

Beyond gradual warming: extreme weather events alter flower phenology of European grassland and heath species

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Abstract

Shifts in the phenology of plant and animal species or in the migratory arrival of birds are seen as 'fingerprints' of global warming. However, even if such responses have been documented in large continent-wide datasets of the northern hemisphere, all studies to date correlate the phenological pattern of various taxa with gradual climatic trends. Here, we report a previously unobserved phenomenon: severe drought and heavy rain events caused phenological shifts in plants of the same magnitude as one decade of gradual warming. We present data from two vegetation periods in an experimental setting containing the first evidence of shifted phenological response of 10 grassland and heath species to simulated 100-year extreme weather events in Central Europe. Averaged over all species, 32 days of drought significantly advanced the mid-flowering date by 4 days. The flowering length was significantly extended by 4 days. Heavy rainfall (170 mm over 14 days) had no significant effect on the mid-flowering date. However, heavy rainfall reduced the flowering length by several days. Observed shifts were species-specific, (e.g. drought advanced the mid-flowering date for *Holcus lanatus* by 1.5 days and delayed the mid-flowering date for *Calluna vulgaris* by 5.7 days, heavy rain advanced mid-flowering date of *Lotus corniculatus* by 26.6 days and shortened the flowering length of the same species by 36.9 days). Interestingly, the phenological response of individual species was modified by community composition. For example, the mid-flowering date of *C. vulgaris* was delayed after drought by 9.3 days in communities composed of grasses and dwarf shrubs compared with communities composed of dwarf shrubs only. This indicates that responses to extreme events are context specific. Additionally, the phenological response of experimental communities to extreme weather events can be modified by the functional diversity of a stand. Future studies on phenological response patterns related to climate change would profit from explicitly addressing the role of extreme weather events.

Keywords: climate change, drought, EVENT-experiment, flower phenology, flowering length, functional diversity, heavy rainfall, reproductive period

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Introduction

Along with climate warming, an earlier onset of spring for mid-latitudes and higher latitudes and a significant extension of the growing season have been observed

recently by numerous authors (Menzel & Fabian, 1999; Penuelas & Filella, 2001; Fitter & Fitter, 2002; Walther *et al.*, 2002; Parmesan & Yohe, 2003). However, an important research frontier currently arising from the climate change debate is the expansion from an analysis of trends to an interest in extreme events (e.g. Easterling *et al.*, 2000; Parmesan *et al.*, 2000; Jentsch *et al.*, 2007). Alterations in the magnitude and frequency of extreme weather events – such as heat waves, drought, heavy rainfall, or cold periods – have been experienced in the

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recent past, and their ecological importance is expected to increase in the near future in many parts of the world (IPCC, 2007). However, there is a substantial lack of knowledge on how extreme weather events affect biodiversity and ecosystem functioning (Jentsch & Beierkuhnlein, 2008).

Phenological shifts are regarded as a 'fingerprint' (Walther *et al.*, 2002) of global warming. Menzel *et al.*, (2006) tested an extended dataset from a systematic phenological network across 21 European countries, comprising more than 500 plant species that are differentiated by numerous life history traits, for phenological changes in response to gradual advances of spring and summer. Since 1960, the onset of spring has advanced in the northern hemisphere on average by 2.5–2.8 days per decade, or 4.6 days per 1 degree of temperature increase (Menzel *et al.*, 2006; Memmott *et al.*, 2007; Parmesan, 2007). Phenological response to such gradual change reveals a remarkable biogeographic differentiation; responsiveness of flower phenology to warming is more pronounced in warmer European countries than in colder ones. Additionally, early flowering species react more strongly to temperature increase than late flowering species (Dunne *et al.*, 2003). There is indication that climate change can be accompanied by a multi-faceted divergence in flower phenology. Warming advances the flowering of early flowering species and delays the flowering of late flowering species in a tallgrass prairie in North America (Sherry *et al.*, 2007). There, warming induces the expansion of reproductive periods of some species and the compression of others (Sherry *et al.*, 2007). An emerging research challenge is to assess whether temperature-driven shifts in phenology put the maintenance of crucial plant-animal interactions such as pollination at risk. Desynchronization of previously synchronized life cycles and a disruption of mutually beneficial interactions due to climate change appear possible (e.g. Harrison, 2000; Parmesan, 2007). Memmott *et al.* (2007) predict that between 17% and 50% of all pollinator species will suffer a disruption of food supply, if plant phenology advances as much as 1–3 weeks.

So far, gradual climatic trends such as global warming have been studied in much more detail than sudden events (review in Jentsch *et al.*, 2007). However, we argue that extreme weather events such as drought account for much of the response of biodiversity to climate change. Extreme weather events that are restricted to several days or weeks may occur independently from climatic trends over years and decades. However, with global warming temporal variability of the climate is expected to increase and, thereby also extreme weather events (IPCC, 2007). In our approach, we distinguish a discrete event from a continuous

process by its abruptness, no matter whether the event is recurrent, advanced, expected or normal (White & Jentsch, 2001). Abruptness of an event is a function of magnitude over duration, which is best described relative to the temporal turnover and development scale of an ecological system or – from an organismic perspective – relative to the life cycle of the organism in focus (Jentsch, 2006). The extremeness of an event can be determined with respect to a historical reference period (e.g. by statistical extremity according to extreme value theory). At longer time scales, extreme events may possibly affect selection processes and species evolution (Overpeck *et al.*, 2003) beyond direct ecological interaction. We concentrate on direct or delayed responses of manipulated plant communities to extreme weather events. First evidence suggests that there are important effects of short-term perturbations on [e.g. aboveground plant productivity (Kreyling *et al.*, in press a) invisibility of plant communities (Kreyling *et al.*, in press b) and carbon exchange (Mirzaei *et al.*, 2008).

