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Phenological Sensitivity of Early and Late Flowering Species Under Seasonal Warming and Altered Precipitation in a Seminatural Temperate Grassland Ecosystem

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ABSTRACT

Shifts in flowering phenology of plants are indicators of climate change. The great majority of existing phenological studies refer solely to gradual warming. However, knowledge on how flowering phenology responds to changes in seasonal variation of warming and precipitation regimes is missing. We report the onset of 22 early (flowering before/within May) and 23 late flowering (flowering after May) species in response to manipulated seasonal warming (equal to + 1.2°C; last 100-year summer/winter warming), additional winter rainfall, and modified precipitation variability (including a 1000-year extreme drought event followed by heavy rainfall) over the growing season in two consecutive years for a species-rich temperate grassland ecosystem. The average onset of flowering (over 2 years) was significantly advanced 3.1 days by winter warming and 1.5 days by summer warming compared to control. Early flowering species responded to seasonal warming in both years, while late-flowering species responded in only 1 year to summer warming. The average onset of early flowering species was significantly advanced, 4.9 days by winter warming and 2.3 days by summer warming. Species-specific analysis showed that even within the early flowering community there were divergences. A positive correlation between plant height and shift in flowering onset was detected under winter warming ($R^2 = 0.20$, $p = 0.005$). The average onsets of early and late flowering community were affected by neither winter rain nor growing season precipitation variability. Seasonal differences in warming, and particularly winter warming, might alter community dynamics among early and late flowering species which can cause shifts in the seasonal performances of temperate ecosystems.

Key words: climatic extreme; drought; ecosystem productivity; mesic; plant–climate interactions; phenology; plant trait; rain; seasonal climate change; temperature.

Introduction

Flowering phenology is sensitive to climate changes (Parmesan and Yohe 2003; Root and others 2003; Badeck and others 2004; Sherry and others 2007; Körner and Basler 2010; Cook and others 2012; Ovaskainen and others 2013; Moore and Lauenroth 2017) and biodiversity loss (Wolf and others 2017). Previous studies suggest that flowering phenology is generally shifting to earlier dates in temperate environments (Menzel and Fabian 1999; Menzel and others 2006; Hovenden and others 2008; Bloor and others 2010; Cornelius and others 2014). The shift in timing of flowering phenology can change plant community composition (CaraDonna and others 2014) and plant–pollinator interactions (Memmott and others 2007; Scaven and Rafferty 2013). Climate change-driven phenological shifts also have an impact on the number of flowers, seed set, timing of seed ripening, and seed dispersal (Santandreu and Lloret 1999; Saavedra and others 2003), which in turn affect reproductive fitness of plants. Earlier flowering influences many other plant activities, like leaf expansion, root growth, and nutrient uptake (McKane and others 1990), which can play important roles in niche differentiation among coexisting species. Furthermore, species-specific flowering phenology alters structure of plant communities, gene flow between species and contributes to plant invasion success as the climate warms (Fitter and Fitter 2002; Wolkovich and others 2013).

In Central Europe, the temperature is likely to increase more rapidly in winter than in summer (Kreyling and Henry 2011; Andrade and others 2012; Vautard and others 2013, 2014). This seasonal timing of climatic changes can be more critical for organisms and ecosystems than annual sums or uniform shifts. The great majority of existing phenological studies investigated the flowering phenology only under year-round gradual warming. Studies on how seasonal variation in warming (winter versus summer) shifts flowering phenology of plants are missing. The best predictor of flowering dates of temperate plants is the average air temperature one to two months before flowering onset (Chmielewski and Rötzer 2001; Menzel and others 2006; Nagy and others 2013). Therefore, it is likely that winter warming (October–March) advances phenology of early flowering species (flowering before/within May) and summer warming (April–September) advances phenology of late flowering species (flowering after May).

Besides temperature change, modified precipitation regimes can influence the phenological behavior of plants. Precipitation sums are expected to remain unaffected in Central Europe, but the intra-annual precipitation variability may increase (Jacob 2009; Kotlarski and others 2014). We are not aware of any other study testing for effects of precipitation variability on flower phenology, and few studies have investigated the effects of altered precipitation sum (for example, drought or heavy rainfall) on flowering phenology (Jentsch and others 2009; Bloor and others 2010; Nagy and others 2013).

Existing studies showed that drought can advance (Jentsch and others 2009), delay (Nagy and others 2013), or have no effect (Bloor and others 2010) on flowering phenology. Similarly, heavy rainfall can either advance (Jentsch and others 2009) or have no effect (Cleland and others 2006) on flowering phenology of grassland species. Taken together, the effects of precipitation on flowering phenology reported to date are not consistent. This is probably due to the timing and amount of precipitation treatments, and because the composition of plant communities in the existing studies is not comparable. Most of the phenological studies done with a sudden change in moisture availability involved single or small sets of species and emphasized diverse (species-specific) responses (Cleland and others 2006; Jentsch and others 2009; Bloor and others 2010; Nagy and others 2013). Therefore, it is timely to investigate responses over a large set of species, in order to gain a general overview of how flowering phenology responds under intra-annual precipitation variability in a species-rich temperate grassland ecosystem.

Besides the direct impact of modified moisture regimes that occurs in the period before and during phenological responses, it is important to understand how previous seasons are influencing phenological responses. Increase in winter rainfall is expected in Europe (Zolina 2012) which could have an impact on water storage in deeper soil horizons and on plant performance throughout the following growing season. Shifting limits of growing seasons can be intensified by increased winter rain, leading to earlier flowering onset and an earlier start to the growing season. However, the influence of winter rain on flowering phenology at the community level has not yet been documented.

We investigated the onset of flowering in a species-rich community (22 early flowering and 23 late flowering species) over two consecutive years in a seminatural temperate grassland under multiple seasonal climate change manipulations: winter

warming, summer warming, winter rain addition, and altered precipitation variability in the growing season (low precipitation variability, medium precipitation variability, and high precipitation variability). We hypothesized that (1a) both winter warming and summer warming are advancing the onset of flowering in grassland communities, where (1b) the onset of early flowering species will be advanced by winter warming and the onset of late flowering species will be advanced by summer warming; and that (2) winter rain addition and growing season precipitation variability will shift the onset of early and late flowering species. We expected that onset of flowering will be advanced by winter rain addition and low precipitation variability but delayed by high precipitation variability.

MATERIALS AND METHODS

Experimental Site

This study is part of the EVENT II experiment (Jentsch and Beierkuhnlein 2010) which was established in 2008 on a seminatural temperate grassland at the Ecological Botanical Garden of the University of Bayreuth, Germany (49°55′19″N, 11°34′55″E, 365 m a.s.l.). The regional climate is characterized as temperate and moderately continental with a long-term mean annual temperature of 8.2°C and a long-term mean annual precipitation of 724 mm (1971–2000) with precipitation peaks in December/January and June/July. Phenological data recording was carried out in 2010 and 2011.

