Understanding past, and predicting future, niche transitions based on grass flowering time variation

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One-sentence summary
Major grass clades show strong conservation in how their flowering time is controlled, despite apparently low evolutionary constraints at the genetic level, and a dearth of data for tropical taxa
ABSTRACT
Since their origin in the early Cretaceous, grasses have diversified across every continent on Earth, with a handful of species—rice (Oryza sativa), maize (Zea mays), and wheat (Triticum aestivum)—providing most of the caloric intake of contemporary humans and their livestock. The ecological dominance of grasses can be attributed to a number of physiological innovations, many of which contributed to shifts from closed to open habitats that incur daily (e.g. tropical mountains) and/or seasonal extremes in temperature (e.g. temperate/continental regions) and precipitation (e.g. tropical savannas). In addition to strategies that allow them to tolerate or resist periodically stressful environments, plants can adopt escape behaviors by modifying the relative timing of distinct development phases. Flowering time is one of these behaviors that can also act as a post-zygotic barrier to reproduction and allow temporal partitioning of resources to promote coexistence. In this review, we explore what is known about the phylogenetic pattern of flowering control in grasses, and how this relates to broad- and fine-scale niche transitions within the family. We then synthesize recent findings on the genetic basis of flowering time evolution as a way to begin deciphering why certain aspects of flowering are seemingly so conserved, and what the implications of this are for future adaptation under climate change.

INTRODUCTION
The timing of reproductive development is a critical component of individual plant fitness and is shaped by a combination of environmental signaling pathways that converge at the growing tip (shoot apical meristem; SAM). Internal signals tell the plant about its health, energy resources (e.g. stored carbohydrates), and ability to secure further resources (e.g. leaf area and height); whereas external factors (e.g. temperature, daylength, and water availability) signal existing or upcoming growing conditions for both the plant and its interacting community (e.g. pollinators and pathogens). In both cases, these cues determine whether, when, and how quickly the plant allocates resources to flower production, so the plant survives long enough to produce abundant viable lifetime seed. From a human perspective, flowering time has major consequences for crop production, both in terms of vegetative biomass in the case of vegetables, and inflorescence biomass primarily in the case of grains, fruits, and seeds. The majority of human calories come
from just three species—rice (*Oryza sativa*), bread wheat (*Triticum aestivum*), and maize (*Zea mays ssp. mays*)—all of which are members of the grass family (Poaceae) (Alexandratos and Bruinsma, 2012). In addition to crops and forage grasses that extend beyond these three cereals, the vegetative parts of grasses provide excellent building materials [e.g. bamboo (Bambusoideae spp.)] and reactants for biofuel [e.g. maize and switchgrass (*Panicum virgatum*)]. The fact that grasses cover around 26% of ice-free global land area and have high average root biomass also means they compete with trees as major sequesters of organic carbon, particularly in arid environments (Dass et al., 2018; Lorenz and Lal, 2018).

To meet the needs of a predicted population increase of around two billion by 2050 (UN DESA, 2019), one part of the solution will be to engineer ways to augment the yields of current and/or novel crops as well as to maintain the health of grasslands. A potential caveat to this is the fact that, concomitant with population growth, the global climate is becoming warmer with the expectation of longer and more severe weather events, such as droughts, monsoons, heatwaves, and frigid temperatures (Ummenhofer and Meehl, 2017). Since extreme weather events will affect plant growth and development both directly, based on innate stress tolerance, and indirectly, through variation in the reliability of cues for phenological shifts such as flowering, it is of increasing importance that we understand the extent to which plants are pre-adapted to these novel climates and/or how quickly they can adapt. Evidence so far suggests that grass niche divergence in the past was, on average, less than predicted by future short-term climate change scenarios if populations are to stay in place (Cang et al., 2016). However, these trends *per se* do not negate the possibility that grass populations, species, and perhaps whole clades are capable of responding plastically or adaptively to non-analogous conditions (Humphreys and Linder, 2013).

Although there are several excellent reviews of flowering time control focused on a few model plant species (e.g. Song et al., 2016; Bouché et al., 2017; Cho et al., 2017), here we synthesize recent insights into the evolutionary history of flowering time within the grass family as whole. In doing so, we aim to (1) determine the importance of flowering time evolution in explaining current patterns of niche differentiation in grasses, (2) predict the ability of grass species to evolve phenologically in the future, (3) highlight new discoveries of genetic pathways that can be manipulated to affect better and more reliable yields in diverse and changing climates, and (4) identify avenues worthy of future research.
HISTORICAL PATTERNS OF GRASS NICHE DIFFERENTIATION

Grasses first evolved as understory forest herbs (Kellogg, 2001; Osborne and Freckleton, 2009; Bouchenak-Khelladi et al., 2010) during the mid-Cretaceous an estimated 105–125 million years ago (MYA) (Strömberg, 2011; Gallaher et al., 2019; Schubert et al., 2019). Evidence suggests that the early grass habitats were in the common Gondwanan landmass of South America and Africa (Bouchenak-Khelladi et al., 2010; Strömberg, 2011) at a time when the continent was largely dominated by tropical forests (Chaboureau et al., 2014). Although mostly aseasonal in temperature, the Cretaceous climate would have had marked wet and dry seasons (Ghosh et al., 2018), similar to the tropical savannas of today (Furley, 1999). Around 71–97 MYA, the grasses diversified into two main clades, namely BOP (Bambuosideae-Oryzoideae-Pooideae) and PACMAD (Panicoideae-Aruninoideae-Chloridoideae-Micrairoideae-Aristidoideae-Danthoniodieae), that comprise the bulk of the current 12,000 species (Prasad et al., 2005; GPWG II, 2012; Schubert et al., 2019) (Fig. 1). Soon after, ancestors of Pooideae and the PACMAD clades moved independently into more open habitats, leaving the Bambusoideae and Oryzoideae predominantly under closed forest canopy and at transitional forest margins (Bouchenak-Khelladi et al., 2010; Gallaher et al., 2019).

The transition from closed to open habitats in grasses was followed by the first evolutionary origins of C4 photosynthesis, starting with the ancestor of Chloridoideae around 55 MYA (Gallaher et al., 2019). As global temperatures peaked at the beginning of the Eocene (~55 MYA) (Zachos et al., 2001; Archibald et al., 2010; Mudelsee et al., 2014), fossils indicate that grasses were rare but widespread (Strömberg, 2011). As the Eocene came to a close around 35–40 MYA, a gradual cooling trend troughed abruptly, bringing with it more pronounced temperature seasonality, as well as increased differences in mean annual temperature from the equator to the poles (Zachos et al., 2001; Potts and Behrensmeyer 1992; Eldrett et al., 2009; Archibald et al., 2010). Aridification of both tropical and temperate regions was soon to follow (Quade and Cerline, 1995), probably leading to further origins of C4 photosynthesis in PACMAD grasses as a mechanism to increase water-use efficiency (Edwards and Smith, 2010; Zhou et al., 2018), and allowing the emergence of novel ‘grassland’ biomes in the mid-to-late
Most members of the PACMAD clade continued diversifying in lowland tropical and subtropical regions of the globe during the Oligocene. However, expansion of temperate and continental biomes (Pound and Salzmann, 2017; Beck et al., 2018) created ecological opportunities for several temperate-adapted lineages (Near et al., 2012; Kerhoff et al., 2014; Favre et al., 2016; Meseguer et al., 2018), including Pooideae, the ancestor of which is hypothesized to have arisen in cold micro-niches during part of the Eurasian orogeny (Schubert et al., 2019). A similar trend was also to occur in temperate regions of the southern hemisphere for the PACMAD subfamily Danthonioideae (Linder et al., 2010; Humphreys and Linder, 2013). During interglacial periods of global warming, lower-latitude cool-season grasses likely took refuge in tropical montane areas of the South American Andes, Ethiopian and Tibetan Plateaus, and Eurasian Alps. Based on this biogeographic history, a strong phylogenetic signal of niche partitioning is evident today, with Pooideae and Danthonioideae grasses dominating microthermal (continental) and mesothermal (temperate and cold desert) areas that have monthly average temperatures of 0–18°C in winter to >10°C in summer and 0°C in winter to >10°C in summer, respectively; and non-Danthonioideae PACMAD grasses dominating megathermal [tropical lowland (< 1500 m) and hot desert] forests and savannas characterized by monthly average temperatures > 18°C (Geiger, 1954; Burkart, 1975; Beck et al., 2018) (Fig. 2D).