Here, we focus on flower phenology as a key ecosystem function. We assume that there may be an analogy between the effects of gradual warming and the sudden drought on flowering dynamics. This is because evidence suggests that one of the major determinants of flowering induction, abscisic acid (phytohormone ABA)-mediated signalling, is responsive to an array of abiotic factors including temperature increase (Toh *et al.*, 2008) and drought stress (Heide, 1994; Bray, 1997). Furthermore, increased evapotranspiration due to warming, as well as a reduced soil moisture level due to drought (Kreyling *et al.*, 2008) may affect the leaf water status in a similar way.

Particularly, we assess the effects of extreme weather events and plant community composition on the phenological performance of individual plant species in experimental grassland and heath by addressing the following four hypotheses: (i) extreme drought advances flower onset and expands the flowering period; (ii) extreme heavy rainfall delays flower onset and compresses the flowering period; (iii) advance and delay of mid-flowering date, as well as expansion and compression of the flowering period is correlated with early vs. late seasonal reproduction; and (iv) functional composition of plant communities modifies the effects of extreme weather events on flower phenology.

Material and methods

Experimental design

The EVENT-experiment (Jentsch *et al.*, 2007) is established in the Ecological Botanical Gardens of the University of Bayreuth, Germany (49°55'19"N,

11°34'55"E, 365 m a.s.l.) with a mean annual temperature of 8.2 °C, and a mean annual precipitation of 724 mm (1971–2000). Precipitation is distributed bimodally with a major peak in June/July and second peak in December/January (data: German Weather Service). The experiment was carried out with three fully crossed factors: (1) extreme weather events (drought, heavy rain, and ambient control); (2) community diversity (two species of one functional group, four species of two functional groups, and four species of three functional groups); and (3) two contrasting vegetation types (grassland and heath). The total setup consisted of five replicates of each factorial combination, 90 plots each 2 m × 2 m in total. The factors were applied in a randomized block design with the vegetation types and diversity levels blocked and randomly assigned within each weather manipulation (Jentsch *et al.*, 2007). The originally installed species composition was maintained by periodical weeding. The texture of the previously homogenized and constantly drained soil body consisted of loamy sand (82% sand, 13% silt, and 5% clay) with pH = 4.5 in the upper and pH = 6.2 in the lower soil layer (measured in 1 M KCl). Data acquisition was carried out in the central

square meter of each plot only, in order to circumvent edge effects.

Extreme weather events

The weather manipulations consisted of extreme drought, heavy rainfall and ambient conditions for control. Intensity of the treatments was based on the local 100-year extreme event in each category. Vegetation periods (March to September) of 1961–2000 were used as the reference period (data: German Weather Service). Gumbel I distributions were fitted to the annual extremes, and 100-year recurrence events were calculated (Gumbel, 1958). Drought was defined as the number of consecutive days with <1 mm daily precipitation. Accordingly, a drought period of 32 days and a rainfall extreme of 170 mm over 14 days were applied in the experiment during the peak growing season (Fig. 1) in June 2005 and 2006 [drought manipulation: days of the year (DOY) 160–191 in 2005 and 141–172 in 2006; heavy rainfall manipulation: DOY 178–191 in 2005 and 159–172 in 2006]. Maximum values in the historical dataset were 33 days without rain during June and

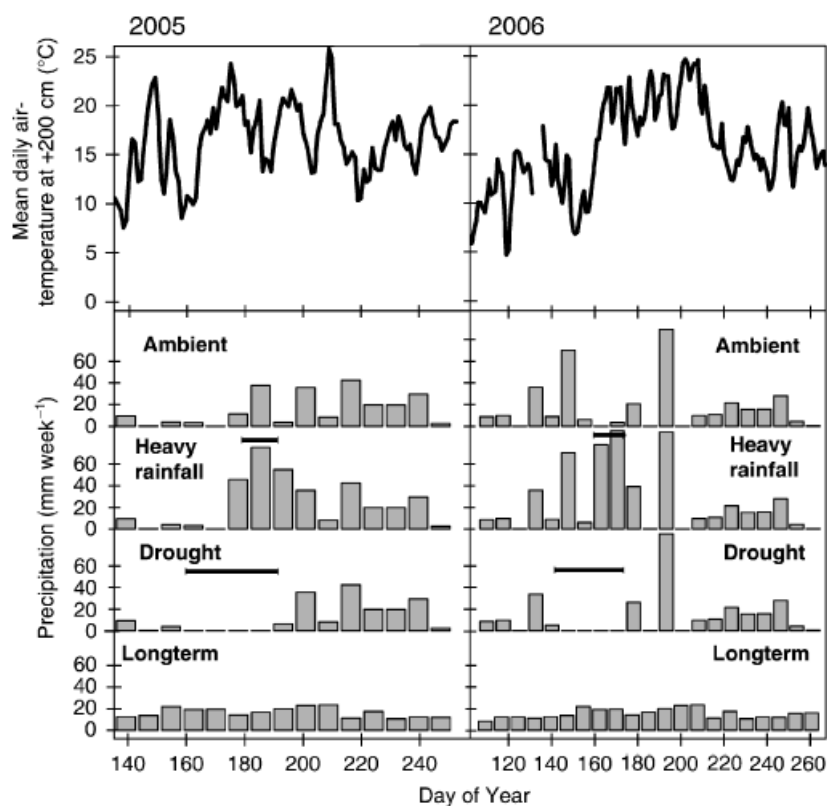


Fig. 1 Mean daily air temperature and weekly precipitation sums in the EVENT-experiment during manipulation and recovery after extreme drought and heavy rainfall events. Grey bars show weekly precipitation for the weather manipulations in comparison with ambient conditions (control) and the long-term mean precipitation 1961–2000 (data: German Weather Service, Station Bayreuth). The timing and duration of the weather manipulations is indicated by the black vertical bars.

July 1976 and 152 mm of precipitation over 14 days in June 1977

Drought was induced with the support of rain-out shelters that permitted nearly 90% penetration of photosynthetically active radiation. Soil moisture was recorded by TDR tube access probe measurements at -10 cm. Near-surface air temperature was slightly increased by the roofs during the weather manipulation period (mean 2005: +1.2 °C; mean 2006: +1.4 °C). Unwanted greenhouse effects were avoided by starting the roof from a height of 80 cm, allowing for near-surface air exchange. After the experimental drought period of 32 days, the roofs were removed.