The soil of the EVENT II experiment is classified as Gleysol (Glaser and others 2013) with a homogeneous, loamy Ap-horizon of about 30 cm depth (43% silt, 42% sand, and 15% clay) and a clayey Bg-horizon. The mean pH-value of the topsoil is 4.1 (1 M KCL). The experimental site is a seminatural grassland, which has not been fertilized for more than 20 years and not plowed for at least 25 years prior to the establishment of the experiment in 2008. This grassland is mown twice a year (end of July/September) to maintain its species composition and the land-use type characteristic. Without mowing the species composition would change over time mainly due to the encroachment of woody species. The seminatural temperate grassland is dominated by tall grasses such as *Alopecurus pratensis* L. (meadow foxtail) and *Arrhenatherum elatius* (L.) P. Beauv. ex J. Presl & C. Presl (tall oatgrass). Grasses represent 75 to 85% of the total plant biomass, whereas the percentage of forb species varies between 15 and 23%. Legumes represent less than 2% with regard to the plant biomass yield. A list of available plant species during the phenological observations in 2010/2011 is provided in the supporting information (Table S1).

Experimental Design

The experiment was carried out in a partly crossed three-factorial design: (1) growing season precipitation variability (levels: ''low,'' ''medium,'' ''high$_{early}$,'' ''high$_{previous\ year\ late}$''), (2) warming (levels: ''winter warming,'' ''summer warming,'' ''control''), and (3) ''winter rain'' (levels: yes or no). Within each precipitation variability treatment, application of winter warming, summer warming, winter rain addition, and control were blocked and randomly assigned. The size of each block was 6 m × 4 m and divided into plots of 1.5 m × 1.5 m (nested design). Each factorial climate treatment plot was replicated five times.

Precipitation Variability Treatment

Here, the effect of intra-annual precipitation variability was investigated, not the direct effects of a drought or heavy rainfall because existing studies suggest that overall precipitation sums are expected to remain unaffected in Central Europe. Rather, the intra-annual precipitation variability may increase (Jacob 2009; Kotlarski and others 2014), in particular during the growing season. To apply the intra-annual precipitation variability, the total amount of precipitation was kept constant, while the precipitation pattern was altered during the growing season (April–September; see supporting information Table S2 for further details). Thus, the following four treatments were applied.

The low precipitation variability plots received at least long-term (1971–2000) weekly average precipitation. If natural rainfall was less than the long-term average sum for the same week, the missing amount was irrigated using portable irrigation systems. Drop size and rainfall intensity resembled natural heavy rainfall events through application by Veejet 80100 nozzles, commonly used in erosion research. At 0.03 MPa water pressure, this system resulted in 2.8 mm water per minute. If weekly rainfall exceeded the long-term average sum, it was not subtracted for the next irrigation. The precipitation amount of the low precipitation variability treatment served as a reference amount and that was kept constant for all precipitation variability treatments, while the temporal precipitation pattern was altered during the growing season (April–September).

The medium precipitation variability plots received ambient precipitation and served as a control for statistical analysis. These plots were irrigated additionally four times (beginning of May, end of June, beginning of August and end of September, see Table S2 for details) to keep total precipitation constant according to the reference amount. These additional irrigations were also implemented on the two high variability treatments, resulting in the same annual amount of precipitation for all treatments.

The two extreme precipitation variability treatments, early high precipitation variability, and previous year late high precipitation variability plots were exposed to a 1000-year drought event in spring and summer, respectively. The duration of this event was calculated by Gumbel statistics and based on the 40-year (1961–2000) time series of a local weather station. The manipulation was done by excluding natural rainfall for 42 days using tunnel-shaped rainout shelters with a base area of 6 m × 8 m and a height of 2.5 m. These were constructed with a steel frame (Hochtunnel, E & R Stolte GmbH, Germany) and covered with a transparent plastic sheet (material: 0.2-mm polyethylene, SPR 5, Hermann Meyer KG, Germany). Greenhouse effects due to rainout shelters were minimized by having 80-cm clearance between the roof and the ground, allowing for near-surface air exchange. Rainout shelters permitted nearly 90% penetration of photosynthetically active radiation. The rainout shelters have a buffer zone of 1 m around the plots toward the shelter edge. Plastic sheet pilings around every plot and around every treatment block reaching down to a depth of 25 cm avoided lateral surface flow and root growth (the vast majority of roots at this site occur above − 20 cm) into and out of the plots.

Rainout shelters were removed from the two extreme precipitation variability treatments after 42 days of drought manipulation. The excluded amount of rainfall was applied with the adjustment to the minimum precipitation variability treatment amount simultaneously at the end of the artificial drought period as one heavy rainfall event within three consecutive days. Additionally, we ran a rainout shelter artifact control treatment to check for shelter artifacts. The rainout shelter artifact control plots were irrigated below the shelters with the same precipitation amounts as the medium precipitation variability treatment (ambient precipitation) after every rainfall. No significant difference in onset of flowering was found between ambient control and rainout shelter artifact control ($F = 0.1$; $p = 0.7341$).

The coefficient of variation (CV = standard deviation × daily mean^{-1} × 100) of precipitation was calculated to test the strength of the precipitation variability treatments (Table S2). In addition, soil moisture in the main rooting zone (− 2 to − 7 cm) in each treatment plot per precipitation block ($n = 5$ for each treatment combination) was logged every hour using frequency domain (FD)-sensors (ECH$_2$O, Decagon devices, Pullman, USA). The soil moisture data are based on the average of all five replicates for each treatment except when missing data occurred due to sensor or logger errors. In both years, the growing season precipitation variability and soil moisture were altered, resulting in lowest variability in low, intermediate variability in medium, and high variability in high$_{early}$ (spring drought) and high$_{previous\ year\ late}$ (summer drought) precipitation variability treatments (Figure 1, Table S2).

