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Abstract

The most accurate understanding of forest functioning during drought is crucial to improve the forecast of future forest productivity. Here we investigate the ecophysiological responses (i.e. primary production, evapotranspiration and water use efficiency) of European beech to drought events with the ecosystem model MuSICA, using as benchmark the observed fluxes at the experimental forest Hesse (France). We show that MuSICA is able to realistically simulate observed drought-induced limitations. Subsequently we use simulation experiments to provide: (1) a quantification of the reduction of ecosystem fluxes during the 2003 drought, (2) a partitioning of heat stress and water limitations during droughts, (3) an analysis of the impact of specific drought trajectories, and (4) an evaluation of the potential impact of projected climate change on the studied forest and (5) over the beech distributional range. Our results show that the 2003 drought resulted in a 17% reduction of annual gross primary production and in a 21% reduction of evapotranspiration at Hesse. The studied forest ecosystem is mostly sensitive to negative precipitation anomalies (82% of the reduced forest productivity in 2003) and almost insensitive to heat stress due to high temperatures (16%). Moreover, we show that the ecosystem fluxes are limited more by fast drought onsets in the early growing season (June-July) than by onsets later in the season. Deciphering the impact of future climate change on beech productivity is complicated by large uncertainties in projected future precipitation and in the severity of extreme dry years. Drastic reduction of ecosystem fluxes is only predicted with climate projections that show marked reductions in precipitation. However, increased CO_2 fertilization in the future will counterbalance negative drought impacts. This modelling-based study improves our understanding of the functioning of

37 an emblematic European tree species during extreme events and informs on potential future forest

38 responses to projected climate change.

Keywords

40 Drought; carbon flux; *Fagus sylvatica* L.; ecosystem model; MuSICA; projected climate change

1. Introduction

42 The frequency of extreme climate events, and especially of droughts, is supposed to increase with future

43 climate change (Prudhomme et al. 2014; Zhao and Dai 2017). Central and Southern Europe in particular

44 are regional hotspots where drought severity and frequency will increase the most (Prudhomme et al.

45 2014). This implies that European forest ecosystems will face new and extreme conditions driving

46 changes in species productivity and distribution (Lindner et al. 2010). Indeed, severe droughts are linked

47 to significant reductions of forest productivity (Granier et al. 2007; Reichstein et al. 2007). Species-

48 specific responses to drought should hence be analyzed thoroughly, in addition to possible interactions

49 between the impact of drought and other projected changes (e.g. increased plant water use efficiency

50 with elevated CO_2; Battipaglia et al. 2013).

51 Among the emblematic European tree species, European beech (*Fagus sylvatica* L.) may be severely

52 impacted by drought during the growing season, resulting in xylem embolism and reduced productivity

53 (Gessler et al. 2007). Beech has already experienced locally increased growth limitations over the 20th

54 century due to drought, which has reduced tree competitiveness in relation to other species

55 (Scharnweber et al. 2011). This loss of competitiveness is especially evident at the southern edge of the

56 species distributional range (Peñuelas et al. 2007). A process-based assessment of the ecophysiological

57 responses of European beech to drought would allow an analysis of the species vulnerability to climate

58 change and would potentially improve future projections of beech growth performance over its

59 distributional range.

60 Such process-based assessment could be performed with ecophysiological models. These models can

61 play an important role in investigations and forecasts of drought impacts on forests because they ensure

62 a coupled representation of the processes behind carbon and water fluxes (Bonan and Doney 2018;

63 Ogée et al. 2003). The selected models should guarantee plausible simulations also at the margin or

64 outside of their calibration environment. Indeed, plausible extrapolations beyond the observed

65 boundary conditions are crucial to accurately predict future ecosystem functioning and carbon budget

66 during extreme events, such as future droughts (Clark et al. 2011).

67 Some studies have already quantified the impact of drought on ecosystem productivity globally (Zhao

68 and Running 2010), on specific regions (Ciais et al. 2005), or on specific forest ecosystems (Reichstein et

69 al. 2007). However, droughts are the result of two components: an increase in temperature-induced

70 plant stress (e.g. effects of temperature on vapor pressure deficit, or the effects on carboxylation rate)

71 and a decrease in water availability driven by low precipitation (Zhao and Dai 2017). The partitioning of

72 heat stress and water limitations during drought events for specific ecosystems is still to be further

73 analyzed. Moreover, each drought has its own climate trigger and its timing of occurrence during the

74 year (Mo 2011), potentially inducing a very specific impact on forests. For example, fast drought onsets

75 in spring followed by average summer conditions can have different impacts on annual ecosystem

76 performance than lesser but constant reduction in water availability during the whole growing season.

77 Impacts due to different drought trajectories should also be better analyzed. Here we focus on the

78 ecophysiological responses (i.e. forest water and carbon fluxes, and ecosystem water use efficiency) of

79 European beech forests using simulation experiments. First, we ensure that the used ecosystem model

80 (MuSICA; Ogée et al. 2003) is able to realistically simulate drought-induced flux reductions at an

81 experimental site, even for much drier periods than used during model calibration. Second, we re-

4

82   compute the local impact of the 2003 drought on ecosystem fluxes using a novel simulation-based

83   approach. Third, we quantify the partitioning of heat stress and water limitations during drought.

84   Fourth, we investigate the impact of different drought trajectories. Fifth, we evaluate the potential

85   impact of projected climate change on the productivity and water use of beech forests locally and, sixth,

86   evaluate the potential impact over the entire species distributional range in Europe.