Heavy rainfall was created using portable irrigation systems. Drop size and rainfall intensity resembled natural heavy rainfall events through application by Veejet 80100 nozzles, used in erosion research (Kehl *et al.*, 2005). The calculated amount of added water was divided into two applications per day to ensure constantly high soil water saturation. If natural precipitation occurred, this amount of rain was subtracted from the respective dose. A lateral surface flow was avoided by plastic sheet pilings around treated plots reaching down to a depth of 10 cm.

A roof artefact control with five replicates of the rain-out shelters was in place in 2006. Adding the same amount of water as occurred naturally in daily resolution below intact shelters during the drought manipulation period did not result in any significant differences between 'ambient control' and 'artefact control' with respect to the 'mid-flowering day' and the 'length of flowering period' neither for individual species (to be precise: for eight out of 10 species, since, unfortunately, we do not have the data for the two legume species) nor for the average over all species, indicating no significant effect from the slightly increased temperature caused by the rain-out shelters.

Experimental plant communities

Overall, grasslands and heath are spatially important ecosystems in Central Europe. Ten wide-spread plant species were chosen from the regional flora. Species were selected with respect to their affiliation to defined functional groups (grasses, herbs, legumes, and dwarf shrubs), to life-span (perennials), to overall importance in nearby and Central European grassland systems, and to the fact that they do naturally grow on substrate similar to the one used in this experiment. One hundred plant individuals per plot in defined quantitative composition were planted in a systematic hexagonal grid with 20 cm distance between individuals in early April (DOY 92) 2005. Grass and herb individuals used in the experiment were grown from seeds in a greenhouse in

the preceding fall, dwarf shrubs were bought from a gardening company as 2-year-old individuals. Thus, all plants were in a juvenile stage under 2 or 4 years of age during manipulation and data acquisition. All plants have been acclimated on site since February 2005, then reaching growth heights of approximately 15 cm. Biomass at planting amounted to 0.1–0.6 g dw Individual⁻¹ for grasses and herbs, to 1.3–3.1 g dw Individual⁻¹ for dwarf shrubs, respectively. These experimental communities represent naturally occurring species combinations. Both, grassland and heath plots were established at two levels of species diversity (two and four species) and three levels of functional diversity (one to three functional groups), resulting in six species combinations or communities in total (Table 1).

Data acquisition and statistical analysis

For each species, weekly observations of the flowering status of four individuals per plot and species were carried out. As a surrogate, the mid-flowering date was calculated, (i.e. the date of the 50 percentile of the flowering curve over time, and flowering length), [i.e. the difference between the dates of the 25 percentile and of the 75 percentile of the flowering curve over time (see Fig. 2 as an example)]. Individuals were counted as 'flowering' when the anthers were visible in at least one flower. *Geranium pratense* had to be excluded from the analysis, because this species did not produce any flowers in most plots.

Phenological shifts of all species combined were analysed using Linear Mixed Effects Models with weather manipulation as a fixed factor and species identity, community composition, block effect of the split-plot design as random factors (Faraway, 2006). The significance of differences between weather manipulation and control were evaluated using Markov Chain Monte Carlo sampling with the level of significance set to $P < 0.05$ in 1000 iterations (Bates & Campbell, 2001). Linear Mixed Effects Models were conducted with the function 'lmer' (Bates & Sarkar, 2007). Since the Markov chain Monte Carlo sampling compares the measured difference to the 95% confidence interval of the permutations, the output is whether or not the data are within this confidence interval. Therefore, instead of decimal values, P can only be reported as being above or below 0.05.

Linear models combined with analysis of variance (ANOVA) were applied to test for significant differences between factorial groups of weather manipulation and functional diversity level (Table 1) for each species separately while accounting for the split-plot design. Before statistical analysis, data were log or square root transformed, if conditions of normality were not met, or

Table 1 Experimental plant communities of two vegetation types (grassland, heath) were used at three functional diversity levels, resulting in six community compositions

Abbreviation	Vegetation type	Diversity level	Description	Species
G2 ⁻	Grassland	A	Two species, one functional group (grass)	<i>Arrhenatherum elatius</i> , <i>Holcus lanatus</i>
G4 ⁻	Grassland	B	Four species, two functional groups (grass, herb)	<i>Arrhenatherum elatius</i> , <i>Holcus lanatus</i> , <i>Plantago lanceolata</i> , <i>Geranium pratense</i>
G4 ⁺	Grassland	C	Four species, three functional groups (grass, herb, legume herb)	<i>Arrhenatherum elatius</i> , <i>Holcus lanatus</i> , <i>Plantago lanceolata</i> , <i>Lotus corniculatus</i>
H2 ⁻	Heath	A	Two species, one functional group (dwarf shrub)	<i>Calluna vulgaris</i> , <i>Vaccinium myrtillus</i>
H4 ⁻	Heath	B	Four species, two functional groups (dwarf shrub, grass)	<i>Calluna vulgaris</i> , <i>Vaccinium myrtillus</i> , <i>Agrostis stolonifera</i> , <i>Deschampsia flexuosa</i>
H4 ⁺	Heath	C	Four species, three functional groups (dwarf shrub, legume shrub, grass)	<i>Genista tinctoria</i> , <i>Vaccinium myrtillus</i> , <i>Agrostis stolonifera</i> , <i>Deschampsia flexuosa</i>

G, grassland; H, heath; 2/4, number of species; -, without legume; +, with legume.