Warming Treatment

According to seasonally differing temperature change during the last 100 years (Deutscher Wetterdienst 2015, see also in Table 1) and current projections (Jacob 2009; IPCC 2013), the warming treatments were carried out during the winter half of the year (October–March, called "winter warming") or summer half of the year (April–September, called "summer warming"). The temperatures were increased using IR-overhead heating lamps (IOT/90 250 W Elstein, Northeim, Germany) at a height of 0.8 m, theoretically resulting in 60 W plot^{-1}. IR-heating lamps were raised to 1 m if tall grasses reached 80 cm. Plots with no warming treatment (control plot) were equipped with dummy lamps. Air temperature at +5 cm (with radiation shield) and soil temperature at − 2 cm were recorded on an hourly basis by thermistors (B57863-106 S302-F40, EPCOS AG, München, Germany) in one warmed and one ambient plot per precipitation block. All data collection took place in the center of each plot directly below the lamp to avoid potential edge effects created by temperature gradients with distance from the lamp. The air temperature at +5 cm above ground was raised on average by 1.0°C in winter warming plots and by 1.3°C in summer warming plots during the manipulation periods (Table 1 and supporting information Figure S1). Soil temperature at − 2 cm was raised by 1.4°C in winter warming plots and by 1.1°C in summer warming plots, respectively. Winter warming reduced the snow cover by more than one-half in winter warming plots (Supporting information Figure S2).
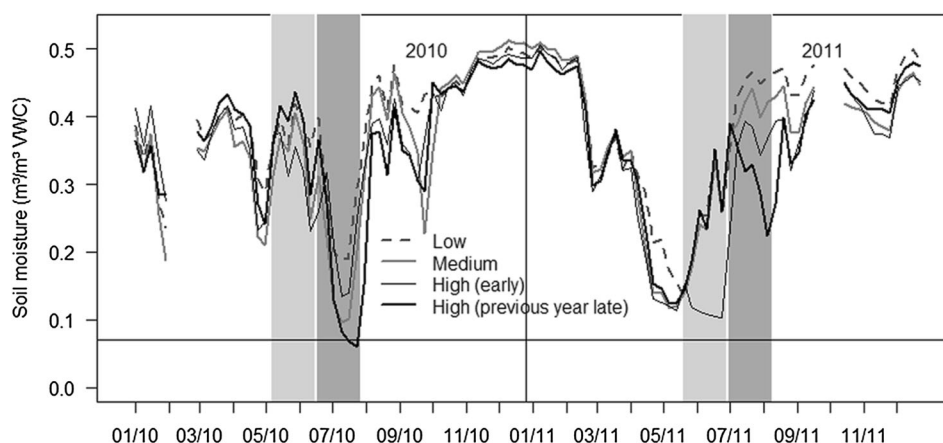
Figure 1. Soil moisture ($- 2$ to $- 7$ cm) under the precipitation variability treatments over the two consecutive study years (2010 and 2011). Data were collected from each treatment plot per precipitation block ($n = 5$) in 1-h intervals. Three-day mean soil moisture (calculated from each 1-h mean) per treatment is shown here. Gray shade indicates the period of early variability, and dark gray shade indicates the period of late variability. The permanent wilting point (pF = 4.2) is indicated by the horizontal straight line.

Table 1. Mean Air ($+ 5$ cm) and Soil ($- 2$ cm) Temperatures During the Experiments

(mean °C)	Ambient (mean ± SD °C)	Warming (mean ± SD °C)	Warming realized (mean °C)	Long-term temperature[a] (mean °C)	Historical warming[b] (mean °C)
Air temperature					
Winter 2009/2010	1.5 ± 5.6	2.5 ± 5.8	+ 1.0	2.6	+ 1.1
Winter 2010/2011	2.2 ± 3.8	3.2 ± 4.5	+ 1.0		
Summer 2010	14.8 ± 6.0	15.9 ± 5.8	+ 1.1	14.0	+ 1.1
Summer 2011	14.2 ± 6.4	15.6 ± 6.3	+ 1.4		
Soil temperature					
Winter 2009/2010	2.6 ± 3.7	4.0 ± 4.2	+ 1.4		
Winter 2010/2011	2.5 ± 2.9	3.8 ± 3.6	+ 1.3		
Summer 2010	14.4 ± 4.7	15.5 ± 4.4	+ 1.1		
Summer 2011	14.0 ± 5.0	15.0 ± 4.7	+ 1.0		

Mean seasonal temperature values and standard deviation of ambient versus warming treatment for summers and winters (2010–2011) and the respective temperature change due to warming are given here.
[a]*Mean climate data for 1960–1990 at ~ 1 km² resolution (Hijmans and others 2005).*
[b]*Deutscher Wetterdienst (2015) for the period of 1881–2014.*

Winter Rain

Independent from the focus on precipitation variability over growing season, we further simulated a winter rain addition because in Europe precipitation is likely to increase in winter (Zolina 2012). The winter rain treatment was carried out from November to February. The control plots received ambient precipitation throughout the whole winter. In addition to ambient precipitation, the winter rain plots received 15 l/m² (= mm, once in a month) water for four consecutive months in mid-November, mid-December, mid-January, and mid-February (60 l/m² in total), which corresponds to

an additional 60-mm precipitation in each winter rain plot. Winter rain addition increased the soil moisture in both years (at least 8–10 weeks) but had no effect on the snow cover (Supporting information Figure S3).

Flowering Phenology, Cover and Biomass

The onset of flowering was recorded weekly in 2010 (starting in March until the end of June) and in 2011 (starting in April until the end of June) for 45 plant species in the central square meter of each plot in order to minimize edge effects. The onset of flowering was considered as the first day an open flower

with visible anthers was observed. The documentation of the onset of flowering was conducted until the biomass harvest at the peak growing season in both years (21 June 2010 and 4 July 2011, respectively). Standing plant biomass of all species was harvested from the core of each plot (0.1 m^2 rectangle). Collected samples were sorted to species and dried to a constant weight at 75°C and weighed (Ohaus Navigator TM, Ohaus Corporation, Parsippany, NJ, USA; accuracy ± 0.01 g). Species-specific plant cover (%) was visually estimated by the same two individuals before each harvest. As the recording of the onset of flowering stopped with the biomass harvests, which corresponds with the end of the spring drought (= ''high$_{early}$'' treatment), the impact of the previous years 2009 and 2010, respectively, (such as ecological stress memory effects, see Walter and others 2013) was examined for the summer drought treatment (= ''high$_{previous\ year\ late}$'' treatment). According to Jäger (2011), plants were classified as early flowering species, if their onset of flowering started before/within May and all plants flowering after May were classified as late flowering species. However, four early flowering species (according to Jäger 2011) were adjusted as late flowering species (*Crepis biennis, Dactylis glomerata, Poa pratensis,* and *Trifolium repens*) as the onset of their flowering did not start before May in our experiment. Similarly, two late flowering species (according to Jäger 2011) were adjusted as early flowering species (*Leontodon hispidus* and *Vicia cracca*) as the onset of their flowering started before May in our experiment (Table S1).

Statistical Analysis

Analysis of variance (ANOVA) combined with linear mixed effect models was applied to test for the main effects of the factors, warming (levels: ''winter warming,'' ''summer warming,'' ''control''), growing season precipitation variability (levels: ''low,'' ''medium,'' ''high$_{early}$,'' ''high$_{previous\ year\ late}$''), winter rain (levels: yes or no), year (level: 2010 and 2011) and the interaction of each factor with the factor ''flowering'' (levels: ''early flowering'' or ''late flowering'' groups), on the response variables, onset, plant cover and biomass at the community level. The nested design with the warming and the winter rain treatments nested within the precipitation variability treatments was accounted for by random effects. Plot-wise ($n = 5$ for each factor combination) average day of onset of flowering was used for community analysis. An average day of onset for early and late flowering community was calculated from the responses of all

species within a plot. Plot replication was used as a random factor.

