1 **Timing of drought in the growing season and strong legacy effects**
2 **determine the annual productivity of temperate grasses in a**
3 **changing climate**

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10   **Abstract**

11   The frequency of extreme weather events, such as droughts, is assumed to increase leading to alterations of ecosystem

12   productivity and thus the terrestrial carbon cycle. Although grasslands typically show reduced productivity in response

13   to drought, their effects have been shown to vary quite dramatically. Here we tested in a two-year field experiment, if the

14   resistance and the resilience of grasses towards drought varies throughout a growing season and if the timing of drought,

15   thus, influences drought-induced reductions in annual net primary production (NPP) of grasses. For the experiment we

16   grew six temperate and perennial C3 grass species in a field as monocultures. The grasses were cut six times during the

17   growing season and subject to 10-week drought treatments that occurred either in the spring, the summer or the fall.

18   Across all species, drought-induced losses of productivity in spring were smaller (-20% to -51%) than in summer and fall

19   (-77% to -87%). This suggests a higher resistance to drought in spring when the productivity of the grasses is the highest

20   and plants are in their reproductive stage. After the release of drought, we found no prolonged suppression of growth. In

21   contrast, post-drought growth rates of formerly drought-stressed swards outperformed the growth rates of the control

22   swards. In 2014, the overcompensation after drought release was similar in all seasons, but differed in 2015. The strong

23   overcompensation of growth after drought release resulted in relatively small overall drought-induced losses of annual

24   ANPP (aboveground NPP) that ranged between -4% to -14% and were not affected by the timing of the drought event.

25   Our results show that (i) the resistance of growth rates in grasses to drought varies across the season and is positively

26   correlated with growth rates in the control, (ii) that positive legacy effects of drought indicate a high resilience of

27   temperate grasses to drought, and (iii) that the high resilience can compensate immediate drought effects on total annual

28   biomass production to a large extent.

1. Introduction

Temperate permanent grasslands cover 38% of the agricultural area of Europe and deliver essential ecosystem services (Pilgrim et al., 2010; Suttie et al., 2005). These services include the production of fodder for livestock and the dairy industry (Voigtländer and Boeker, 1987), the maintenance of biodiversity (Lachat et al., 2010), and the sequestration of substantial amounts of carbon (Schulze et al., 2009). Climate projections forecast significant rainfall reductions in summer for central Europe (CH2018, 2018; Fischer et al., 2015). Such drought periods will influence physiological processes of ecosystems and consequently affect the ecosystem services that are delivered from permanent European grasslands (Reichstein et al., 2013).

Numerous studies have attempted to quantify the effects of drought on grassland ecosystems in the past decade. In general, these studies have confirmed that drought-induced water limitation typically leads to a reduction of net primary productivity (NPP) (Gherardi and Sala, 2019; Wilcox et al., 2017; Wu et al., 2011). Importantly, however, these studies have also shown that the response of ecosystems to experimental drought can vary quite dramatically (Gherardi and Sala, 2019; Gilgen and Buchmann, 2009; Grant et al., 2014; Hoover et al., 2014; Wilcox et al., 2017). Among others, the drought response of grasslands has been shown to depend on the severity of the experienced drought (Vicca et al., 2012; Wilcox et al., 2017), and important secondary factors such as the type of grassland affected (Byrne et al., 2013; Gherardi and Sala, 2019; Sala et al., 2015; Wilcox et al., 2017), the intensity of land use (Vogel et al., 2012; Walter et al., 2012), the plant functional composition (Gherardi and Sala, 2015; Hofer et al., 2016, 2017a; Mackie et al., 2018), or the biodiversity of an ecosystem (Isbell et al., 2015; Kahmen et al., 2005; Wagg et al., 2017). These secondary factors that affect the responses of terrestrial ecosystems to drought are just beginning to be understood (Reichstein et al., 2013; Wu et al., 2011). Defining their impact on the drought response of terrestrial ecosystems is yet essential for quantitative predictions of drought effects on the carbon cycle and for the ultimate inclusion of drought responses of terrestrial ecosystems in coupled land surface models (Schiermeier, 2010; Smith et al., 2014).

Grassland ecosystems often show a pronounced seasonality, where plants undergo different phenological, physiological, morphological or ontogenetic stages throughout a year (Gibson, 2009; Voigtländer and Boeker, 1987). Temperate European grasslands for example, are highly productive early in the growing season during reproductive growth, while they show much lower growth rates during vegetative stages in summer and fall (Voisin, 1988). Several studies have addressed how the seasonal timing of drought affects aboveground NPP (ANPP) of North American C4 grasslands (Nippert et al., 2006; Petrie et al., 2018). It has been suggested that moisture availability during stalk production of the dominant C4 grass species in mid-summer is particularly important for maintaining the annual productivity of these grasslands (Denton et al., 2017; La Pierre et al., 2011). For C3 dominated temperate grasslands, this would imply that spring, when grasses flower and have the highest growth rates, is the time when the productivity should be most susceptible to drought and that productivity should be less prone to drought-induced losses in the summer and fall.

61   Empirical evidence how the seasonal timing of a drought event affects the productivity of temperate C3 dominated

62   grasslands is, however, missing.

63   The impact of drought on the annual NPP of ecosystems depends on the immediate effects of drought on

64   productivity (determined by the drought resistance of the ecosystem), but also on potential legacy effects that occur after

65   drought release (determined by the drought resilience of the ecosystem) (Sala et al., 2012; Seastedt and Knapp, 1993). In

66   particular, legacy effects of drought are a critical yet rarely explored component that can strongly affect the impact of

67   drought on the annual NPP of an ecosystem (Ingrisch and Bahn, 2018; Petrie et al., 2018; Sala et al., 2012). Previously it

68   was believed that the drought history (e.g. previous year annual precipitation deficit) of an ecosystem is crucial for the

69   annual NPP and that the magnitude of the drought history negatively influences current NPP (Mackie et al., 2018;

70   Reichmann et al., 2013; Sala et al., 2012; Yahdjian and Sala, 2006). In contrast, there is now increasing evidence that

71   drought stressed plants or ecosystems can respond to drought release also with an overcompensation of their physiological

72   activity or growth (Griffin-Nolan et al., 2018; Hofer et al., 2017a; Shen et al., 2016). Following an experimental drought,

73   tropical and temperate tree seedlings have, for example, exhibited higher net photosynthesis rates than seedlings that had

74   not experienced a drought event (Hagedorn et al., 2016; O'Brien et al., 2017). In grasslands, Hofer et al. (2016) recently

75   showed that formerly drought-stressed swards had a higher productivity in the post-drought period than non-stressed

76   control swards and that the species richness of a grassland contributes to this effect (Kreyling et al., 2017; Wagg et al.,

77   2017). Even across growing seasons it has been suggested that the previous growing season precipitation patterns can

78   have positive legacy effects on the current year productivity of ecosystems (Shen et al., 2016). As legacy effects can

79   either worsen or diminish immediate drought effects on annual NPP, their assessment is essential to determine if the

80   sensitivity of annual NPP to the timing of drought is driven by the resistance or resilience of the system (Petrie et al.,

81   2018; Shen et al., 2016). This requires, however, a detailed analysis of not only annual NPP, but the assessment of biomass

82   increase (i.e. productivity) during and after the release of a drought event.

83   In the work that we present here, we experimentally assessed if the drought response of the annual NPP of six

84   different grasses that are common in temperate C3 grasslands depends on the timing of the drought event in the growing

85   season. To do so, we determined the drought resistance and resilience for these grasses in different times of the growing

86   season. Specifically, we tested in our study,

87   i)   if the timing of a drought event within the growing season (e.g. spring, summer, fall) has an effect on

88   the immediate aboveground productivity reduction – i.e. the resistance of an ecosystem,

89   ii)   if the timing of a drought event within the growing season affects the resilience of an ecosystem, and

90   iii)   how the combination of resistance and resilience in different times of the growing season impact the

91   annual aboveground productivity of drought-stresses C3 grasses.

