

Flowering phenology as a functional trait in a tallgrass prairie

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Summary

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- The timing of flowering is a critical component of the ecology of plants and has the potential to structure plant communities. Yet, we know little about how the timing of flowering relates to other functional traits, species abundance, and average environmental conditions.
- Here, we assessed first flowering dates (FFDs) in a North American tallgrass prairie (Konza Prairie) for 431 herbaceous species and compared them with a series of other functional traits, environmental metrics, and species abundance across ecological contrasts.
- The pattern of FFDs among the species of the Konza grassland was shaped by local climate, can be linked to resource use by species, and patterns of species abundance across the landscape. Peak FFD for the community occurred when soils were typically both warm and wet, while relatively few species began flowering when soils tended to be the driest. Compared with late-flowering species, species that flowered early had lower leaf tissue density and were more abundant on uplands than lowlands.
- Flowering phenology can contribute to the structuring of grassland communities, but was largely independent of most functional traits. Therefore, selection for flowering phenology may be independent of general resource strategies.

Introduction

The timing of flowering is a critical component of the ecology of plants and can be an important component of community assembly as flowering phenology influences not only the relative abundance of species in a given ecosystem, but also their presence or absence (Rathcke & Lacey, 1985; Sargent & Ackerly, 2008; Crimmins *et al.*, 2011). One manner in which flowering phenology affects the composition of plant communities is through its effect on species interactions. Overlap of flowering times among species is almost inevitable in most communities, generating the potential for strong competition, but also facilitation, for pollination resources (Rathcke & Lacey, 1985). Independent of pollination, flowering phenology indirectly affects species interactions, as flowering times may be associated with other aspects of performance, such as canopy development (Cleland *et al.*, 2006), that influence competition for resources required for vegetative growth. While many temperate woody species flower before leaves are produced, most temperate grassland species flower at the time of maximum vegetative biomass (Mooney *et al.*, 1986; Sun & Frelich, 2011), causing species with similar flowering times to also compete for limiting soil resources and/or light. Flowering phenology can also influence plant success independently of species interactions. Flowering when environmental stress is typically high, such as when temperatures are frequently cold or soil moisture is typically low, can also lower plant fecundity if not lead to the species' local extirpation (Lacey *et al.*, 2003; Inouye, 2008).

If the timing of flowering is an important component of community assembly, there should be general rules that pattern variation in flowering for a community (Armbruster *et al.*, 1994; Morales *et al.*, 2005; Elzinga *et al.*, 2007). If flowering time is neutral within a growing season and uninfluenced by species interactions and environmental conditions within the growing season then a null-model such as the mid-domain hypothesis (Morales *et al.*, 2005) may accurately predict the pattern of flowering phenology at the community level. The mid-domain hypothesis predicts that flowering for a flora should be greatest in the middle of the growing season as a consequence of the constraints of species placement in a bounded growing season (Morales *et al.*, 2005). If flowering time, however, is critical to competition for pollinators and other resources (Kochmer & Handel, 1986; Rathcke, 1988; Godoy *et al.*, 2009) or avoidance of environmental stress (Reich & Borchert, 1984; Penuelas *et al.*, 2004), patterns may deviate from null model expectations. For example, in many grasslands, soil moisture stress can strongly limit plant production and reproduction. Even in grasslands where growing season length is dictated by temperatures, soil moisture stress can be high in the middle of the growing season as leaf area develops, temperatures peak, precipitation declines, and soil moisture is depleted (Briggs & Knapp, 1995; Nippert *et al.*, 2006; Craine *et al.*, 2010). In such grasslands, midsummer soil moisture stress in many grasslands is frequent even in years with above-average precipitation (Nippert *et al.*, 2011).

If flowering time for a species influences its exposure to environmentally stressful conditions and its interspecific interactions

(Brody, 1997; Augspurger, 2009; Devaux & Lande, 2010) then it could also be part of a larger plant strategy that incorporates other functional traits. Flower production and maintenance as well as subsequent reproduction is resource-intensive (Ashman & Schoen, 1994; Obeso, 2002), which might tend to favor reproduction during times of low environmental stress. For example, high leaf tissue density is favored under conditions of low nutrient availability in grasslands and considered part of a broader low-nutrient strategy (Craine *et al.*, 2001; Craine, 2009; Craine & Towne, 2010). Thus if nutrient availability varies seasonally, species that flower during periods of low nutrient availability might also have high leaf tissue density. Seasonal variation in drought could also generate links between plant functional traits and flowering phenology. For example, when stresses become severe enough to constitute a disturbance (e.g. prolonged drought), species with high-activity, rapid-turnover tissues would be favored. For example, severe droughts that generate widespread mortality across all species can favor annuals over perennials (Weaver, 1968). If the probability of drought varies seasonally, times of typical low soil moisture could be more likely to have species with traits that confer drought resistance, while times after the drought could be associated with species that have traits associated with disturbance, such as low leaf tissue density.

Ultimately, if flowering phenology is not neutral and is associated with responses to environmental conditions and plant functional traits then flowering phenology should also be linked to species abundance on a landscape (Willis *et al.*, 2010). For example, if environmental stress varies over the course of a growing season, species that flower during stressful times might be less abundant, linking flowering time and abundance. Competition for pollinator resources could in turn strengthen associations between abundance and flowering time driven also by patterns of environmental stress. If competition for pollination resources is an important associate of flowering time, then there might be fewer species that flower during the same time as the most abundant species to minimize competition. This would lead to fewer less-abundant species flowering at the time when more-abundant species flower.