In addition, species-specific flowering onsets were analyzed separately if there were at least three replicates of a species in a season in any single treatment ($n = 3$) and in the respective control ($n = 3$). Based on this criterion, 13 early flowering species and 12 late flowering species were suitable for species-specific data analysis (Table 4). ANOVA combined with linear mixed effect models (LMEMs) were applied to test the onset of flowering at the species level. Replication and year (if no significant variation between years) were used as random factors. Furthermore, regression analysis between biomass (gm^{-2}) and onset (day of the year) of flowering species was conducted separately under control and warming treatments (as warming treatments had significant effects on community-average flowering onset) to see whether a phenological shift could explain any changes in biomass responses. Biomass, as opposed to cover, was selected for this analysis as the community-average biomass of late flowering species significantly differed under warming treatments compared to control, whereas cover responses of both early and late flowering species and biomass of only early species did not significantly differ under warming compared to control. Regression analysis between plant height (cm) and shift in flowering onset (actual effect size of warming in terms of how many days flowering was shift in comparison with the control) was conducted. Regression analysis was done with linear least-squares regression (function ''lm''). Relative treatment effects on biomass (gm^{-2}) and onset (day of the year) of each species were also calculated ($\Delta = $ (treatment − control)/control.

Homogeneous groups of factor combinations were identified by Tukey's HSD post hoc comparisons. The level of significance was set at $p < 0.05$. LMEMs were conducted with the function ''lme'' and Tukey HSD post hoc comparisons by the function ''glht.'' Plot-wise average onset of flowering (of the year) was calculated by the function ''aggregate.'' The five packages multcomp (Simultaneous Inference in General Parametric Models, version:1.3-2, Hothorn and others 2008), lme4 (Linear mixed-effects models using Eigen and S4, version: 1.0-6, Bates and others 2015), sciplot (Scientific Graphing Functions for Factorial Designs, version: 1.1-0, Morales and R Development Core Team 2012), Rmisc (Ryan miscellaneous, version: 1.5, Hope 2013) and ggplot2 (An implementation of the Grammar of Graphics, version: 1.0.0, Wickham 2009) were used for data analysis

and graph preparation in R version 3.2.1 (R Core Team 2015).

RESULTS

Effects of Seasonal Climate Warming

At the community level, winter warming significantly advanced the onset of flowering in both years 2010 and 2011 ($p = 0.0001$, by 3.1 days; $p < 0.0001$, by 3.1 days, respectively, Figure 2, Table 2). Summer warming significantly advanced the onset of flowering in the overall grassland community in 2010 ($p = 0.0001$, by 2.7 days), but not in 2011 (Figure 2). The advanced phenological shift in response to seasonal warming was mainly caused by early flowering species. Winter warming significantly advanced the onset of early flowering species by 3.8 days in 2010 and by 6.1 days in 2011 ($p < 0.0001$ in both years) (Figure 2). Winter warming had no statistically significant effect on the onset of late flowering species in both years. On the other hand, summer warming advanced the onset of early flowering species by 3.5 days ($p = 0.0004$) and of late flowering species by 2.8 days ($p = 0.0012$) in 2010, but not in 2011.

The warming treatments significantly altered plant cover and biomass production of early versus late flowering species (warming × flowering (early/late); cover, $F = 5.1$, $p = 0.0095$; biomass, $F = 8.7$, $p = 0.0002$, Table S3). Winter warming significantly increased the biomass production (66%) and tended to increase the cover (13%) of late flowering species compared to control, while early flowering species showed neither a significant change in cover nor in biomass in response to winter warming (Figure 3). Summer warming showed no significant change in biomass or cover for any of the two species groups compared to control (Figure 3).

At the species level, warming effects on the onset of flowering were species-specific (Table 3). Seasonal warming significantly advanced the onset of eight (seven early and one late flowering) grassland species in at least 1 year (see Table 3 for details). Surprisingly, most of these early flowering grassland species (six out of seven) are short in height (≥ 50 cm). No single-species effects of winter warming in 2010 and summer warming in 2011 were detected in any late flowering species. No significant correlations between single-species biomass (gm^{-2}) and onset (day of the year) of both early and late flowering species were detected under any seasonal warming treatments (regression data not shown, relative treatment effects on sin-gle-species biomass are shown in Table 3). However, significant positive correlations between plant height and onset of flowering were detected, irrespective of warming treatment ($R^2 = 0.39$, $p = 0.001$; Supporting information Figure S5). Interestingly, plant height was also related to the impact of winter warming on phenological shift ($R^2 = 0.20$, $p = 0.005$; Figure 4).

Effects of Additional Winter Rain and Growing Season Precipitation Variability

At the community level across species, additional winter rain and growing season precipitation variability had no effect on the onset of flowering in any of the 2 years (winter rain × year, $p = 0.8538$; precipitation variability × year, $p = 0.2523$; Table 2; years did not differ for winter rain and precipitation variability, and therefore, average onset over 2 years is shown in Figure 5). Additional winter rain had no significant single and interaction effects on cover and biomass for both early and late flowering species compared to control (Supporting information Table S3 and Figure S4). Precipitation also had no significant effects on biomass for early and late flowering species compared to control (Supporting information Table S3 and Figure S6).

However, a few species-specific responses were detected (average onset over 2 years is shown in Table 3) under precipitation treatments. The addition of winter rain and low precipitation variability advanced the onset of at least one early and one late-flowering species. No significant species-specific responses were detected under the spring drought ($high_{early}$ precipitation variability) treatment. However, the summer drought ($high_{previous\ year\ late}$ precipitation variability) treatment delayed the onset of one early flowering and advanced onset of one early and one late flowering species (Table 3).