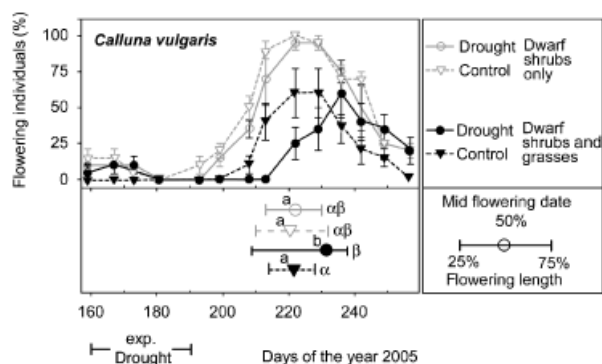


Fig. 2 Phenological shifts due to extreme weather events as a function of functional diversity, using flowering pattern of *Calluna vulgaris* after drought as an example. Given are mean \pm SE of weekly observations of the flowering of four individuals in five replications. Below the flowering curves, vertical lines indicate the mid-flowering date (date of the 50 percentile of the flowering curve over time), horizontal bars indicate flowering length (difference between the dates of the 75 percentile and the 25 percentile of the flowering curve over time). Homogeneous groups according to Tukey's HSD *post hoc* comparison are given in Latin letters for the mid-flowering date and in Greek letters for the flowering length.

to improve homogeneity of variances. Both characteristics were tested by examining the residuals vs. fitted plots and the normal qq-plots of the Linear Models (Faraway, 2005). All statistical analyses were performed using R (R Development Core Team, 2006; *R: A Language and Environment for Statistical Computing*, R Foundation for Statistical Computing, ISBN 3-900051-07-0, URL <http://www.R-project.org>, Vienna, Austria).

Divergence between early and late flowering species was studied by separating flowering periods before and

after the 200th day of the year and examining mixed models of these two groups separately. Three species (*Genista tinctoria*, *Lotus corniculatus*, *Plantago lanceolata*) performed two distinct flowering periods, one before and one after the 200th day of the year, consequently, their first flowering period was placed in the early flowering group and the second into the late flowering group.

Results

In the following, we characterize the effects of extreme weather events on flower phenology over 2 consecutive years in terms of two key parameters: 'mid-flowering day' and 'length of flowering period'. Further, we distinguish seasonally early from late reproducing species and report on interactions between extreme weather events and plant diversity modifying phenological response.

Climatic characteristics between years

The year 2005 was characterized by dry conditions (Fig. 1) before the beginning of the drought manipulation (only 4 mm of precipitation in 15 days before the onset of manipulation), which had already led to a minimum in soil water content. During the drought treatment, soil water content remained at this minimum, thus differing from the control, which received natural precipitation. During the heavy rainfall manipulation in 2005, it took nearly 2 weeks until soil moisture had reached its maximum, and soil moisture exceeded the field capacity of the soil only briefly. The year 2006 was characterized by wet conditions when the

drought manipulation started, followed by relatively dry conditions afterwards, when the rainfall manipulation began. The difference between drought manipulation and the control was therefore smaller in 2006 than in 2005, even though soil moisture values below the wilting point ($pF = 4.2$, Boden, 1996) occurred longer in the drought manipulation.

Drought impact on the mid-flowering date and the length of the flowering period

In our field experiment, on average over all species, drought resulted in an advance of the mid-flowering date by 4 days in 2005, but in no significant reaction in 2006 (Fig. 3). At the species level, however, unidirectional shifts did not generally occur, especially in 2005 (Table 2). For example, drought significantly advanced the mid-flowering date of *Holcus lanatus* and delayed the mid-flowering date of *Calluna vulgaris*. Even though few significant weather manipulation effects were found at the species level in 2006, phenological shifts

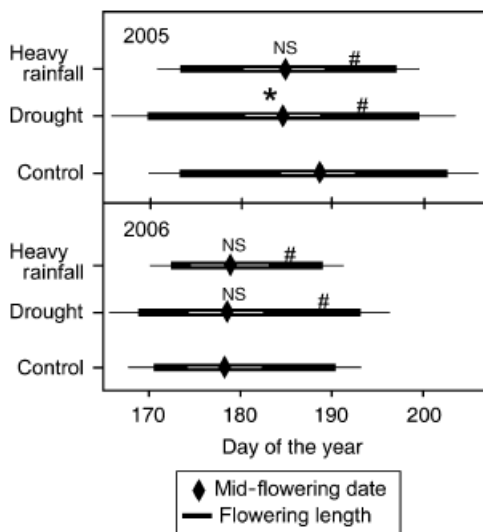


Fig. 3 General effects of extreme weather events on the mid-flowering date and flowering length of 10 common European species (Table 1). For each species, weekly observations of the flowering status of four individuals in five replications were used to obtain the mid-flowering date (date of the 50 percentile of the flowering curve over time) and flowering length (difference between the dates of the 25 percentile and of the 75 percentile of the flowering curve over time). Average values over all functional diversity levels were taken for each species which occurred in more than one community composition. Significant differences between weather manipulation and the control ($P < 0.05$) according to Markov Chain Monte Carlo sampling of Linear Mixed Effects Models are marked by '*' for the mid-flowering date and '#' for the flowering length. Thin white bars represent the standard error of the mid-flowering date, thin black bars indicate the standard error of the flowering length.

appeared to be more homogenous than in 2005. The mid-flowering date of most species was advanced after drought (seven out of nine species) in 2006.

Furthermore, drought resulted in a significant expansion of the flowering period by about 4 days compared with the control in both years (Fig. 3). At the species level, the length of the flowering period was rather consistently modified, especially in 2006, where drought expanded flowering period of all species (Table 2). Four species bloomed well after the treatment period.

Finally, there were no significant differences between 'ambient control' and 'artefact control' with respect to 'mid-flowering day' and 'length of flowering period' neither for individual species (to be precise: for eight out of 10 species, since, unfortunately, we do not have the data for the two legume species) nor for the average over all species.

Heavy rain impact on the mid-flowering date and length of the flowering period

Heavy rainfall had no significant effect on the mid-flowering date in either year on average over all species. However, at the species level, the mid-flowering date of most species was delayed after heavy rainfall (seven out of nine species) in 2006.

In contrast to drought, heavy rainfall caused a significant compression of the flowering period by 5.4 days in 2005 and by 3.3 days in 2006 on average over all species. Compression of the flowering period occurred in seven out of nine species (Table 2).