ECOLOGICAL SORTING AND FLOWERING TIME

Tropical lowlands versus tropical highland and temperate/continental regions

As a result of both historical and ongoing processes, current grass distributions span all continents, and encompass a range of habitats that vary along several climate axes (Fig. 2). According to the climate zones of Köppen, alluded to above (Geiger, 1954; Beck et al., 2018), these include tropical lowland, dry desert and semi-arid, temperate, continental, and polar (<10°C each month) climates; as well as lowland (> 1500 m) tropical regions (Burkart, 1975). Whereas temperature is thought to be the main factor limiting plant growth and reproductive
output in mesothermal, microthermal, and polar climates (Fig. 2A,B), seed set and growth in the
tropics are strongly influenced by light (e.g. in tropical forests) and hydric conditions (e.g. in
tropical savannas) (Ma et al., 2013) (Fig. 2A,C). In some cases, optimal conditions for flowering,
such as high accumulated heat units, light intensity, and water availability, are also the cues that
prompt development of inflorescences, flowers, and fruits. In others, different stages of
reproductive development are triggered by sub-optimal conditions, such as drought, low
temperatures, and/or short days, as a way to preempt the impending growing season (Cho et al.,
2017). For example, whereas long-day taxa flower only when photoperiod exceeds a specific
critical threshold, short-day taxa flower when photoperiod is below a critical threshold (Itoh et
al., 2010; Brambilla et al., 2017). Although the latter conditions result in fewer daily light units
for growth, in some climates (e.g. lowland subtropics) they correlate with the rainy season, thus
providing a cue to avoid drought conditions that occur when daylength is relatively long (Weller
et al., 2019) (Fig. 2C).

The most diverse grass ecosystems in lowland tropical regions are the tropical savannas that can
be classified into two main types: hyperseasonal (monsoon) and seasonal (Sarmiento, 1983). In
some hyperseasonal climates, water-logging of soil during the monsoon can cause root hypoxia
such that the growing season commences primarily in the dry season after the winter solstice, as
the days are getting longer. However, in most tropical savannas, vegetative growth or ‘green-up’
is coincident with the long rainy season of the spring, summer, and early autumn (Sarmiento,
1983; Parihar and Pathak, 2006; Higgins et al., 2011; Ma et al., 2013; Pei et al., 2015) (Fig.
2A,C). Although green-up and flowering tend to be continuous for tropical savanna grasses
throughout the rainy season, evidence suggests that communities are composed of mixed guilds
that flower at the beginning, middle, and end of the season, presumably as a mechanism to
reduce competition for resources (Sarmiento, 1983). Nonetheless, several studies have shown a
peak in grass flowering after the summer solstice when the days are getting shorter (Sarmiento,
1983; Pei et al., 2015). The fact that inter-annual variation in the onset and duration of the rainy
season can have major consequences for the timing of green-up, and hence flowering, suggests
that precipitation is a key determinant of flowering time in tropical ecosystems, albeit indirectly
through its effect on vegetative growth (Ma et al., 2013). However, the exact date of
reproduction during the long growing season is likely also shaped directly through precipitation-
and/or photoperiod-responsive flowering genetic pathways. In the latter case, the aforementioned pattern of increased flowering during the shortening of daylengths predicts that the majority of tropical savanna grasses will be short-day responsive (see later section); this generally fits with the phylogenetic pattern of short-day responsive grasses primarily in the PACMAD clade (Tothill, 1977).

In contrast to the tropical lowlands, mesothermal, microthermal, and polar biomes above 30–40° in latitude are currently dominated by members of grass subfamily Pooideae, particularly in the northern hemisphere (Hartley, 1973; Livingstone and Clayton, 1980; Sage, 1999; Bremond et al., 2008) (Fig. 2D). These grasses face a range of relatively short growing seasons edged by low-to-freezing temperatures, such that inductive signals for flower production are predominantly cold, short days that mark the non-growing season and warm, long days that mark the growing season (Fig. 2B). Furthermore, many ancestrally temperate/continental Pooideae lineages have either migrated or diversified into tropical montane habitats, such as in the South American páramos where 49% of grasses are of mesothermic or microthermic origin (van der Hammen and Cleef, 1986; Ricardi et al., 1997; Marquez, 2004). The resulting biogeographic pattern of migration from mesothermic/microthermic regions to tropical highlands—an example of ecological sorting—is often interpreted as being due to the ancestral cold hardiness of dominant highland taxa (Engler, 1904), including genera such as Agrostis, Bromus, Calamagrostis/Deyeuxia, and Festuca (Saarela et al., 2017). What is less well understood is whether cues (i.e. temperature and photoperiod) commonly used in mesothermic, microthermic, and polar regions to avoid winter flowering, but facilitate rapid spring flowering, similarly helped in the transition to tropical alpine zones by matching the reproductive transition with favorable conditions.

In terms of temperature, although páramos are notorious for daily fluctuations ranging from –7°C to 30°C, this variation also changes seasonally, with lower night and higher day temperatures occurring during the relatively cloud-free dry season from November to March and April to October north and south of the equator, respectively (Luteyn, 1999) (Fig. 2C). Thus, cues such as freeze-thaw cycles or hours below freezing could potentially discriminate between dry and wet seasons. Similarly, if ancestral populations from mesothermic and microthermic regions are primarily long-day flowering (see later section), this predicts peaks of flowering...
between the winter and summer solstices in related tropical highland species. Potentially at odds
with the long-day flowering hypothesis are studies showing abundant Pooidae grass flowering
after the summer solstice in the Venezuelan páramo (Marquez, 2004). However, other studies
have documented flowering of similar Venezuelan species before the summer solstice (Smith
and Klinger, 1985) or a general lack of grass flowering between May to August in highland
Ecuador (Matson and Bart, 2014). Explicit tests based on rigorous flowering counts and
controlled experiments will be needed to test both the temperature- and daylength-based
flowering hypotheses for highland tropical grasses.