DISCUSSION

Effects of Seasonal Climate Warming on Onset of Flowering

Our results support the first hypothesis that both winter and summer warming advance the onset of flowering of plant species in a species-rich temperate grassland ecosystem. In addition, we found higher phenological sensitivity of grassland species to winter warming. On average over 2 years, winter warming (air, + 1.0°C; soil, + 1.4°C) advanced the onset of flowering of the temperate grassland
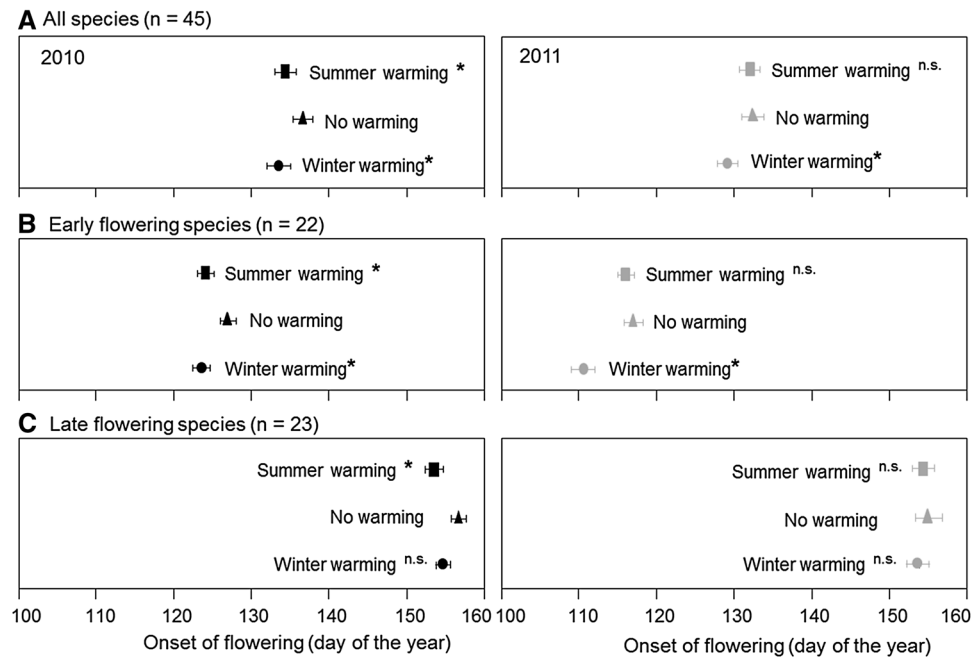
Figure 2. Community-average onset of flowering under winter and summer warming **A** all species, **B** early flowering species **C** late flowering species. Average onsets of flowering and standard error per plot ($n = 5$ per treatment) in a temperate grassland ecosystem are shown here. Significant treatment effects compared to control are marked by asterisks ($p < 0.05$). n.s. not significant.

Table 2.   ANOVA Results of the Treatment Effects on Community-Average Phenological Responses

Factors	numDF	denDF	F value	p value
Warming (control, winter, summer)	**2**	**64**	**9.5**	**0.0002**
Precipitation variability (4 treatments)	3	64	0.8	0.4792
Winter rain (no, yes)	1	64	0.9	0.3455
Year (2010, 2011)	**1**	**190**	**135.1**	**< .0001**
Warming × flowering (early or late)	**2**	**190**	**6.2**	**0.0024**
Precipitation × flowering	3	190	1.3	0.2690
Winter rain × flowering	1	190	1.0	0.3283
Precipitation × warming	6	64	0.7	0.6869
Precipitation × winter rain	3	64	1.2	0.3240
Precipitation × warming × flowering	6	190	1.7	0.1165
Precipitation × winter rain × flowering	3	190	0.3	0.8308
Warming × year	**2**	**190**	**3.2**	**0.0441**
precipitation × year	3	190	1.4	0.2523
Winter rain × year	1	190	0.0	0.8538
Flowering × year	**1**	**190**	**97.6**	**< .0001**
Warming × flowering × year	2	190	2.4	0.0949
Precipitation × flowering × year	3	190	0.4	0.7772
Winter rain × flowering × year	1	190	0.6	0.4355
Precipitation × warming × year	6	190	1.5	0.1799
Precipitation × winter rain × year	3	190	0.5	0.6979
Precipitation × warming × flowering × year	6	190	0.2	0.9735
Precipitation × winter rain × flowering × year	3	190	0.1	0.9402

Significant results ($p < 0.05$) are marked bold. Flowering species: early or late; early flowering species if their onset starts before/within May and late flowering species if their onset starts after May
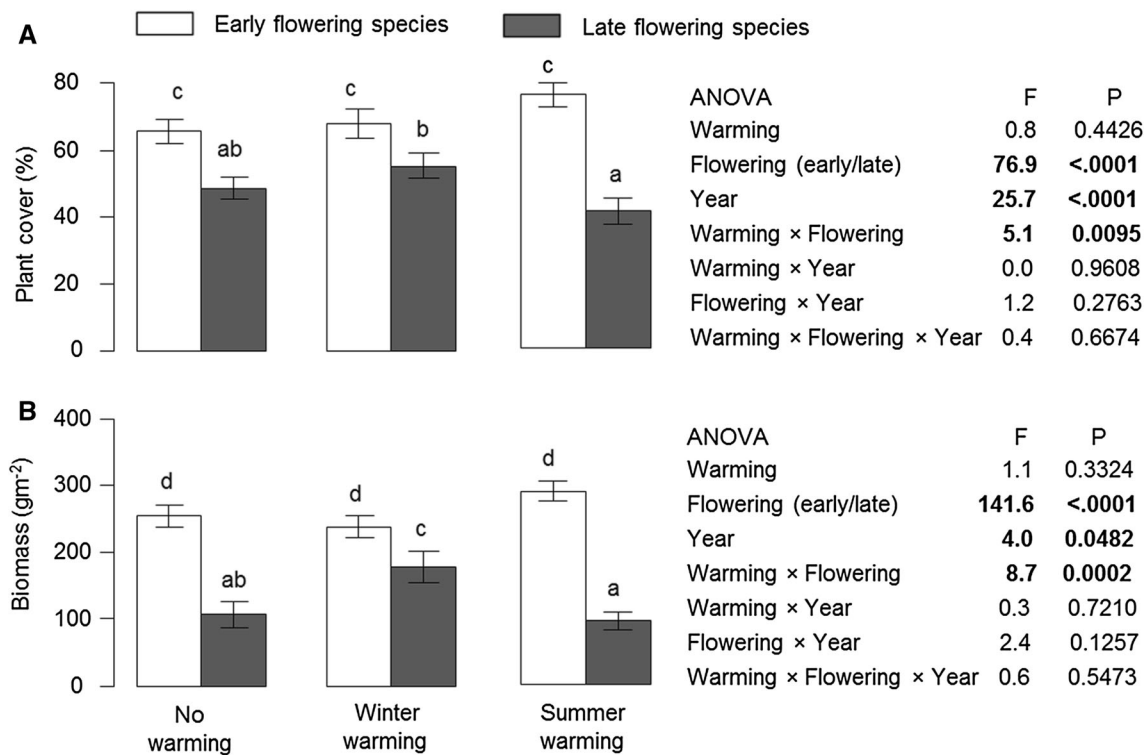
Figure 3. Responses of early versus late flowering community **A** plant cover (%) and **B** biomass (gm^{-2}) at peak growing season under warming treatments. Average community responses and standard error per plot are shown ($n = 5$ per treatment). Significant results ($p < 0.05$) are marked bold.

community by 3.1 days, while summer warming (air, $+ 1.3°C$; soil, $+ 1.1°C$) advanced flowering by only 1.5 days. Advanced flowering due to temperature increase was reported for many plant species and regions (Sherry and others [2007]; Körner and Basler [2010]; Cook and others [2012]; Moore and Lauenroth [2017]). In temperate Europe, it was found that plant phenology is shifting $- 2$ to $- 5$ days per $1°C$ year-round temperature increase (Chmielewski and Rötzer [2001]; Menzel and others [2006]).