2. Materials and Methods

2.1. The Hesse forest experimental station

89   We used the data of the Hesse forest experimental station (Granier et al. 2008) to optimize the MuSICA

90   ecosystem model for beech forests. The Hesse site (+48.7° latitude, +7.1° longitude, 300 m elevation) is

91   a European beech forest located in north-eastern France (Moselle) in the center of the species

92   distributional range. Hesse belongs to the ICOS infrastructure (www.icos-ri.eu) and there are 20 years of

93   ecosystem fluxes and ecophysiological measurements available at the site. Hesse is a drought-sensitive

94   ecosystem and extreme dry years, such as 2003, produce significant anomalies on the observed carbon

95   dynamics (Granier et al. 2007). We used measured ecophysiological traits for the initialization of the

96   model parameters (Dufrêne et al. 2005) and soil water content at three soil depths (SWC; 0.1, 0.3 and

97   0.55 m), carbon fluxes (net ecosystem exchange - NEE; and gross primary production - GPP; NEE was

98   partitioned into GPP and ecosystem respiration using the night-time approach of Reichstein et al. 2005)

99   and evapotranspiration (ET) for further parameter optimization and validation.

2.2. The MuSICA ecosystem model

101   MuSICA is a mechanistic ecosystem model primary developed to simulate water, carbon and energy

102   exchanges over the soil-vegetation-atmosphere continuum (Domec et al. 2012; Giuggiola et al. 2016;

103   Klein et al. 2014; Ogée et al. 2003; Ogée et al. 2004; Wingate et al. 2010). MuSICA discretizes the

104   ecosystem in several air and soil layers. In this project, we used 15 layers in the soil and 10 layers in the

105 vegetation. Carbon fluxes depend on the coupling between photosynthesis (Farquhar et al. 1980) and

106 stomatal conductance (Leuning 1995), as well as on the simulation of respiration, leaf light interception

107 (Sinoquet et al. 1990), convection and turbulent transport (Raupach 1989) in each air layer. Soil water

108 fluxes are a mixture of preferential and matrix flows, the latter ones being described by Richards'

109 equations (Braud et al. 1995).

2.3. Model calibration and validation

111 MuSICA was optimized using as target half-hourly SWC, NEE and ET measurements of the year 2002,

112 which had normal climate conditions. ET observations were corrected to ensure energy balance closure

113 as proposed by Mauder et al. (2013). All MuSICA parameters were initialized according to our best

114 knowledge of the ecophysiological traits of the Hesse experimental forest. Subsequently, we used

115 Morris parameter screening (Morris 1991) to quantify the sensitivities of the target variables to the

116 individual model parameters of MuSICA (Cuntz et al. 2015). The Morris parameter screening analyses

117 the variations of the target variables with respect to variations in the model parameters (Saltelli et al.

118 2004). The identified sensitive parameters were further optimized using a differential evolution

119 algorithm (Abbass et al. 2001; Mier 2017). Finally, the 2003 dry year was used to verify that MuSICA

120 realistically simulates drought-induced ecosystem limitations as well as daily variations of observed

121 water-related variables during extreme dry periods. This calibration/validation scheme was specifically

122 designed because drought severity is supposed to increase with future climate change and, therefore,

123 plausible model extrapolations are crucial.

2.4. Local simulation experiments

125 Once MuSICA was optimized for Hesse, we performed several local simulations modifying the 2003

126 temperature and precipitation input data. These simulations were grouped in four experiments (Table

127 1). Experiment 1 quantifies the reduction of fluxes during the 2003 drought. Experiment 2 provides

128 partitioning of heat stress and water limitations during drought. Experiment 3 studies the impact of

129 alternative drought trajectories having the same severity than the 2003 drought but different timing of

130 occurrence over the growing season (i.e. faster or slower drought onset). Experiment 4 analyzes the

131 impact of future climate change on the studied forest. All simulations use the 2003 half-hourly variability

132 to avoid potential impacts of different structures of rainy/dry, warm/cold, sunny/cloudy days. Only the

133 monthly temperature and precipitation mean values were modified and were specific to each

134 simulation:

135
$$T\_new_{i,y} = T\_ref_i + \Delta_{i,y} \qquad (1)$$

136
$$P\_new_{i,y} = P\_ref_i \cdot \lambda_{i,y} \qquad (2)$$

137 where $T\_new_{i,y}$ ($P\_new_{i,y}$) is the new temperature (precipitation) mean value of the month i and the

138 simulation y, T_ref_i (P_ref_i) is the reference temperature (precipitation) mean value of the month i of

139 the median observed climate at Hesse (1997-2013), $\Delta_{i,y}$ is the climate anomaly of temperature for the

140 specific simulation y, and $\lambda_{i,y}$ is the climate anomaly factor of precipitation for simulation y. Specific

141 simulations and their climate anomalies are detailed in Table 1. Each simulation was preceded by a one

142 year spin-up period, which was subsequently discarded from following analyses, where MuSICA was

143 forced by the meteorology of an average year.

144 The impact of future climate change in experiment 4 was analyzed using an ensemble of six EURO-

145 CORDEX simulations forced by an RCP8.5 (Table 2; Jacob et al. 2014; data downloaded from the Pierre

146 Simon Laplace Institute node of the Earth System Grid Federation). This extreme RCP was selected to

147 emphasize the potential impact of climate change on forest ecophysiology and analyze forest responses

148 under extreme climate conditions. Furthermore, the role of increased CO_2 concentration in the future

149 was isolated by the production of MuSICA simulations at Hesse with both current and future CO_2 values.