Niche partitioning and phylogenetic signal for flowering behaviors within transitional
zones

Relatives of species from megathermal and mesothermal/microthermal zones often coexist in
seasonally dry and humid mesothermal regions, suggesting that the latter climates might be very
active areas for ecological transitions, similar to altitudinal gradients in tropical mountain C4 to
C3 grasses (Cabido et al., 2003). For example, in the pampas of South America (Burkart, 1975)
and parts of the Tibetan Plateau in central Asia (Chang, 1981), BOP and PACMAD grasses are
present in almost equal share. In both regions, Pooidae (e.g. Poa, Calamagrostis, Bromus, and
Achnatherum sp.) tend to flower as the days lengthen in spring/early summer, whereas remaining
taxa (e.g. Panicum, Setaria, and Eragrostis) reproduce as the days shorten in late summer/early
autumn (Burkart, 1975; Miller 1990). Part of this pattern might be explained by the ability of
ancestrally mesothermic/microthermic species to continue vegetative growth over mild winters,
such that they are ready to flower quickly as temperatures increase. On the other hand, it is likely
that physiological variation in photoperiodic and temperature responses will interact with
internal cues to precisely define the timing of reproduction. Prairies of midwestern USA show
similar partitioning of flowering time between cool-season Pooidae and warm-season
PACMAD grasses. Many cool-season prairie grasses (e.g. Agropyron smithii and Bromus
japonicus) are known to flower more rapidly under long- versus short-day conditions, and vice
versa for warm-season (e.g. Panicum virgatum and Andropogon furcatus) taxa (Benedict, 1940;
Sherry et al., 2007).
Based on available data, it is clear that history, as assessed by phylogenetic signal, has a major role in shaping the contemporary niche space of grasses, with Pooideae dominating cool, open habitats; Bambusoideae dominating forest habitats; and PACMAD dominating warm, open habitats. Furthermore, the fact that grasses within the Pooideae or PACMAD clades display similar flowering times in relation to moisture, daylength, and/or temperature suggests strong conservation of flowering time control that might be linked to past and ongoing ecological sorting. In the remaining sections, we explore whether these broadly conserved patterns are due, at least in part, to constraints on the evolution of flowering-time pathways by comparing the physiological and genetic basis of the reproductive transition across phylogenetically representative taxa. We also investigate evidence for the evolution of flowering-time behaviors correlated with finer-scale niche shifts, i.e. within the two major grass BOP and PACMAD clades.

FLOWERING TIME RESULTS FROM A SERIES OF DEVELOPMENTAL EVENTS

In order to understand factors that control the timing of plant flowering (next sections), it is important to first recognize that flowering time is contingent on several physiological phase transitions. Each of these transitions defines a narrowing path of development, ending in the production of determinate floral meristems. Similar to angiosperms as a whole, grasses are in the so-called juvenile phase of development immediately following germination, at which time they are usually unable to respond to signals that would normally induce flowering (Yang et al. 2011). Although the juvenile phase can vary considerably in length, even between populations of the same species (Heide et al., 1994; Foerster et al., 2015), it is often marked by specific morphological features, such as waxy glabrous leaves in the Panicoideae species maize (Orkwiszewski and Poethig, 2000; Lauter et al., 2005).

Juvenility requires the expression of genes that simultaneously promote juvenile features (e.g. APETALA2 (AP2)-like genes such as maize glossy15) and suppress adult features. Suppression of the adult phase is largely, but not exclusively, defined by the expression of a functionally conserved microRNA, miR156, that represses several members of the SQUAMOSA PROMOTER
BINDING PROTEIN LIKE (SPL) transcription factors, whose protein-product targets are floral induction genes such as FRUITFULL (FUL) and LEAFY/FLORICAULA (Chuck et al., 2007; Curaba et al., 2013; Wang et al., 2015; Hibara et al., 2016). The transition to adult growth is then marked by an age-dependent reduction of miR156 and a concomitant increase in miR172, partly induced by SPL genes when the SPLs are de-repressed (Tripathi et al. 2018). Similar to the repression of SPLs by miR156, miR172 transcriptionally degrades several juvenile-phase AP2 genes, whereas SPL proteins act to reduce vegetative branching and promote the expression of inflorescence meristem identity genes (Wang et al., 2015). In some taxa, the action of SPL genes might be sufficient to cause an immediate shift to inflorescence development. In others, however, adult-phase plants will be physiologically competent to enter the reproductive phase, but will require further permissive signals to do so (An et al., 2015). A major field of research is to understand how environmental signals interplay with the miR156/AP2 and miR172/SPL regulons to determine timing of the juvenile-to-adult and vegetative-to-reproductive phase transitions; and to assess the implications of this timing on green-up (perennials only), biomass, and yield, the latter particularly in crop species.

CONSTRAINTS ON GRASS FLOWERING TIME EVOLUTION FROM A DEVELOPMENTAL GENETIC PERSPECTIVE

Many of the genes known to be involved in grass flowering time are part of a more ancient genetic network that has been evolving since the origin of land plants (Brambilla et al., 2017). The extent to which genes have been coopted for novel flowering-time functions is complicated by the tendency of traits to evolve convergently in response to similar environmental conditions, skewed taxonomic sampling, and mistaken orthology that often occurs following reciprocal loss of homeologs/paralogs generated after segmental or whole genome duplications (WGDs). In the case of grasses, the rho WGD that occurred prior to their diversification (McKain et al., 2016) led to a doubling of the genome, possibly increasing the family’s adaptive potential in the face of novel environmental stress (Van der Peer et al., 2017). However, Schnable et al. (2012) found little evidence for rampant reciprocal paralog loss that, in combination with extensive conservation of gene content and collinearity (Bennetzen and Freeling, 1997), simplifies to a certain extent comparative genomic and functional analyses within the group. Nonetheless, it is
important to bear in mind that the aforementioned caveats can potentially cloud inferences of the
direction, tempo, number of origins, and underlying mechanisms for niche/flowering trait
transitions, laid out in the following sections.

Highs and lows of temperature-induced flowering

As outlined in previous sections, it has long been recognized that environmental temperature
shapes plant physiology, collectively via its impact on growth rate, survival, phenology, and
reproductive output (Bykova et al., 2012). Generally speaking, whereas most plants grow well
between 18–28°C, relatively low and high temperatures can be physically (e.g. due to ice crystal
formation) and/or biochemically (e.g. due to enzyme denaturation) prohibitive to growth and
reproduction, such that they place strong selective pressures on populations to either migrate or
adapt, the latter by evolving avoidance and/or tolerance strategies (Preston and Sandve, 2013;
Fjellheim et al., 2014; Lohani et al., 2019). Although perhaps not as reliable as photoperiodic
cues (see next section), annual shifts in both day and night temperatures are used by many
temperate plants to predict favorable and unfavorable seasons for flowering and seed set. In the
Poaceae grasses, for example, many taxa gain floral competency earlier with an extended period
of above freezing cold (vernalization) (Ream et al., 2012). By being responsive to vernalization
and having an epigenetic ‘memory’ of cold exposure (He and Li, 2018), individuals can avoid
the detrimental effects of precocious flowering on the occasional warm winter day, but will be
readied for rapid flowering in the spring. The latter can be particularly valuable when the
-growing season is short. On the other hand, climatic fluctuations resulting in shorter or warmer
winters can cause delayed spring flowering if vernalization is not saturating, possibly rendering
vernalization responsiveness maladaptive. Such late flowering has already been observed for
some species within the Anthropocene across Europe and the Tibetan Plateau (Menzel, 2006; Yu
et al., 2010). For tropical highland plants, there are data to support pre-adaptation to low night
temperatures based on the cold hardiness of ancestral lineages (e.g. Prentice et al., 1992). A
lesser explored question is whether such tropical highland taxa can detect and use subtle
variations in seasonal montane temperatures to attain floral competency, similar to their
temperate/continental ancestors.
In the temperate Pooideae crops wheat and barley (*Hordeum vulgare*), vernalization-mediated flowering involves a simple feedforward mechanism comprising both repressors and promoters of the reproductive transition (Fig. 3). Prior to cold exposure, the CCT domain–family protein VERNALIZATION 2 (VRN2) localizes throughout the aboveground tissues to repress transcription of VRN3/FT-like2 (FTL2), and hence block flowering (Yan et al., 2006). With the onset of cold, epigenetic changes at the VRN1/FUL1 locus gradually causes its upregulation (Oliver et al., 2013; Huan et al., 2018). Once it crosses a particular transcriptional threshold, the protein product of VRN1/FUL1 acts to repress the VRN2 floral repressor, resulting in floral competency, and then activates VRN3/FTL2 for flowering once conditions become inductive (Yan et al., 2006). Interestingly, VRN1/FUL1 is upregulated by cold in vernalization-responsive taxa across Pooideae (McKeown et al., 2016; Zhong et al., 2018). Together with ancestral trait reconstructions, this suggests that vernalization responsiveness had a single origin in this subfamily, evolving at or around its base (McKeown et al., 2016). By contrast, VRN2 and at least a couple of other known cold-responsive floral repressors in wheat/barley only appear to be involved in the vernalization pathway in core Pooideae (Woods, McKeown et al., 2016; Woods et al. 2017; Zhong et al., 2018) (Fig. 3). These data collectively suggest two alternative hypotheses: either vernalization responsiveness in or beyond the Pooideae evolved once, followed by developmental drift of some of the underlying genes; or it evolved multiple times through the independent (parallel) recruitment of VRN1/FUL1 and a handful of lineage-specific floral repressors. Functional analysis of VRN1/FUL1 genes and their paralogs from vernalization-responsive grass species outside Pooideae will be useful to distinguish between these two hypotheses, particularly since VRN1/FUL1 homologs are not part of the vernalization pathway in more distantly-related species such as *Beta vulgaris* (Amaranthaceae) and *Arabidopsis thaliana* (Preston and Sandve, 2013). It will also be useful to follow-up on cold-responsive candidate genes that are coexpressed with VRN1/FUL1 across vernalization-responsive Pooideae (Zhong et al., 2018) to determine if they function in flowering time or other aspects of cold adaptation.