To test for evidence that flowering time is important to competition for resources and avoidance of environmental stress, we compared interspecific patterns of the timing of flowering of a North American tallgrass prairie (Konza Prairie) with a suite of functional traits, environmental data, and species abundance across three ecological contrasts. We assessed dates of first flowering for 430 herbaceous species with near daily surveys of the vegetation. Patterns of flowering phenology were then determined for the Konza flora as well as for groups defined by species' photosynthetic pathway, life history, and whether the species were native or not to North America.

To better understand the interplay of flowering phenology with environmental conditions, functional traits, and abundance, we focus on three main hypotheses. First, if the probability of species flowering over the growing season is influenced by environmental stress, then the greatest number of species should begin flowering when growing conditions are the least stressful, which would be when soils are the warmest and wettest.

Flowering should be reduced during times of consistent extreme temperatures and/or minimum soil moisture. We test this hypothesis by comparing the frequency of first flowering dates (FFDs) across species with long-term records of air temperatures, precipitation, and soil moisture. Secondly, if environmental stress is a determinant of flowering for a given species, species that flower during the most stressful times should have traits that confer resistance to environmental stress or low resource availability. To test this hypothesis, we examined relationships between flowering time and average leaf tissue density – a proxy for stress tolerance – for *c.* 400 species, as well as relationships over a smaller number of species with other functional traits such as physiological drought tolerance and photosynthetic rates that are associated with plant resource strategies.

Lastly, to determine whether the timing of flowering contributes to the abundance of a species, we examined relationships between flowering time and abundance across three main ecological contrasts at Konza: topography, fire, and grazing. At Konza Prairie, uplands have shallower soils than lowlands and species that are more physiologically drought-tolerant (Craine *et al.*, 2011). We compared watersheds that are burned annually in the spring with those that are infrequently burned because annual spring burning might preferentially decrease the abundance of early flowering species (Howe, 1994). Finally, we compared the abundance of species with different flowering times in areas grazed by bison with those not grazed by bison. Although grazing decreases the abundance of C₄ grasses and increases species richness (Knapp *et al.*, 1999; Collins & Smith, 2006), we do not know, for example, whether grazing increases the richness of species that flower late in the growing season as a consequence of competitive release.

Materials and Methods

The study was conducted at Konza Prairie Biological Station, a 3487 ha native tallgrass prairie located in northeastern Kansas, USA (39.08°N, 96.56°W) (Knapp *et al.*, 1998). Mean annual temperature is 13°C, with average monthly temperatures ranging from -3°C in January to 27°C in July. Annual precipitation for Konza Prairie averaged 844 mm from 1983 and 2009, with *c.* 75% falling in the April–September growing season and peak precipitation in June. The vegetation at Konza is primarily unplowed native tallgrass prairie. Woody species form gallery forests in riparian areas, and can be abundant in specific watersheds, depending upon fire frequency (Briggs *et al.*, 2002). The known vascular flora of Konza Prairie comprises 597 species, of which 59 are woody. Of the 539 herbaceous species, 122 are graminoids, 411 are eudicots, and six are ferns. Graminoid species consist of C₄ Poaceae (51 species), C₃ Poaceae (38 species), C₃ Cyperaceae (26 species), and C₄ Cyperaceae (seven species). Of the herbaceous eudicots, 397 species utilize the C₃ photosynthetic pathway and 14 have the C₄ photosynthetic pathway.

At Konza, grazing, burning, and landscape position are the main environmental contrasts that affect plant communities other than climate. Grazing on three watersheds by reintroduced native bison began in October 1987 and expanded to another

three watersheds in 1992. Stocking rate increased over time so that grazing intensity removes *c.* 25% of the grass production (Towne, 1999). Compared with areas without bison, grazed areas are more diverse (Collins & Smith, 2006), have higher abundance of forbs (Towne *et al.*, 2005), and greater nutrient availability (Johnson & Matchett, 2001; Veen *et al.*, 2008). Annually burned watersheds tend to have lower nutrient availability (Blair, 1997) than infrequently burned watersheds. Lastly, upland and lowland positions differ mainly in soil depth. Upland soils are shallow (often < 25 cm) (Schimel *et al.*, 1991) and are generally cherty, silty clay loams overlying limestone and shale layers (Udic Argiustolls, Florence series). By contrast, lowland soils are deeper and derived from colluvial and alluvial deposits (Pachic Argiustolls, Tully series). Lowland soils are less xeric (Schimel *et al.*, 1991; Nippert & Knapp, 2007b) and support greater productivity and flowering (Heisler & Knapp, 2008; Craine *et al.*, 2010).

Herbaceous species on Konza were surveyed for first flower appearance almost daily from March to October 2010 (129 d sampled over 189 d period), throughout Konza. When a species was found to be flowering for the first time, the date was recorded and the plant collected. Occasionally, some outlier individuals flowered well before the majority of other individuals in their population but these nonrepresentative samples were not collected. We assessed FFDs for a total of 430 herbaceous species (Table S1).