92

2. Materials and methods

2.1 Research site

The experiment was performed in the years 2014 and 2015 near Zurich, Switzerland (47°26'N, 8°31'E, altitude: 490 m a.s.l., mean annual temperature: 9.4°C, mean annual precipitation: 1031 mm) on an eutric cambisol soil. For the experiment, we established six perennial C3 grass species in monoculture that are commonly used in agricultural practice in August 2013 on 96 plots (3 × 5 m). The plants were sown on a highly productive field that yields typically around 12 t grass dry matter per year and hectare (i.e. 1200 g m^{-2}). The establishment followed the basic procedures of sowing permanent highly productive grasslands, where before sowing, the existing vegetation at the site (which was a winter wheat) was plowed. Establishment of the grasses in the growing season before the experiment started followed best practice and guaranteed full establishment of the swards (including vernalisation during winter) and full productivity in the following year. The six grasses were *Lolium perenne* L. early flowering (LPe; cultivar 'Artesia'), *Lolium perenne* L. late flowering (LPl; cultivar 'Elgon'), *Dactylis glomerata* L. early flowering (DGe; cultivar 'Barexcel'), *Dactylis glomerata* L. late flowering (DGl; cultivar 'Beluga'), *Lolium multiflorum* Lam. var *italicum* Beck (LM; cultivar 'Midas'), and *Poa pratensis* L. (PP; cultivar 'Lato'). Phosphorous, potassium and manganese were applied following national Swiss fertilization recommendations for intensely managed grasslands at the beginning of each growing season (39 kg P ha^{-1}, 228 kg K ha^{-1}, 35 kg Mg ha^{-1}). In addition, all plots received the same amount of mineral N fertilizer as ammonium-nitrate (280 kg N ha^{-1}, divided into six applications per year). The solid N fertilizer was applied at the beginning of the growing season (80 kg N ha^{-1}) and after each of the first five cuts (40 kg N ha^{-1} each time).

2.2 Experimental design

Each of the six grass species was subject to four treatments: one rain-fed control and three seasonal drought treatments (spring, summer, fall) (see Fig. 1). We used a randomized complete block design with four blocks representing the four replicates. Each block contained all the 24 plots (six species times four treatments) fully randomized. A drought treatment lasted for ten weeks. Drought was simulated using rainout shelters that excluded rainfall completely on the treatment plots. The rainout shelters were tunnel-shaped and consisted of steel frames (3 × 5.5 m, height: 140 cm) that were covered with transparent and UV radiation transmissible greenhouse foil (Lumisol clear, 200 my, Hortuna AG, Winikon, Switzerland). To allow air circulation, shelters were open on both opposing short ends and had ventilation openings of 35 cm height over the entire length at the top and the bottom at both long sides. Gutters were installed to prevent the water from flowing onto adjacent plots, and a 0.75 m boarder zone at each plot was not considered for measurements to prevent a possible effect of lateral water flow in the soil. These shelters and plot design had previously been successfully used in other grassland-drought experiments (Hofer et al., 2016, 2017a, 2017b). Rain-fed controls were subject to the natural precipitation regime. However, when soil water potential (Ψ_{Soil}) sank below -0.5 MPa due to naturally dry conditions,

125   control plots were additionally watered with 20 mm of water (300 l per plot). Watering happened once on June 16th and

126   17th 2014 and three times in 2015 (7.7., 14.7., 11.8.).

127

2.3   *Environmental measurements*

129   Relative humidity and air temperature were measured hourly at the field site using VP-3 humidity, temperature and vapor

130   pressure sensors (Decagon Devices, Inc., Pullman, WA, USA). Measurements were conducted in control and treatment

131   plots under the rainout shelters (n=2). Information on precipitation and evapotranspiration was provided by the national

132   meteorological service stations that were in close proximity of our research site (average of the two surrounding

133   meteorological stations Zurich Affoltern in 1.4 km distance and Zurich Kloten in 4.5 km distance). Ψ_{Soil} was measured

134   in 10 cm depth on an hourly basis using 32 MPS-2 dielectric water potential sensors (Decagon Devices, Inc., Pullman,

135   WA, USA). The soil water potential sensors were evenly distributed over the field and treatments. Daily means of all

136   measurements were calculated per treatment, but across grasses since no grass-specific alterations in Ψ_{Soil} were expected

137   (Hoekstra et al., 2014) or measured (n=8).

138

2.4   *Harvests*

140   Aboveground biomass was harvested six times per year in five-week intervals in 2014 and 2015, resulting in six growth

141   periods per year (see Fig. 1). Aboveground biomass was also harvested once in spring 2016. Such a high frequency of

142   harvests is typical for highly productive grasslands used for fodder production. For the purpose of our study this high-

143   resolution biomass sampling allows the analyses of the immediate drought effects and the impacts of drought that occur

144   after the release of drought on productivity. The harvests were synchronized with the drought treatments and occurred

145   five and ten weeks after the installation of the shelters on a respective treatment. For the harvest, aboveground biomass

146   was cut at 7 cm height above the ground and harvested from a central strip (5 × 1.5 m) of the plot (5 × 3 m) using an

147   experimental plot harvester (Hege 212, Wintersteiger AG, Ried/I., Austria). The fresh weight of the total harvest of a plot

148   was determined with an integrated balance directly on the plot harvester. Dry biomass production was determined by

149   assessing dry weight – fresh weight ratios of the harvested biomass. For this a biomass subsample was collected for each

150   plot and the fresh and dry weight (dried at 60°C for 48 h) were determined. After the harvest of the aboveground biomass

151   in the central strip of a plot, the remaining standing biomass in a plot was mowed 7 cm above the ground and removed.

152

2.5   *Roots*

154   Belowground biomass of four grasses (DGe, DGl, LPe and LPl) was harvested six times per year, at the end of each

155   drought period and six to eight weeks after drought release, from the respective treatment and control plots using a manual

156   soil auger with a diameter of 7 cm. For each plot samples of the upper 14 cm soil were taken from two different spots

157 (one sample directly from a tussock and one from in between tussocks) and pooled as one sample per plot. All samples

158 were washed using a sieve with a mesh size of 0.5 cm × 0.5 cm and weighed after drying (at 60°C for 72 h).

159

160 *2.6 Determining drought impacts on productivity*

161 In order to allow the comparison of grassland productivity in the different treatments across the two years we standardized

162 the productivity that occurred in between two harvest periods (i.e. during five weeks) for growth related temperature

163 effects and calculated temperature-weighted growth rates for each of the six grasses (DMYTsum, see Menzi et al. (1991)).

164 For this purpose, we determined temperature sums of daily mean air temperature above a baseline temperature of 5°C

165 (Tsum) for each growth period (i.e. 5 weeks prior to harvest). Dry matter yield (DMY) of a given harvest was then divided

166 by the temperature sum of the corresponding time period to obtain temperature-weighted growth rates (henceforth referred

167 to simple as growth rate):

168

169   $DMYTsum = DMY(g\ m^{-2})/Tsum(°C).$      Eq. (1)

170

171 To determine the absolute change of growth (ACG) of a drought treatment on aboveground growth rate we calculated the

172 difference between temperature-weighted growth rates in a drought treatment (drt) and the corresponding control (ctr):

173

174   $ACG = DMYTsum(drt)-DMYTsum(ctr).$      Eq. (2)

175

176 To determine the relative change of growth (RCG) due to drought, we calculated percentage change of temperature-

177 weighted growth rates:

178

179   $RCG = 100\times(DMYTsum(drt)/DMYTsum(ctr)-1).$      Eq. (3)

180

181 Annual ANPP as an average of the different grasses was determined by adding up the dry matter yields of the six harvests

182 of a growing season. These data were not temperature-corrected (DMY).

183

184 We further calculated the sensitivity (S) of annual ANPP to the different drought treatments to quantify the response

185 relative to the amount of precipitation change, as suggested by previous studies (Huxman et al., 2004; Knapp et al., 2017;

186 Wilcox et al., 2017):

187

188   $S = (DMY(ctr)-DMY(drt))/(PPT(ctr)-PPT(drt))$      Eq. (4)

189

190   with PPT being the amount of precipitation in the treatment (drt) and control (ctr).

191

2.7   Data analysis

193   Relative and absolute changes in DMYTsum due to drought, the season of drought, and the tested grasses were analyzed

194   using linear mixed-effects regression (Pinheiro and Bates, 2000). Temperature-weighted growth rate (DMYTsum) was

195   regressed on the fixed variables season (factor of three levels: spring, summer, fall), drought (factor of two levels: control,

196   drought treatment) and grass (factor of six levels: LPe, LPl, DGe, DGl, LM, PP), including all interactions. To account

197   for repeated measurements of the control plots over time (as the control for every seasonal drought treatment was the

198   same), plot was specified as a random factor, thereby accounting for potential correlation of DMYTsum over time.

