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Climate change and the flowering time of annual crops

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Abstract

Crop production is inherently sensitive to variability in climate. Temperature is a major determinant of the rate of plant development and, under climate change, warmer temperatures that shorten development stages of determinate crops will most probably reduce the yield of a given variety. Earlier crop flowering and maturity have been observed and documented in recent decades, and these are often associated with warmer (spring) temperatures. However, farm management practices have also changed and the attribution of observed changes in phenology to climate change *per se* is difficult. Increases in atmospheric $[CO_2]$ often advance the time of flowering by a few days, but measurements in FACE (free air CO_2 enrichment) field-based experiments suggest that elevated $[CO_2]$ has little or no effect on the rate of development other than small advances in development associated with a warmer canopy temperature. The rate of development (inverse of the duration from sowing to flowering) is largely determined by responses to temperature and photoperiod, and the effects of temperature and of photoperiod at optimum and suboptimum temperatures can be quantified and predicted. However, responses to temperature, and more particularly photoperiod, at supraoptimal temperature are not well understood. Analysis of a comprehensive data set of time to tassel initiation in maize (*Zea mays*) with a wide range of photoperiods above and below the optimum suggests that photoperiod modulates the negative effects of temperature above the optimum. A simulation analysis of the effects of prescribed increases in temperature (0–6 °C in +1 °C steps) and temperature variability (0% and +50%) on days to tassel initiation showed that tassel initiation occurs later, and variability was increased, as the temperature exceeds the optimum in models both with and without photoperiod sensitivity. However, the inclusion of photoperiod sensitivity above the optimum temperature resulted in a higher apparent optimum temperature and less variability in the time of tassel initiation. Given the importance of changes in plant development for crop yield under climate change, the effects of photoperiod and temperature on development rates above the optimum temperature clearly merit further research, and some of the knowledge gaps are identified herein.

Key words: Climate change, crops, flowering time, maize, photoperiod, tassel initiation, temperature.

Introduction

A changing climate

The recent fourth assessment report of the Intergovernmental Panel on Climate Change (IPCC, 2007*a*, *b*) provided clear evidence of changes in climate due to human activities. The concentration of greenhouse gases in the atmosphere has progressively increased over the last century or so. For example, $[CO_2]$ has increased from pre-industrial levels of 280 ppm to 379 ppm and mean temperature has increased by 0.76 °C over the same time period. Recent temperature changes have been particularly marked, such that the warming trend in the last 50 years has been 0.13 °C per decade, nearly double that of the preceding 100 years. Projections to the end of this century suggest that mean global temperature will increase by 1.8–4.0 °C (range 1.1–6.4 °C), depending on the greenhouse gas emission scenario, accompanied by changes in rainfall patterns and an increase in climate variability (IPCC, 2007*a*, *b*). Such climate changes are expected to have far-reaching impacts on ecosystems worldwide.

Crop production is inherently sensitive to variability in climate. Some of the early studies of the impacts of climate

change on crops highlighted the importance of changes in crop development at warmer temperatures in determining the impact of climate change on crop yield. For example, the yield of wheat declined by ~5–8% (Wheeler *et al.*, 1996) or 10% (Mitchell *et al.*, 1993) per 1 °C rise in mean seasonal temperature. The timing of anthesis and grain maturity was earlier at warmer temperatures in both studies, thus shortening the duration of growth and reducing grain yield. Under climate change, other factors, such as the enhanced rate of net photosynthesis at elevated [CO_2], will offset to some extent such decreases in yield due to temperature warming, and changes in precipitation patterns and the frequency of extreme weather events will further complicate impacts on crop yields. Nevertheless, it is clear that the impacts of climate change on crop productivity will be greatly influenced by how climate affects the rate of crop development, and hence the timing of crop growth.

The timing of flowering, a critical stage of development in the life cycle of most plants when seed number is determined, is important for adaptation both to the abiotic stresses of temperature and water deficit, and to biotic (pest and disease) constraints (Curtis, 1968) within the growing season. For example, in many annual crops, brief episodes of hot temperatures (>32–36 °C) can greatly reduce seed set, and hence crop yield, if they coincide with a brief critical period of only 1–3 d around the time of flowering (Matsui *et al.*, 1997; Vara Prasad *et al.*, 2000; Wheeler *et al.*, 2000; Jagadish *et al.*, 2008). Therefore, the moderation of crop development will be critical to the impacts of climate change on yield in two ways: through determining the season length, and hence the availability of radiation, water, and nutrient resources for growth; and by affecting the exposure of the crop to climate extremes. Adaptation to moderate changes in climate that influence temperature, season length, and planting dates, as well as the occurrence of abiotic stress, can be achieved by selecting varieties with appropriate flowering times and crop durations (Fig. 1: Ludlow and Muchow, 1990; Richards, 2006). Farmers (landraces) and plant breeders (cultivars) have very successfully selected/manipulated life cycle duration and phenology to maximize the range of environments in which crops grow as well as their yield (Evans, 1993; Roberts *et al.*, 1996) at least for current climates. A major challenge for crop improvement is how to plan for future climate change.