For most species that were encountered in a flowering state, a series of leaf traits were measured on nonsenescent leaves of a range of ages. Some species flower with few leaves present (e.g. *Spiranthes vernalis*), while others have too highly dissected leaves to measure accurately (e.g. *Lomatium foeniculaceum*). Consequently, leaf traits for these species were not measured. Thus we were able to measure leaf traits on a range of ages of nonsenescent leaves for 391 species. After collection in the field, plants were stored in a plastic bag with a small amount of water until leaf area could be measured on a LI-3100 leaf area meter (Li-Cor, Lincoln, NE, USA) later that day. Thickness was measured with calipers on typically three to five leaves on an area adjacent to any midrib or major secondary veins. Leaves were then dried at 65°C for 2–3 d and weighed. Leaf volume was calculated as the product of leaf area and thickness, and leaf tissue density was calculated as the ratio of dry mass to volume.

Dried leaf matter was then ground and analyzed on a Delta Plus mass spectrometer (ThermoScientific, Bremen, Germany) in combination with a CE 1110 elemental analyzer (Carlo Erba, Milan, Italy) for C and N concentrations as well as C and N isotope ratios (see Supporting Information, Notes S1).

Statistical analyses

To assess whether community-level phenology patterns deviated from a simple mid-domain neutral model, we first smoothed univariate community-level patterns with a kernel density smoothing function ($h = 12$) and tested for a significant departure from unimodality in community-level flowering phenology using Hartigan's dip test (Hartigan & Hartigan, 1985) with significance tested using 999 reps of a Monte-Carlo approach (package

dipTest in R 2.12.0). Patterns of FFD across the growing season were compared for phytotaxonomic functional groups (C_3 and C_4 Cyperaceae, Poaceae, and eudicot species) as well as for species native and not native to North America and across three longevity categories (annual, biennial, or perennial). To compare categories, means were compared with ANOVA while the timings of peak FFD were compared nonstatistically (i.e. visually) on smoothed curves.

To determine whether peaks and troughs in flowering were associated with climate parameters, patterns of FFD were compared with mean daily temperature and mean daily precipitation collected from Konza and averaged over 25 yr. In addition to temperature and precipitation, patterns of FFD were compared with soil moisture which was measured biweekly during the growing season for 25 yr (1984–2008) at two points in the lowlands of an annually burned ungrazed watershed. Soil moisture was measured with a neutron depth moisture gauge (Troxler Electronic Incorporated, Research Triangle Park, NC, USA) in thin-walled aluminum access tubes buried 2 m deep. Data on soil moisture at 25 cm are used here as they likely are most important for water relations of the majority of species (Nippert & Knapp, 2007a; Craine *et al.*, 2010). Soil moisture data were expressed as an index of apparent field capacity (Craine *et al.*, 2010).

In addition to the leaf traits measured on most species, FFDs were compared with seven additional functional traits previously measured on plants grown under controlled conditions (Tucker *et al.*, 2011). These functional traits relate to resource capture and retention and are those likely to represent plant resource strategies, such as adaptations to low water, light, or nutrient availability or to high-resource environments (Craine, 2009). Functional traits included maximum photosynthetic rates, maximum stomatal conductance, physiological drought tolerance, leaf angle, average fine root diameter and tissue density, and fraction of biomass in roots. Functional trait data existed for 86–93 of the species measured here, depending on the trait. Seed mass data for 335 species were acquired from the Seed Information Database of the Royal Botanic Gardens, Kew (<http://data.kew.org/sid>). In addition to the traits examined here, we analyzed the relationships between flowering phenology and species' geographic climate envelopes, flowering color, phylogenetic patterns, and foliar C and N isotope ratios from leaves collected in the field. Details on the methods and results for these metrics are presented in Notes S1.

Lastly, to better understand whether FFDs were related to abundance of species, we compared FFDs with the abundance of species across a number of ecological contrasts (Craine & Towne, 2010): landscape position (upland and lowland), grazing by native bison (grazed and ungrazed), and burning (frequent, annual burning vs infrequent, *c.* every 20 yr). Species abundance was determined on 16 watersheds from 1994 to 2009. The fire treatments for most watersheds have been in place since 1983, except for four watersheds which had their fire treatments (annually burned and unburned) reversed in 2001. These four watersheds were classified by their current treatment. In each watershed, 40 plots for determining species abundance are divided evenly between the shallow xeric upland soils and the

mesic lowland soils. In addition to examining relationships with average abundance, relationships were also examined with the differences in log-transformed abundance between uplands and lowlands, frequently and infrequently burned, and grazed and ungrazed. The latter two metrics can be considered the species' long-term responses to fire and grazing.

Results

General patterns and differences among groups

Among the 430 herbaceous species observed in flower at Konza, the first species to flower was the annual forb *Holosteum umbellatum* on March 30. The last species to begin flowering was the perennial forb *Gentiana puberulenta* on October 5. The total range of FFDs was 189 d. Based on smoothed curves, FFDs peaked on June 14 with 0.83% of the flora (3.6 species) flowering on that day (Fig. 1a). There was a secondary peak on August 21, with 0.38% of the flora flowering, that followed an intermediate trough on August 8 (Hartigan's dip test, $P = 0.02$).