199   DMYTsum was natural log-transformed prior to analysis to improve homogeneity and normal distribution of residual

200   variance. This transformation also implies that the regressions provide the inference to relative changes in DMYTsum,

201   namely RCG. A temporal compound symmetry correlation structure was initially imposed on the residuals, yet, it turned

202   out that the estimated correlation parameter was very small. A likelihood ratio test indicated its non-significance ($p>0.5$)

203   and it was finally omitted. However, inspection of residuals revealed clear differences in their variance among seasons

204   and control and drought plots, and the residual variance parameter was defined as $Var(e_{jk}) = \sigma^2\delta_{jk}^2$, with δ being a ratio to

205   represent $j \times k$ variances, one for each of three seasons j under control and drought conditions k (Pinheiro and Bates,

206   2000). The R^2 of explained variance of fixed effects was computed following Nakagawa and Schielzeth (2013). This

207   model was applied to DMYTsum at each second growth period under drought and the second post-drought growth period

208   in 2014 and 2015.

209   Root dry weight was analyzed in a similar way, i.e. it was natural log-transformed prior to analyses and the same

210   explanatory factors were applied except that the factor grass had only four levels (only LPe, LPl, DGe and DGl measured).

211   Here, estimation of a single residual variance parameter e_i was sufficient to fulfill the model assumptions.

212   Annual ANPP was analyzed by one-way analysis of variance. The first factor season-treatment consisted of the

213   four levels control, spring drought, summer drought, and fall drought. The second factor grass consisted of six levels,

214   representing the six grasses.

215   All statistical analyses were done using the statistical software R, version 3.5.1 (R Foundation for Statistical

216   Computing, Vienna, Austria, 2018). Graphics were implemented with the package *ggplot2*, version 2.1.0 (Wickham,

217   2016).

3. Results

3.1 Precipitation, evapotranspiration and soil water potential

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219   *3.1 Precipitation, evapotranspiration and soil water potential*

220   Over the entire growing season, the year 2015 was exceptionally dry, while 2014 showed normal climatic conditions for

221   the experimental site. The difference between rainfall (634 and 568 mm for 2014 and 2015, respectively) and

222   evapotranspiration (356 and 447 mm for 2014 and 2015, respectively) was 278 mm in 2014 and only 121 mm in 2015

223   for the unsheltered control plots. The shelter periods reduced the total annual precipitation in the different treatments

224   between 17.9 % and 37.0 % and the precipitation of the growing season (duration of the experiment, approx. March –

225   November) by between 23.1 % and 45.8 % (see Table 1).

226   In 2014 Ψ_{Soil} was severely reduced in the drought treatments and reached values around the permanent wilting

227   point (-1.5 MPa) for the entire second half of the sheltered periods in all treatments (spring, summer, fall) (Fig. 2b-e,

228   Table 2). Due to low rainfall in June 2014, Ψ_{Soil} dropped not only in the sheltered summer drought treatment, but also in

229   the control and the fall drought treatment (that was not yet sheltered). Ψ_{Soil} recovered in the treatment plots after each

230   sheltered period and reached Ψ_{Soil} values comparable to the ones in the control plots. Because of the lack of rain in June

231   2014, the full rewetting of the spring drought treatment occurred only in the second post-drought growth period after the

232   spring drought shelter period, while after the summer drought treatment rewetting occurred already in the first post-

233   drought growth period.

234   In 2015, drought treatments reduced Ψ_{Soil} in all seasons (Fig. 2g-k). However, an intense rain event caused some

235   surface runoff in the field on May 1st 2015, which partly interrupted the spring drought treatment. Still, for the second

236   growth period of the spring drought treatment of 2015 the median of Ψ_{Soil} was at -0.77 MPa, a value comparable to that

237   of the second growth period of the summer drought treatment (-0.83 MPa) (Table 2). In 2015 Ψ_{Soil} reached lower values

238   during the shelter period in the fall treatment than during the shelter period in the spring and summer treatments. Due to

239   a lack of rain in 2015, Ψ_{Soil} recovered only partly after the end of the shelter period in the spring and summer drought

240   treatments and remained significantly below that of the control plots for both post-drought growth periods (Table 2).

241   Watering of the control plots during natural dry conditions lead to quick increases in Ψ_{Soil} to values close to saturation

242   (=0 MPa).

243   Daily mean air temperature under the rainout shelters was between 2.9°C lower and 3.5°C higher than in the

244   control.

245

3.2 Varying growth rates throughout the growing season

246   *3.2 Varying growth rates throughout the growing season*

247   The temperature-weighted growth rates of the investigated six grasses in the control plots showed a clear seasonal pattern

248   (Fig. 3a). In both years, it was highest during the second growth period in spring and sharply declined to values that were

249   two- to eight-fold smaller in summer and fall. Except for the second growth period growth rates of the grasses were lower

250   in 2015 than in 2014. Root biomass increased towards summer and slightly decreased after summer in 2014 (Fig. 3b).

251

252   *3.3*   *Seasonality of drought resistance*

253   The growth rates of the six grasses were barely affected by the exclusion of rain during the first five weeks of sheltering

254   (Fig. 4). However, during the second sheltered growth period (weeks six to ten), the drought treatments strongly reduced

255   temperature-weighted growth rates in all seasons, in both years, and in relative and absolute terms (Figs. 4, 5 and 6, Table

256   3). In both years, the relative drought-induced changes in growth rates compared to the controls were smallest in spring

257   (2014: -51%, 2015: -20%) and clearly larger in summer (2014: -81%, 2015: -85%) and fall (2014: -77%, 2015: - 84%)

258   (Fig.4a, Table 3; season x treatment $p<0.001$). As such, the drought resistance of temperate grasses throughout the

259   growing season was largest in spring and positively correlated with their productivity (Fig. 5). This pattern was generally

260   observed for all six grasses tested (Fig. 6a) even though there was a significant season × treatment × grass interaction

261   (Table 3). In 2014 this interaction mainly derived from DGl and PP showing an exceptionally large drought induced

262   growth reduction in fall. In 2015 it was explained by an especially low drought response of DGl in spring and strong

263   responses of DGl in summer and LPe and PP in fall (Fig. 6a).

264   In 2014 the absolute drought-induced reduction of growth across all six grasses was largest in spring (-0.5 g m^{-2}

265   °C^{-1}), followed by summer (-0.4 g m^{-2} °C^{-1}) and was lowest in the fall (-0.1 g m^{-2} °C^{-1}) (Fig. 4b). Likewise, in 2015 the

266   absolute reduction of the growth rate in the drought treated plots was largest across the six grasses in spring (-0.2 g m^{-2}

267   °C^{-1}), but slightly lower in summer (-0.1 g m^{-2} °C^{-1}) and fall (-0.1 g m^{-2} °C^{-1}).

268   The average standing root biomass across four of the grasses was not significantly affected by any of the drought

269   treatments of 2014 (Fig. 7).

270

271   *3.4*   *Seasonality of post-drought resilience*

272   When compared to corresponding controls, relative (and absolute) changes in temperature-weighted growth rates after

273   drought release showed positive treatment effects in 2014 (Fig. 8, Table 4). Across all six grasses, the relative increases

274   in post-drought growth rates were 41% after the spring drought treatment, 31% after the summer drought treatment and

275   53% after the fall drought treatment, and did not differ among the seasons (Table 4; season × treatment p=n.s.). In 2015,

276   the relative increases in post-drought growth rates were 5% after the spring drought treatment, 15% after the summer

277   drought treatment and 52% after the fall drought treatment, and did differ among the seasons (Table 4; season × treatment

278    $p<0.001$). Increased growth rates were also observed in the first harvest in 2015 and 2016 for all the plots that had received

279   a drought treatment in 2014 and 2015, respectively (Fig. 4). In this first harvest of 2015, growth rate increases were 110%

280   after the spring, 36% after the summer and 53% after the fall drought treatments of 2014. In the first harvest of 2016,

281   growth rate increases were 10% after the spring, 31% after the summer and 51% after the fall drought treatments of 2015.

282   When compared across the different grasses, the only grass that tended to have a weaker resilience (lower or no

283   increase of growth rate during post-drought) was LM (Fig. 8); but there was no significant difference among the grasses

284   (Table 4; treatment x grass p=n.s.). In 2015 again LM showed the weakest resilience of all the grasses after all drought

285   treatments, the effect being significant (Table 4; treatment x grass $p<0.001$).