Early vs. late seasonal reproduction in plants

Our assumption was that shifts in the mid-flowering date as well as alterations to the flowering period are correlated with seasonal reproductive traits. However, in our field experiment, the advance and delay of the mid-flowering date (Fig. 4) was not generally correlated with plant traits of early vs. late reproduction (i.e. there was no significant shift in mixed models separated by early and late flowering species). Likewise, an extension and compression of the flowering period (Fig. 4) was not correlated with plant traits of early vs. late reproduction (i.e. there was no significant difference in mixed models separated by early and late flowering species).

Interaction between extreme weather events and plant diversity

Community composition significantly modified the phenological response of individual species prone to extreme weather events (see Table 2). For example, a delay of the mid-flowering date of *C. vulgaris* by 9.3

Table 2 Shifts in the mid-flowering date and flowering length compared with the control

Weather manipulation	Species	2005			2006				
		Shift (days)	p_{wm}	p_{dl}	$p_{wm \times dl}$	Shift (days)	p_{wm}	p_{dl}	$p_{wm \times dl}$
(a) Mid-flowering									
Heavy Rainfall									
	<i>A. elatius</i>	0.5	0.510	0.394	0.260	-3.6	0.025	0.932	0.380
	<i>H. lanatus</i>	-1.0	0.646	0.515	0.115	0.8	0.271	0.150	0.340
	<i>P. lanceolata</i>	-1.5	0.711	0.181	0.638	3.9	0.220	0.662	0.625
	<i>G. pratense</i>	X				#			
	<i>L. corniculatus</i>	-26.6	0.003			-4.1	0.114		
	<i>V. myrtillus</i>	-3.5	0.593	0.468	0.931	1.0	0.442	0.038	0.645
	<i>C. vulgaris</i>	1.6	0.240	0.584	0.321	0.1	0.944	0.153	0.184
	<i>G. tinctoria</i>	0.2	0.934			6.3	0.049		
	<i>A. stolonifera</i>	1.5	0.450	0.241	0.144	0.2	0.544	0.550	0.761
	<i>D. flexuosa</i>	X				0.1	0.834	0.723	0.010
	All species	-3.6	ns			0.81	ns		
Drought									
	<i>A. elatius</i>	0.5	0.979	0.040	0.398	-0.4	0.366	0.527	0.489
	<i>H. lanatus</i>	-1.5	0.344	0.070	0.145	-2.1	0.021	0.426	0.284
	<i>P. lanceolata</i>	0.6	0.960	0.057	0.010	-5.8	0.146	0.070	0.207
	<i>G. pratense</i>	X				#			
	<i>L. corniculatus</i>	-18.3	0.129			4.5	0.292		
	<i>V. myrtillus</i>	-3.4	0.568	0.555	0.770	-0.6	0.535	0.066	0.311
	<i>C. vulgaris</i>	5.7	0.731	0.493	0.880	-1.5	0.534	0.121	0.862
	<i>G. tinctoria</i>	-18.3	0.212			13.4	0.199		
	<i>A. stolonifera</i>	-0.5	0.749	0.819	0.560	-0.7	0.165	0.040	0.082
	<i>D. flexuosa</i>	-0.7	0.949	0.447	0.642	-0.4	0.297	0.098	0.061
	All species	-3.98	<0.05			0.71	ns		
(b) Flowering length									
Heavy Rainfall									
	<i>A. elatius</i>	0.1	0.897	ns	ns	-0.8	0.208	0.957	0.394
	<i>H. lanatus</i>	-0.8	0.782	ns	ns	-1.8	0.012	0.441	0.455
	<i>P. lanceolata</i>	-3.3	0.485	ns	ns	-6.5	0.800	0.246	0.609
	<i>G. pratense</i>	X				#			
	<i>L. corniculatus</i>	-36.9	0.001			-6.6	0.136		
	<i>V. myrtillus</i>	X				-0.5	0.768	0.954	1.000
	<i>C. vulgaris</i>	2.9	0.011	0.001	0.004	-3.7	0.009	0.048	0.936
	<i>G. tinctoria</i>	-4.7	0.757			-7.4	0.948		
	<i>A. stolonifera</i>	1.2	0.150	0.018	0.037	-1.0	0.111	0.077	0.848
	<i>D. flexuosa</i>	X				-0.5	0.369	0.536	0.112
	All species	-5.4	<0.05			-3.3	<0.05		
Drought									
	<i>A. elatius</i>	-0.2	0.979	0.041	0.394	0.2	0.571	0.502	0.747
	<i>H. lanatus</i>	-9.6	0.001	0.667	0.567	0.2	0.724	0.786	0.979
	<i>P. lanceolata</i>	3.6	0.893	0.477	0.049	13.3	0.041	0.195	0.453
	<i>G. pratense</i>	X				X			
	<i>L. corniculatus</i>	1.6	0.242			9.9	0.210		
	<i>V. myrtillus</i>	X				1.3	0.627	0.985	0.880
	<i>C. vulgaris</i>	9.6	0.008	0.483	0.126	1.6	0.495	0.183	0.684
	<i>G. tinctoria</i>	16.9	0.437			11.7	0.352		
	<i>A. stolonifera</i>	-2.1	0.503	0.018	0.210	1.3	0.294	0.128	0.936
	<i>D. flexuosa</i>	X		0.861	0.940	0.9	0.139	0.960	0.281
	All species	2.2	<0.05			4.38	<0.05		

Average values over all functional diversity levels are shown for species which occurred in more than one community composition (X: no data). Significant differences between weather manipulation and the control (p_{wm}) are in bold, for single species obtained by Analysis of Variance, for all species combined according to Markov Chain Monte Carlo sampling of Linear Mixed Effects Models. For all species occurring in more than one community composition, p_{dl} indicates significance of functional diversity according to ANOVA, and $p_{wm \times dl}$ indicates significance of interaction between weather manipulation and functional diversity according to ANOVA.