The genetic and environmental moderation of the timing of flowering is therefore central to the responses described
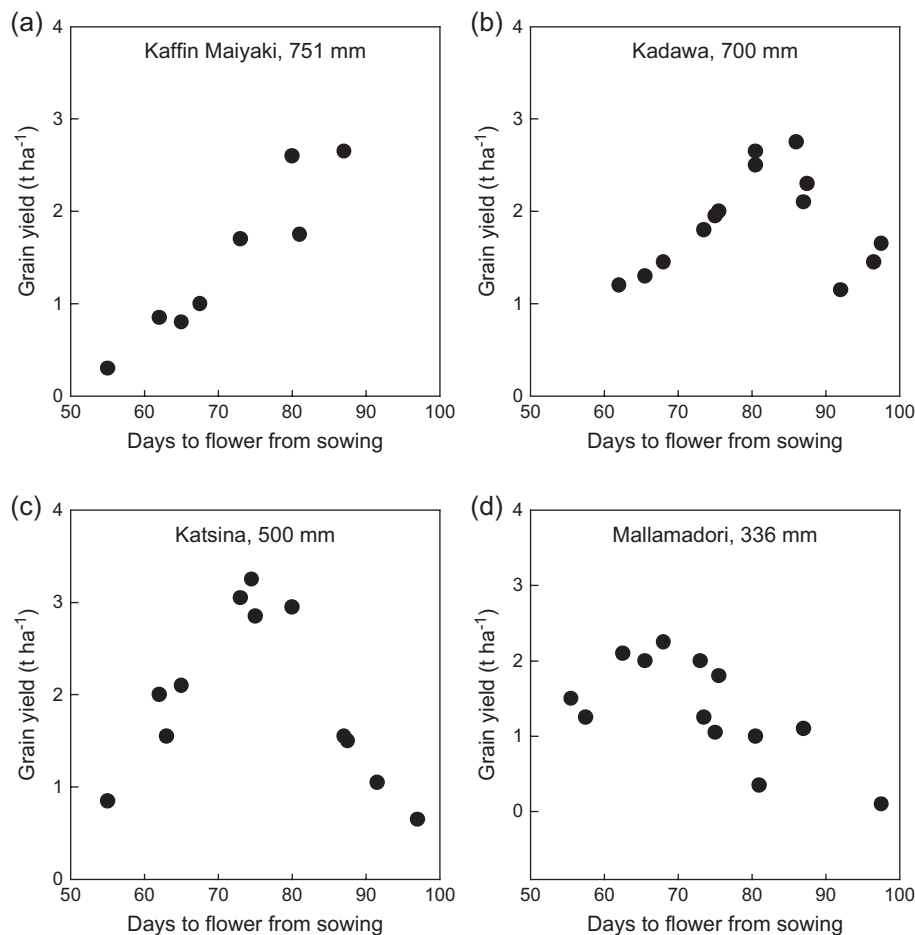
Fig. 1. Relationship between grain yield and time to flowering of a range of sorghum landrace genotypes grown at four locations varying in rainfall in northern Nigeria. At the highest rainfall location, Kaffin Maiyaki, yield is proportional to duration to flowering. As rainfall decreases and season length is reduced, the yield of later flowering genotypes is reduced and the optimum flowering time changes from >90 d to ~70 d. Redrawn from Flower (1996) with permission.

above. The timing of flowering within a season is largely determined by responses to temperature and photoperiod, and in whole plants at suboptimal temperatures these quantitative responses are reasonably well understood (Roberts and Summerfield, 1985; Wallace and Yan, 1998). However, responses to temperature and photoperiod at supraoptimal temperatures are poorly understood—though clearly these will become more important as the frequency of high temperature events increases under projected climate change. In recent years molecular biology has also greatly contributed to our understanding of flowering gene pathways (Baurle and Dean, 2006; Tsuji *et al.*, 2008), although the effects of temperature and temperature×photoperiod interactions on these pathways have not been studied.

In this review studies of phenology in annual cropping systems, mostly with cereals and legumes, over the last 50 years that looked for evidence for changes in phenology in the recent past are first considered. Secondly, whole-plant responses of flowering to CO_2, temperature, and photoperiod are described, with particular emphasis on responses and interactions at high and supraoptimal temperatures. Thirdly, how genotypic variation in responses to temperature and photoperiod may be exploited to provide adaptation to climate change, and how this is simulated in climate change impact studies, is examined. The review concludes by identifying some key knowledge gaps in current understanding of the impacts of climate change on the flowering time of crops.

Past changes in phenology of cropping systems

Earlier flowering and maturity have been observed and documented in crop plants (Williams *et al.*, 2004; Hu *et al.*, 2005; Menzel *et al.*, 2006; Tao *et al.*, 2006; Estrella *et al.*, 2007), as well as in natural communities (Fitter and Fitter, 2002), over the last 50 years from phenology networks and individual records. Menzel *et al.* (2006), for example, report that 78% of all observations in 21 European countries showed earlier flowering, with an advance in phenological events of 2.5 d per decade on average. In Germany, the phenology of 78 agricultural and horticultural events between 1951 and 2004 were, on average, 1.1–1.3 d earlier per decade (Estrella *et al.*, 2007). Likewise, winter wheat cv. Kharkof grown in the USA Great Plains has flowered 0.8–1.8 d earlier per decade (depending on location) since 1950 (Hu *et al.*, 2005).

