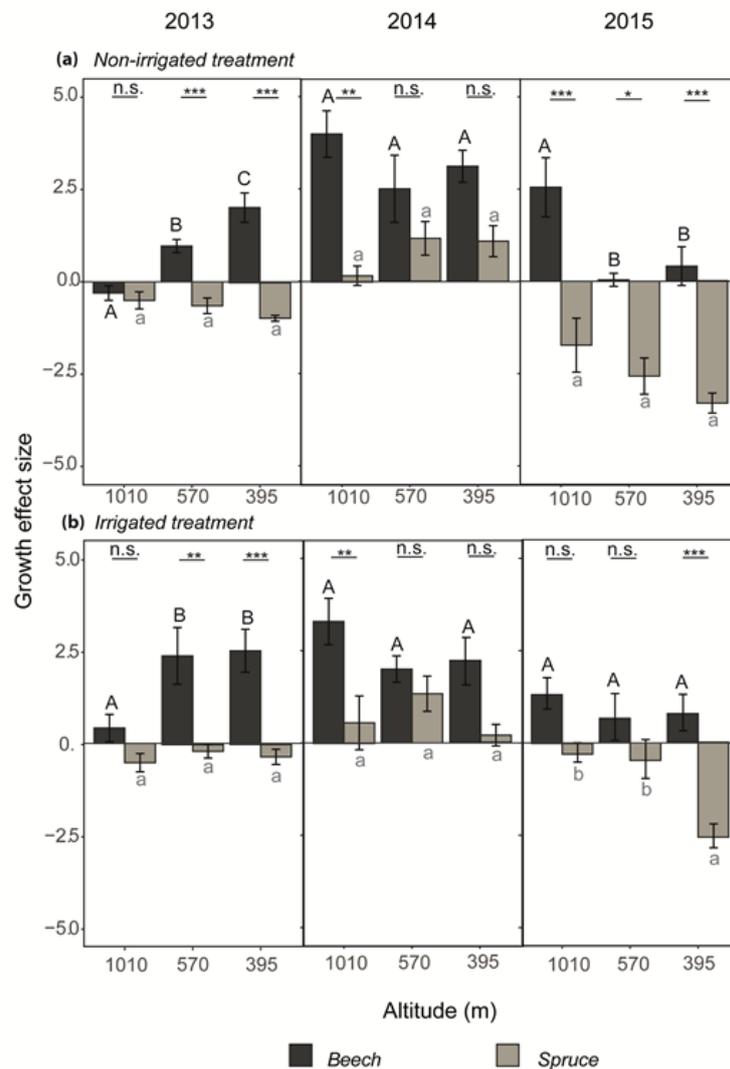


444

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 (\pm 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

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



463

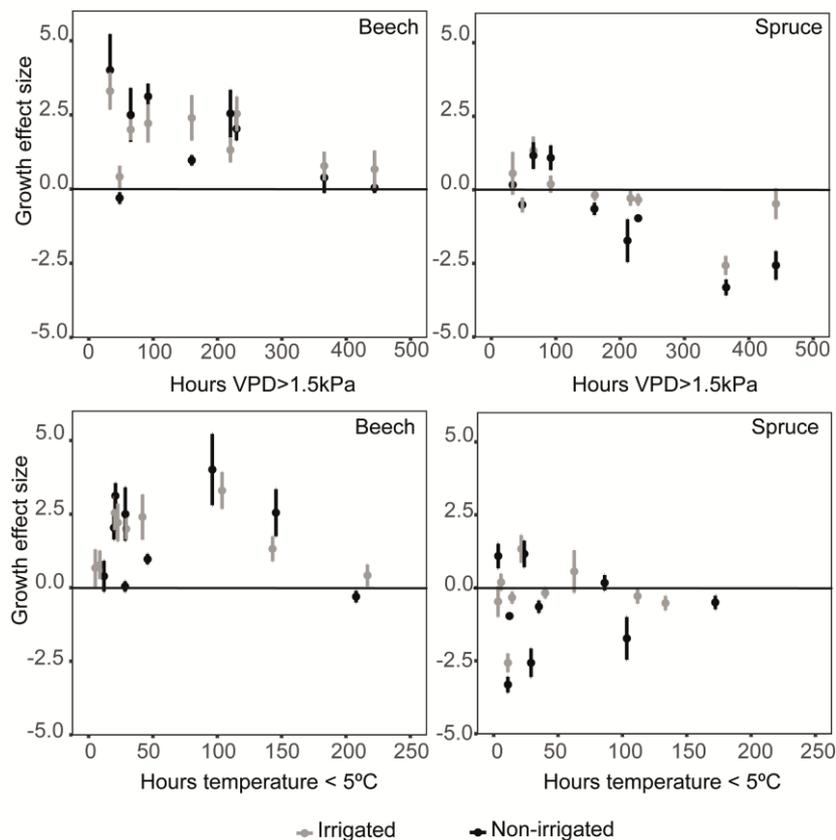
Signif. codes: 0 '****' 0.001 '***' 0.01 '**' 0.05 '*' n.s. >0.05