On average, species with the C_3 photosynthetic pathway flowered 33 d earlier than species with the C_4 photosynthetic pathway (June 13 \pm 2 vs July 16 \pm 6, $P < 0.001$) (Fig. 1b,c). Among the five functional groups, FFD was earliest for the C_3 Cyperaceae (mean FFD, May 10 \pm 10 d), C_3 Poaceae (May 24 \pm 8 d)

and C_3 eudicots (June 16 \pm 2 d). Although C_4 Poaceae (July 15 \pm 6 d) and C_4 eudicots (July 24 \pm 15 d) flowered, on average, distinctly later than the C_3 functional groups, there was little difference in the timing of flowering for the first or last species of C_3 and C_4 Poaceae. For example, the first C_3 Poaceae species to flower was *Poa pratensis* on April 21, whereas the first C_4 Poaceae species to flower was *Bouteloua dactyloides* on April 27, which was before all C_3 grasses except *P. pratensis*. *Tripsacum dactyloides*, another C_4 grass, also flowered early in the season, with the FFD on April 28. Conversely, C_3 Poaceae species flowered, on average, before the C_4 Poaceae species, but some C_3 Poaceae species began to flower when most C_4 Poaceae were flowering. For example, the FFDs for *Leersia virginica* and *Leersia oryzoides* were July 23 and September 9, respectively. Further reducing evidence for the role of photosynthetic pathway in timing of flowering, C_3 eudicots flowered throughout the entire growing season (see earlier discussion).

The nonnative species that have become established at Konza characteristically flower in the first half of the growing season (Fig. 1d,e). Species not native to North America flowered on average 21 d earlier than native species (May 31 \pm 5 d vs June 21 \pm 2 d, $P < 0.001$). The early average FFD for nonnative species was associated with a near absence of nonnative species flowering late in the season. Only four nonnative species flowered after August 1 (6% of the nonnative community) as opposed to

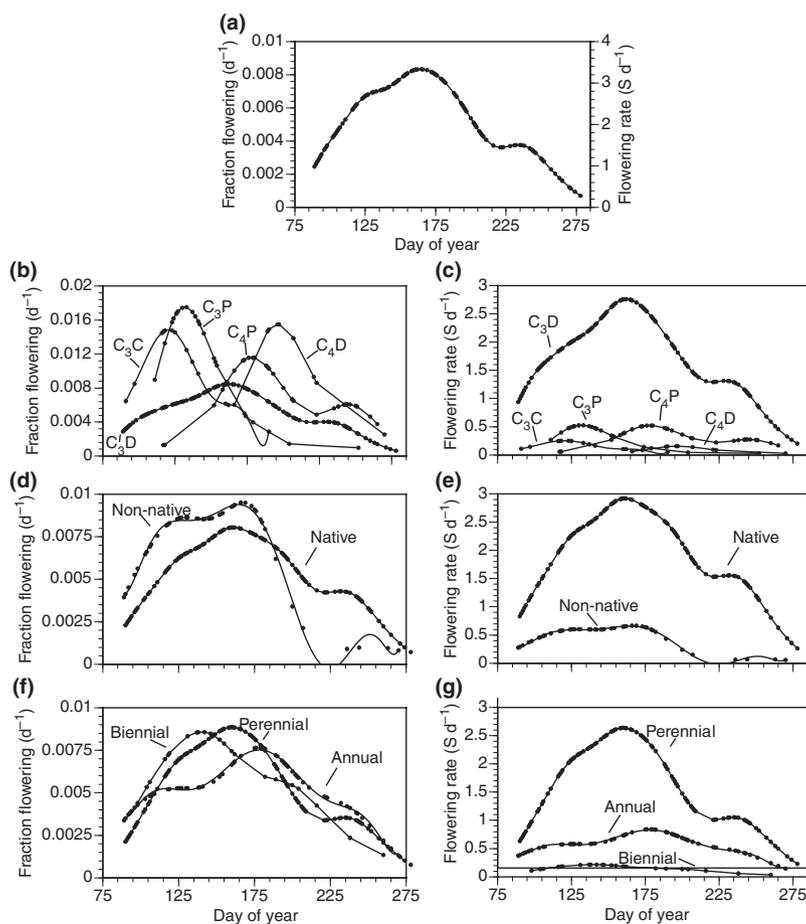


Fig. 1 (a) Patterns of first flowering dates (FFDs) for Konza herbaceous flora expressed as a fraction of all recorded species, flowering per d or number of species (S) flowering per d ($S d^{-1}$). Also shown are FFDs compared between: (b, c) functional groups (C_3 Cyperaceae, C_3 eudicots, C_4 euDicots, C_3 Poaceae, and C_4 Poaceae); (d, e) native and nonnative species; and (f, g) life history groups (annual, biennial, and perennial species).