286   Root dry weight of the treatment plants showed no alterations in growth compared to the control in either of the

287   post-drought periods (Fig. 7).

288

289   **3.5   *Effects of seasonal drought on annual biomass production***

290   The cumulative annual aboveground biomass production (i.e. annual ANPP) of the controls averaged across all six grasses

291   differed strongly between the two years (Fig. 9a), with 2014 (1303 g m^{-2} a^{-1}) being 37% more productive than 2015 (949

292   g m^{-2} a^{-1}). The strong reduction in biomass production in 2015 was most probably related to the naturally occurring lack

293   of rain in summer and fall (Fig 2). This is evident from the two spring growth periods being equally productive in the

294   unsheltered plots (control, summer and fall drought) in 2015 and in 2014 (Fig. 9a). The annual ANPP of the treatments

295   was significantly different from control in both years. In 2014, the largest drought effect on the annual ANPP across all

296   grasses resulted from the summer treatment, which reduced productivity significantly by 14% (185 g m^{-2}) compared to

297   the control. Spring and fall drought treatments in 2014 resulted in a non-significant 4% (53 g m^{-2}) and 6% (74 g m^{-2})

298   reduction of annual ANPP across all grasses, respectively. In 2015, drought treatments in the summer and fall significantly

299   caused a 10% and 11% reduction of annual ANPP across all grasses (-97 g m^{-2} and -105 g m^{-2}), respectively, while the

300   spring drought treatment reduced annual ANPP across all grasses by only 4% (34 g m^{-2}), which was not significant (Fig.

301   9a).

302   The sensitivity of annual ANPP to drought differed between the treatments in both years of the experiment. In

303   2014, the annual ANPP was most sensitive to drought in the summer, while annual ANPP was less sensitive to rainfall

304   reduction in the spring but also fall (Fig. 9b). In 2015, the sensitivity increased within the growing season so that annual

305   ANPP was least sensitive to spring drought and most sensitive to fall drought (Fig. 9b).

306

4. Discussion

307 In our study we experimentally assessed if the drought resistance and resilience of six different temperate perennial C3

308 grasses varies throughout the growing season and if the timing of a drought event, thus, has an influence on drought

309 induced reductions in annual NPP of these grasses. All six temperate grasses showed a clear seasonal pattern of drought

310 resistance in both years. The drought-induced reduction of growth was smaller under spring drought (-20% and -51% for

311 the two years) than under summer and fall droughts (between -77% and -87%). Thus, the investigated grasslands were

312 more resistant to drought in the spring when productivity of temperate grasses is generally the highest and they were least

313 resistant in summer and fall, when their productivity is much lower. Moreover, the examined grasslands did not show any

314 negative legacy effects such as a prolonged suppression of growth after rewetting following the end of the drought

315 treatments. In contrast, after the release of drought, temperature-weighted growth rates of the grasses in the treatment

316 plots surprisingly outperformed the growth rates of the grasses in the controls for extended periods of time. This suggests

317 a high resilience of all six grasses that we investigated. As a consequence of the high resilience, the seasonal drought

318 treatments resulted in only moderate drought-induced reductions in annual aboveground NPP between -4% to -14% -

319 despite the strong immediate effects of drought - and no clear effects of the timing of drought on annual NPP were

320 detected. With this our study shows (i) that the resistance of growth rates in different grasses to drought varies throughout

321 the growing season and is positively correlated with growth rates in the control, (ii) that positive legacy effects of drought

322 on plant productivity indicate a high resilience of temperate C3 grasses throughout the entire growing season, and (iii)

323 that the high resilience can strongly compensate for immediate seasonal drought effects on productivity, resulting in total

324 annual NPP that is only marginally reduced in the drought treated plots compared to the controls.

4.1 Differences in the climatic conditions between the two years

327 While the first experimental year (2014) was characterized by more or less normal climatic and thus growth conditions,

328 the summer of 2015 was exceptionally dry in all of central Europe (Dietrich et al., 2018; Orth et al., 2016). These

329 conditions led to a reduction of the annual NPP of the control plots by 37% in 2015 compared to 2014 (Fig. 9a). The lack

330 of rain in the second half of the 2015 growing season i.e. between the third harvest in June and the last harvest in October

331 (Fig. 2) was of importance for our experiment, especially for the response of the treatments during the recovery phase

332 after the removal of the shelters. In this period, the amount of rainfall was only 153 mm in 2015 while it was 405 mm in

333 2014. Thus, positive legacy effects directly following drought treatments were much smaller or absent following the

334 spring and summer treatments in 2015 due to a missing rewetting (Figs. 2, 4 and 8). Yet, strong positive legacy effects in

335 response to the 2015 treatments were observed in the first harvest of 2016 when the experimental site was fully rehydrated.

336 This highlights the general occurrence of positive drought legacy effects in the investigated grasslands once the soil

337 moisture has recovered from the drought treatments.

339   Intense rains between the first and second harvest of the year 2015 caused some water flow into the treatments.

340   This resulted in a partial reduction of drought stress in the treatment plots (Fig. 2h). Yet, the median of the soil water

341   potential was still clearly reduced in the treatment plots compared to the control and, consequently, we observed a

342   reduction of growth rates in the second spring harvest in 2015 despite this event (Figs. 4, 6). We therefore conclude that

343   the partial reduction in drought stress did weaken the immediate drought response during the growth period concerned,

344   but that this does not question the overall drought responses of the grasslands that we report here.

345

346   *4.2   Grasses were most resistant to drought in spring, the most productive part of the growing season*

347   Previous studies have indicated that the timing of drought is relevant for the reduction of annual NPP of ecosystems

348   (Bates et al., 2006; Denton et al., 2017; La Pierre et al., 2011; Nippert et al., 2006). It has been argued that the variable

349   drought sensitivity of ecosystems throughout the growing season could be linked to different phenological stages of

350   dominant plant species, where plants in reproductive stages and periods of high growth are particularly susceptible to

351   drought (Bates et al., 2006; Craine et al., 2012; Dietrich and Smith, 2016; Heitschmidt and Vermeire, 2006; O'Toole,

352   1982). We found, however, that relative reductions in temperature-weighted growth rates were lowest in the spring

353   treatments 2014 and 2015 as compared to the summer and fall treatments. The highest resistance of plant growth rates to

354   drought occurred, thus, when the plants showed the highest growth rates in the control and when the investigated grasses

355   were in their reproductive stages (Fig. 5). With this, our findings are in contrast to previous studies that have suggested

356   temperate grasslands and crops to be particularly susceptible to drought early in the growing season when their growth

357   rates are the highest and plants are in reproductive stages (Bates et al., 2006; Craine et al., 2012; Dietrich and Smith,

358   2016; Heitschmidt and Vermeire, 2006; Jongen et al., 2011; O'Toole, 1982; Robertson et al., 2009). Our study does

359   support, however, findings of El Hafid et al. (1998) and Simane et al. (1993), who detected that spring droughts have the

360   least impact on annual productivity of wheat. Importantly, most of the previous studies that have reported the effects of

361   drought timing on grasslands or other ecosystems report effects on annual NPP but have not differentiated immediate and

362   long-term legacy effects of drought events as we did in our study. As drought impacts on annual NPP combine immediate

363   and post drought legacy effects, it is difficult to directly compare the results we present here on variably seasonal drought

364   resistance of temperate C3 grasses to previous work reporting the influence of drought timing on annual NPP.

365   One possibility for the higher drought resistance of grasses during spring is that grasses invest more resources

366   towards the stress resistance of their tissue in this part of the growing season when they have not only the largest growth

367   rates, but also reproduce. Such a resource allocation strategy could allow drought stressed grasses to remain

368   physiologically active in this critical part of the growing season. Osmotic adjustment is one mechanism that reduces the

369   effects of drought on the physiological performance of the plant (Sanders and Arndt, 2012). This is achieved through the

370   active accumulation of organic and inorganic solutes within the plant cell. Thus, osmotic potential increases and the plant

371 can withstand more negative water potentials in the cell while maintaining its hydraulic integrity (Sánchez et al., 1998).