Despite uncertainty about the number of times FUL-like genes have been recruited to vernalization-mediated floral competency in grasses, the fact that the VRN1-targeted repressor of flowering is different across Pooideae might suggest only moderate constraint on the ability of
this trait to evolve. From the opposite perspective, the apparent multiple losses of, or reduced
requirement for, vernalization responsiveness under both artificial (Zhang et al., 2012; Ergon et
al., 2016; Nishiura et al., 2018) and natural (McKeown et al., 2016) selection suggests that, all
other things being equal, temperate lineages would have had the opportunity to establish in
tropical habitats by gradually or abruptly losing their vernalization responsiveness. In the case of
transitions to tropical mountain regions, as far as we know there has only been a test for
vernalization responsiveness in one grass species [Nassella pubiflora (Pooideae); native to
western and southern South America] (McKeown et al., 2016). Perhaps surprisingly, this taxon
has retained a weak vernalization response; whether this was retained due to exaptive forces
remains to be seen.

In addition to low temperatures regulating phase change in grasses, it is becoming increasingly
clear that high temperatures also play a role (Fig. 3). In bread wheat and barley, high
temperatures (e.g., 25°C versus 18°C) can either accelerate or decelerate the transition to
flowering depending on the genotype, and the daylength conditions in barley (Hemming et al.,
2012). In the bread-wheat cultivar ‘Charger’, delayed flowering with high temperatures appears
to be mediated by decreased levels of VRN1/FUL1 and VRN3/FTL2 alongside increased levels of
VRN2 transcripts, providing a mechanistic link between cold- and heat-regulated flowering (Kiss
et al., 2017; Dixon et al., 2019). Indeed, Dixon et al. (2019) recently demonstrated that certain
vernalization-responsive wheat cultivars can lose their epigenetic memory of winter, or be
‘devernalized’, during high-temperature exposure after a non-saturating period of vernalization.
The fact that high temperatures do not appear to affect VRN1/FUL1, VRN2, or VRN3/FTL2 levels
in barley genotypes that show temperature-driven flowering time differences begs the question as
to the number of origins of high temperature–flowering pathways in grasses, and to the
prevalence of devernalization (Hemming et al., 2012). Elucidating the evolutionary history of
devernalization will be an important avenue of discovery since it is suspected to be an important
adaptation to highly variable and extreme climates, both of which are predicted to become more
common during Anthropocene climate change. The possibility of high temperature as a cue for
flowering more generally across grasses also opens up the possibility that subtropical plants use
high temperatures as a cue to flower rapidly after seasonal drought.
Photoperiod is the most stable seasonal cue in a changing climate

Even more so than temperature, photoperiod is a highly reliable cue of the changing seasons, the magnitude of annual change being determined by degrees north or south of the equator. As such, plants have evolved the ability to detect yearly changes in photoperiod, even in cases where it varies as little as 30 min (Borchert et al. 2005; Itoh et al., 2010). Despite general agreement that grasses evolved in tropical climates during the mid-Cretaceous (Gallaher et al., 2019; Schubert et al., 2019), the latitudinal origins of grasses, and by extension the selective pressures that might have shaped their early flowering-time behavior in response to photoperiod, remain a mystery.

A day-neutral grass last common ancestor seems unlikely given that transitions to day-neutral flowering often involve loss-of-function mutations (Eckardt, 2000; Izawa, 2007; Turner et al., 2013; Mascheretti et al., 2015) and there is strong conservation of photoperiod flowering pathways between grasses and other angiosperms (Matsubara et al., 2014; Woods et al., 2014). On the other hand, there appears to be a general trend of long-day photoperiodism in the core group Pooideae [e.g. Brachypodium distachyon, wheat, oat (Avena sativa), and ryegrass (Lolium perenne)] (Gardner and Loomis, 1953; Turner et al., 2013; Woods et al., 2014), but short-day photoperiodism in PACMAD (e.g. maize, Setaria viridis, and Miscanthus sacchariflorum) (Benedict, 1940; Evans, 1962; Jensen et al., 2013; Doust et al., 2017) and Oryzoideae (e.g. rice) (Eckardt, 2000) grasses, tentatively suggesting that the ancestral grass transitioned to flowering under short days during periods of high precipitation. Within the family, the apparent lack of photoperiodic flowering control in the Bambusoideae and early diverging lineages of Pooideae (Brachyelytreae and Nardeae) (pers. obs.) posit that long-day flowering evolved immediately after the divergence of Nardeae from the remaining Pooideae, easily facilitating contemporaries of the latter to flower quickly at the onset of temperate and/or highland–tropical growing seasons (Fjellheim and Preston, 2018).

Alternatively, the early origin of vernalization-responsive flowering (McKeown et al., 2016) might have been a sufficient prerequisite to the Pooideae’s shift into temperate regions, with transitions to long-day photoperiodism evolving secondarily as clades moved closer toward the poles. From a molecular standpoint, comparison of model grass flowering-time pathways is
starting to provide a framework for distinguishing between these two major evolutionary scenarios, as well as for predicting the ability of populations to shift between photoperiod-sensitive or insensitive states. However, much basic work is left to do to determine the extent to which the primarily tropical BOP-PACMAD sister lineages use photoperiod to control flowering, and whether these photoperiodic signals are equally important in both lowland and highland tropical grasses.

The mechanism by which grasses and other plants determine daylength is based on the activation and inactivation of phytochrome (PHY) photoreceptors by red light and far-red light/dark, respectively, in the context of a 24-hr period (Song et al. 2015). For example, in the case of the long-day plant A. thaliana (Brassicaceae), the transcription factor CO oscillates in expression as defined by the 24-hr (circadian) clock. Measurements of CO transcripts have shown that mRNA levels are highest in the afternoon; however, CO mRNA is only stably translated into a functional protein that promotes flowering in the presence of light-regulated enzymes (Valverde et al., 2004). Thus, CO protein levels are only high during the coincidence of high CO mRNA and late-afternoon light, the latter characteristic of temperate summers. Such an ‘external coincidence model’ of flowering has been extrapolated to both long-day grasses, such as wheat and barley (Mulki and von Korff, 2016), and short-day grasses, such as rice and sorghum (Sorghum bicolor) (Itoh et al., 2010; Murphy et al., 2011), although the need for stabilization of CO and its protein product in these species remains to be demonstrated. Nevertheless, it is clear that, despite having many photoperiod-pathway genes in common, some key differences exist between long-day grasses and A. thaliana, as well as between long-day, short-day, and day-neutral grasses. The latter are particularly interesting from the perspective of niche transitions in grasses.