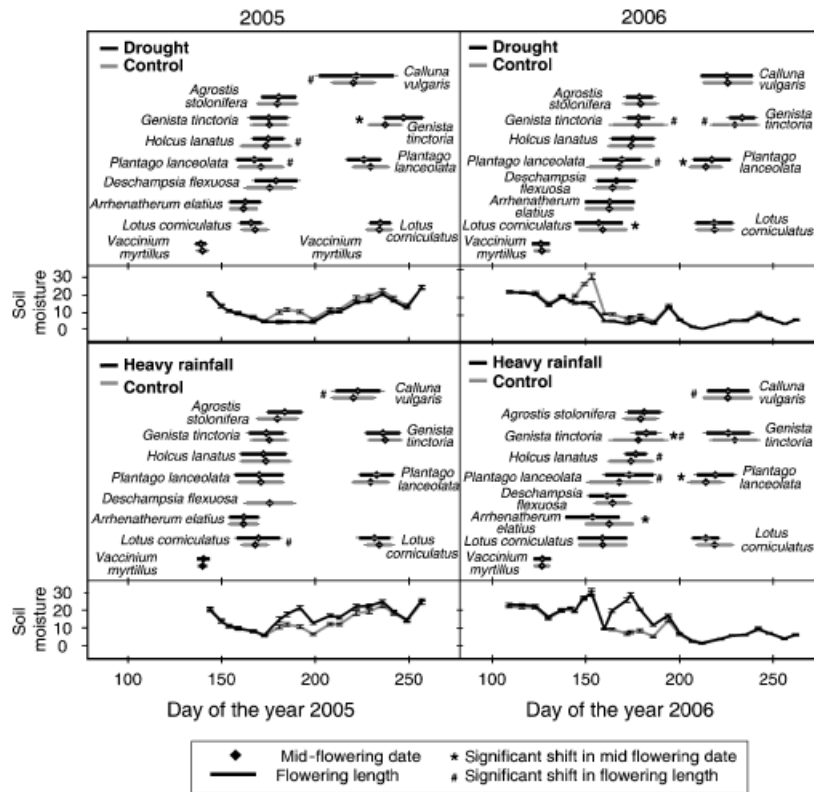


Fig. 4 Phenological response of 10 common European plant species to extreme weather events, separated into early (species name left of flowering bar) and late (species name right of flowering bar) flowering species. For each species, weekly observations of the flowering status of four individuals in five replications were used to obtain the mid-flowering date (date of the 50 percentile of the flowering curve over time) and flowering length (difference between the dates of the 25 percentile and of the 75 percentile of the flowering curve over time). Average values over all functional diversity levels are displayed for each species which occurred in more than one community composition. Significant differences between weather manipulation and the control according to ANOVA ($P < 0.05$) are marked by '*' for the mid-flowering date and '#' for flowering length. Thin white bars represent the standard error of the mid-flowering date, thin black bars indicate the standard error of the flowering length. Soil moisture is given in vol% at 12 cm soil depth measured by a TDR tube access probe in every plot. Displayed are mean and standard errors over all species compositions.

days in communities composed of two grasses and two dwarf shrubs compared with communities composed of two dwarf shrubs only was found in the drought manipulation (Fig. 1). No similar pattern was observed for the control, resulting in a significant interaction effect between the drought and the functional diversity level for *C. vulgaris*. Interestingly, all modifications of phenological shifts due to interaction with plant diversity were greater with increasing diversity levels (Fig. 5). A delay in the mid-flowering date of *Deschampsia flexuosa* by 2.7 days after heavy rainfall and of *P. lanceolata* by 15.3 days after drought in communities containing no legumes compared with communities containing a legume was found. Remarkably, the flowering length of *P. lanceolata* even differed by 26.2 days and that of *Agrostis stolonifera* by 5.7 days after drought in communities containing no legumes compared with communities containing a legume dwarf

shrub. Diversity level, a surrogate of community composition and species richness, had no effect on soil moisture.

Discussion

Effects of a sudden drought on flower phenology

The experimental data are in accordance with our hypothesis stating that extreme drought events advance flower onset (the mid-flowering date) and extend the flowering period of Central European plant species. Changes in the flowering period were highly significant and uniform over both years of observation (Fig. 2). The magnitude of shift (around 4 days) observed in our data is remarkable when compared with findings from long-term observational datasets accounting for gradual warming over recent decades. Generally, global