372 Santamaria et al. (1990) found that early- and late flowering cultivars of *Sorghum bicolor* L. developed a different pattern

373 of osmotic adjustment (continuous increase of osmotic adjustment vs. first increase and later decrease of osmotic

374 adjustment), hinting that drought tolerance may vary between seasons. In a companion paper we report physiological data

375 for the six grasses from the same experiment. We show that at a given soil water potential, foliar water potentials were

376 less negative and stomatal conductance was higher in plants drought stressed in the spring compared to plants drought

377 stressed in the summer or fall (Hahn et al. in prep). This suggests indeed that for a given drought level, grasses remain

378 physiologically more active in the spring than in the summer or fall. The exact physiological mechanisms that explain the

379 higher drought resistance of the investigated grasslands in the spring and their higher drought susceptibility in the summer

380 and fall remain yet unknown and require further detailed ecophysiological and biochemical assessments.

381 An alternative explanation for different immediate drought effects on growth rates throughout the growing

382 season are experimental artefacts causing different experimentally induced drought severities throughout a growing

383 season. This could be by either residual moisture dampening the experimentally induced drought more in the spring than

384 in the summer or fall. Alternatively, higher evaporative demand of the atmosphere in the summer compared to the spring

385 or fall could have enhanced experimentally induced drought effects in the summer. De Boeck et al. (2011) explain for

386 example the higher drought susceptibility of growth in three herbs in the summer compared to spring by a higher

387 evaporative demand of the atmosphere in the summer compared to spring or fall. In our study, however, soil water

388 potential data indicate that ten weeks of drought treatment reduced plant available water in the soil to mostly equal levels

389 in spring, summer and fall (Fig. 2). In addition, we found only small differences in median VPD between the spring,

390 summer and fall drought treatment period (Fig. 2). This suggests that stronger drought stress in summer and fall compared

391 to spring cannot explain alone the different resistances of plant growth to drought throughout the growing season. Along

392 these lines, Denton et al. (2017), who performed a similar experiment as we report here but in a C4 grassland in North

393 America, also did not find that these seasonal differences in the experimentally induced drought severity are the reason

394 for variable drought effects on the growth rates throughout the growing season.

395

396 *4.3   No increased root biomass in the top soil layer*

397 In the entire experiment, root biomass increased only in one out of the four investigated grasses (DGe) in response to

398 drought in summer as well as in the post-summer drought period. This confirms the findings of Byrne et al. (2013),

399 Denton et al. (2017) and Gill et al. (2002), who did not find any changes in belowground biomass in response to drought.

400 In a similar setting, Gilgen and Buchmann (2009) found no changes in belowground biomass to simulated summer

401 drought in three different temperate grassland sites (from lowland to alpine grassland). While Denton et al. (2017) ascribe

402 the missing drought response in belowground biomass to modest precipitation alterations in their experiment, we can

403   exclude this a factor in our experiment since the soil water potential under drought was significantly reduced compared

404   to the soil water potential in the controls in every season. Contrary to that, several studies have shown that drought can

405   maintain or increase root growth while inhibiting shoot growth (Davies and Zhang, 1991; Hofer et al., 2017a; Saab et al.,

406   1990). In an experiment by Jupp and Newman (1987), *L. perenne* increased lateral root growth under low Ψ_{Soil} indicating

407   an increased investment in root growth under water limited conditions. In our experiment the *L. perenne* grasses did not

408   show a trend towards increased investment in root growth, neither during drought nor after drought-release, contradicting

409   the results of Jupp and Newman (1987). Such differences in the response of root biomass in different studies as described

410   above may derive from the soil layer that was investigated. Hofer et al. (2017a) have shown that the response of root

411   growth into ingrowth bags depended on the soil depth: root growth of *L. perenne* decreased in the top soil layer (0-10

412   cm), but increased in deeper soil layers of 10-30 cm. Thus, the superficial root sampling (0-14 cm) in our experiment

413   might mask increased root growth in deeper soil.

414

415   ### *4.4   Positive legacy effects of drought periods*

416   Several previous studies have suggested that drought events can lead to negative legacy effects on the productivity of

417   ecosystems (Petrie et al., 2018; Reichmann et al., 2013; Sala et al., 2012). We found, however, that growth rates of

418   previously drought-stressed plots were significantly larger than in the corresponding control plots after rewetting,

419   indicating positive legacy effects and a high resilience of the investigated grasses (Figs. 4 and 8). Interestingly, we did

420   not only observe growth rates that were larger in the treatment plots than in the control plots immediately after the drought

421   release, but observed larger growth rates in all treatment plots compared to the control plots even in the first harvests of

422   the following growing season (Fig. 4). This pattern was consistent for both years of the experiment. Bloor and Bardgett

423   (2012) and also Denton et al. (2017) found that drought events promote soil fertility and nutrient retention following

424   drought release. Likewise, Gordon et al. (2008) found an increase in microbial activity after a rewetting event, possibly

425   leading to a rapid and sudden influx of plant available nitrogen in the soil (Mackie et al., 2018; Schimel and Bennett,

426   2004). Hofer et al. (2017a) also attributed growth increases relative to control plots in post-drought periods to nitrogen

427   availability in the soil and Karlowsky et al. (2018) found evidence that interactions between plants and microbes increase

428   plant nitrogen uptake in grasslands after rewetting events. It could, thus, be that the enhanced productivity in the treatment

429   plots following drought release is the result of increased microbial activity leading to enhanced nitrogen availability

430   and/or changes in resource limitation following drought release as suggested by Seastedt and Knapp (1993) in their

431   Transient Maxima Hypothesis.

432   We applied nitrogen fertilizer in our experiment to each plot after each harvest, also at the beginning and in the

433   middle of a drought treatment. Since we applied the fertilizer in form of water-soluble pellets, it is possible that nitrogen

434   fertilizer pellets accumulated in the drought-treated plots during the treatment phase. The rewetting of the soil could have

435 resulted in a massive release of nitrogen fertilizer from these pellets so that plant growth rates in formerly drought-stressed

436 plots were stimulated by the release of this fertilizer and, thus, larger than those of the control plots. However, Hofer et

437 al. (2017a) observed strongly increased N availability and plant growth rates after drought release not only in plots that

438 received mineral fertilizer during the drought treatment period, but also in plots that did not receive any N fertilizer during

439 drought. We suggest therefore that the release of accumulated fertilizer nitrogen in the treatment plots might explain

440 some, but not all post-treatment growth responses in the formerly drought treated plots in our study.

441 Hagedorn et al. (2016) have shown that rewetting events trigger intrinsic processes that lead to a sudden increase

442 of photosynthesis in young beech trees. Moreover, Arend et al. (2016) found a rapid stimulation of photosynthesis

443 immediately after rewetting that continued until the end of the growing season, partly compensating the loss of

444 photosynthetic activity during drought. Hofer et al. (2017b) found an increased root mass and increased water-soluble

445 carbohydrate reserves in the stubbles of drought stressed *L. perenne* at the end of a drought stress period. Both of which

446 could have contribute to increased growth rates observed in their study once rewetting had occurred. Also, drought-

447 induced shifts in plant phenology could lead to a shift in high productive stages, e.g. leading to peak growth rates not in

448 spring, but in summer (O'Toole and Cruz, 1980). With the data we collected throughout our experiment, we cannot clearly

449 identify the mechanisms behind the strong post-drought growth increase that extended even into the next growing season.

450 In the end, several biogeochemical and ecophysiological mechanisms might be responsible for the overcompensation of

451 growth following drought release.

452

453 **4.5   The grasses only slightly differed in drought resistance and resilience**

454 During the seasonal drought events the six tested grasses showed a mostly universal response with only slight and not

455 consistent differences in their growth rate reductions. Post-drought legacy effects differed among the different grasses in

456 the second year (grass x treatment; *p*=n.s. for 2014 and *p*<0.001 for 2015). *D. glomerata* and *P. pratensis* showed a high

457 potential for resilience and overcompensation after drought, while *L. multiflorum* generally showed the lowest resilience.

458 Wang et al. (2007) found that plant communities consisting of less productive species were more resistant to drought than

459 plant communities consisting of more productive species. The fact that inter-specific differences in the responses to the

460 drought stress and to the following rewetted post-drought period in our study were smaller than in other studies, may be

461 related to the fact that all six tested grasses belong to a relatively narrow functional group of productive fast-growing

462 grasses with high demands for mineral N in the soil. The availability of mineral N in the soil was found to be a key factor

463 for the response during as well as after drought for non-leguminous species (Hofer et al., 2017a, 2017b).