One key difference between the flowering pathways of temperate cereals, rice, and sorghum is how the putative CO ortholog—HvCO1 in barley, HEADING DATE 1 (HD1) in rice, and SbCO in sorghum—interacts with other members of the CCT domain family (Fig. 3). As mentioned previously, the CCT-domain family gene VRN2 (also known as GRAIN NUMBER, PLANT HEIGHT, AND HEADING DATE 7 [GHD7] in rice) is a negative regulator of flowering that is downregulated by VRNI/FUL1 during vernalization, specifically in core Pooideae taxa.
However, VRN2 transcription is also promoted under long days, and this aspect of its regulation, as well as its repression of flowering, appears to be conserved in other members of the grass BOP clade (e.g. rice) and the PACMAD clade (e.g. sorghum and maize) (Xu et al., 2008; Hung et al., 2012; Murphy et al., 2014; Woods, McKeown et al., 2016). Although not completely worked out, the long-day function of VRN2/GHD7 in at least rice and sorghum appears to be mediated through transcriptional and post-transcriptional interactions with PHYs, the latter of which is antagonized by the signaling protein GIGANTEA (GI) (Hung et al., 2012; Yang et al., 2014; Zheng et al., 2019). In short-day rice, GI sensitizes leaves to early-morning blue light, causing induction of \textit{EARLY HEADING DATE 1 (EHD1)} when dawn GHD7 expression is low-to-absent and the interval between red and blue-light perception is long (Itoh et al., 2010). Since this dual-gating system results in high \textit{HD3a} expression with 13-h daylength or less, and rapid transcriptional reduction with 13.5-h daylength or more, it provides a potential mechanism for sub-equatorial grasses more generally to detect small changes in photoperiods across the year. A similar model is likely to explain the critical threshold of short-day flowering in sorghum (Sanon et al., 2014), although this needs to be explicitly tested.

In rice and possibly sorghum, but not wheat or barley, Ghd7 also forms a repressive complex with Hd1 such that Hd1 switches from an indirect promoter (via \textit{EHD1}) of the \textit{VRN3/FTL2} ortholog \textit{HD3a} under short days to an indirect repressor of \textit{HD3a} under long days (Murphy et al., 2011; Nemoto et al., 2016; Zhang et al., 2017) (Fig. 3). Indeed, delayed flowering under long days in several rice accessions has been linked to variation at the \textit{GHD7} locus, and is associated with increased biomass, yield, and abiotic stress tolerance (Okada et al., 2017; Herath et al., 2019). HD1 and another CCT-domain protein (PSEUDORESPONSE REGULATOR 37 (PRR37)) can further be switched-out to form a heterotrimeric NUCLEAR FACTOR Y (NF-Y) complex with GHD8/OsNF-YB11 and NF-YC. This complex promotes \textit{GHD7} (Wang et al., 2019) and represses \textit{HD3a} expression, the latter via direct binding of its promoter (Goretti et al., 2017), again delaying flowering under long days. Interestingly, wheat also forms an NF-Y complex under long days, in this case between NF-YA and NF-YB and either VRN2 or the functional HD1 homolog CO2 (Li et al., 2011). The balance of \textit{VRN2} and \textit{CO2} expression under long days determines exactly what complex will form; without cold the VRN2 NF-Y complex dominates to repress flowering, whereas with cold the CO2 NF-Y complex dominates to promote...
flowering. Currently \textit{PRR37/PPD-H1} is not known to be part of the NF-Y complex in wheat or barley, perhaps explaining why, in contrast to rice and sorghum (Koo et al., 2013; Casto et al., 2019), the protein product of this gene promotes flowering (Guedira et al. 2016). Increased expression of \textit{PRR37/PPD-H1} is associated with daylength insensitivity to promote both long- and short-day flowering in oat (An et al., 2020), whereas recessive mutations cause late flowering in wheat and barley under long days (Guedira et al. 2016).

From the perspective of flowering pathway evolution, if the ancestor of the BOP-PACMAD clade was short-day flowering, the PHY-VRN2/GHD7-CO/HD1, HD1-GHD8-NF-Y, and PRR37-GHD8-NF-Y modules could explain repression of flowering specifically under long days. Repression of \textit{VRN2/GHD7} by cold, as well as a loss of binding affinity between the \textit{VRN2/GHD7} and CO/HD1 proteins, and antagonism between \textit{VRN2/GHD7} and CO2, might then have evolved secondarily to allow Pooideae species to flower during the long days of temperate/continental spring and summers. Although day-neutral alleles of \textit{VRN2/GHD7} exist in rice and maize, it is most likely that these were derived during domestication, and thus do not represent the ancestral state at this locus (Hung et al., 2012; Zhang et al., 2017; Je et al., 2018). The ancestor of rice (\textit{Oryza rufipogon}), for example, is a perennial short-day flowering grass that spans a large geographic range from eastern India and Indochina to southern China. Under domestication, repeated unconscious selection on annual rice varieties for day-neutral flowering and several other traits (e.g. increased drought and cold tolerance), greatly facilitated range expansion of both subspecies: \textit{indica} in the lowlands of tropical Asia and \textit{japonica} in upland Asia, Africa, and the Americas (Londo et al., 2006; Chen et al., 2016). Beyond cultivated species, available data currently limit our understanding of how common shifts are in daylength-regulated flowering time at the population level. Nonetheless, it is known that day-neutral flowering has also evolved multiple times simultaneously with the spread of tropical Australian Panicoideae grasses (i.e. \textit{Heteropogon contorus}, \textit{Bothriochloa bladhii}, \textit{Themeda australis}, and \textit{Dicanthium tenuiculum}) into the subtropics and warm, temperate regions (Tothill, 1977).

In addition to \textit{VRN2/GHD7}, \textit{CO/HD1}, and \textit{PRR37/PPD-H1}, grasses have several other CCT-domain genes, many of which are also demonstrated players in the flowering-time pathway (Zhang et al., 2015; Zheng et al., 2017). For example, barley has nine CCT-domain genes, of
which at least four (HvCO1, HvCO2, PPD-H1, and VRN-H2) are upregulated under long days and one is responsive to short days (HvCO9). In accessions with a functional VRN-H2 gene, HvCO1 and HvCO2 initially act as floral repressors under long days by positively regulating VRN-H2; however, once VRN-H2 levels decrease, HvCO2 promotes flowering by indirectly regulating the expression of HvFT1 by way of PPD-H1 (Mulki and von Korff, 2016) (Fig. 3). Under short-day conditions, not only are HvCO1 and HvCO2 not transcriptionally active, but flowering is actively repressed by HvCO9 (Kikuchi et al., 2012). Whether this repression of short-day flowering is specific to temperate Pooideae awaits testing of orthologous gene function in short-day taxa such as rice and sorghum. It will also be interesting to determine how the other CCT genes are wired into this complex network, and if changes to their regulation, protein binding affinities, and cellular functions can account for differences in photoperiodic induction across grasses and crop cultivars.