464 Fig. 3. The effect size (1350 m as the control site) of the biomass increase along the gradient and
 465 throughout the three years for both species and for the non-irrigated (a) and irrigated (b)
 466 treatments. The larger the absolute value, the higher the impact of the local conditions on the
 467 relative biomass increase (standardized by GSL). Different upper- and lowercase letters represent
 468 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 ($\Delta \% d^{-1}$) was calculated for each sapling.

471 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	***					
		AOVPD1.5	***	0.48	8	242.1	251.2	-113.1

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

503

504 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.

517 Contrasting growth responses of beech and spruce saplings exposed to simulated 518 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 R2 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 R^2 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 (Cocoza 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**

661 The quantitative assessment of the impacts of an increase in the AOV_{VPD1.5} and ABT₅
662 on tree growth provided new insights for assessing climate-growth relationships. The
663 higher sensitivity of spruce than beech to increasing VPD could account for the limited
664 growth of spruce at the lower altitudes. We used a scatterplot of VPD vs. growth effect
665 size to determine the approximate upper limit threshold for each species. The lower
666 tolerance limit of spruce (~100 h) compared to beech (~300 h) partly could account for
667 the contrasting growth responses between these species. The negative impacts of extreme
668 conditions also depended on the conditions of the site, i.e. the impact on growth was not
669 the same at 1010 and 395 m for the same duration of increased VPD, mainly due to the
670 differences in the limitation of tree growth at higher and lower altitudes (temperature vs.
671 water deficit). The absence of a clear response of spruce to the length of cold spells during
672 the growing season suggested that spruce growth was limited by other variables. In
673 contrast, beech growth was negatively affected by an ABT₅ above 200 h during the
674 growing season. The large range of responses of both species under this threshold of 200
675 h indicated that lower temperatures were not the main limitation to growth at the recipient
676 sites. Our results suggest that both spruce and beech are limited by increasing air dryness
677 but present different degrees of tolerance. The final GAMMs identified VPD as the main
678 explanatory variables of the increases in biomass for both species. As second main
679 explanatory variable the precipitation rate during the growing season (mm/day GS) was
680 determinant factor for beech while the number consecutive days without precipitation
681 during the growing season was for spruce. This leads to a differentiation between the
682 main factor which is common for both species (VPD) and more species-dependent factors
683 related to precipitation and consecutive days without rain.

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

694 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.