150 Indeed, a 2.17-time increase in CO_2 concentration is forecast at the 2080-2100 horizon in RCP8.5

151 scenarios. The annual ecosystem fluxes (F) of the obtained MuSICA simulations y were compared

152 between each other by percent change (PC) computations relative to the fluxes of the reference

153 simulation (median climate):

154 $$PC = \frac{F_y - F_{Ref}}{F_{Ref}} 100 \ (\%) \tag{3}$$

155 *2.5. Regional simulation experiments*

156 Experiment 4 described in the previous section was extended to analyze the potential impact of

157 projected climate change on European beech ecophysiology over the entire species distributional range

158 as defined by Caudullo et al. (2017). The MuSICA temperature and precipitation input data were

159 modified using the same EURO-CORDEX simulations (Table 2; all EURO-CORDEX data were extracted

160 over a regular 0.5° grid) and the same equations described earlier (Eq. 1 and 2). This climate forcing was

161 used to simulate European beech GPP and ET during extreme dry years at two time horizons (2006-2026

162 and 2080-2100; an extreme year was defined with median monthly temperature and precipitation of six

163 extreme dry years, one per simulation). We also took into account the impact of spatially different soil

164 properties. We used USDA soil classification and soil texture data available at "soilgrids.org" to estimate

165 MuSICA soil parameters, such as van Genuchten water retention parameters and saturated hydraulic

166 conductivity, using the Rosetta computer program (Schaap et al. 2001).

167 3. Results

168 *3.1. Validation of MuSICA simulations during dry periods*

169 MuSICA accurately simulates daily variation of GPP, ET and SWC at the Hesse European beech forest

170 (Figs. 1 and S1-S2). The typical annual cycle of drying and rewetting of the soil profile is well caught by

171 the model (Fig. 1, red and blue points). Furthermore, MuSICA simulations show similar performance

172 over both, the 2002 calibration year and the 2003 validation year (Fig. 1), the latter was characterized by

173 reduced precipitation and a severe 4-month drought starting in June and ending in late September (Fig.

174   S3). Finally, observed drought-induced ecosystem limitations are well simulated, such as the limitation

175   of evapotranspiration by soil water availability (Fig. 2). At Hesse, ecosystem fluxes begin to be limited by

176   water availability once soil water in the top 70 cm drops below about 250 kg/m^3, corresponding to

177   values of relative extractable soil water (REW) lower than 0.3.

178   *3.2. Mining forest responses to drought with simulation experiments*

179   The first simulation experiment allowed a precise quantification of the reduction of ecosystem fluxes at

180   Hesse during the 2003 drought. Comparison of the simulation with a median climate but diurnal

181   variations of 2003 (2003_median_climate, red) and the full 2003 dry climate (2003, black) in Figure 3

182   shows that there is a reduction of cumulated annual GPP by 17% and a reduction in total ET by 21% at

183   Hesse due to higher temperatures and less precipitation. This suggests that such an important drought

184   had only a slight impact on water use efficiency (evapotranspiration decreased slightly more than

185   productivity). Interestingly, the divergence between the two simulations started only 1.5 months after

186   the beginning of the 2003 heatwave in early June (Fig. S3). This is the time needed to dry out the soil

187   profile to the threshold of about 250 kg/m^3 in the top 70 cm, or REW = 0.3, when plants start

188   experiencing water stress (Fig. 2).

189   The second experiment allowed the partitioning of heat stress and water limitations at Hesse during

190   drought. Comparing the simulation with a median climate but diurnal variations of 2003

191   (2003_median_climate, red), the simulation with median climate and the 2003 temperature anomalies

192   only (2003_T_limited, blue), the simulation with median climate and the 2003 precipitation anomalies

193   only (2003_P_limited, green), and the simulation with full 2003 dry climate (2003, black) in Figure 3, we

194   can observe that water limitations caused by low precipitations are responsible for most of the observed

195   reductions in GPP and ET. Heat stress due to high temperature is instead very low for GPP and negligible

196   for ET.

197 Subsequently, we show that droughts with same severity but diverse trajectories (i.e. timing of drought

198 onset and recovery over the growing season) have different impacts on the ecosystem (Experiment 3;

199 Table 1 and Fig. 4). The beech forest in Hesse shows very similar annual sums of GPP and ET if there is

200 still some precipitation in June-July, which was the case in 2003 and is the case in the slow-onset

201 scenario (black and purple lines). However, the forest is sensitive to fast drought onset. If there is a

202 different precipitation timing with almost no precipitation in June-July, SWC decreases earlier than in

203 2003, leading to a longer drought-limited period, which cannot be compensated during drought release

204 later in the year (orange line). Note that all simulations in Fig. 4 have the same precipitation amount

205 over the growing season (Table 1).

206 Our fourth experiments allowed an evaluation of the impact of projected climate change at the studied

207 forest. Fig. 5 shows the expected changes between present and future forest performance over median

208 climatological years (*Median_futur vs. 2003_median_climate*; dark blue) and extreme dry years

209 (*Xtreme_futur vs. Xtreme_today*; light blue). The same figure also allows the comparison of the expected

210 impact of future extreme dry years (*Xtreme_futur vs. 2003_median_climate*; green) and of present

211 extreme dry years (*Xtreme_today vs. 2003_median_climate*; red) relative to present median conditions.

212 All CORDEX simulations used in Fig. 5 agree in projecting an important increase in temperature over the

213 growing season (median increase of +3.0 °C; Fig. S4). Conversely, there is a large spread in the

214 magnitude and sign of the precipitation change (Fig. 5; dark and light blue), which is the most influential

215 parameter modifying ecosystem fluxes in MuSICA at Hesse. MuSICA, forced by these climate inputs and

216 by stable, current CO_2 concentrations, projects only slight changes in GPP and ET during a median year

217 (Fig. 5, dark blue) and an extreme year (Fig. 5, light blue) of 2080-2100. Although EURO-CORDEX climate

218 simulations show hotter and drier extreme years in the future than today (Fig. 5, green and red), the

219 reduction of the ecosystem fluxes relative to present median conditions remains very similar. Indeed,

220 the simulated climate of extreme dry years in EURO-CORDEX is less severe than the observed extreme

10

221   year 2003, so that the soil water threshold of 250 kg/m^3 in the top 70 cm, or REW = 0.3, is rarely reached

222   in the MuSICA simulations. The picture changes drastically if we include the future increase in CO_2

223   concentration projected by RCP8.5 simulations at the 2080-2100 horizon (2.17 current CO_2). Over a

224   median year (Fig. 5, dark blue), GPP increases by 36% in this case, ET decreases by 17%, leading to very

225   high water use efficiency (+64%). We computed that a 1.22-time increase in CO_2 concentration (+89

226   ppm) would be enough to counterbalance future negative drought impacts on carbon fluxes (i.e. the

227   green horizontal bar in the fourth column of Fig. 5, showing the percent change in GPP with increased

228   atmospheric CO_2, which would then be located at the zero line).