As is hopefully becoming clear, much of the diversity in how grasses respond to different photoperiodic and temperature signals is based on either the partitioning of functioning or neo-functionalization of gene duplicates that have an ancestral role in some aspect of a conserved flowering-time pathway (Ream et al., 2012; Fjellheim and Preston, 2018; Xu and Chong, 2018). Duplicate genes are akin to standing variation whereby neutral or near-neutral mutations in extra copies can become favorable as the external conditions change (Katju and Berghthorsson, 2013). Beyond CCT-domain genes (Okada et al., 2017), members of the FT and FUL (Preston and Kellogg, 2006) gene families are good candidates as selective targets for past and future flowering adaptation. Another trend is that all taxa appear to have both repressors and promoters of flowering that are active under both long and short days. This suggests that photoperiod has been an important cue for flowering throughout the lifespan and range of the grass family, as is observed at the cultivar level in most cereal crops (Liu et al., 2015; Manrique et al., 2019).

In the case of FT-like evolution, it was recently reported that in long-day B. distachyon, FT-LIKE 9 (FTL9) delays flowering under long days and promotes flowering under short days through daylength-dependent interactions with the florigen activation complex (FAC)-agent FD1 and another FT-like protein, FT1 (Qin et al., 2019). Under short days, FT1 is virtually absent from the transcriptome, thus allowing the complex of FTL9 and FD1 to weakly foster the floral
transition. By contrast, in long-day conditions, when FT1 levels are high, an alternative FT1-FD1 would be a much stronger instigator of the floral transition, except that competition with FTL9 for FD1 binding ameliorates this response (Qin et al., 2019). A similar antagonism has been found between the FT-like proteins HD3a and RICE CENTRORADIALIS (RCN) through competitive FD1 binding (Kaneko-Suzuki et al. 2018). Thus, the decision to flower under long days versus short days can come down to the number and strength of interactions mediated by a handful of fundamentally conserved genes. Together, these data suggest that shifts between long-day, day-neutral, and short-day flowering might occur through a few simple mutations. As such, the general lack of described long-day taxa in the PACMAD grasses (but see Evans and Knox, 1969), or short-day taxa in the Pooideae, tentatively points to constraints on traits other than photoperiod-regulated flowering, or to genetic pleiotropy.

Intersection of temperature- and photoperiod-regulated flowering

As well as different daylengths being inductive for flowering, it has been shown in several vernalization-responsive temperate crops (e.g. wheat, barley, ryegrass, and oat) that short days can compensate for vernalization through a phenomenon often termed short-day vernalization (Purvis and Gregory, 1937; Sampson and Burrows, 1972). As in the case of true vernalization, short-day vernalization causes plants to become competent to make the reproductive transition. However, flowering per se only occurs rapidly when the same plants are then subject to inductive conditions, these usually being the warm, long days of temperate spring and summer. In the obligatory long day flowering Pooideae species B. distachyon, the presence or absence of a short-day vernalization response is determined by a single amino acid change in FTL9 that appears to have evolved only once in the species (Woods et al., 2019). Silencing of FTL9 in short-day, vernalization-responsive accessions blocks flowering in individuals exposed to short days followed by long days, but plants from the same population will still flower when short days are swapped for low temperatures. Thus, the two types of vernalization can be unlinked at the genetic level, although both FTL9 and VRN3 are negatively regulated by VRN2 under long days, and in both cases upregulation of VRN1/FUL1 is involved (Woods et al., 2019).
In the context of climate change, where rising temperatures and more extreme weather events are already manifest, compensation between the long-day photoperiod and low-temperature pathways might either buffer against unpredictable short-term temperature cues or be a source of maladaptation when daylength is not a good predictor of growing conditions. However, the fact that these two flowering pathways are semi-independent, particularly in their control of different FT-like gene paralogs that have traditionally been recognized as integrators of different pathways (Woods et al., 2019), suggests a history of adapting to climates where different seasonal cues become unlinked. Important avenues of research will be to determine the prevalence across grasses of cold and short-day vernalization responsiveness, as well as the history of photoperiodic shifts in flowering. This can then be used to elucidate whether the genetic architecture of these pathways facilitates evolutionary flexibility broadly across the family, and will have implications for agricultural practices where crops can be specifically designed for a range of uses and habitats.

HOW IMPORTANT ARE OTHER ENVIRONMENTAL FACTORS IN FLOWERING TIME?

In addition to temperature and photoperiod, flowering time can be affected by a range of external factors, including salinity, herbivory, and drought (Cho et al., 2017). Since current and future projected climate change suggests rapid alterations to several of these factors simultaneously, predicting how these changes will affect flowering time plasticity and evolution ultimately depends on the level of cross-talk (i.e. pleiotropy and epistasis) between these pathways. Although there are many examples of plants escaping from stress through non-plastic, adaptive early flowering (e.g. Shavrukov et al., 2017; Hamann et al., 2018), actual stress-induced flowering requires a direct causal link between a perceived stress and plasticity of the flowering time–pathway response (Franks, 2011). Thus, demonstrating stress-induced flowering requires evidence of phenotypic plasticity that occurs as a direct result of the stress in question, which then leads to precocious or delayed flowering relative to some measure of biomass.

Low water availability and/or high evapotranspiration (drought) has been found to impact flowering time differently across angiosperms. In A. thaliana, for example, drought promotes
and delays flowering under long and short days, respectively; both responses are mitigated by mutations in the photoperiod pathway gene GI (Han et al., 2013; Riboni et al., 2013) and, under long days, by abscisic acid (ABA)–pathway mutants that promote flowering through their loss of TWIN SISTER OF FT (TSF), FT, and SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1 (SOC1) regulation (Cho et al., 2017). Drought also affects flowering time in rice, although the direction of effect varies across cultivars (Lafitte et al., 2007; Galbiati et al., 2016; Groen et al., 2020). For early-flowering, drought-induced genotypes, little is known about the genetic basis for this trait; the ABA pathway has been implicated in the late-flowering genotypes, but the genes involved appear to be different to those mediating this response in A. thaliana (Zhang et al., 2016; Cho et al., 2017). In the case of wheat and barley, flowering time is generally hastened by drought (McMaster and Wilhelm, 2003; Park et al., 2016). Indeed, a recent study showed that bread-wheat TaVRN1 and TaFT1 are upregulated in leaves under drought relative to well-watered conditions, where they are co-expressed with the CCAAT Binding Factor (CBF) transcriptional repressor TaDR1 (Zotova et al., 2019) (Fig. 2). This apparent coregulation of vernalization-responsive VRN1/FUL1 by cold and drought in bread wheat is particularly interesting given known links between cold-acclimation and drought-pathway genes (e.g. CBF genes) (Chew and Halliday, 2011; Hao et al., 2017), and the fact that, at least in barley, VRN1/FUL1 directly negatively regulates CBF2, CBF4, and CBF9, causing reduced freezing and drought tolerance (Oh et al., 2007; Deng et al., 2015). Much work remains to be done to determine when, and how many times, a drought-induced flowering pathway evolved in grasses, what genes are involved, and to what extent it facilitated independent transitions into seasonally dry or flooded habitats.