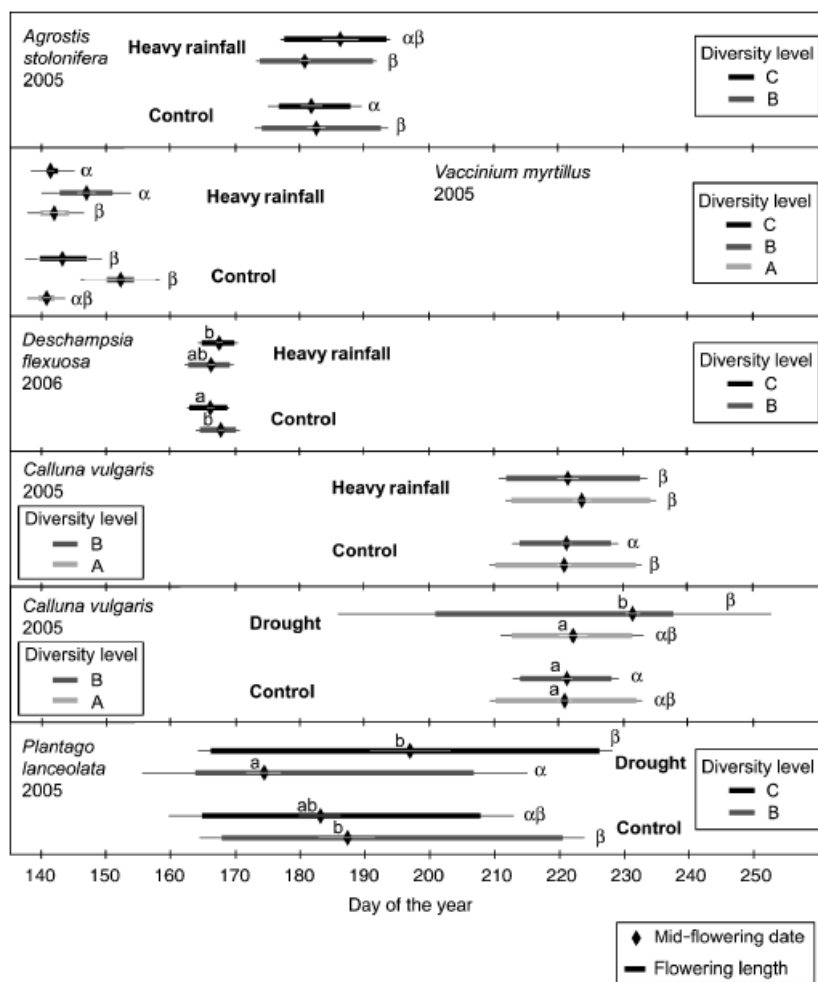


Fig. 5 Shifts in the mid-flowering date and flowering length as affected by the functional diversity level (see Table 1) for all species exhibiting a significant interaction effect between weather manipulation and functional diversity (Table 2). Homogeneous groups according to Tukey's HSD *post hoc* comparison are shown in Latin letters for the mid-flowering date and in Greek letters for the flowering length if the respective interaction was significant. Thin white bars represent the standard error of the mid-flowering date, whereas thin black bars indicate the standard error of the flowering length. Please note that the data in the panels are from shrubland, except for *Plantago*, which is from grassland.

warming has advanced the first flowering date of plants by 4 days °C⁻¹ on average in the temperate zone (Memmott *et al.*, 2007). This phenological shift due to gradual warming is of the same magnitude as the phenological shift due to a single extreme drought event according to our data. Other experiments confirm that summer drought may result in early flowering (Franks *et al.*, 2007). In contrast, for Mediterranean plants, evidence suggests that dry conditions delay flowering phenophases (Penuelas *et al.*, 2004; Llorens & Penuelas, 2005), especially for drought sensitive species (Ogaya & Penuelas, 2003).

With experimental data, there might be obfuscation between drought and warming effects on flower phenology. Ultimately, we cannot determine whether the advance of flowering and extension of flowering length

observed in our drought treatment was really due to drought or to warming, or to a combination of both. However, there were no significant differences between 'ambient control' and 'artefact control' with respect to 'mid-flowering day' and 'length of flowering period' neither for individual species nor for the average over all species. The increase in temperature due to an installation of rainout shelters was statistically not significant and lasted only for a limited period of 32 days. However, we acknowledge that this period may have been the sensitive period for stimulating subsequent flowering-related dynamics.

Possible links between drought and warming include the effects on leaf water status either due to reduced soil moisture content during drought or due to higher evapotranspiration during warming. Moreover, drought

and warming could analogously affect abscisic acid-mediated signalling (Toh *et al.*, 2008), which is a major driver of flowering dynamics. However, in this study we did not analyse plant physiological pathways, but monitored the effects of extreme weather events on flower phenology. Thus so far, we can hardly offer a discussion about the mechanisms that account for how extreme weather events affect the start and duration of flowering times. Possible ways are event-driven production of extra flower buds, abortion of flower buds, longer duration of individual flowers or mechanical damage of individual flowers. However, we have not yet recorded data tracking the fate of individual buds and flowers.

Studies focusing on climate warming that monitor many plant species over large areas and long time scales report comparable phenological shifts of 2 days per decade for Central Europe (Menzel & Fabian, 1999), 4.5 days per decade for the British Isles (Fitter & Fitter, 2002), 1.2–2.0 days per decade for North America (Walther *et al.*, 2002), and 1.4–2.3 days per decade for global datasets (Penuelas & Filella, 2001; Parmesan & Yohe, 2003). All these studies agree that the observed shifts are highly correlated with changes in mean temperature, especially in the months preceding the phenological event. Furthermore, our study provides evidence, that phenological shifts may be driven by soil moisture dynamics. However, the different patterns in shifting the mid-flowering day after drought in 2005 (significant shift) and 2006 (no significant shift) may be due to alternative mechanisms. Firstly, the 2 consecutive years were characterized by relatively dry (2005) vs. humid (2006) weather conditions indicating the crucial role of precipitation pattern or soil water status before a drought event for phenological dynamics. Secondly, the individual plant age moved on from 1 year to the next, so that sensitivity to drought and competitive ability may have changed inconsistently between growth forms due to their particular carbon allocation strategy and status in the life cycle. For example, a smaller root/shoot ratio may account for higher drought sensitivity in juvenile plant individuals.

Published findings on the effect of warming on the length of the flowering period only exist for a few species and remain controversial. Some authors report no warming effects on the length of flowering period for particular dwarf shrubs (Llorens & Penuelas, 2005) and for subalpine angiosperms (Price & Waser, 1998). Others found compression of flowering period for particular chamaephytic species (Llorens & Penuelas, 2005), or an extension of the flowering period for subalpine herbs and grasses (Dunne *et al.*, 2003), where soil moisture was generally not significant for the duration of flowering.

The effects of drought on the timing of the flowering period is also ambiguous, and shifts in both directions are reported for two Mediterranean dwarf shrubs (Llorens & Penuelas, 2005). In another study, water stress increased the duration of flowering by up to 15 days in *Lesquerella fendleri* (Ploschuk *et al.*, 2001). Compared with phenological point data such as flower onset, the flowering period or length has received little attention up to now, although it might be ecologically more important than the flowering onset, (e.g. for plant–pollinator interactions and pollination success).