229   We also compared the performance of potential European beech forests under current and future

230   extreme dry years over the entire species distributional range (Fig. 6). The results show that the species

231   is potentially vulnerable to climate change at its southern and western range, where projected

232   precipitation changes are large (Fig. S4). European beech forests in the Alps and in the north-eastern

233   part of the distribution range are insensitive to temperature and precipitation changes (Fig. 6, top row).

234   Indeed, water availability over the growing season is not a limiting factor for European beech in the Alps,

235   while CORDEX simulations project a precipitation increase in the north-eastern part of the species range

236   (Fig. S4). As it was the case for the Hesse forest, beech productivity is highly enhanced (the first and the

237   third quartiles of the GPP change are +40 and +55 %, respectively) if we include in our simulations the

238   increase of future CO_2 concentrations, with a clear southwest-northeast gradient of increased forest

239   productivity due to projected precipitation changes (Fig. 6, bottom row).

4. Discussion

241   Drought frequency over the 21st century will increase by more than 20% in Central and Southern Europe

242   and the dynamic response of vegetation to these droughts is highly uncertain (Prudhomme et al. 2014).

243   We thus need ecophysiological models able to capture key forest processes and to provide plausible

244 extrapolations over severe dry periods in order to assess the impact of increased drought frequency on

245 forest functioning and carbon budgets (Clark et al. 2011; Williams et al. 2018). In our case, we used the

246 MuSICA ecosystem model (Ogée et al. 2003) to analyze the ecophysiological responses of European

247 beech to drought events. The model showed high skills in reproducing key variables and drought-

248 induced ecosystem limitations over an independent verification year with severe drought (year 2003;

249 Figs. 1-2). MuSICA thus seems an appropriate tool to extrapolate the ecosystem responses to future

250 droughts.

251 Our work refines the results of previous studies and points out important forest processes and

252 dynamical responses in a climate change context. Previous studies quantified a reduction of ecosystem

253 fluxes (GPP and ET) of more than 30% at the Hesse beech forest in 2003 (Granier et al. 2007; Reichstein

254 et al. 2007). Our results give instead a much more conservative estimate (−17% for GPP and −21% for

255 ET). Previous studies used the preceding 2002 year as reference for their quantifications. We rather

256 used a novel anomaly-based approach, attenuating the impact of specific years and of different climate

257 structures such as of wet/dry, warm/cold, or sunny/cloudy days between the dry year 2003 and the

258 reference.

259 We confirm here the key role of water limitations for reduced forest productivity during the 2003

260 drought (Granier et al. 2007; Reichstein et al. 2007). Furthermore, we are able to disentangle the

261 partitioning between heat stress and water limitations during drought. The results represented in Figure

262 3 estimate that 82% of the reduced forest productivity in 2003 can be attributed directly to low

263 precipitation. Only 16% of the reduced forest productivity comes from heat stress in the model, while

264 only 2% comes from combined effect of heat stress and water limitations. This low impact of

265 temperature is surprising because high temperatures influence plant biochemistry and increase vapor

266 pressure deficit, dampening stomatal conductance and enhancing soil water evaporation. Granier et al.

267 (2000) measured a difference of about 23% between ecosystem evapotranspiration and stand

268   transpiration at Hesse. They concluded that this difference could at least partly be due to soil

269   evaporation. They argued, though, that measurement uncertainties in both, ecosystem

270   evapotranspiration and stand transpiration, are so large that they cannot be proven to be significantly

271   different. This led Betsch et al. (2011) to neglect soil evaporation in their analysis of drought effects on

272   the Hesse beech forest. However, high temperatures should also affect plant biochemistry. Optimum

273   temperatures for biochemical reactions, such a carboxylation, were found to be above 35 °C for *Fagus*

274   *sylvatica* (Kattge and Knorr 2007), which are rarely reached in Hesse. However, maximum daily

275   temperatures of the sunlit leaves increased from 39 (August 1st) to 48 °C (August 8th) during the hottest

276   spell of summer 2003, inducing a progressive and almost complete cessation of photosynthesis and

277   transpiration, especially in the upper canopy layer (Fig. S5). Such high temperatures have the potential

278   to damage sun-exposed leaves (e.g. burned epidermis). Although these carry-over effects of heat stress

279   are not accounted for in the model, the rather good agreement of MuSICA with ecosystem-scale water

280   and CO_2 flux observations during and after the 2003 heat wave, indicates that these effects have only a

281   minor influence at the ecosystem scale and that water limitations remain crucial.

282   An important point of our study is the demonstration that rain seasonality matters, i.e. specific drought

283   trajectories over the growing season can potentially drive different impacts to ecosystem fluxes.