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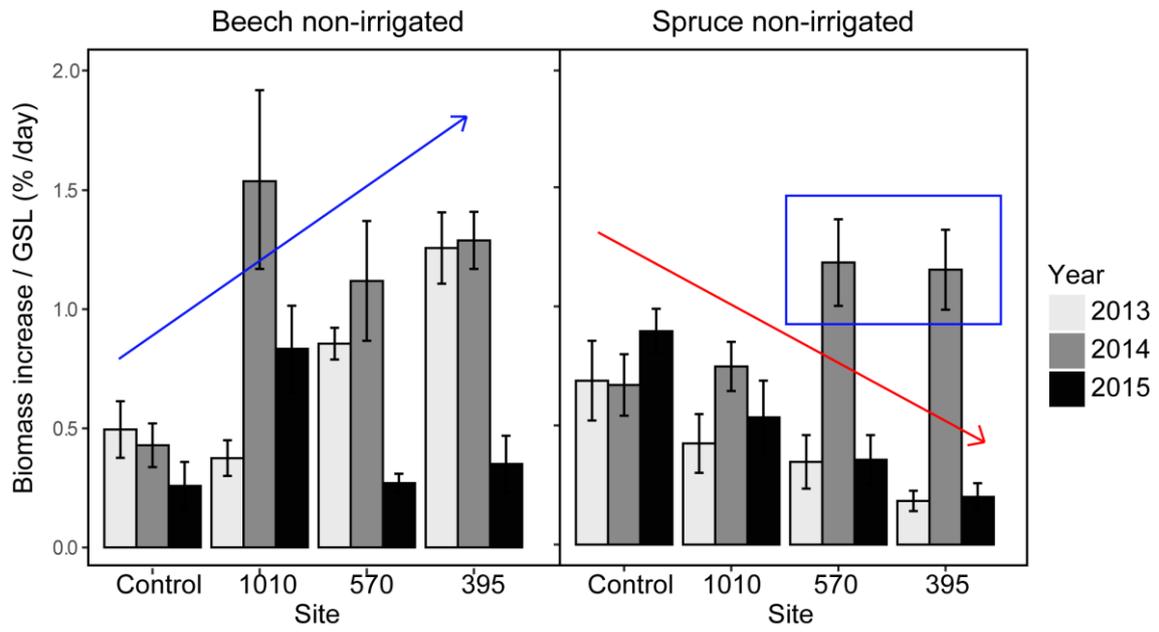
700 **Supplementary information**