Probably, warming remains the most important driver of phenological shifts – observed as linear trends over the years – in the northern hemisphere (Root *et al.*, 2003; IPCC, 2007). It has been demonstrated that phenology is responsive to the temperature of the preceding months (Menzel *et al.*, 2006). However, our results suggest, that a single extreme drought event can have effects on flower phenology of similar or higher magnitude than gradual warming. We suppose that, taking the impact of extreme weather events on flower phenology into account, unexplained inter-annual variance observed so far in datasets solely based on gradual warming might be reduced. Zavaleta *et al.* (2003) came to a comparable conclusion in a study of grassland phenological response to elevated temperature, carbon dioxide, precipitation, and nitrogen deposition. They state that individual species were more sensitive to interannual variability and extreme events than to mean changes in environmental and resource conditions. Drought-induced modifications in the timing of flowering are known to affect the flower number and seed set (Saavedra *et al.*, 2003), which in turn affect reproductive fitness.

Effects of heavy rainfall on flower phenology

Our experimental data are partly in accordance with the hypothesis stating that heavy rainfall events compress the flowering period of plant species. However, our data suggest that heavy rainfall events do not influence the mid-flowering date. Generally, little is known about either the effects of heavy rainfall or of increased and reduced annual precipitation on flower phenology (Rathcke & Lacey, 1985; Ashton *et al.*, 1988). A compression of the flowering period by increased rainfall intensities combined with longer intervals of drought is reported from a tallgrass prairie in Kansas (Fay *et al.*, 2000). An advance of phenological development after additional water supply has been reported for woody species of higher latitudes (Wielgolaski, 2001). An increased amount of precipitation together with an increase in the length of the rainy season by 3 weeks in spring had no consistent impact on phenology in an

annual Californian grassland (Cleland *et al.*, 2006), and a double precipitation treatment without changes in the rainfall timing had no significant effect on flowering phenology in a perennial grassland in Oklahoma (Sherry *et al.*, 2007).

Divergence of flower phenology after extreme weather events

Our experimental data on 10 common European species including herbs, grasses, and dwarf shrubs provide no evidence for a divergence in the advance and delay of the mid-flowering date or an extension and compression of the flowering period as a function of early vs. late seasonal reproductive period. Analyses of large phenological datasets suggest that flower phenology responds most sensitively to mean monthly temperatures in the month of flower onset and the 2 preceding months (Menzel *et al.*, 2006). In our experiment three out of 10 species (*G. tinctoria*, *L. corniculatus*, *P. lanceolata*) performed two distinct flowering periods during the course of a year, which were affected by the simulated extreme weather events (Fig. 4). Also, the impact of a single extreme weather event in spring may vary by temporal distance to flower onset dates of various species.

Interaction between extreme weather events and functional diversity

The interaction between extreme weather events and community composition seems to play a crucial role in phenological shifts. The number of significant interactions for the seven species occurring in more than one community composition indicates that this phenomenon is no singular case, but rather a common feature (Table 2).

Facilitation by other growth forms is known to improve individual species performance (Bertness & Callaway, 1994; Bertness & Leonard, 1997). Increased disturbance and physical stress levels are thought to reduce the intensity and importance of competition and to increase the importance of facilitation (Holmgren *et al.*, 1997; Bertness, 1998; Brooker & Callaghan, 1998; Sthultz *et al.*, 2007). Callaway & Walker (1997) present examples of reduced importance of competition and increased facilitation in climatically extreme years compared with strong competition within low-stress years. The same kind of response is described for bunchgrass communities in the Rocky Mountains (Greenlee & Callaway, 1996). Kikvidze *et al.* (2006) recently showed that interactions between two dominant grassland species and their associated communities switched from competition during the early part of the growing sea-

son, when conditions were favourable, to facilitation during the late part of the growing season, when the site became more xeric. Species diversity on its own may enhance facilitation (Hacker & Gaines, 1997), and the presence of certain functional groups such as legumes is known to facilitate other species (Pugnaire & Luque, 2001; Spehn *et al.*, 2002; Beierkuhnlein & Nesshoever, 2006). Most of these studies used biomass production as a response parameter, however, facilitative neighbor effects are also reported for phenological events in harsh environments (Wipf *et al.*, 2006).

In contrast to facilitative effects, dwarf shrubs are known to be very tolerant to drought but to suffer from high competition from fast-growing grass species, especially at the juvenile stage (Hester *et al.*, 1991). Hence, the observed drought effect from 2005 of flowering reduction in dwarf shrubs growing in a mixture with grasses could be explained by the increased competition for water. Surprisingly, simulated drought had no significant effect on summed community aboveground net primary productivity (ANPP), not even for the dry year of 2005 in the heath community composed of grasses and dwarf shrubs (Kreyling *et al.*, in press a). Only the productivity of the dwarf shrub *Vaccinium myrtillus* decreased after drought when growing with the grasses *Agrostis stolonifera* and *D. flexuosa*.

Generally, a significant interaction between an extreme weather event and functional diversity might be due to the fact that shifts in phenology are promoted as a consequence of resource partitioning due to higher functional diversity. For all significant interactions between species in a community setting (Table 2), no facilitative effect of higher functional diversity was found. All shifts were more pronounced in the more diverse communities (Fig. 5), with some species exhibiting shifts into different directions depending on the specific level of functional diversity. Thus, facilitation is not a direct function of functional diversity.

Conclusions

Phenological shifts are obviously driven by other factors besides temperature and photoperiodic conditions (e.g. Sawa *et al.*, 2007). We propose that field observations of altered phenological patterns related to climate change would profit from addressing the role of extreme weather events. Soil-drying might be a major environmental cue for phenological shifts. Especially with the emerging phenological network datasets, which comprise data from many countries, it seems promising to broaden the debate on the effects of climate warming in ecosystems by including phenological responses to extreme weather events. Available climate data series with daily resolution should be

screened for such events. On short-term time scales, extreme weather events might be even more powerful than gradual warming in disturbing the synchronization between organisms (e.g. Both *et al.*, 2006) and community organization, because their occurrence and return interval is much less predictable and the vigor of their effects may reach a decadal scale of warming. Furthermore, interaction effects of extreme weather events with plant diversity are emerging as a one of the most challenging research frontiers in studying shifts in plant phenology. Understanding the ecosystem effects of extreme weather events is indispensable. Extreme events are forecasted to increase in magnitude and frequency along with ongoing climate warming, potentially having far-reaching consequences for ecology and evolution.

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