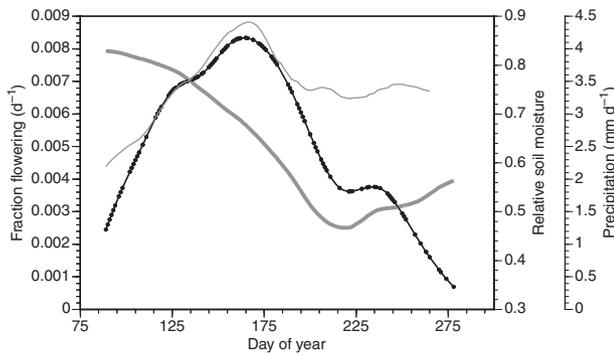


Fig. 2 Fraction of Konza flora flowering each day (black line with embedded circles). Each circle represents a day where a new species in flower was observed. Also shown are an index of soil moisture (thick gray line) and average daily precipitation (thin gray line).

73 native species (19% of the native community). Among species that flowered before August 1, 27% of the nonnative community and 18% of the native community flowered before May 1. Average flowering times among annuals, biennials, and perennial species were not significantly different ($P = 0.68$) (Fig. 1f,g). The earlier flowering of nonnative species could not be ascribed to a greater proportion of C_3 species being nonnative than native. There was no difference in the proportion of native and nonnative species that are C_3 and C_4 ($P = 0.57$).

Both peak FFDs and the early August trough in FFDs corresponded to mean climate parameters (Fig. 2). Across the years, soil moisture averaged 83% of maximum on March 30, and then declined throughout the growing season, reaching a low of 47%

of maximum soil moisture by August 7, which corresponded with the August 8 FFD trough. Peak first flowering was also coincident with peak precipitation. The mean temperature on the day the first species flowered was 9.3°C , while the mean temperature on the day the last species began flowering was 15.8°C .

Relationships with functional traits

Among the leaf traits measured on plants in the field, species that flowered later had relatively high leaf tissue density ($r^2 = 0.07$, $P < 0.001$) (Fig. 3). Based on the relationship with flowering time, the leaf tissue density of the last species flowering would be 68% greater than the first species flowering. Species that flowered later had marginally thinner leaves ($r^2 = 0.01$, $P = 0.02$), lower $[\text{N}_\text{L}]$ ($r^2 = 0.05$, $P < 0.001$), and higher $[\text{C}_\text{L}]$ ($r^2 = 0.02$, $P = 0.008$) than early-flowering species (Fig. 3). Based on these relationships, the last flowering species would be 10.9 mg N g^{-1} lower and 19.8 mg C g^{-1} higher than the first flowering species.

When flowering times were compared with ecophysiological traits measured under common conditions, FFD was not related to photosynthetic rate, stomatal conductance, physiological drought tolerance, leaf angle, root diameter, root tissue density, or root fraction ($r^2 < 0.04$, $P > 0.05$ for all). Relationships were not significant even when controlling for average differences between the two phylogenetic clades (monocots and eudicots; data not shown). Species with small seeds did not flower earlier or later than species with larger seeds. There was no relationship between log-transformed seed mass and flowering time ($P = 0.73$, $n = 335$).

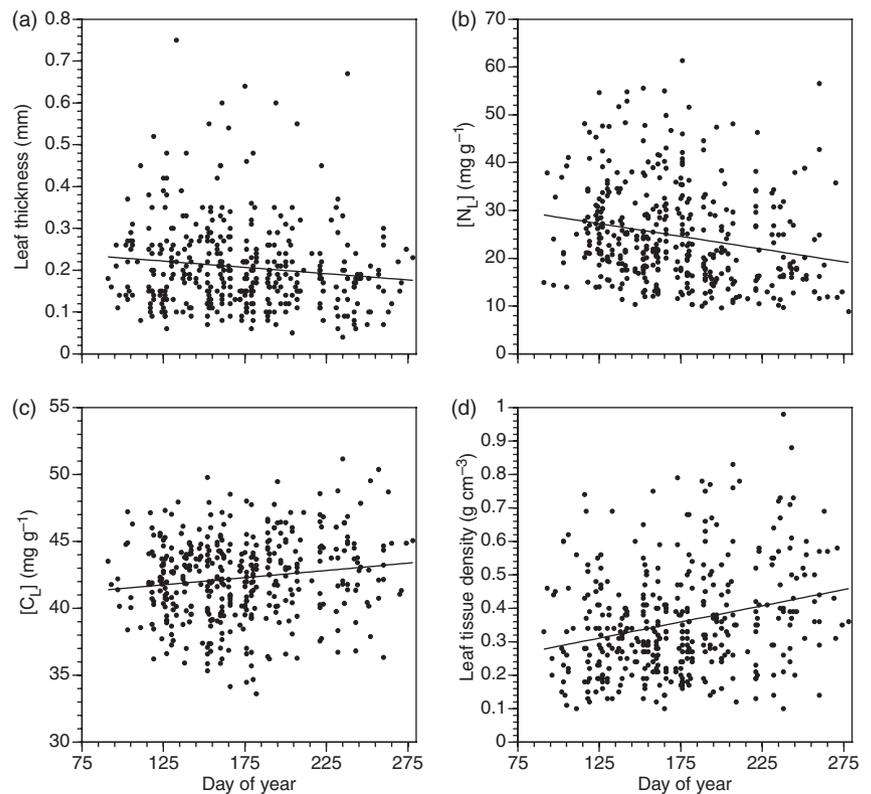


Fig. 3 Bivariate regressions between first flowering date and leaf thickness ($y = 0.26 - 0.00030x$, $r^2 = 0.01$, $P = 0.02$) (a); foliar N concentrations ($[\text{N}_\text{L}]$; $y = 33.7 - 0.052x$, $r^2 = 0.04$, $P < 0.001$, $n = 365$) (b); foliar C concentrations ($[\text{C}_\text{L}]$; $y = 40.4 + 0.011x$, $r^2 = 0.02$, $P = 0.003$, $n = 365$) (c); and leaf tissue density ($y = 0.19 + 0.00097x$, $r^2 = 0.07$, $P < 0.001$, $n = 392$) (d).