464

465 **4.6   Small to moderate impact of seasonal drought on annual aboveground net primary production**

466   Although the immediate effects of drought on growth rates were severe in all three seasons in our study, the overall effects

467   on total annual ANPP of 4 to 14% were only small to moderate compared to drought effects observed in other studies

468   (Gherardi and Sala, 2019; Wilcox et al., 2017; Wu et al., 2011) (Fig. 9a). We also did not find any consistent effects of

469   the drought timing on annual NPP, contrary to other studies (Denton et al., 2017; La Pierre et al., 2011; Nippert et al.,

470   2006; Petrie et al., 2018). This is likely a consequence of the small overall drought effects on annual ANPP in our study.

471   The small drought effects on annual ANPP that we report here can be explained by the high resilience of growth rates in

472   the treatment plots following the drought release. This is in particular evident in the spring treatment, where we observed

473   on the one side the largest absolute reduction in growth in response to drought, but at the same time also the strongest

474   positive legacy effects after drought, leading to relatively small total drought effects on annual aboveground ANPP.

475   Because the fall drought treatment period lasted until the end of the vegetation period, the positive post-drought legacy

476   effects for this treatment were not included in the calculation of annual biomass production. Nevertheless, the fall drought

477   treatment in 2014 did also not strongly affect the annual aboveground ANPP. This is because the growth period affected

478   by the fall drought treatment, was the least productive part of the growing season, and, thus contributed only little to the

479   annual productivity.

480   The overall effect of drought on annual ANPP might also be small compared to other studies because our study

481   was conducted in highly productive grasslands that according to best practice management were harvested six times in

482   the growing season. The drought treatments occurred, however, only in two out of these six growth periods throughout

483   the growing season. In addition, the first sheltered growth period generally did not show a reduced growth rate (Fig. 4),

484   because the soil with its water holding capacity acted as a buffer. With the absence of negative legacy effects, the impact

485   of the immediate drought effect of one drought stressed growth period on annual NPP was therefore diluted by the five

486   other harvests of the vegetation period (Finn et al., 2018).

487   The majority of studies that have assessed the impact of drought on grassland productivity have either assessed

488   immediate drought effects, i.e. drought resistance (Bollig and Feller, 2014; Kahmen et al., 2005; Walter et al., 2012;

489   Wang et al., 2007), or have assessed the net effects of drought on annual NPP (Gherardi and Sala, 2019; Wilcox et al.,

490   2017; Wu et al., 2011). Our study highlights that it is important to also quantify immediate and post-drought effects –

491   even in the following growing season – if the causes of drought reduced annual productivity are to be understood.

492   Effects of drought on annual aboveground NPP of grasslands have been shown to vary, depending on the severity

493   of the experienced drought (Vicca et al., 2012; Wilcox et al., 2017), ecosystem type (Byrne et al., 2013; Gherardi and

494   Sala, 2019; Sala et al., 2015; Wilcox et al., 2017), the intensity of land use (Vogel et al., 2012; Walter et al., 2012), the

495   plant functional composition (Gherardi and Sala, 2015; Hofer et al., 2016, 2017a; Mackie et al., 2018), or the biodiversity

496   of an ecosystem (Isbell et al., 2015; Kahmen et al., 2005; Wagg et al., 2017). In accordance with work in C4 grasslands,

497   our study shows that the timing of a drought event in the growing season is crucial for the immediate effects of a drought

498   on grassland productivity. Importantly, however, our study also shows that strong positive legacy effects can occur after

499   rewetting and that these legacy effects are even important in spring of the next year. These effects can partially compensate

500   the strong immediate drought effects and lead relatively small overall seasonal drought effects on annual ANPP.

501   Author contributions:

502   AK and AL planned and designed the research. CH and SEH performed the experiments. CH analysed the data and wrote

503   the manuscript. AK and AL co-wrote the manuscript.

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708

709 Tables

710 Table 1: Amount of rainfall fallen in the experiment and associated amount of excluded rainfall during the sheltered

711 drought periods in the years 2014 and 2015. Growing season precipitation refers to the period of time between the set-up

712 of the shelters and the last harvest of each year.

		2014		
annual precipitation	growing season precipitation	spring	summer	fall
		excluded precipitation (mm)		
937.1	717.9	167.4	308.8	241.7
		excluded precipitation annually (%)		
		17.9	33.0	25.8
		excluded precipitation in growing season (%)		
		23.2	43.0	33.7
		2015		
annual precipitation	growing season precipitation	spring	summer	fall
		excluded precipitation (mm)		
801.9	648.5	296.9	204.7	149.9
		excluded precipitation annually (%)		
		37.0	25.5	18.7
		excluded precipitation in growing season (%)		
		45.8	31.6	23.1

713

714 Table 2: (a) Median of soil water potential and (b) average air temperature during the two growth periods of the drought

715 treatments and the two post-drought growth periods as well as the corresponding periods of the rain-fed control. n.a.: not

716 available.

a) Growth period	Control			Treatment		
	spring	summer	fall	spring	summer	fall
2014			MPa			
1st drought	-0.03	-0.41	-0.01	-0.09	-0.72	-0.73
2nd drought	-0.01	-0.01	-0.01	-1.44	-1.44	-1.61
1st post-drought	-0.41	-0.01	-0.01	-1.1	-0.05	-0.01
2nd post-drought	-0.01	-0.01	n.a.	-0.01	-0.02	n.a.
2015			MPa			
1st drought	-0.01	-0.02	-0.14	-0.08	-0.45	-0.85
2nd drought	-0.01	-0.25	-0.34	-0.77	-0.83	-1.34
1st post-drought	-0.02	-0.14	n.a.	-0.57	-0.73	n.a.
2nd post-drought	-0.25	-0.34	n.a.	-0.7	-0.88	n.a.
b) Growth period	Control			Treatment		
	spring	summer	fall	spring	summer	fall
2014			°C			
1st drought	10.3	18.0	16.6	11.0	19.0	17.3
2nd drought	10.9	18.0	15.2	11.5	18.7	15.8
1st post-drought	18.0	16.6	7.1	18.0	16.6	7.1
2nd post-drought	18.0	15.2	n.a.	18.0	15.2	n.a.
2015			°C			
1st drought	7.1	16.2	20.3	7.6	16.9	20.5
2nd drought	13.3	22.7	13.0	14.4	23.7	13.5
1st post-drought	16.2	20.3	n.a.	16.2	20.3	n.a.
2nd post-drought	22.7	13.0	n.a.	22.7	13	n.a.

717

718 Table 3: Summary of analysis for the effects of season, drought treatment, grass, and their interactions on temperature-

719 weighted growth rates (DMYTsum, natural log-transformed) from the second growth period during drought (weeks six

720 to ten). The inference (F- and p-values) and the R^2 refer to the fixed effects from the linear mixed model. df_{num}: degrees

721 of freedom term, df_{den}: degrees of freedom of error.

Effect	df_{num}	df_{den}	2014		2015	
			F-value	p	F-value	p
Season (spring, summer, fall)	2	36	1051.1	<0.001	2655.3	<0.001
Treatment (control vs. drought)	1	72	341.9	<0.001	642.9	<0.001
Grass	5	72	9.4	<0.001	14.2	<0.001
Season × Treatment	2	72	25.9	<0.001	366.2	<0.001
Season × Grass	10	36	6.8	<0.001	10.3	<0.001
Treatment × Grass	5	72	2.9	0.018	2.0	0.094
Season × Treatment × Grass	10	72	3.3	0.001	3.4	0.001
R^2			0.901		0.965	

722

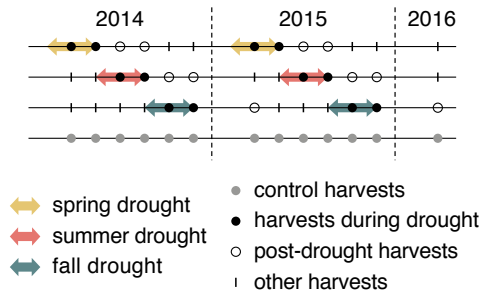
723   Table 4: Summary of analysis for the effects of season, drought treatment, grass, and their interactions on temperature-

724   weighted growth rates (DMYTsum, natural log-transformed) from the second post-drought growth period (weeks six to

725   ten). See Table 3 for additional explanation.