In addition to phenology observations, Menzel *et al.* (2006) also reported that farmers' activities, such as sowing and harvesting, also occurred earlier, indicating a change in crop season length. Other studies have also shown that season length has increased, at least in mid to northern latitudes (White *et al.*, 1999; Menzel *et al.*, 2003), and this is associated with warmer temperatures in winter and spring. However, many of these changes in the timing of farming activities are driven by changes in farm management

practices and the introduction of new cultivars. So, although several studies have associated these changes in phenology with warmer seasonal or winter/spring temperatures, earlier flowering in crop species may be related more to the earlier onset of farming activities than to temperature and hence past climate change *per se*. In addition, changes in crop management may also counter direct effects of temperature warming and the timing of farm operations, for example through a change to a longer duration variety. Therefore, studies that robustly attribute observed changes in phenology in ecosystems to changes in climate are rare for natural ecosystems (Root *et al.*, 2005) and not found for managed ecosystems.

Effect of CO_2 on flowering

The effect of $[CO_2]$ on growth and development has been studied in many crop species. Springer and Ward (2007) recently summarized the effect of $[CO_2]$ on flowering time in 23 crop species in 33 papers that included experiments in growth cabinets/glasshouses, open-topped chambers, and field-based FACE (free air carbon enrichment) facilities. The majority of papers compared current ambient with a doubling of $[CO_2]$, i.e. the expected $[CO_2]$ beyond 2070 depending on future greenhouse gas emissions. Effects of intermediate $[CO_2]$ representing short- and medium-term changes in $[CO_2]$ are not commonly reported, although changes to flowering time would be hard to detect at these intermediate $[CO_2]$.

Approximately half the studies cited by Springer and Ward (2007) reported earlier flowering time, and only four out of 33 [Hesketh and Hellmers, 1973; Rogers *et al.*, 1984; Ellis *et al.*, 1995 (two species)] reported delayed flowering in response to increased $[CO_2]$. Earlier flowering was reported in most crop species studied, including short-day [soyabean (*Glycine max*), rice (*Oryza sativa*), and cowpea (*Vigna unguiculata*)] and long-day [barley (*Hordeum vulgare*), pea (*Pisum sativum*), and faba bean (*Vicia faba*)] species. The four papers reporting a delay in flowering were on maize, sorghum, and soyabean, all short-day species. It has been suggested that short-day and long-day species respond differently to $[CO_2]$ (Marc and Gifford, 1984; Reekie *et al.*, 1994). However, the four reports of delayed flowering were all from controlled-environment experiments, and there are no reports of delayed flowering from field-based experiments of short-day species.

Given that some authors have questioned the influence of artefacts associated with controlled environments on plant responses to climate (Long *et al.*, 2005), the most reliable guide to $[CO_2]$ effects on flowering should be those reported from the FACE experiments. In FACE experiments, $[CO_2]$ treatments are imposed on crops growing in large fields under well-managed farm conditions, i.e. as near 'natural' conditions as possible (Ainsworth *et al.*, 2008). In general, the FACE experiments reported in Springer and Ward (2007), along with more recent FACE papers, suggest that $[CO_2]$ has little or no effect on flowering time in either C4

species (e.g. maize; Leakey *et al.*, 2006) or C3 species (e.g. rice, Shimono *et al.*, 2009). One FACE experiment on potato (*Solanum tubersosum*) by Miglietta *et al.* (1998) does show flowering occurring 5–7 d earlier at 460–660 μmol mol^{-1} than at ambient [CO_2], but this was associated with increased canopy temperature according to the paper (though no data were presented). Although reductions in stomatal conductance (g_s) are commonly reported in FACE experiments at high [CO_2] (Ainsworth and Long 2005; Ainsworth *et al.*, 2008), and this can increase canopy temperature (Fig. 1b; Long *et al.*, 2006), canopy temperature is not usually given.

At high [CO_2], tissue temperatures are usually increased due to lower conductance, and care is therefore required when interpreting such data (Ainsworth *et al.*, 2008). For example, Vara Prasad *et al.* (2006) observed tissue temperature in sorghum to be 1.2–2.7 °C warmer at high than at ambient [CO_2] at ambient daytime air temperatures of 32–44 °C. In this particular experiment, high [CO_2] delayed flowering slightly at 36 °C compared with 32 °C, suggesting a temperature×CO_2 interaction. However, this delay can be explained by higher tissue temperatures that were reported, resulting in mean temperature exceeding the optimum temperature (T_o; see Fig. 2) and hence causing a delay in flowering.

Temperature and effects on phenology

Given the apparent lack of a direct effect of [CO_2] on rate of development, then temperature, and interactions with temperature, will be the most important aspect of human-induced climate change for crop development. The duration from sowing to flowering and maturity in plants without a vernalization requirement, or where that requirement has been met, is largely determined by responses to temperature and photoperiod (Roberts and Summerfield, 1987; Wallace and Yan, 1998). While photoperiod-insensitive or day-neutral types are important in modern agriculture, especially in warm short-season environments, photoperiod sensitivity is the norm and is a very powerful adaptive mechanism (e.g. soyabean: Evans 1993; Roberts *et al.* 1996). In this section, the basic framework used to quantify responses to temperature and photoperiod in whole plants is given, and a close look is taken at responses above and below the optimum temperature, and tissue versus air temperature.