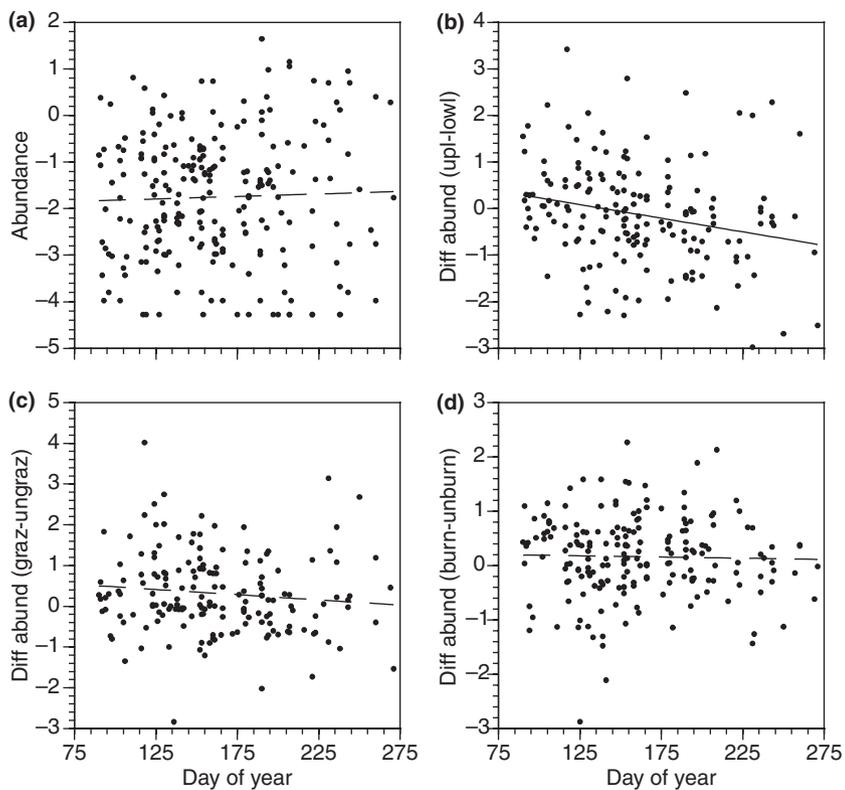


Fig. 4 (a) Relationship between log-transformed abundance and first flowering dates (FFDs). Also shown are relationships between FFDs and the difference in log-transformed abundance between uplands and lowlands ('diff abund (upl-lowl)') ($y = 0.82 - 0.0058x$, $r^2 = 0.05$, $P = 0.002$, $n = 170$) (b); grazed and ungrazed watersheds ('diff abund (graz-ungraz)') (c); and burned and unburned watersheds ('diff abund (burn-unburn)') (d). A value of 1 for differential abundance represents a species that is 10 times more abundant in uplands than in lowlands, whereas a value of -1 represents a species that is 10 times more abundant in lowlands than in uplands. Dashed lines are not significant at $P < 0.05$.

Relationships with abundance

Across all contrasts, species that flowered earlier were not more or less abundant than species that flowered later ($P = 0.08$; Fig. 4a). Species that were more abundant in uplands did not flower earlier or later than species that were less abundant in uplands ($P = 0.71$). Likewise, species that were more abundant in lowlands did not flower earlier or later than species that were less abundant in lowlands ($P = 0.19$). Yet for species found in both uplands and lowlands, those that were differentially more abundant in uplands than in lowlands flowered earlier than those that were more abundant in lowlands than in uplands ($r^2 = 0.05$, $P = 0.004$, $n = 168$; Fig. 4b). Based on the relationship between FFD and the differential abundance of species in uplands and lowlands, for every 52 d earlier that a species flowered, it was two times more abundant in uplands than in lowlands. Part of the reason that the difference in abundance between uplands and lowlands was significant but the relationships with abundance were not significant was that species found in lowlands but not in uplands tended to flower later in the growing season and were found at low abundance. When these species were excluded from analyses, species that flowered later were significantly more abundant in the lowlands than species that flowered earlier ($r^2 = 0.05$, $P = 0.002$, $n = 170$). There was still no relationship between flowering time and abundance in the uplands when including only species found in both uplands and lowlands.

Species' flowering phenology was not associated with the species' responses in abundance to grazing or burning. Species that were more abundant in grazed watersheds did not begin flowering earlier or later than species that were less abundant in grazed

watersheds, and the same was true for their abundance in ungrazed watersheds ($P > 0.1$ for both). Likewise, species that increased in abundance with grazing did not flower earlier or later than species that declined with grazing (Fig. 4c, $P = 0.16$). Flowering phenology was not associated with the relative abundance of species in frequently burned ($P = 0.15$) or infrequently burned regions ($P = 0.39$), or with species' response to burning (Fig. 4d; $P = 0.73$).