284   European beech forests are more sensitive to fast drought onset in the early growing season (Fig. 4)

285   because the soil profile dries out earlier, leading to water limitations during times of highest incoming

286   radiation and hence highest ecosystem fluxes. This result is similar to what D'Orangeville et al. (2018)

287   found for eastern North American forests using tree-ring data but partially contrasts with the findings of

288   Granier et al. (2007) and Arend et al. (2016) pointing out that rainfall events during drought can rapidly

289   restore ecosystem fluxes. Although fluxes increase after rainfall in the fast onset scenario, they cannot

290   close the overall gap with the fluxes of alternative drought trajectories having the same severity but

291   slower onset (i.e. the actual 2003 drought trajectory and the experiment 2003_slow_onset). For this

292 reason, a more in-depth analysis of the projected changes in drought seasonality should be sought (see

293 Mo 2011). For example, do we have any indication that crucial months for beech forest productivity,

294 such as June, are becoming drier relative to other months? How much precipitation deficit is needed

295 during these crucial months to significantly reduce ecosystem fluxes and how long does it take to the

296 soil profile to dry (e.g. 1.5 months in 2003 at Hesse; Fig. 3)? Such drought analysis should not be

297 performed with simplistic drought indices, which respond mainly to temperature changes and result in

298 biased interpretations (e.g. Thornwaite equation for potential ET; see Sheffield et al. 2012).

299 Our comparison of the impact of current and future extreme dry years on European beech forests

300 reveals important key findings. First, the large uncertainties in the future trends of precipitation limit the

301 predictability of forest responses at specific sites and at European scale (see Fig. 5). This known issue

302 cannot fully be resolved due to the impact of high internal climate variability on precipitation (Knutti and

303 Sedláček 2013). Furthermore, we confirmed that caution should be paid when using climate model

304 simulations to analyze extreme years (see Asadieh and Krakauer 2015); climate models are constructed

305 to simulate climate and hence dampen interannual variations of meteorology. Observed severe

306 droughts at specific sites are more extreme than those simulated at the corresponding grid cells (see red

307 and black dots in Fig. 5). Consequently, drastic reductions of ecosystem fluxes at the Hesse forest (a

308 humid site only sensitive to extreme dry years) are only projected for those simulations with lower

309 precipitation amounts at the 2080-2100 horizon compared to today (Fig. 5; see points surrounded by

310 circles). This is consistent with the important role of critical thresholds in relative extractable water

311 determining forest responses to drought (Granier et al. 2007). These thresholds are clearly reached

312 more often over the southern and the western part of the beech distributional range (Fig. 6), where the

313 species has already shown its vulnerability to climate change (Hacket-Pain et al. 2016; Peñuelas et al.

314 2007). Although our analysis of the potential impact of future droughts on beech forests relies on

315 MuSICA's performance for Hesse, drought response traits of beech trees only show small differences

316   according to tree provenance (Aranda et al. 2014). In all cases, increased CO_2 fertilization in the future

317   (+2.17-time increase of CO_2 concentrations in the RCP8.5 scenarios at the 2080-2100 horizon) will

318   compensate negative drought impacts (Fig. 6). This response is consistent with retrospective studies

319   based on tree-ring $\delta^{13}C$ data, which show important increases in water use efficiency of beech trees over

320   the past century (up to 44%; Duquesnay et al. 1998). This response is also consistent with the increased

321   productivity of European forests projected by other modelling studies over the next century (Davi et al.

322   2006; Gea-Izquierdo et al. 2017). However, controlled experiments under a CO_2-enriched atmosphere

323   seem to show a more moderate CO_2 fertilization effect with almost no changes in productivity (Bader et

324   al. 2013). The effects of nutrient limitations should hence be included in future studies (see Luo et al.

325   2004; Norby et al. 2010).

5. Conclusion

327   In this study, we used the MuSICA ecosystem model (Ogée et al. 2003) to analyze the potential impact

328   of present and future droughts on fluxes and processes of European beech forests. Using MuSICA, we

329   were able to simulate realistic carbon and water fluxes at the leaf- and soil-level, and to quantify

330   precisely the impact of drought. Severe droughts may reduce European beech GPP and ET annual fluxes

331   by 20%. We demonstrated that low precipitation limits beech forest productivity much more than heat

332   stress. Beech forest ecosystems are also sensitive to the timing of drought onset over the growing

333   season. Finally, our results show a good adaptation of European beech ecosystems to projected climate

334   change because increased CO_2 concentration in the future will enhance plant water use efficiency

335   counterbalancing negative drought impacts. However, large uncertainties exist as simulated trends in

336   ecosystem fluxes depend mainly on projected trends and anomalies of precipitation, which are both

337   largely uncertain in climate model projections. This study represents a step forward to a more complete

338   ecophysiological understanding of the potential impact of drought on the productivity and seasonal

339 dynamics of European beech forests, which should be enhanced in the future by the inclusion of

340 additional processes such as nitrogen limitations, legacy/carry-over effects after extreme events, or

341 growing season and phenological changes.

342

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352

Competing interests

354 Declarations of interest: none.

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Tables

Table 1. *Local MuSICA simulations at Hesse used in the four experiments.*

Experiments*	Simulation name	Monthly temperature	Monthly precipitation	Daily/hourly variability	Temperature/precipitation annual anomalies
1, 2, 3	2003	2003	2003	2003	2003
1, 2	2003_median_climate	Median climate (1997-2013)	Median climate (1997-2013)	2003	Median climate
2	2003_only_P_limited	Median climate (1997-2013)	2003	2003	Median climate/2003
2	2003_only_T_limited	2003	Median climate (1997-2013)	2003	2003/Median climate
3	2003_fast_onset	Anomalies added to June-September: +2, +1, -1, -2 (°C)	Anomalies of June-September: 10%, 20%, 30%, 40% of total precipitation over the period	2003	2003
3	2003_slow_onset	Anomalies added to June-September: -2, -1, +1, +2 (°C)	Anomalies of June-September: 40%, 30%, 20%, 10% of total precipitation over the period	2003	2003
4	Xtreme_today	Modified by deltas relative to extreme dry years in CORDEX simulations at the 2006-2026 horizon	Modified by change factors relative to extreme dry years in CORDEX simulations at the 2006-2026 horizon	2003	Extreme simulated years at the 2006-2026 horizon
4	Median_futur	Modified by deltas relative to median years in CORDEX simulations at the 2080-2100 horizon	Modified by change factors relative to median years in CORDEX simulations at the 2080-2100 horizon	2003	Median simulated years at the 2080-2100 horizon
4	Xtreme_futur	Modified by deltas relative to extreme dry years in CORDEX simulations at the 2080-2100 horizon	Modified by change factors relative to extreme dry years in CORDEX simulations at the 2080-2100 horizon	2003	Extreme simulated years at the 2080-2100 horizon

* Experiments are defined in the section "Local simulation experiments". The same simulation can be used in more than one experiment.