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

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

715

716

717 Supplementary Table S1 Ecophysiological measurements in leaves performed twice during the growing seasons 2013 and 2014 at each elevation (m). The mean
 718 values of predawn leaf water potential Ψ_p (MPa), midday leaf water potential Ψ_m (MPa) and leaf stomatal conductance ($\text{mmol g}^{-1} \text{s}^{-1}$) \pm the standard error (SE)
 719 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												
1350	Beech	Ψ_p	-0.1 \pm 0.02				-0.2 \pm 0.09				-0.1 \pm 0.01				-0.2 \pm 0.03			
		Ψ_m	-1.5 \pm 0.00				-2.4 \pm 0.41				-1.9 \pm 0.13				-1.4 \pm 0.22			
		Gs	0.8 \pm 0.74				4.1 \pm 0.70				1.7 \pm 0.30				2.9 \pm 0.33			
	Spruce	Ψ_p	-0.3 \pm 0.03				-0.5 \pm 0.08				-0.3 \pm 0.04				-0.5 \pm 0.04			
		Ψ_m	-1.2 \pm 0.09				-1.6 \pm 0.18				-1.4 \pm 0.05				-1.1 \pm 0.20			
		Gs	0.9 \pm 0.12				1.1 \pm 0.30				1.5 \pm 0.22				1.8 \pm 0.18			
1010	Beech	Ψ_p	-0.3 \pm 0.05	-0.1 \pm 0.01			-0.1 \pm 0.03	-0.2 \pm 0.02			-0.1 \pm 0.00	-0.1 \pm 0.03			-0.2 \pm 0.05	-0.2 \pm 0.03		
		Ψ_m	-1.2 \pm 0.27	-1.8 \pm 0.32			-2.4 \pm 0.07	-2.6 \pm 0.20			-2.3 \pm 0.15	-2.2 \pm 0.12			-1.4 \pm 0.46	-2.1 \pm 0.09		
		Gs	3.2 \pm 0.40	3.9 \pm 0.25			6.7 \pm 0.57	5.8 \pm 1.13			2.5 \pm 1.02	3.7 \pm 0.90			7.0 \pm 0.78	6.6 \pm 1.79		
	Spruce	Ψ_p	-0.3 \pm 0.05	-0.2 \pm 0.04			-0.5 \pm 0.08	-0.5 \pm 0.03			-0.2 \pm 0.04	-0.4 \pm 0.15			-0.4 \pm 0.08	-0.5 \pm 0.04		
		Ψ_m	-1.1 \pm 0.09	-1.3 \pm 0.10			-1.8 \pm 0.06	-1.8 \pm 0.12			-1.7 \pm 0.09	-1.7 \pm 0.23			-1.3 \pm 0.03	-1.0 \pm 0.17		
		Gs	1.1 \pm 0.13	1.3 \pm 0.09			1.2 \pm 0.23	1.4 \pm 0.16			1.7 \pm 0.44	1.9 \pm 0.15			1.0 \pm 0.44	1.4 \pm 0.26		
570	Beech	Ψ_p	-0.1 \pm 0.06	-0.1 \pm 0.08			-0.7 \pm 0.16	-0.8 \pm 0.30			-0.1 \pm 0.01	-0.1 \pm 0.00			-0.2 \pm 0.02	-0.2 \pm 0.03		
		Ψ_m	-2.1 \pm 0.13	-1.9 \pm 0.12			-2.8 \pm 0.12	-2.9 \pm 0.05			-2.3 \pm 0.01	-2.5 \pm 0.24			-1.5 \pm 0.20	-1.9 \pm 0.22		
		Gs	3.8 \pm 1.06	3.0 \pm 0.22			1.6 \pm 0.35	3.2 \pm 1.20			2.5 \pm 0.16	3.1 \pm 0.94			3.9 \pm 0.44	3.6 \pm 0.38		
	Spruce	Ψ_p	-0.2 \pm 0.09	-0.4 \pm 0.09			-0.4 \pm 0.05	-0.4 \pm 0.05			-0.2 \pm 0.03	-0.1 \pm 0.16			-0.4 \pm 0.01	-0.4 \pm 0.10		
		Ψ_m	-1.5 \pm 0.19	-1.3 \pm 0.12			-1.9 \pm 0.13	-1.6 \pm 0.22			-1.7 \pm 0.18	-1.5 \pm 0.28			-1.1 \pm 0.16	-1.0 \pm 0.08		
		Gs	1.0 \pm 0.10	0.9 \pm 0.06			0.6 \pm 0.09	0.6 \pm 0.19			1.2 \pm 0.19	1.2 \pm 0.42			1.1 \pm 0.17	1.2 \pm 0.16		
395	Beech	Ψ_p	-0.3 \pm 0.10	-0.2 \pm 0.06			-0.5 \pm 0.37	-0.7 \pm 0.38			-0.1 \pm 0.01	-0.1 \pm 0.01			-0.2 \pm 0.04	-0.2 \pm 0.02		
		Ψ_m	-1.9 \pm 0.09	-1.8 \pm 0.12			-3.0 \pm 0.31	-2.2 \pm 0.22			-2.5 \pm 0.18	-2.4 \pm 0.12			-2.5 \pm 0.17	-2.0 \pm 0.24		
		Gs	3.4 \pm 0.65	3.5 \pm 0.73			2.5 \pm 0.67	2.9 \pm 0.64			4.3 \pm 0.45	1.8 \pm 0.18			5.2 \pm 0.30	4.8 \pm 1.03		
	Spruce	Ψ_p	-0.2 \pm 0.09	-0.2 \pm 0.04			-0.6 \pm 0.00	-0.6 \pm 0.11			-0.2 \pm 0.04	-0.2 \pm 0.02			-0.4 \pm 0.07	-0.3 \pm 0.03		
		Ψ_m	-1.2 \pm 0.03	-1.2 \pm 0.12			-1.7 \pm 0.25	-2.2 \pm 0.18			-1.6 \pm 0.03	-1.4 \pm 0.24			-0.9 \pm 0.14	-0.9 \pm 0.17		
		Gs	1.2 \pm 0.28	1.3 \pm 0.12			0.6 \pm 0.15	0.6 \pm 0.31			1.1 \pm 0.46	0.9 \pm 0.44			1.3 \pm 0.38	1.1 \pm 0.20		

720

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