EVIDENCE FOR RELEASED CONSTRAINT ON GRASS FLOWERING EVOLUTION

Despite evidence for strong phylogenetic signals in the environmental control of grass flowering time (see previous sections), other behaviors related to flower development appear relatively labile. For example, many grasses and other plants are able to partition their shoot meristems, such that some are maintained in, or reset to, the vegetative state even when the main SAM is producing flowers and seed (Robinson and Wareing, 1969). Such spatial variation in phase
change allows for multiple transitions to flowering (iteroparity) throughout a plant’s lifespan, and usually coincides with a multi-year lifecycle (perenniality) (Begonzi and Albani, 2011). Despite the apparent flexibility of iteroparous perenniality, whereby individuals can capitalize on well-established above- and below-ground resources, many grasses have evolved alternative life strategies, mainly in the form of semelparity (once flowering), annuality (single-year lifecycle), or both. In the case of predominantly semelparous perennial and woody forest bamboos, spectacular cases of mast flowering in predictable 15–16 year cycles have been explained through selection for outcrossing replenishment, satiation of intense seed predation, and maximization of fuel for forest fires to increase canopy gaps and seedling recruitment (Keeley and Bond, 1999; Guerreiro et al., 2014; Linder et al., 2018). The latter provides a potential clue to both the proximate and ultimate causes of this bizarre flowering behavior, and is hypothesized to have facilitated transitions from forest margins to forest understories (Keeley and Bond, 1999). As both water availability and heat units increase, the speed of succession by trees increases. Thus, it is hypothesized that these factors set the ecological timeframe for masting and interact as long-term proximate cues to trigger flowering (Keeley and Bond, 1999). In other grasses, both C3 and C4, semelparity is most often linked to annuality, and there is strong evidence that these traits have evolved repeatedly in response to dry, minimally shaded, and highly seasonal environments, most likely to mitigate increased adult mortality through increased seed recruitment (Liu et al., 2019). Several species (e.g. the Pooideae taxa *Festuca vivipara*, *Poa alpina vivipara*, and *Deschampsia alpina*) adapted to harsh tundra conditions also present the phenomenon of pseudovivipary, wherein vegetative shoots are derived from floral structures (Tooke et al., 2005). Such ‘floral reversion’ appears to be environmentally induced as a back-up to failing seed set; the genetic basis for this trait remains a subject of investigation.

In the context of sustainable agriculture, there is a growing interest in ‘perennializing’ annual crops to make them more resource-use efficient. This requires an understanding of the physiological and developmental basis of iteroparous perenniality in different environmental contexts, as well as an awareness of potential factors that might facilitate switches between annuality and perenniality in different clades. A recent study on Pooideae grasses inferred 51 independent shifts from the perennial to annual habit and demonstrated a link between the origin of annuality and an undefined precursor trait (Lindberg et al., 2020). Further investigation into
the nodes of origin for the precursor trait(s) revealed that they correspond to an increase in belowground to aboveground biomass ratio, suggesting that changes in resource allocation are critical for the evolution of growth habit, and by extension in the engineering of more efficient crop grasses. Future work will be required to determine if the same or different growth traits are correlated with habit in grasses outside Pooideae.

Although the developmental basis for iteroparity/semelparity and perenniality/annuality has not been fully worked out for grasses, studies in model Brassicaceae perennials suggest that it involves both a temporal and spatial control component that is absent or repressed in semelparous annual taxa. For example, in both annual A. thaliana and perennial Arabis alpina, FLOWERING LOCUS C/PERPETUAL FLOWERING1 (FLC/PEP1) is expressed in SAMs to maintain vegetative growth, with its downregulation causing de-repression of flowering. However, in A. alpina, reduced PEP1 levels only induce flowering in some SAMs, the others being held in an incompetent juvenile state by the spatially-specific expression of another floral repressor, TERMINAL FLOWER1 (TFL1) (Bergonzi and Albani, 2011). Interestingly, a similar pattern of expression has been found for the TFL1 orthologue in perennial ryegrass (Pooideae) (Jensen et al., 2001), but how it is spatially controlled is still not understood. In the case of the “woody” Moso bamboo (Phyllostachys edulis, Bambusoideae), which generally proliferates clonally, annual cycles of shoot elongation from rhizomes appear to be controlled by signals that control flowering in other grasses (e.g. temperature, photoperiod, and precipitation), and indeed shoot growth is correlated with expression of the flowering-time ‘florigen’ gene FLOWERING LOCUS T (FT). It is hypothesized that this mismatch between FT expression and asexual reproduction is due to a functional switch of FT from promoter to repressor of flowering, or the presence of an additional component that makes the SAM partially insensitive to the action of FT (Gamuyao et al., 2017).

CONCLUDING REMARKS AND FUTURE PERSPECTIVES

In this review we set out to address the extent to which evolution of different flowering-time behaviors have shaped and/or reinforced the broad and varied niche space of grasses. Clearly, much of what we know about the control and genetic basis of grass flowering comes from
studies of crop and forage grasses, the exceptions often being members of temperate/continental clades; there is a dearth of data from tropical-lowland and -highland taxa. Nonetheless, the fact that model grasses span both major BOP and PACMAD clades provides opportunities for generating general hypotheses about the direction and tempo of flowering behavior evolution, and at least what behaviors correlate with potentially stressful habitats. Based on the data presented, it seems likely that the early grasses inherited and maintained an ancient photoperiod pathway, allowing them to time flowering during particular seasons based on cycles of rainfall, drought, light quality, and phenology of the surrounding biome. Molecular, ecological, and phylogenetic data so far support the hypothesis that the first grasses were facultative short-day flowering, although this remains to be explicitly tested (see Outstanding Questions). A second, even lesser-explored question, is whether the grass last common ancestor had flowering pathways that were directly responsive to drought and other stressors (e.g. high temperatures), and if so, how important these pathways were for shaping the grass distributions that we see today. Addressing these questions will require observations of flowering time under a range of control and field conditions for phylogenetically and geographically diverse taxa, including those in clades sister (i.e. Pueliodieae, Pharoideae, and Anomochloideae) to the BOP and PACMAD grasses (GPWG II, 2012), and follow-up studies on the genetic basis of these behaviors. Since the origin of these ancestral grasses, a number of large-scale niche shifts, including transitions into more open, drier, and colder environments have taken place both in situ during climate change, orogeny, and landmass movement, and ex situ as individual species migrated toward the poles (Fig. 1). For contemporaneously temperate/continental species and populations (e.g. temperate japonica rice), it seems highly likely that changes in the control of flowering time contributed to these shifts, along with changes in whole-plant physiology. Vernalization-responsive flowering, for example, is prevalent across Pooideae, and conservatively has evolved at least once more in the southern hemisphere PACMAD species Themeda triandra (Panicoideae) (Evans and Knox, 1969; McKeown et al., 2016). Variability in the duration and minimum temperature required to saturate the requirement both across and within species further speaks to the role of vernalization responsiveness in local adaptation (Evans and Knox, 1969), although most studies on this have been conducted outside of Poaceae (e.g. Calcedo et al., 2004; Van Dijk and Hautekeete, 2014). Long-day photoperiodism in flowering has likewise shown to
be prevalent in at least core Pooideae crops and forage grasses, facilitating rapid flowering once competency has been attained. Even so, explicit tests of photoperiodic flowering are so shallow across grasses that it is difficult to determine the rate and direction of evolution. This is particularly true when it comes to interpreting the importance of short-day photoperiodism in sub-tropical and tropical regions, and the prevalence of short-day vernalization in tropical to temperate/continental shifts. On the other hand, the fact that warm-season PACMAD grasses in temperate/continental regions generally flower after cold-season Pooideae grasses suggests the retention of an ancient short-day pathway in their tropical ancestors.

The relative lack of evolution in short-day clades (but see Evans and Knox, 1969) does not appear to be due to constraints at the genetic level, since both long- and short-day plants have pathways for flowering under both conditions, and day-neutral flowering is a common derivation in crops. Rather, it might be explained by strong selection to reduce competition in mid-latitude temperate transition zones. In the future, some exciting avenues of research will be to determine if secondary shifts from temperate to tropical regions are correlated with the loss of long-day flowering, either in the direction of short-day photoperiodism or day neutrality; to consider if these changes are contingent on elevation; and to assess the genetic bases for these modifications. Since the evolution of annuality is correlated with seasonal drought in temperate regions, it will also be interesting to determine if tropical climates additionally select for this trait, and to characterize its history across PACMAD grasses. Although much work needs to be done, the increasing availability of paleoclimatic, phenological, and genetic data at different geographical and phylogenetic scales is revealing the complex nature of flowering time control and its relationship to an ever-changing fitness landscape. Given this dynamic past, it seems likely that the grass flowering-time toolkit comprises handy variation for future challenges within the Anthropocene, and is already being utilized for major improvements in crop yields (e.g. Okada et al., 2017).