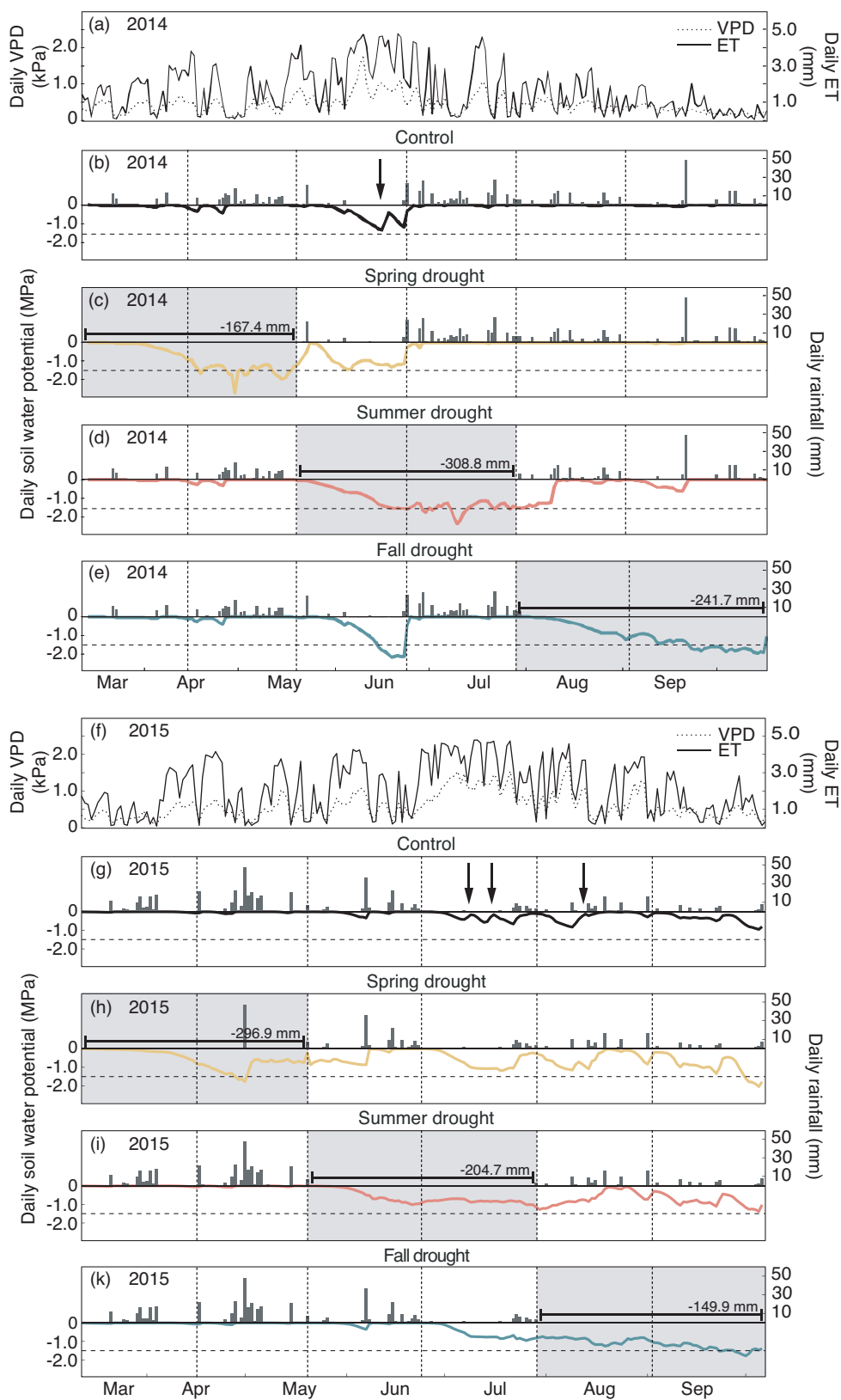
Effect	df_{num}	df_{den}	2014		2015	
			F-value	p	F-value	p
Season (spring, summer, fall)	2	36	783.4	<0.001	1428.6	<0.001
Treatment (control vs. drought)	1	72	63.5	<0.001	25.5	<0.001
Grass	5	72	18.4	<0.001	39.4	<0.001
Season × Treatment	2	72	1.8	0.180	16.6	<0.001
Season × Grass	10	36	15.7	<0.001	9.6	<0.001
Treatment × Grass	5	72	0.9	0.517	6.4	<0.001
Season × Treatment × Grass	10	72	2.2	0.025	0.8	0.621
R^2			0.810		0.944	

726

727   Figures

728

729   Fig. 1: Experimental design; experiment lasted two consecutive years (2014, 2015) with six evenly distributed harvests

730   in both years and one additional harvest in the beginning of 2016. Arrows indicate the duration of each drought treatment

731   (ten weeks). Each treatment was replicated four times with each of six grasses.

733   Fig. 2: (a, f) Daily evapotranspiration (ET) and vapor pressure deficit (VPD), (b-e, g-k) daily rainfall and soil water

734   potential (Ψ_{Soil}) in 10 cm depth over the growing seasons 2014 (a-e) and 2015 (f-k) for the control and drought treatment

735   (sensors per treatment: n=8). Grey shaded areas represent the experimental drought when rainfall was excluded. Dashed

736   horizontal line shows permanent wilting point (Ψ_{Soil}=-1.5MPa). Dashed vertical lines represent dates of harvest. Arrows

737   indicate watering events (in control plots only).

738

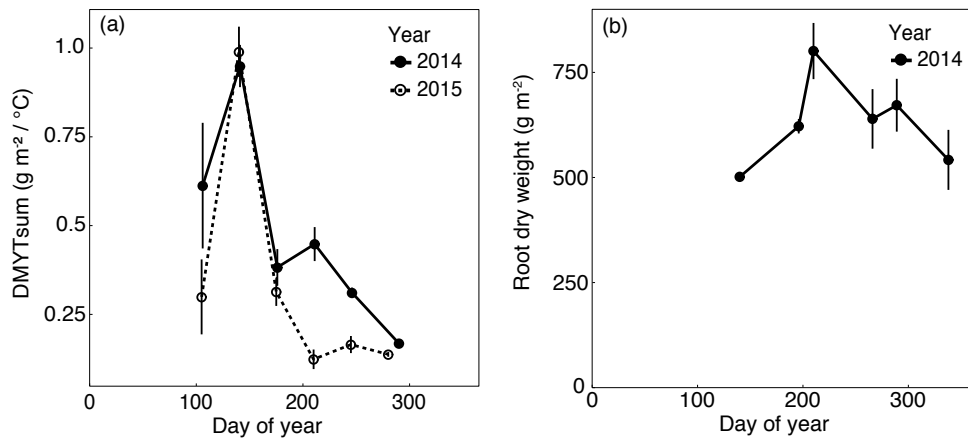
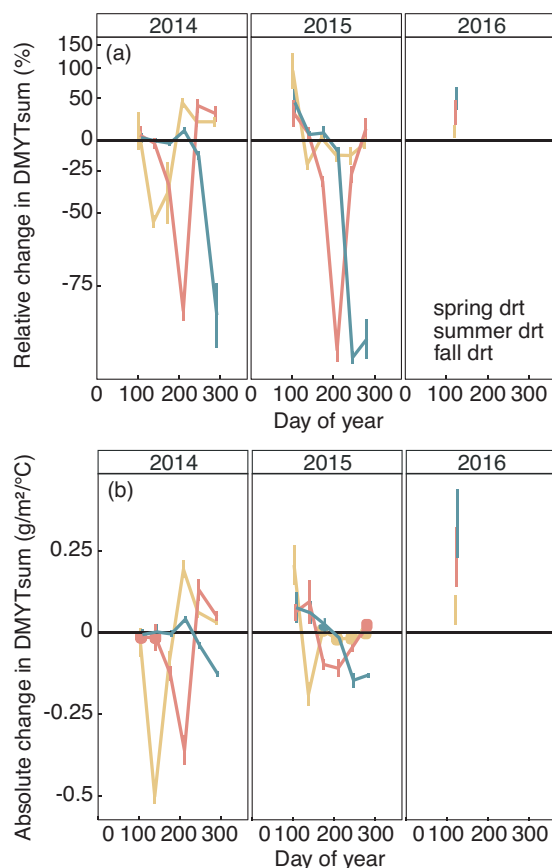



Fig. 3: (a) Temperature-weighted growth rates (DMYTsum) of aboveground biomass of rain-fed control plots in 2014

and 2015; values are means across all six investigated grasses and four replicates (n=6, ± se) and b) belowground biomass

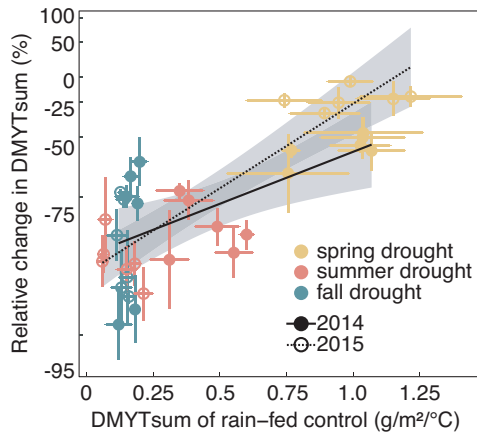
of rain-fed control plots in 2014; values are means across the four grasses *L. perenne* early (LPe) and late (LPl) flowering

and *D. glomerata* early (DGe) and late (DGl) flowering (n=4, ± se).