Discussion

Environmental stress and climatic constraints on flowering

Understanding the role of plant phenology in structuring plant types and communities has long been an active research focus (Parrish & Bazzaz, 1979; Ollerton & Lack, 1992; Parmesan & Yohe, 2003; Menzel *et al.*, 2006), but this has resulted in little consensus about its role in ecological communities. Climate shapes Konza flowering patterns both by setting the seasonal bounds for flowering and by shifting stressors during the growing season. Low temperatures that define the start and end of the growing season place fundamental limits on the period of plant flowering in many temperate systems (Larcher, 2003; Schwartz, 2003; Inouye, 2008).

Although the community flowering curve of Konza may be characterized as a neutral model with multiple bounds throughout the growing season, more parsimoniously, flowering phenology is an important mechanism to avoid environmental stress within the growing season, which structures plant assemblages and diversity patterns across Konza's grassland habitats. Although

the hump-shaped seasonal pattern of community flowering broadly fits a bounded neutral model such as the mid-domain (Morales *et al.*, 2005), the flowering patterns are as parsimoniously, if not more so, explained by species flowering tracking patterns of within-season environmental stress. Further evidence supporting community-level flowering being nonneutral at Konza is the late-season trough in flowering that corresponds to a seasonal maximum in soil moisture stress. Although specific patterns in soil moisture vary across years, the long-term effects of repeated drying during this period would likely select against species that begin flowering during a period of typically high environmental stress. The species that do begin flowering during this period are a mix, including many species that are likely to occupy sites that would be least impacted by drought or have other strategies to avoid it. For example, many of the species that first begin to flower during this period are summer annuals, for example, *Ambrosia artemisiifolia*, and would occupy disturbed sites where competition for water might be low, even in a dry year. Other species that flower during this period, such as *Lobelia cardinalis*, *Lobelia siphilitica*, and *Amaranthus tuberculatus*, are considered wetland species. Still others such as *Desmodium sessilifolium* and *Helianthus maximiliani* are deeply rooted and would be able to tap deeper soil water (Weaver, 1968).

Resource strategies and functional groups

Flowering time is expected to be a highly important niche trait (Donohue, 2005; Fargione & Tilman, 2005; Godoy *et al.*, 2009; Johnson, 2010). Yet, we found relatively few links between most functional traits and flowering time. If water and nutrient availability decline as the growing season progresses, flowering phenology has the potential to covary with functional traits that are associated with resource availability. Along these lines, Konza species that flowered later in the growing season had higher leaf tissue density. Leaf tissue density has been shown to be associated with species that perform well when nutrients are limiting (Craine *et al.*, 2001) as well as species that are physiologically tolerant of drought (Tucker *et al.*, 2011). As such, it is possible that as the season progresses, nutrient and water availability decline such that late-flowering species would benefit from having high leaf tissue density.

Although soil moisture declines at Konza as the growing season progresses and species water-use efficiency has been shown to increase over time as soils dry out in other ecosystems (Smedley *et al.*, 1991), there was no relationship between FFDs and physiological drought tolerance. Examining patterns of carbon isotopes in leaves, late-flowering species at Konza actually showed lower, not higher, water-use efficiency than early-flowering species (Supporting Information Fig. S3). This is unlikely to be the result of increasing water availability for a given location over this time, but instead likely represents late-flowering species occupying wetter sites on average. As such, there was no support for the idea that the high leaf tissue density of late-flowering species was associated with an increased ability to endure water stress. If water stress was not driving the increase in leaf tissue density over time, then it is likely that declining nutrient availability might

underlie it. Although we did not see a decline in foliar $\delta^{15}\text{N}$ (Fig. S3) that would suggest lower N availability later in the season (Craine *et al.*, 2009), foliar N concentrations of late-flowering species were lower, consistent with the general decline in N concentrations over time seen for individual species (Rao *et al.*, 1973) and the seasonal decline in soil N mineralization and soil respiration previously observed (Turner *et al.*, 1997; Johnson & Matchett, 2001). With few linkages between flowering phenology and functional traits, more research is necessary to understand the linkages that are present and to search for other functional traits that might be associated with flowering phenology.

Outside of the associations with resource-related traits, most other traits studied were orthogonal to flowering. Flowering timing was distributed relatively evenly across species with different flower colors (Fig. S1). Annuals did not necessarily flower earlier or later than perennials, most likely because of the presence of both winter and summer annuals at Konza (Towne, 2002). Furthermore, although C_3 grasses on average flowered earlier than C_4 grasses, photosynthetic pathway was not diagnostic for flowering time. C_4 grasses such as *B. dactyloides* and *T. dactyloides* flowered before almost all of the C_3 grasses, while there were C_3 grasses and C_3 eudicots that flowered after most C_4 grasses had begun flowering. Thus, while the generality of early-flowering C_3 and late-flowering C_4 grass species was maintained on average, both groups had species that suggested phenological divergence from the general trend might be common. Similarly, while there was nonrandom phylogenetic signal in flowering time (Fig. S2), and some taxa exhibited characteristic seasonal patterns of flowering, there was a great deal of variation in flowering time within broader clades (Wilczek *et al.*, 2009, 2010).