Table 2. *EURO-CORDEX RCP8.5 simulations used to define the projected climate change.*

| Regional climate model	Driving global climate model	Member
ALADIN53	CNRM-CERFACS-CNRM-CM5	r1i1p1
RCA4	ICHEC-EC-EARTH	r12i1p1
WRF331F	IPSL-IPSL-CM5A-MR	r1i1p1
CCLM4-8-17	MOHC-HadGEM2-ES	r1i1p1
REMO2009	MPI-M-MPI-ESM-LR	r1i1p1
REMO2015	NCC-NorESM1-M	r1i1p1

Figures

492 Figure 1. Simulated versus observed daily values of water-related variables and forest productivity at

493 Hesse during the 2002 calibration year and the 2003 dry validation year. From top to bottom: gross

494 primary productivity, evapotranspiration, soil water content in the top 70 cm. For soil water content, red

495 (blue) points correspond to daily values before (after) August 15, which is in the middle of the yearly dry

496 period at Hesse. Grey lines are the one-to-one lines.
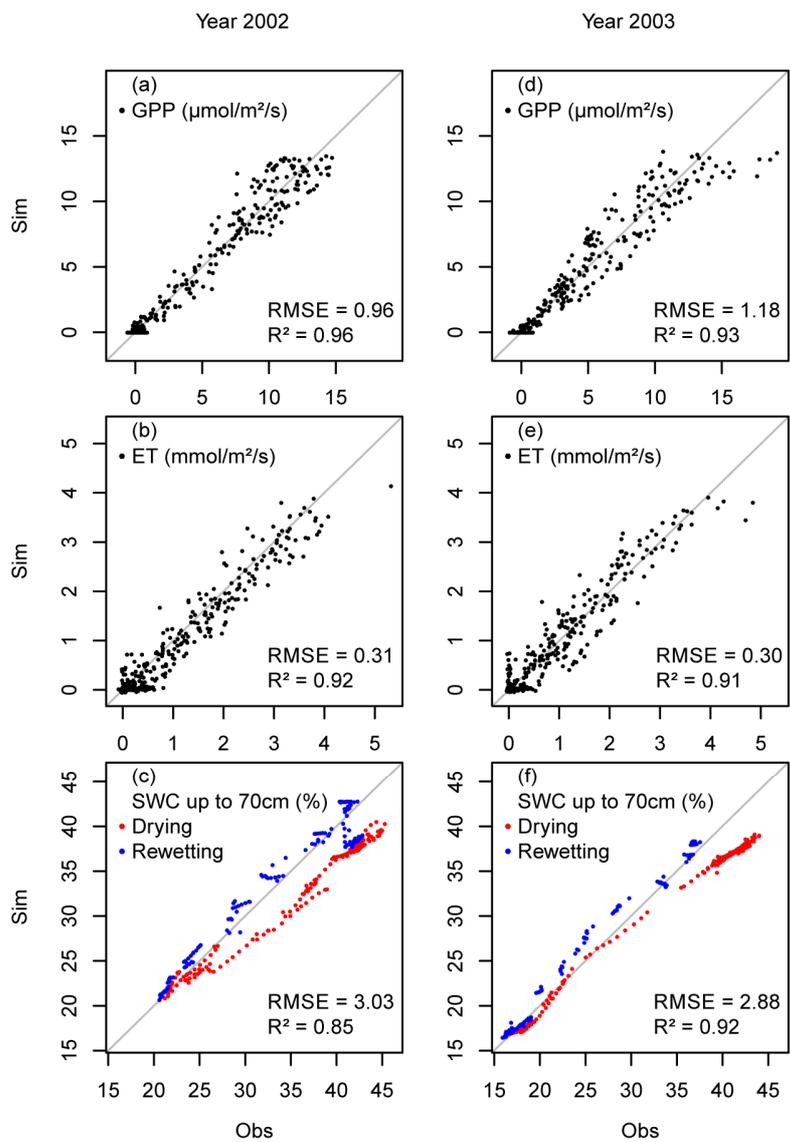
497

498   Figure 2. Impact of soil water availability on evapotranspiration (2001-2008): daily mean observed

499   (black) and simulated (red) evapotranspiration versus soil water content in the top 70 cm for May to

500   September. The upper envelope lines with larger circles show the 95th percentiles of the

501   evapotranspiration data divided in 15 equally spaced bins of soil water content. Only sunny days with

502   mean daily net radiation greater than 100 W/m^2 were considered.
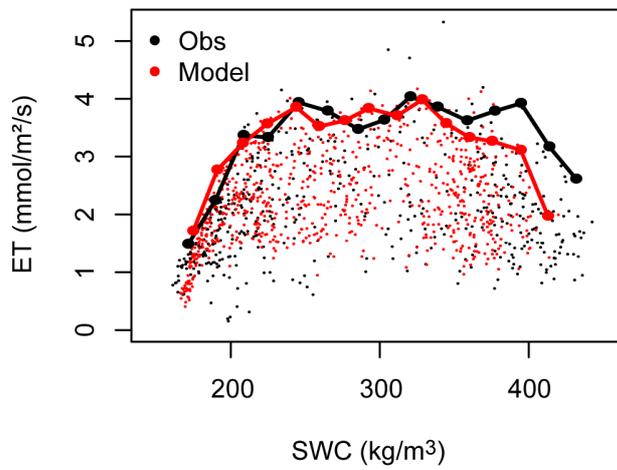