Phases of development sensitive to temperature or photoperiod

The rate of development of plants is generally responsive to photoperiod for only part of their life cycle (i.e. between emergence and flowering), though some post-flowering processes such as the rate of flower initiation are affected by photoperiod and can therefore influence the duration of the seed-filling period (Summerfield *et al.*, 1998). In contrast, temperature affects the rate of development throughout the life cycle (Roberts and Summerfield, 1985). Three distinct stages of pre-flowering development can be identified in plants (Table 1), namely the pre-inductive or juvenile, inductive, and post-inductive phases. Photoperiod only affects the duration of the inductive phase (Roberts and Summerfield, 1987; Yin *et al.*, 1997b), and in photoperiod-sensitive cultivars the effects of photoperiod are usually substantial and are the major determinant of flowering time (Table 1). In most annual crop species examined, the duration of the pre-inductive or juvenile phase is short [days not weeks: soyabean (Collinson *et al.*, 1992); lentil (Roberts *et al.*, 1986)], the most important exception being in rice (*O. sativa*) where the duration of the pre-inductive phase (sometimes called the basic vegetative phase or BVP, though this includes part of the inductive phase) may exceed 50 d (Vergara and Chang, 1976). A long juvenile trait has also been identified in soyabean (Hinson, 1989).

Typically the response to temperature of many plant processes, including the rate of development (inverse of days to flower; Fig. 1), is described in terms of cardinal temperatures (base or minimum, T_b; optimum, T_o; and maximum or lethal, T_m temperature) and the thermal sum (θ) or rate (inverse of the duration). This response can be quantified by simple bi-linear or broken stick models with a sharply defined T_o or by linear models with a flat-top/plateau response that have a maximum rate of development over a range of temperatures. Curvilinear quadratic or beta-function models (Yin *et al.*, 1997a) that have a near optimal rate of development over a range of temperatures have also been used. This basic response to temperature is affected by photoperiod in photoperiod-sensitive genotypes and therefore must be determined under short-day or inductive
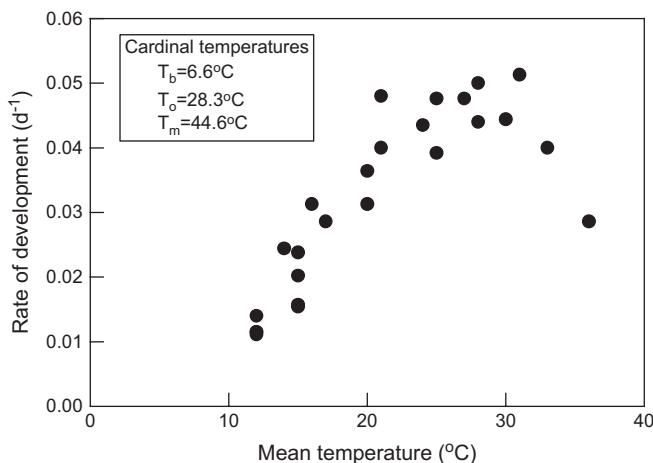

Fig. 2. Effect of temperature on the rate of development (1/days to tassel initiation) between sowing and tassel initiation in maize (*Zea mays*) cv. Tuxpeño grown in short, inductive photoperiods (≤12 h to ensure minimal confounding with photoperiod effects) in controlled-environment chambers. The cardinal temperatures describe the response of rate to temperature, where: T_b (base temperature) is that temperature at and below which the rate is zero; T_o (optimum temperature) is that temperature at which the rate is maximal; and T_m, where the rate is again zero. Original data from Ellis *et al.* (1992) and additional unpublished data.

Cardinal temperatures
T_b=6.6°C
T_o=28.3°C
T_m=44.6°C

Table 1. Durations of the pre-inductive (JUV), inductive (PSP), and post-inductive (PIP) phases in rice cv. Peta at two temperatures and photoperiods

JUV and PIP were not determined at 11.5 h. Source: Collinson et al. (1992).

Mean temperature (°C)	Photoperiod (h)	Duration in days [°Cd (T_b=10 °C) in parentheses]			
		JUV	PSP	PIP	Total
23.8	13.5	39 (533)	83 (1145)	22.8 (315)	144 (1984)
	11.5	–	19 (264)	–	81 (1102)
28.7	13.5	30 (540)	113 (2143)	20.7 (387)	163 (3047)
	11.5	–	14 (252)	–	63 (1179)

photoperiod (Roberts and Summerfield, 1987; Yan and Wallace, 1998). These differences in model/interpretation are not particularly important in most natural growing seasons in current climates, where mean daily temperatures are mostly close to but below the T_o; the choice of model under these circumstances makes little difference to the predicted number of days to flowering (see Sinclair, 1991; Summerfield et al., 1993; Wallace and Yan, 1998). However, in future climates where temperature is expected to exceed T_o more frequently, the choice of temperature response function will be much more significant, and this is discussed further below.

Ambient or tissue temperature?