Taken together, our results suggest that flowering phenology does not fit into a general resource strategy in any direct way. Previous work suggests important functional traits should covary with flowering time (Golluscio & Sala, 1993; Thuiller *et al.*, 2004); however, others have suggested phenology as a plant trait may be often neutral (Ollerton & Lack, 1992) and thus correlations with resource use or related traits may be rare, as has been found in other recent analyses (Willis *et al.*, 2010) where correlations with a variety of traits were uncommon. Overall, general direct tests such as those presented here are sorely needed across a broader array of species and regions before a general framework can emerge.

Spatial and temporal patterns of abundance

Increasingly, researchers have speculated about (Augsburger, 2009; Crimmins *et al.*, 2010) and sometimes documented (Chapin *et al.*, 1995; Inouye, 2008; Willis *et al.*, 2010) how shifts in phenology may be associated with changes in abundance. However, we found no simple links between flowering time and abundance. Community flowering appeared to vary strongly with environmental stress, for example, low temperatures or low soil moisture. Yet, species that flowered during periods of higher soil moisture stress were as abundant as those that flowered at other times. Further, flowering during the peaks of community-wide

flowering, or later in the season when plant biomass is highest (Schimel *et al.*, 1991), did not correspond to species' abundance.

Furthermore, we found no relationship between disturbance – via either grazing or fire – and flowering phenology. Management regimes in some systems can alter community-level phenology via selection pressure (Ollerton & Lack, 1992), accelerating, for example, the flowering of species in habitats with consistent late-season cutting regimes (Lack, 1982). In Konza, however, flowering dates were equally variable across species more abundant in grazed or burned plots vs control plots. The lack of linkage between species' flowering phenology and abundance response to grazing – which is continuous throughout the year – might not be as surprising as the lack of effect for the seasonally constrained fires. Most burning occurs in March–April, as many species begin flowering. However, species with flowering times during this period do not tend to be less abundant in burned areas – suggesting that the co-occurrence of flowering and disturbance does not penalize overall abundance, at least in the presence of grazers. This could suggest that flowering time is an effectively neutral trait for these species (Ollerton & Lack, 1992) or effects may be more nuanced. For example, early-season species tend to have higher variability in their FFDs across space and time (Menzel *et al.*, 2006), and therefore early-season species at Konza may vary their flowering between burned and unburned areas, delaying flowering in burned areas. Understanding the full effects of fire on phenology would thus require landscape-level studies focused on intraspecific variation in flowering.

First flowering time was, however, associated with the topographical patterning of abundance on the landscape. Konza is characterized by a heterogeneous landscape of cooler, moister lowland sites and hotter, drier upland sites (Nippert *et al.*, 2011). Many species show differential abundance between these two dominant microhabitats. Species with higher abundance on upland sites tended to flower earlier than those more common on lowland sites. Such an effect could be driven by climatic differences: species that do best on upland sites are those adapted to flower before upland sites rapidly dry out, while, conversely, lowland species may flower slightly later as a result of cooler lowland temperatures. Thus, within Konza, the interaction of flowering time and abundance suggests small, topographic differences in climate play a role in the spatial patterning of the plant community.

Predicting future community composition

Based on how closely Konza community flowering tracked temperature and soil moisture, informed predictions about how future climate change may alter community temporal patterning are possible. In Konza, where regional climate models consistently predict warmer future temperatures along with a more variable precipitation regime (Christensen *et al.*, 2007), a series of growing-season shifts may alter flowering. First, as found with many floras globally, early-season species may shift earlier as thermal sums required to trigger flowering are met earlier. Alongside this, species invasions from donor floras may increase (Wolkovich & Cleland, 2010) as the Konza season expands to increase overlap in phenological climatic space with other regions.

Additionally, if the mid-growing season drought becomes more pronounced, this might reduce the number of species flowering during the early-August trough in flowering. Evidence of a such a shift towards a novel midseason gap (or decrease) in flowering has already been suggested in other floras observationally (Aldridge *et al.*, 2011) and via experiments (Sherry *et al.*, 2007).

That said, our approach did not quantify intraspecific variation in flowering in response to changes in environmental factors. Better predictive capacity will require an approach that scales from intraspecific to community levels and contrasts patterns across a landscape for each species. A plant's phenology also extends beyond the timing of first flowering to include peak flowering and other reproductive events, as well as vegetative flowering such as the phenology of leaf production and stem elongation. At this point, more research is necessary to understand how coordinated the different phenological components of plant growth are across species, which may aid in understanding broader plant strategies and patterns of plant performance (Wilsey *et al.*, 2011).

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Patterns of first flowering dates for Konza herbaceous flora partitioned by flowering color and expressed as a fraction of all recorded species flowering per d or number of species flowering per d.

Fig. S2 Phylogenetic distribution of first flowering dates (FFDs) for angiosperm species at Konza.

Fig. S3 Relationships between first flowering dates and foliar carbon and nitrogen isotope ratios.

Table S1 Species sampled in the study along with their functional group, whether the species are native or not, and their photosynthetic pathway

Notes S1 Results and details on methods of analysis for the relationships between flowering phenology and species geographic climate envelopes, flowering color, phylogenetic patterns, and foliar C and N isotope ratios.

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