743   Fig. 4: (a) Relative (RCG) and (b) absolute (ACG) changes in temperature-weighted growth rates (DMYTsum) of the

744   respective drought (drt) treatment compared to the control (ctr) for 2014, 2015 and 2016. Values are means ± se across

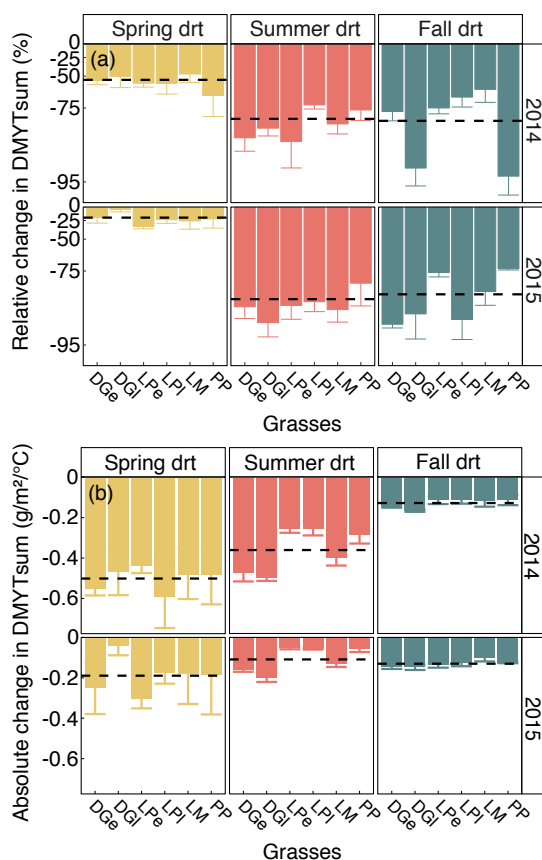
745   all six investigated grasses each in four replicates. Values below the horizontal black line indicate reduced growth

746   compared to the control. Values above the line indicate an increase of growth.

747   RCG=100×(DMYTsum(drt)/DMYTsum(ctr))-1); displayed on log-scale); ACG=DMYTsum(drt)–DMYTsum(ctr).

748

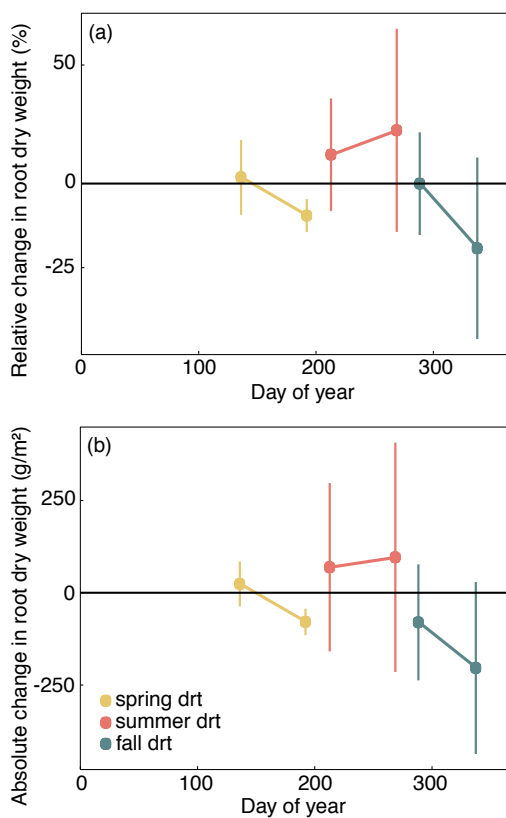
749   Fig. 5: Relative changes of temperature-weighted growth rate due to drought (RCG; %) as a function of temperature-

750   weighted growth rate (DMYTsum) of the corresponding rain-fed control plots (g/m^2/°C). Values are means ± se for all

751   six investigated grasses each in four replicates.

752   Fig. 6: (a) Relative (RCG) and (b) absolute (ACG) changes in temperature-weighted growth rates (DMYTsum) for the

753   second growth period (weeks six to ten) of the respective drought (drt) treatment for 2014 and 2015 for the individual

754   grasses. Values are means of four replicates ± se. Dashed black lines represent the means across all grasses. See Fig. 4

755   for additional explanation.

756   Fig. 7: (a) Relative and (b) absolute changes in root dry matter at the end of each drought treatment and after six to eight

757   weeks after drought-release in 2014. Values are means ± se of four grasses of *L. perenne* (LPe and LPl) and *D. glomerata*

758   (DGe and DGl) each in four replicates.

759

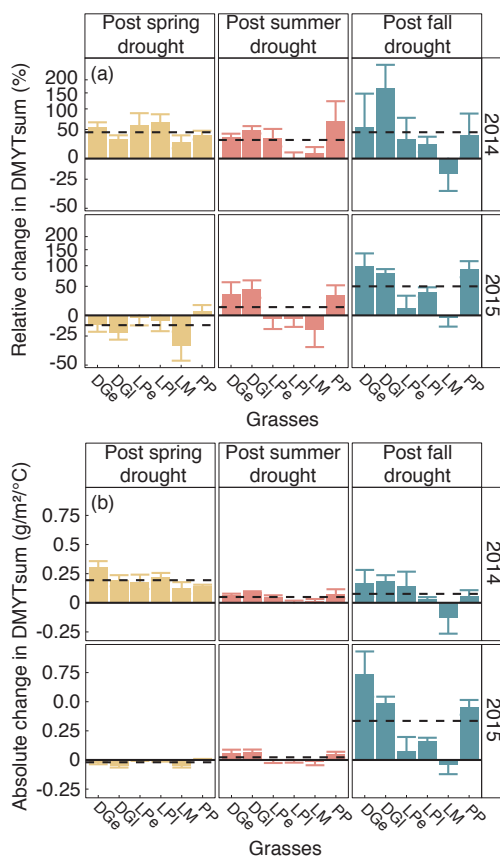
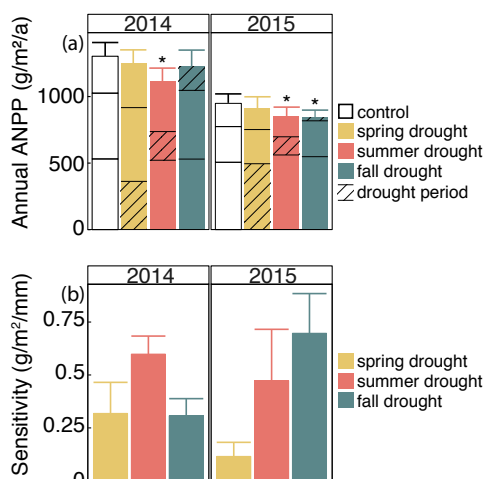



Fig. 8: (a) Relative (RCG) and (b) absolute (ACG) changes in temperature-weighted growth rates (DMYTsum) for the

second post-drought growth period (weeks six to ten) in 2014 and 2015 after the respective drought (drt) treatment for

the individual grasses. Values are means of four replicates ± se. Post-drought growth period of the fall drought treatment

is the first growth period of the following year. See Fig. 4 for additional explanation.

764

765 Fig. 9: (a) Annual ANPP under rain-fed control and under the three seasonal drought treatments and (b) sensitivity of the

766 three seasonal drought treatments in the years 2014 and 2015. Values are means ± se across all six investigated grasses

767 each in four replicates. Bars in (a) are stacked according to growth in spring (bottom part), summer and fall (top part).

768 Significant differences to the control are marked with * ($p<0.05$).