Vautard and others ([2014]) expect that during the twenty-first century most of Europe will be warming up more than the global average with stronger warming in Central Europe during winter months compared to the summer season. The IPCC states a ''high confidence'' for cold days as well as cold nights to decrease all over Europe. This is why it is particularly interesting that the present study found flowering phenology of a seminatural temperate grassland community to be more responsive to a $1°C$ temperature increase in winter (October–March) than to a $1°C$ increase in summer (April–September).

Nevertheless, the hypothesis that the onset of early flowering species will be particularly ad-vanced by winter warming and the onset of late flowering species will be rather advanced by summer warming, was only partly supported by the present study. In accordance with our expectations, winter warming significantly advanced the onset of early flowering species in both years (2010, by 3.8 days; 2011, by 6.1 days) but had no effect on late flowering species in either of the 2 years. Winter warming effects in both years are related to the direct impacts of rising air and soil temperature during the two months (February and March) preceding the onset of early flowering species (as indicated by $1.2°C$ warming compared to control, see Tables [1] and [2]). The lower winter warming effects on early flowering species in 2010 compared to 2011 could potentially be due to the differences in ambient winter air temperature compared to the long-term mean. In our study site, the long-term mean air temperature in winter (October–March) is $2.6°C$ (Hijmans and others [2005]). However, the ambient air temperature in winter 2010 and 2011 was 1.5 and $2.2°C$, respectively. Lower ambient air temperature during winter 2010 compared to 2011 indicates a delayed start of the growing season in 2010. Therefore, the onset of early flowering species started about 10 days later in 2010 compared

Table 3. Shift in the Onset of Flowering and Biomass Responses of the Single Early and Late Flowering Species to the Seasonal Climate Treatments

Species	Plant height (cm)	Winter warming Year 2010	Winter warming Year 2011	Summer warming Year 2010	Summer warming Year 2011	Winter rain Both years	Low precipitation variability Both years	High_early precipitation variability Both years	High_previous year late precipitation variability Both years
Early flowering species									
Alopecurus pratensis	45	− 5.3 (− 0.15)	− 10.0 (− 0.14)	− 1.8 (+ 0.8)	− 4.5 (+ 0.23)	− 1.2 (+ 0.16)	+ 0.5 (+ 0.01)	+ 0.2 (− 0.14)	+ 0.3 (− 0.05)
Anthoxanthum odoratum	17	− 2.2 (− 0.16)	− 8.8 (− 0.16)	− 0.7 (− 0.27)	− 0.2 (− 0.23)	− 1.8 (− 0.40)	− 0.7 (+ 0.42)	− 1.9 (+ 0.41)	+ 0.5 (− 0.43)
Bellis perennis	6	− 6.9 (+ 2.34)	− 3.5 (0.00)	− 8.0 (− 0.08)	+ 3.6 (0.00)	− 5.1 (+ 0.21)	− 1.0 (− 0.03)	3.0 (− 0.02)	+ 0.5 (− 0.10)
Cerastium holosteoides	15	− 4.1 (+ 2.76)	− 1.4 (− 0.21)	− 5.3 (+ 0.46)	− 0.8 (− 0.49)	+ 0.7 (− 0.07)	+ 0.9 (− 0.15)	− 0.5 (− 0.01)	− 2.4 (− 0.15)
Plantago lanceolata	23	+ 0.7 (+ 0.24)	− 4.2 (+ 0.92)	− 3.2 (+ 0.17)	+ 6.7 (+ 0.33)	+ 0.6 (− 0.06)	− 3.7 (+ 0.65)	− 4.9 (+ 1.62)	− 3.5 (+ 1.20)
Ranunculus acris	51	− 3.8 (− 0.13)	− 5.6 (− 0.63)	− 5.4 (+ 1.22)	+ 1.4 (− 0.70)	− 0.3 (− 0.42)	− 5.7 (− 0.19)	− 0.7 (+ 0.06)	− 2.3 (+ 0.83)
Rumex acetosa	51	− 0.2 (− 0.08)	− 5.3 (+ 0.22)	− 0.3 (− 0.22)	0.0 (+ 0.12)	+ 0.2 (− 0.02)	− 1.2 (+ 0.11)	+ 0.6 (− 0.15)	− 0.4 (− 0.16)
Taraxacum officinale	23	− 10.4 (+ 1.20)	− 5.1 (+ 0.67)	− 5.2 (+ 7.17)	+ 1.0 (+ 3.62)	+ 0.7 (+ 0.35)	+ 1.7 (− 0.65)	− 0.1 (+ 1.90)	− 0.5 (− 0.02)
Trifolium dubium	20	− 4.4 (− 0.46)	− 12.3 (0.00)	− 10.3 (+ 1.42)	NA	− 7.2 (+ 0.04)	− 10.5 (− 0.72)	− 8.4 (− 0.63)	− 9.2 (+ 0.82)
Veronica arvensis	14	− 13.4 (− 0.40)	NA	− 10.1 (0.00)	NA	− 2.2 (− 0.69)	+ 2.7 (0.00)	+ 3.7 (− 0.76)	+ 3.8 (+ 2.33)
Veronica chamaedrys	28	NA	− 2.8 (0.00)	− 7.7 (0.00)	+ 7.2 (0.00)	+ 1.0 (0.00)	+ 0.3 (0.00)	+ 7.6 (0.00)	+ 14.3 (0.00)
Veronica serpyllifolia	18	− 10.0 (0.00)	NA	− 7.7 (0.00)	NA	− 10.5 (0.00)	− 4.3 (0.00)	+ 9.7 (0.00)	+ 0.3 (0.00)
Vicia sepium	65	− 7.8 (+ 2.48)	− 28.3 (+ 89.9)	NA (+ 32.4)	− 22.5 (+ 6.75)	− 7.5 (+ 3.83)	+ 11.9 (− 0.53)	NA	+ 20.5 (− 0.64)
Late flowering species									
Arrhenatherum elatius	110	− 0.9 (+ 1.77)	+ 2.1 (+ 0.62)	− 1.9 (+ 0.13)	− 1.0 (+ 0.42)	− 1.7 (+ 0.17)	+ 1.5 (+ 0.49)	− 1.2 (+ 0.31)	+ 0.8 (+ 0.11)
Centaurea jacea	85	NA (− 0.69)	− 1.2 (+ 2.03)	NA (− 0.98)	+ 0.4 (− 0.91)	− 1.4 (− 0.92)	+ 2.7 (+ 3.67)	+ 4.6 (+ 5.18)	− 4.5 (+ 8.72)
Dactylis glomerata	62	NA (+ 1.13)	− 3.0 (+ 0.81)	NA (− 0.19)	− 11.8 (− 0.13)	+ 0.2 (+ 0.87)	− 1.2 (− 0.18)	− 4.6 (− 0.75)	3.6 (− 0.02)
Festuca rubra	50	NA (− 0.25)	+ 3.0 (+ 0.88)	NA (− 0.74)	+ 2.3 (− 0.45)	+ 2.9 (− 0.71)	− 3.4 (+ 0.74)	− 0.7 (− 0.32)	− 3.6 (− 0.23)
Galium album	75	0.0 (+ 0.79)	+ 2.3 (+ 14.14)	− 5.1 (+ 8.6)	− 1.1 (+ 15.91)	− 0.1 (+ 0.23)	− 2.1 (+ 3.99)	− 2.5 (+ 0.95)	+ 1.3 (− 0.76)
Holcus lanatus	33	− 1.3 (+ 0.49)	− 10.3 (+ 0.86)	− 6.6 (− 0.08)	− 3.9 (+ 0.12)	− 3.2 (− 0.03)	+ 0.3 (+ 0.25)	− 1.5 (+ 0.13)	− 0.2 (− 0.17)
Hypochaeris radicata	60	NA (+ 0.88)	+ 6.5 (− 0.32)	NA (+ 0.86)	+ 8.7 (− 0.95)	+ 9.0 (− 0.74)	− 1.2 (+ 4.84)	+ 1.8 (− 0.74)	− 1.7 (+ 0.41)
Leucanthemum ircutianum	44	0.0 (0.00)	NA	NA (− 0.89)	NA	− 2.4 (− 0.55)	NA	− 3.8 (+ 3.88)	− 8.8 (+ 6.51)
Phleum pratense	53	NA (− 0.10)	+ 0.1 (+ 1.38)	NA (− 0.18)	− 0.3 (+ 5.89)	− 1.6 (+ 0.40)	+ 2.5 (+ 2.31)	+ 3.5 (− 0.32)	− 0.3 (− 0.33)
Poa pratensis	30	− 2.6 (+ 0.16)	0.0 (+ 0.91)	− 1.8 (+ 0.48)	− 1.9 (+ 0.45)	− 0.7 (+ 0.19)	− 1.5 (+ 0.24)	− 2.9 (− 0.21)	− 1.2 (− 0.01)
Poa trivialis	45	NA (+ 1.99)	NA (+ 9.40)	NA (− 0.21)	NA	NA (+ 1.23)	− 0.3 (+ 0.21)	− 5.8 (− 0.46)	NA + (1.99)
Trifolium pratense	53	− 6.2 (− 0.14)	− 4.2 (+ 2.83)	− 5.0 (− 0.11)	NA (− 0.29)	− 9.4 (+ 0.73)	+ 3.9 (− 0.55)	+ 0.8 (− 0.72)	− 3.3 (− 0.19)