503

504 Figure 3. Quantification of the reduction of gross primary production and evapotranspiration due to

505 heat stress, water limitations and combined effects during the 2003 drought. Lines are cumulative sums

506 of daily gross primary productivity and evapotranspiration in 2003, simulated with the full 2003 dry

507 climate (2003, black), simulated with a median climate but diurnal variations of 2003

508 (2003_median_climate, red), simulated with median climate and the 2003 precipitation anomalies only

509 (2003_P_limited, green), simulated with median climate and the 2003 temperature anomalies only

510 (2003_T_limited, blue). Horizontal grey arrows show the time lapse between the start of the drought

511 and the divergence among simulations. Vertical black arrows indicate the 2003 reductions of fluxes

512 between simulations with a median climate and the full 2003 dry climate.
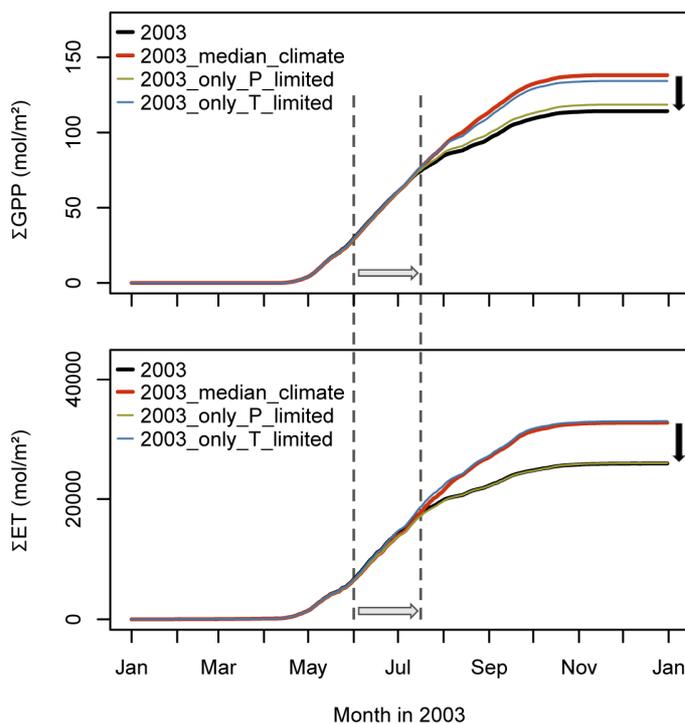
513

514   Figure 4. Quantification of the impact of different hypothetic drought trajectories. Lines are cumulative

515   sums of daily gross primary productivity and evapotranspiration in 2003, simulated with the full 2003

516   dry climate (2003, black) and with modified versions of the 2003 climate. In the simulations

517   "2003_fast_onset" and "2003_slow_onset ", the 2003 temperature and precipitation values were

518   modified to have a faster or slower drought onset but same overall anomalies over the growing season
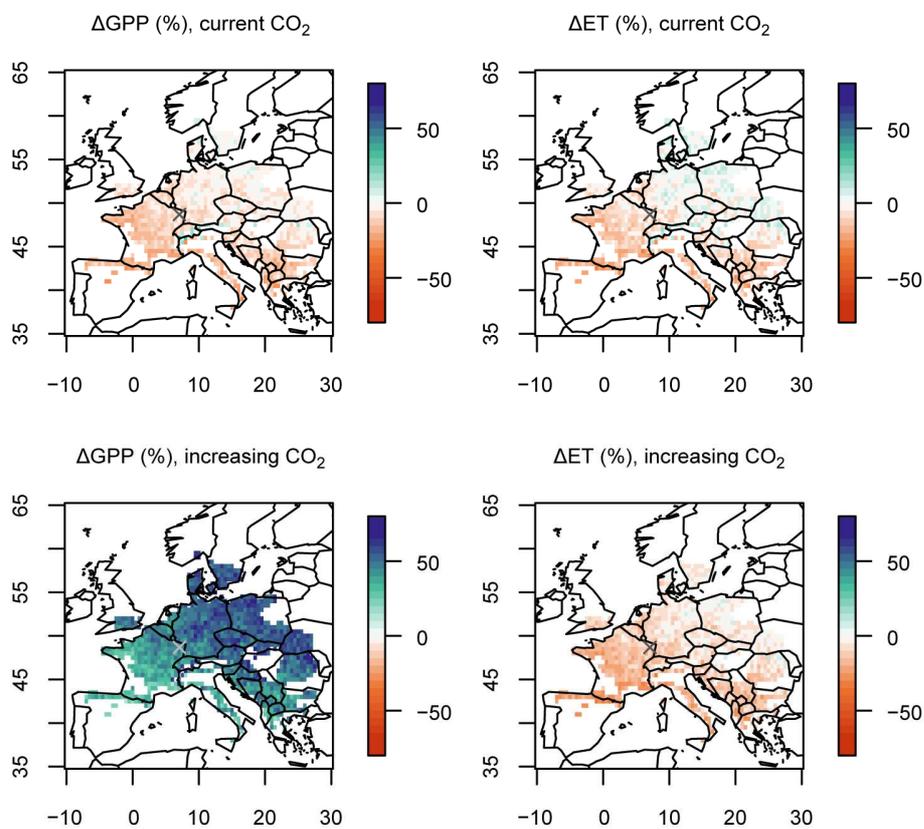
519   (see Table 1).