Ambient air temperature is the usual 'temperature' used to quantify responses to temperature, although of course for plant processes it is the temperature nearest/approximating that of the growing point or meristem that matters (Jamieson et al., 1995). In many temperate crops, such as wheat, both soil and air temperature influence development; soil temperature while the apex is close to the ground, air temperature thereafter (Jamieson et al., 1995) Similarly, in irrigated or flooded rice systems, water temperature, not air temperature, controls development until the apex is above the water (Collinson et al., 1995). It is therefore important in quantifying and modelling responses to climate change to use the appropriate 'temperature' driver, and not simply ambient air temperature. However, it is also necessary to remember that climate model output used for climate change impacts studies will provide values of surface temperature that can be viewed as similar to the 2 m temperature recorded in weather stations. Therefore, quantitative relationships between the rate of development and temperature will often include a degree of uncertainty due to differences between where temperature is measured and where it is perceived by the plant.

Perhaps less obvious is that significant differences between air and tissue temperature are often found in controlled environments, and these differences may be critical for interpreting interactions where temperatures are close to the optimum. For example, Vara Prasad et al. (2000) recorded peanut (Arachis hypogeae) flower bud temperatures for plants raised in growth cabinets to be 0.4–4.3 °C below ambient air temperature over the range 28–

48 °C. This has obvious implications for the quantification of responses to temperature for application to natural environments. Large differences between air and tissue temperatures can also arise where environmental conditions decrease transpirational cooling, for example with severe water deficits or at elevated [CO_2] (Ainsworth et al., 2008).

Photoperiod and temperature interactions

Most crop plants respond to photoperiod, and in general short- and long-day plants respond in a similar manner with photoperiods longer or shorter, respectively, than the critical or base photoperiod delaying flowering (e.g. maize, a short-day species in Fig. 3). In quantitative types, flowering is delayed but not prevented in the non-inductive photoperiod, whereas in qualitative types, if the photoperiod transgresses a critical threshold, flowering will not occur. While qualitative responses have been observed in some crop plants [e.g. pigeonpea (Carberry et al., 2001); soyabean (Roberts et al., 1996)], the photoperiod in most growing seasons does not transgress the ceiling or maximum photoperiod, or does so only for a short period, and hence most crop plants are effectively quantitative short- or long-day plants. One exception to this may be sorghum in parts of West Africa (Dingkuhn et al., 2008).

Most whole-plant crop models (e.g. DSSAT, APSIM) assume that photoperiod effects are additive to those of temperature, which is the basic underlying driver of development, though others have argued from observations that there is a photoperiod by temperature (P×T) interaction (Wallace and Yan, 1998). The P×T interaction manifests itself as a hyperbolic response to photoperiod (Vaksmann et al., 1998; Wallace and Yan, 1998), variation in the critical photoperiod with temperature (Roberts and Summerfield, 1987), or variation in the optimum temperature with photoperiod (Wallace and Yan, 1998). Sensitivity analyses, however, generally show that fixing critical photoperiods and optimum temperatures does not significantly reduce the accuracy of predictions (Carberry et al., 2001). More recently, a threshold- or appetence-type response has been proposed wherein the threshold or target for floral initiation to occur is reduced through time (Dingkuhn et al., 2008). An effect of rate of change of photoperiod has also been proposed (Clerget et al., 2004; Borchet, 2005), and was included in the AFRC wheat model (Weir et al., 1984). As

a general rule, all models predict flowering time fairly accurately in crops growing in their normal growing season where days are becoming more inductive and temperatures are favourable (March to July in temperate latitudes north of the equator; June to October in tropical/subtropical latitudes north of the equator; December to April in tropical and subtropical latitudes south of the equator); they work less well outside these norms when, for example, days are becoming less inductive (e.g. post-rainy season crops) or crops are planted before the longest day [e.g. sorghum in West Africa (Clerget et al., 2004; Dingkuhn et al., 2008)].

Most crop models assume that photoperiod only affects rate of development at and below T_o; above T_o, only temperature affects the rate. However, the effect of photoperiod at temperatures $>T_o$ has not been studied extensively and this is clearly of importance for accurately predicting phenology in future climates. Crop models such as DSSAT and APSIM effectively assume that at temperatures $>T_o$ the rate of development is only affected by temperature. In most current seasons and environments there will not be many days where temperature exceeds T_o and therefore this approach broadly works. However, in future climates where mean temperatures will be higher, the optimum temperature is likely to be exceeded more frequently, so interactions $>T_o$ may be more significant. This is likely to be more so in crop species such as wheat (Triticum aestivum) and common bean (Phaseolus vulgaris) that originated in temperate climates but are now widely grown in more tropical environments and which have comparatively low values for T_o of <25 °C (Wallace and Yan, 1998). Crop species that originated in the tropics (e.g. rice, sorghum, millet, and peanut) generally have higher values for T_o, often between 25 °C and 30 °C, and sometimes as high as 35 °C (Yin et al., 1997b; Clerget et al., 2004).

It is really only in controlled environments, where temperature and photoperiod can be controlled independently and supraoptimal temperatures can be applied, that these interactions can be investigated. In a series of experiments with maize (Zea mays) over several years (Ellis et al., 1992), genotype Tuxpeňo was grown at constant temperatures and photoperiods ranging from 12 °C to 36 °C and 9 h to 16 h, respectively. The duration from sowing to tassel initiation (the first easily observed sign of reproductive apical development, cf double ridges in wheat) was recorded in 67 P×T treatments and modelled using a linear, additive regression technique (compare the responses in Figs 2 and 3) assuming plants were sensitive to photoperiod from emergence (Roberts and Summerfield, 1987). The resultant modelled durations are shown as a contour graph (Fig. 4).