Relative treatment effects on biomass are given in the parentheses (if species are present in both control and treatment plots). Effects of seasonal warming on the onset of flowering differed between years (warming × year, p = 0.0441, Table 3). Therefore, responses to warming treatment are shown separately for both years. Averages over both years (2010 and 2011) are shown for the precipitation treatments as responses did not differ between years (Table 3). Positive (+) values indicate delay and negative (−) values indicate the earlier onset of flowering date in days compared to control. Significant (ANOVA, p < 0.05) effects between control (the mid-variability treatment for the precipitation variability treatments) and the treatments are marked bold for the flowering onset. For biomass, positive (+) values indicate relative increase and negative (−) values indicate relative decrease by treatments compared to control (relative responses = (treatment − control)/control). "NA" if the onset of flowering was not observed at least three times in the specific treatment or in the respective control plot. Plant height data are collected from TRY data base (Kattge and others 2011).
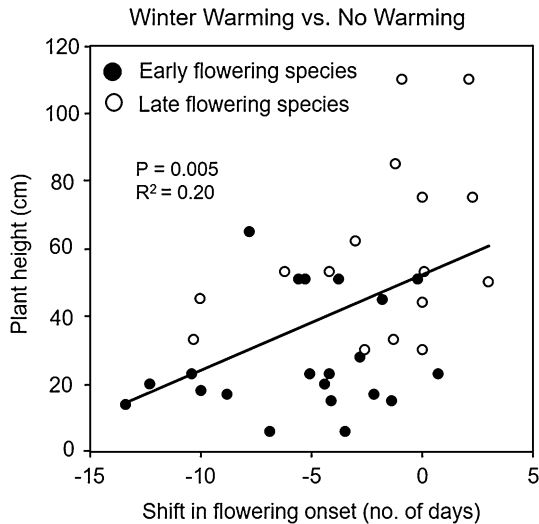
Figure 4. Correlation between shift in flowering onset and plant height under winter warming. Species-specific responses of 13 early flowering species and 12 late flowering species during the years 2010 and 2011 are shown here (see methods and Table 3 for details). Plant height data are collected from TRY data base (Kattge and others 2011).
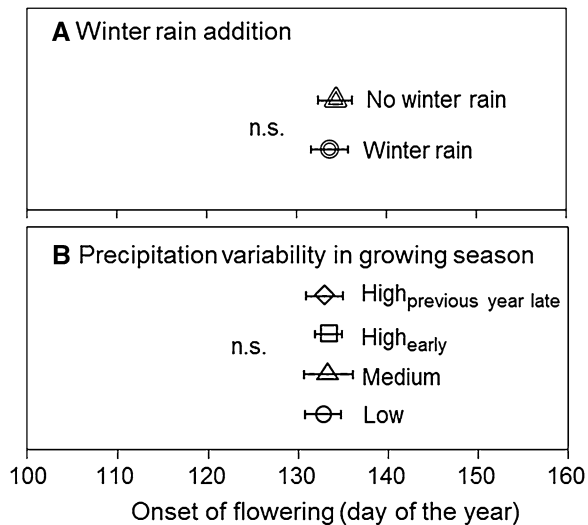

Figure 5. Community-average onset of flowering of a temperate grassland community under **A** winter rain addition and **B** four precipitation variability treatments during the growing season. Average onsets of flowering and standard error per plot are shown ($n = 5$ per treatment). *n.s.* not significant.

to 2011, irrespective of treatment. Summer warming advanced the onset of early and late flowering species in 2010 by 3.5 and 2.8 days, respectively, while no effects were observed in 2011. The missing effect in 2011 for the summer

warming is also probably due to the earlier start of the growing season in that year. The majority of early flowering species had already started flowering in March, which is before the summer warming even started in April 2011.