520
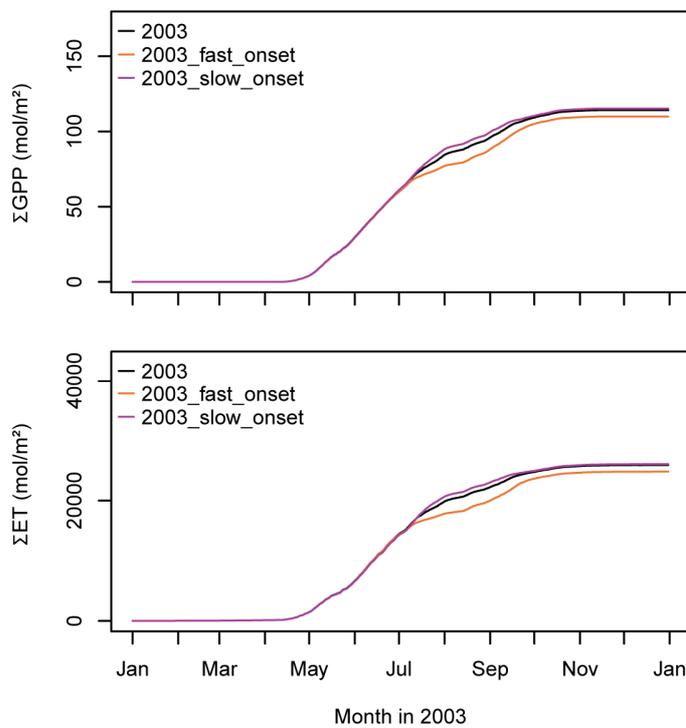
Figure 5. Comparison of annual gross primary productivity, evapotranspiration and water use efficiency (net assimilation divided by transpiration) at the Hesse beech forest under current and future (2080-2100) climate from six EURO-CORDEX simulations; future MuSICA simulations use either current atmospheric CO_2 levels or projected, increased atmospheric CO_2 concentrations (2.17-time increase). Each point represents the percent change (Eq. 3) of MuSICA input climate (May-September mean temperature and precipitation) from Regional Climate Models (Table 2) and of MuSICA simulated fluxes. The points for the simulation with driest projected climate are surrounded by circles. Horizontal bars represent the median of the six simulations. The specific MuSICA simulations are given in Table 1. *Xtreme_future vs. 2003_median_climate*, for example, means the percent change in the annual sum if MuSICA is driven by the most extreme year of specific CORDEX simulations over 2080-2100 compared to MuSICA driven by the median climate of 1997-2013. Black dots, showing the estimated impact of the observed 2003 drought at Hesse, are given for comparison.
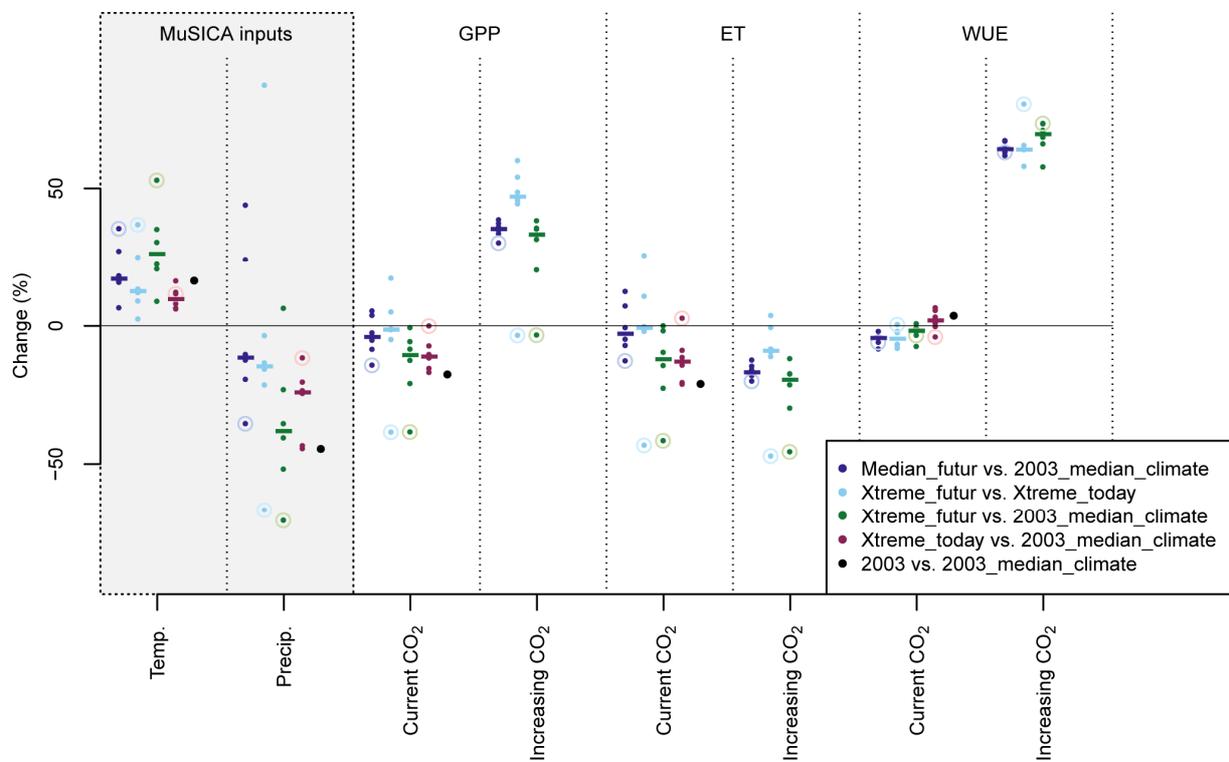
Figure 6. Comparison of gross primary productivity and evapotranspiration of potential European beech forests under current and future (2080-2100) extreme dry years over the species distributional range. Forcing temperature and precipitation used to drive MuSICA simulations are derived from the median of six extreme years, one pear each EURO-CORDEX simulation. Percent changes are computed as described in Eq. 3. The top row uses current atmospheric CO_2 concentration and the bottom row uses future CO_2 levels (2.17 current CO_2). The grey cross in Eastern France is the location of the Hesse forest experimental station.