Tassel initiation occurred between 18 d and 111 d after sowing, and the cardinal temperatures were typical for maize (T_b=6.7, T_o=28.3, and T_m=44.6 °C). The genotype was sensitive to photoperiod (Fig. 3); at 25 °C, days to tassel initiation increased from 22 d to 36 d as the photoperiod increased from 12 h to 16 h, i.e. an increase in duration of ~60%. This large and comprehensive data set suggests that photoperiod has an effect on rate of development up to and beyond T_o in addition to any negative effect of supraoptimal temperatures. So, for example at 30 °C and 11 h photoperiod, tassel initiation will occur ~20 d after sowing, whereas at 15 h and the same temperature tassel initiation will occur after 26 d. While
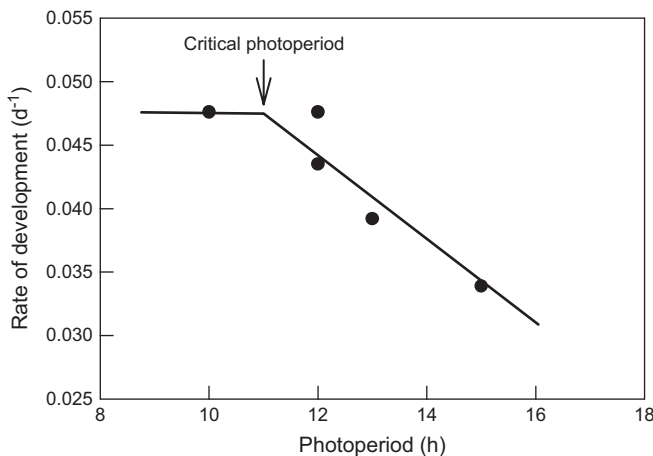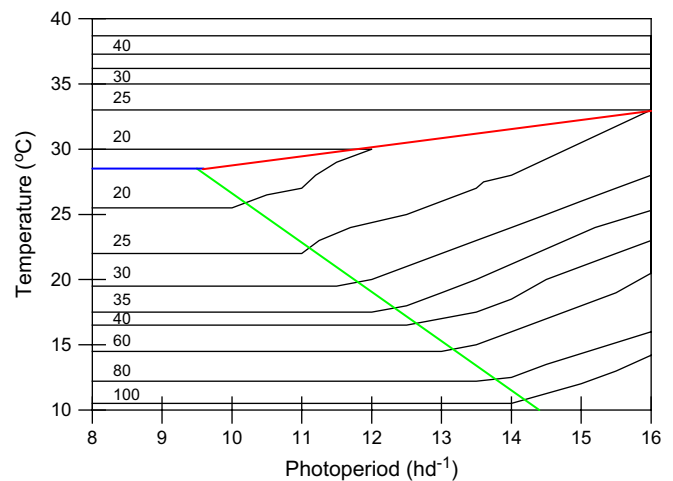
Fig. 3. Response of rate of development (1/days to tassel initiation) to photoperiod in maize cv. Tuxpeňo grown at 25 °C in controlled-environment chambers. The critical photoperiod is that point above which (in the case of a short-day plant) the rate of development is reduced by the photoperiod. A constant temperature minimizes the confounding effects of temperature on rate. Lines fitted by eye. Original data from Ellis et al. (1992) and additional unpublished data.

Fig. 4. Contour plot showing modelled durations from sowing to tassel initiation in response to temperature and photoperiod in maize cv. Tuxpeňo. The blue line shows the minimum duration to tassel initiation at the optimum temperature; the green line shows the critical photoperiod; and the red line shows the upper temperature limit of the response to photoperiod. The area between the green and red line therefore shows where the rate of development is determined by photoperiod and temperature; the area to the left of the green line and below the blue line where the rate is determined by suboptimal temperature only; and the area above the blue and red lines where the rate is determined by supraoptimal temperature only. Original data from Ellis et al. (1992) and additional unpublished data.

these effects may seem small, this delay is equivalent to a 30% increase in duration to the first sign or reproductive development; were days to flowering to be modelled these delays would be much more marked.

Molecular/genetic aspects of flowering response to climate change

Little is known about the molecular mechanisms that control flowering times in response to ambient temperature, other than for the vernalization response, even in *Arabidopsis* (Baurle and Dean, 2006). Similarly little is known about the response of flowering pathway genes to elevated [CO$_2$].

Flowering time (usually measured by leaf number) in wild-type *Arabidopsis* responds to temperature in a similar manner to other plants, occurring sooner at warm (up to ~27 °C) than at cool (16 °C) temperatures (Blazquez *et al.*, 2003; Thingnaes *et al.*, 2003; Balasubramanian *et al.*, 2006). Comparisons of mutants of the photoperiod, gibberellin, and autonomous pathways have shown that ambient temperature (growth temperature) is sensed through genetic pathways involving *FCA* and *FVE*, and integrated through *FT* (Flowering Locus T) (Blazquez *et al.*, 2003; Lee *et al.*, 2007), and that temperature leads to a photoperiod-independent activation of *FT* (Balasubramanian *et al.*, 2006). Temperature also affects responses of phytochrome mutants (Blazquez *et al.*, 2003; Halliday *et al.*, 2003); for example, *PHYA* (Phytochrome A) is not able to promote flowering at cooler temperatures, a response that might contribute to P×T interaction. However, while warm/short days (27 °C/8 h) apparently induce flowering at the same time as cool/long days (16 °C/16 h) in *Arabidopsis* (Balasubramanian *et al.*, 2006), temperature cannot usually compensate for non-inductive photoperiod in most crop plants.