FIGURE LEGENDS

**Figure 1.** Relationships and ages of the grass subfamilies in the context of major climatic and geological events. The dated phylogeny (top) is based on estimates in Gallaher et al. (2019)
(error bars not shown) and historical events throughout grass evolution (bottom) are based on Zachos et al. (1992), Moores and Fairbridge (1997), Veizer et al. (2000), McLoughlin (2001), Levin et al. (2004), Coxall et al. (2005), Gee and Stephenson (2006), Rowley and Currie (2006), DeCelles et al. (2007), Dupont-Nivet et al. (2007), Eldrett et al. (2009), Bouchenak-Khelladi et al. (2010), Bywater-Reyes et al. (2010), Strömberg (2011), Passchier et al. (2013), Sun et al. (2013), Abbate et al. (2015), Evenstar et al. (2015), Sharkov et al. (2015), Carter et al. (2017), Liu et al. (2017), Pound and Salzman (2017), and Gallaher et al. (2019). Sizes of triangles reflect relative number of species (Soreng et al. 2017). Ellipses represent inferred time periods for each ecological (light green), climatic (blue-green), or geological (grey) event.

Figure 2. Overview of climatic factors potentially controlling timing of grass flowering. Temperature is most likely the defining factor in high latitude and altitude regions in microthermal and mesothermal climates, whereas precipitation patterns is the expected defining factor in low latitude mesothermal and megathermal climates. (A) Length of growing season based on UNEP (2019). (B) Onset of growing season defined by temperature. Data from WorldClim v1.4 data set, Bioclim variable 6, 2.5 km2 resolution (Hijmans et al., 2005). (C) Onset of rainy season redrawn from Bombardi et al. (2017). (D) Temperature regimes based on the Köppen-Geiger climatic zones with macrothermal climate equaling climate zone A (tropical) and hot regions of B (dry), mesothermal climate equaling climate zone C (temperate) and cold regions of B (dry), and microthermal climate equaling climate zone D (continental) (Geiger, 1954; Beck et al., 2018).

Figure 3. Latitudinal and phylogenetic bias of photoperiod- and temperature-regulated flowering in grasses. Pooideae (e.g., wheat, domesticated in the middle east) is bias toward the mixed meso- (light green) to microthermal (light blue) zone north of the equator (thick blue line), whereas PACMAD taxa (e.g., *Sorghum*, domesticated in northeast Africa; rice, domesticated in the Chinese Yangtze River Valley) are concentrated in megathermal (light pink) regions. Differences in the flowering behaviors of temperate/continental and subtropical/tropical crops involved changes in the connections between response pathways, and a relatively conserved set of proteins such as those in the CONSTANS (CO) family (purple). It is unclear exactly if and
how temperature regulates CO-like proteins in rice and Sorghum as illustrated by question marks. SD, short day; LD, long day.

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ADVANCES

- The prevalence of short-day flowering in grasses suggests ancient adaptation to precipitation seasonality in tropical climates.
- Vernalization responsiveness and long-day photoperiodism likely led to early Pooidae diversification in temperate/continental regions, with shifts from perenniality to annuality allowing tolerance to arid seasonal climates.
- Vernalization, devernalization, and short-day vernalization pathways converge on the flowering promoter VRN1 in wheat.
- Transitions between cold- and heat-induced attainment of floral competency and long- and short-day photoperiodic grass flowering involved modified interactions mainly between CCT domain, MADS-box, and FT-like proteins.
- Conservation of flowering-time behavior in grasses is attributed to ecological sorting, niche partitioning to limit competition, and/or genetic pleiotropy of flowering-time genes in stress responses.
OUTSTANDING QUESTIONS

- To what extent does flowering behavior limit grass species distributions?
- What internal factors constrain broad-scale phylogenetic patterns of grass flowering time control?
- Was the grass ancestor short-day, long-day, or day-neutral flowering?
- Is photoperiod or precipitation the dominant flowering time control in tropical ecosystems?
- How common are shifts between short-day, long-day, and day-neutral flowering pathways at fine taxonomic scales?
- Are taxa outside Pooidae vernalization-responsive; how many times did this trait evolve?
- Are seasonal changes in diurnal temperature variation a cue for highland tropical grass flowering?
- What is the prevalence of high temperature-regulated flowering in grasses; does it have a phylogenetic signal?
- How important are non-temperature stress flowering pathways in grasses; what genes are involved?
- What external signals affect bamboo flowering?
Figure 1. Relationships and ages of the grass subfamilies in the context of major climatic and geological events. The dated phylogeny (top) is based on estimates in Gallaher et al. (2019) (error bars not shown) and historical events throughout grass evolution (bottom) are based on Zachos et al. (1992), Moores and Fairbridge (1997), Veizer et al. (2000), McLoughlin (2001), Levin et al. (2004), Coxall et al. (2005), Gee and Stephenson (2006), Rowley and Currie (2006), DeCelles et al. (2007), Dupont-Nivet et al. (2007), Eldrett et al. (2009), Bouchenak-Khelladi et al. (2010), Bywater-Reyes et al. (2010), Strömberg (2011), Passchier et al. (2013), Sun et al. (2013), Abbate et al. (2015), Evenstar et al. (2015), Sharkov et al. (2015), Carter et al. (2017), Liu et al. (2017), Pound and Salzman (2017), and Gallaher et al. (2019). Sizes of triangles reflect relative number of species (Soreng et al. 2017). Ellipses represent inferred time periods for each ecological (light green), climatic (blue-green), or geological (grey) event.
Figure 2. Overview of climatic factors potentially controlling timing of grass flowering. Temperature is most likely the defining factor in high latitude and altitude regions in microthermal and mesothermal climates, whereas precipitation patterns is the expected defining factor in low latitude mesothermal and megathermal climates. (A) Length of growing season based on UNEP (2019). (B) Onset of growing season defined by temperature. Data from WorldClim v1.4 data set, Bioclim variable 6, 2.5 km2 resolution (Hijmans et al., 2005). (C) Onset of rainy season redrawn from Bombardi et al. (2017). (D) Temperature regimes based on the Köppen-Geiger climatic zones with macrothermal climate equaling climate zone A (tropical) and hot regions of B (dry), mesothermal climate equaling climate zone C (temperate) and cold regions of B (dry), and microthermal climate equaling climate zone D (continental) (Geiger, 1954; Beck et al., 2018).
Figure 3. Latitudinal and phylogenetic bias of photoperiod- and temperature-regulated flowering in grasses. Pooideae (e.g., wheat, domesticated in the middle east) is bias toward the mixed meso- (light green) to microthermal (light blue) zone north of the equator (thick blue line), whereas PACMAD taxa (e.g., Sorghum, domesticated in northeast Africa; rice, domesticated in the Chinese Yangtze River Valley) are concentrated in megathermal (light pink) regions. Differences in the flowering behaviors of temperate/continental and subtropical/tropical crops involved changes in the connections between response pathways and a relatively conserved set of proteins, such as those in the CONSTANS (CO) family (purple). It is unclear exactly if and how temperature regulates CO-like proteins in rice and Sorghum as illustrated by question marks. SD, short day; LD, long day.
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