Correlation between single-species biomass and the flowering onset of early and late flowering species was not statistically significant. However, community-average cover and biomass data show that winter warming significantly increases the biomass of late flowering species, while winter warming has no effects on cover or biomass of early flowering species compared to no warming. This indicated that the smaller response in phenology of the late flowering species might simply be an artifact of increased biomass of those species rather than true changes in phenology, whereas the phenological response of the early flowering species could not be related to increased cover or biomass.

In summary, our main finding of the early flowering species being more responsive in their phenology is a true phenological effect. Furthermore, the present study added that phenological sensitivity differs not only between early and late flowering species but also within the early flowering community. We found a significant correlation between plant height and shift in flowering onset, which indicates that early flowering short grassland species were more sensitive to winter warming than early flowering tall species whose reproductive organs are not so close to the soil surface and more exposed to wind. Taken together, we conclude that advanced flowering phenology in response to gradual warming in a temperate grassland ecosystem is mainly due to the high phenological sensitivity of early flowering species to winter warming.

Species-specific flowering onset demonstrates that one-third of the early flowering species exhibit a significant response to seasonal warming. This shows non-uniform responses also within the early flowering community. The general tendency of phenological advance of early flowering species, however, is in accordance with previous findings in a North American natural prairie (Sherry and others 2007). Still, the observed phenological shift of late flowering species toward earlier flowering does not match the findings of Sherry and others (2007) who found warming to delay the onset of late flowering species. Obviously, phenological responses can be specific for regional climate and ecosystems. Also, temperate managed grasslands (for example, hay meadows) cannot be directly compared to continental natural prairies because of

Table 4. Predicted Onset (First Flowering Date) of Temperate Grassland Plants for the Twenty-First Century

Predicted increase in temperature for 2081–2100 (IPCC 2013)	Predicted shift in onset of grassland plants in 2081–2100	
	Winter warming	Summer warming
(a) All species		
0.3–1.7°C (RCP2.6)	− 0.8 to − 4.4 days	− 0.4 to − 2.1 days
1.1–2.6°C (RCP4.5)	− 2.8 to − 6.7 days	− 1.4 to − 3.3 days
1.4–3.1°C (RCP6.0)	− 3.6 to − 8.0 days	− 1.8 to − 3.9 days
2.6–4.8°C (RCP8.5)	− 6.7 to − 12.4 days	− 3.3 to − 6.0 days
(b) Early flowering species		
0.3–1.7°C (RCP2.6)	− 1.2 to − 6.9 days	− 0.6 to − 3.3 days
1.1–2.6°C (RCP4.5)	− 4.5 to − 10.6 days	− 2.1 to − 5.0 days
1.4–3.1°C (RCP6.0)	− 5.7 to − 12.7 days	− 2.7 to − 5.9 days
2.6–4.8°C (RCP8.5)	− 10.6 to− 19.6 days	− 5.0 to − 9.2 days

[1](a) All species: winter warming (air + soil = 1.2°C) shift –3.1 days, summer warming (air + soil = 1.2°C) shift − 1.5 days; (b) Early flowering species: winter warming (1.2°C) shift − 4.9 days and summer warming (1.2°C) shift − 2.3 days, respectively. Responses of late flowering species are not given here as no significant phenological shift observed over 2 years.
Onset shifts were predicted by linear extrapolation based on the observed results[1] and four global warming scenarios projected by IPCC (2013).

the differences in climate, length of growing season, plant composition and, perhaps most importantly, the dominant management regime of mowing, which systematically removes aboveground biomass. Temperate grass species are adapted to this continuous extraction of biomass also in their phenological rhythms.

Here, we investigated the onset of flowering in the most important temperate European grassland community (managed hay meadow), where many plant species are flowering before June due to their adaptation to seasonality and land-use regimes (Table S1). The observed seminatural ecosystem and its 45 plant species are representative for the large surface of managed grassland in Europe. Therefore, we expect that the detected phenological responses at the level of the community and its species groups are reflecting the phenological responses of European temperate grassland ecosystems to climate warming.

Effects of Winter Rain Addition and Growing Season Precipitation Variability on Onset of Flowering

The present experimental study provides evidence that average flowering onset of a species-rich temperate grassland community responds neither to increased winter rain nor to enhanced seasonal precipitation variability. However, at the species level, a few species responded significantly to these precipitation treatments. Such species-specific re-

sponses are in accordance with previous findings (for example, Jentsch and others 2009; Nagy and others 2013).

Most other studies, however, focused on small sets of species and reported species-specific phenological responses to sudden changes in moisture regimes (Cleland and others 2006; Bloor and others 2010). The present study showed no phenological shift at the community level, indicating that flowering phenology of a species-rich temperate grassland community is stable under modified precipitation amount and variability. This is in line with current studies that confirm a stabilizing contribution of biodiversity on ecosystem functioning in the face of climatic extremes (Isbell and others 2015).

Implications of Climate Change-Driven Phenological Shifts to Plant Functioning

The present study findings indicate that winter warming can alter vegetation dynamics of temperate grassland ecosystems across Europe by changing physiological and morphological activities of early flowering species stronger than that of late flowering species.

Early phenological development can alter reproductive fitness and can play an important role in niche differentiation among coexisting plant species. This is because temperature-dependent advancement of phenology is related to earlier root growth, leaf expansion, seed maturation, higher

plant *N* uptake and also success of exotic species (McKane and others 1990; Santandreu and Lloret 1999; Saavedra and others 2003; Wolkovich and others 2013). These responses could trigger cascading effects in ecosystem functioning (for example, plant–pollinator interactions).

Finally, our study predicts that flowering onset of the studied grassland ecosystem might advance 6.7–12.4 days by winter warming and 3.3–6.0 days by summer warming at the end of twenty-first century under the temperature scenario RCP8.5, if we assume a simple linear relation between warming and shift in phenology (see details in Table 4). Surprisingly, there was no significant evidence of community-level phenological responses to increased winter rain and modified growing season precipitation variability. However, the observed species-specific phenological effects of modified intra-annual precipitation in temperate grasslands hint at possible alterations of population dynamics, dominance patterns, community composition, and ecosystem functioning, respectively.

CONCLUSIONS

Winter warming rather than summer warming emerged as the main driver for advancing flowering phenology of the studied seminatural mesic temperate grassland community. Our findings emphasize the necessity of considering seasonality in climate change impact research. The observed magnitudes of change have the potential to alter ecosystem functioning and community dynamics, for example, by favouring early flowering species over late flowering species. Flowering phenology of the studied temperate grassland ecosystem was largely unaffected by the manipulated precipitation changes, that is, altered summer rainfall variability and increased winter rainfall.

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