In *Arabidopsis*, Springer *et al.* (2008) examined the response to elevated [CO$_2$] in two genotypes, one selected for high seed number at elevated [CO$_2$] and one a random control. They found that flowering was not affected by [CO$_2$] in the control genotype and unsurprisingly the down-regulation of *FLC* (Flowering Locus C) and up-regulation of *SOC1* (Suppressor of Overexpression Constans 1) and *LFY* (Leafy) was similar at ambient and elevated [CO$_2$]. However, in the adapted genotype, flowering was delayed by 7–9 d at elevated [CO$_2$] and this was associated with no down-regulation of *FLC* over the course of the experiment and, as a result, later up-regulation of *SOC1* and *LFY* expression. Elevated [CO$_2$], as expected, increased plant size, and relative increases in the adapted and control genotypes at ambient and elevated [CO$_2$] were proportional to the delay in flowering. The authors suggest that higher sucrose levels may act as a signal to influence flowering. However, it may be that selection for high seed number at elevated [CO$_2$] was associated with later flowering and hence larger plant size and yield.

Models predicting flowering time based on flowering pathway genes have been proposed for *Arabidopsis* (Welch *et al.*, 2003, 2004; Van Oosterom *et al.*, 2004) and these models do predict flowering time in constant photoperiod

and temperature environments. Furthermore, these simple gene network models can generate important physiological parameters, such as critical photoperiods. However, as stated above, none of these models currently quantifies basic (suboptimal) temperature responses and certainly not supraoptimal temperatures; nor do they model temperature×photoperiod interactions.

Simulation of phenology in future climate

One of the most commonly documented impacts of climate change on crops is the shortening of development stages in a warmer climate and the change in areas of crop suitability that result. In many studies this response dominates the impact of climate change on yield. Many simulation studies of changes in areas of crop suitability use simple thermal time relationships to represent the rate of development (Kenny *et al.*, 2000; Fischer *et al.*, 2005), and only a few model the effects of supraoptimal temperatures on the rate of development (Challinor and Wheeler, 2008). Given that we know that photoperiod sensitivity of duration to flowering is a key determinant of crop adaptation to climate, and that many crop varieties are photoperiod sensitive to some extent, it seems important to explore how photoperiod sensitivity may affect the response of crop phenology to temperature warming. For this, the photothermal model of flowering time illustrated in Fig. 4 was used to simulate duration from sowing to tassel initiation in maize cv. Tuxpeño in the current climate at one maize-growing location and at a range of prescribed temperature increases. Specifically, the aim was to determine whether photoperiod sensitivity affected the response of duration from sowing to tassel initiation to increases in mean temperature and to a more variable temperature regime.

One hundred years of current climate at Zaria, Nigeria (11.1°N, 7.7°E), were generated using the MarkSim weather generator (Jones and Thornton, 2000). Another set of 100 years was generated with an increase in temperature variability that was simulated by increasing the diurnal temperature range by 50% compared with the current climate simulations. Temperature increases of +1, +2, to +6 °C were added separately to the daily mean temperature of these two sets of current climates to provide a total of 14 sets of 100 years of climate. The photoperiod on each day was calculated from standard astronomical daylength equations (Keisling, 1982). A sowing date of 15 May, the average date of the start of the rains at this location (Craufurd and Qi, 2001), was used in all simulations. Time to tassel initiation was simulated using the photothermal time model (Fig. 4) with the appropriate temperature and photoperiod sensitivity for maize cv. Tuxpeño (PT model), and with the same temperature sensitivity alone (T model, i.e. no response to photoperiod). The mean and coefficient of variation of duration from sowing to tassel initiation was calculated for each set of 100 years of simulations.

Mean duration from sowing to tassel initiation became progressively shorter with an increase in mean temperature until an apparent optimum, beyond which duration

progressively increased, indicating that current mean temperatures at Zaria are below the optimum (Fig. 5a). Photoperiod sensitivity (PT model) delayed tassel initiation by 6 d in the current climate (zero change in temperature) and changed the response to temperature warming. Most notably, the apparent optimum for this development stage increased from +2 °C without photoperiod sensitivity (T model) to +4 °C with photoperiod sensitivity (Fig. 5a). The interannual variability in the duration from sowing to tassel initiation was similar between the simulations with and without photoperiod sensitivity until +2 °C, beyond which interannual variability in development was greater at a given temperature warming in the absence of photoperiod sensitivity (Fig. 5b). Also, interannual variability in development was greater when the diurnal temperature variability was increased. To explore this further, the change with temperature in the coefficient of variation of duration to tassel initiation between the climate simulations with and without extra temperature variability was examined. Again, photoperiod sensitivity affected the simulated response to temperature warming. The increase in variability of the timing of tassel initiation due to increased temperature variability at +3 °C and warmer was reduced with photoperiod sensitivity (Fig. 5c).

From this preliminary analysis, it is concluded that photoperiod sensitivity changed the response of flowering time to simulated temperature warming that is a typical component of a climate change impacts study. Specifically, the apparent optimum warming for rate of development is warmer, and the increase in the variability of flowering time due to a more variable temperature is less, when the rate of development to flowering is sensitive to photoperiod and temperature, compared with temperature alone. An implication of these results, although they are based on only a single set of simulations for one genotype of maize at one location, is that climate change impact studies that only use thermal time to model crop development may not be capturing the correct response of development to climate change for crop genotypes that are photoperiod sensitive. Given the importance of changes in development in a warmer climate for crop yield and the timing of crop-sensitive phases, this is clearly a topic that merits further research.

Knowledge gaps

In this review, the state of knowledge on the modulation of flowering times in annual crops by photoperiod and temperature has been outlined. Given the importance of timely flowering and maturity for yield in current and future climates, predicting these phenological events is a major challenge for the assessment of the impacts of, and adaptation to, climate change and variability. There is an urgent need to increase our understanding of the processes controlling phenology, particularly at supraoptimal temperatures. This review has identified the following needs for future studies of crops and climate change.
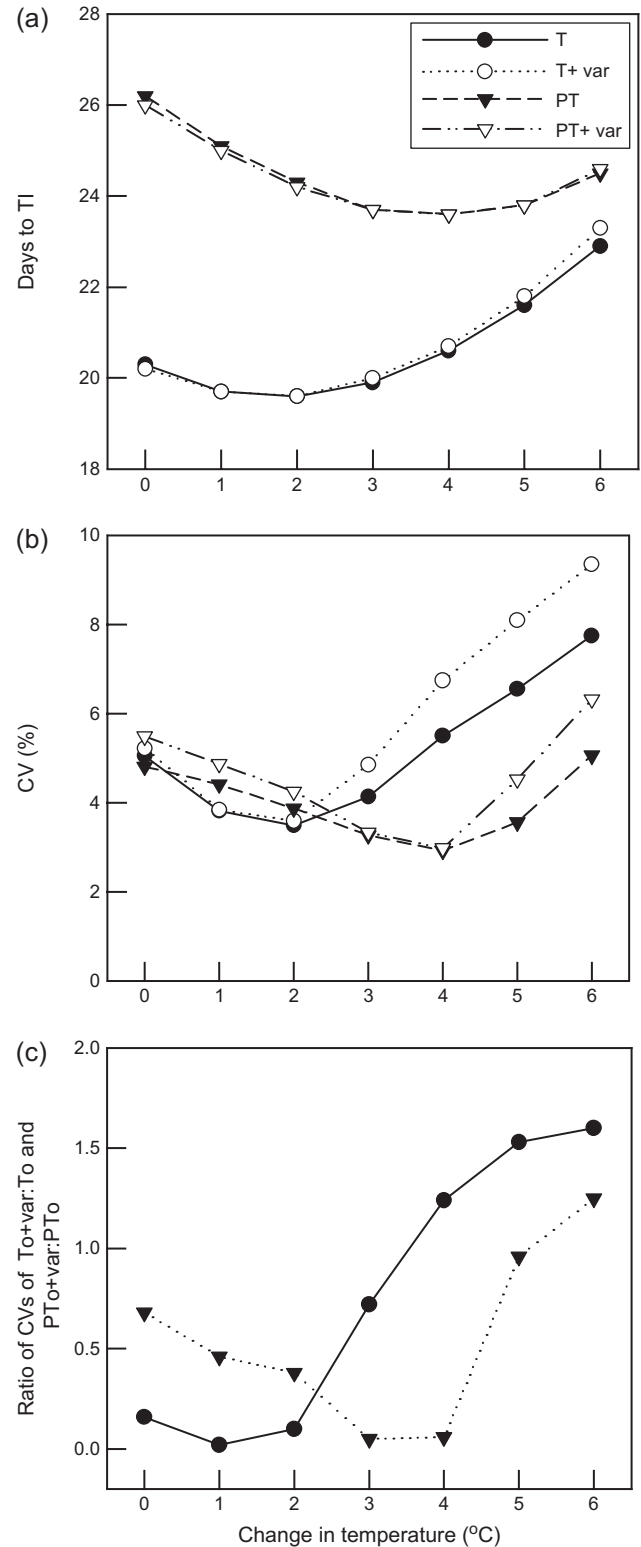

Fig. 5. The simulated effect of an increase in mean temperature and temperature variability (+var) on (a) days to tassel initiation (TI), (b) the coefficient of variation (CV%) of TI, and (c) change in CV% with temperature variability compared with normal in maize cv. Tuxpeño. Models: T, temperature response only; PT, temperature and photoperiod response.

(i) Better representation of plant development, particularly photoperiod sensitivity, in studies of the impacts of climate change on annual crops.

(ii) Improved simulations of the diversity of responses to temperature and photoperiod of crop genotypes used in low input annual cropping systems.

(ii) Data collection of past changes in phenology in cropping systems.

(iv) More observations of the response of the rate of development and temperature by photoperiod interactions above the optimum temperature to inform simulation models of crop development.

(v) More research on the effect of temperature, both sub- and supraoptimal, and interactions with photoperiod, on flowering pathway genes.

(vi) Integration of molecular and whole-plant responses and models.

Acknowledgements

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