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Temperature responses of developmental processes have not been affected by breeding in different ecological areas for 17 crop species

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Summary

- Rates of tissue expansion, cell division and progression in the plant cycle are driven by temperature, following common Arrhenius-type response curves.
- We analysed the genetic variability of this response in the range 6–37°C in seven to nine lines of maize (*Zea mays*), rice (*Oryza* spp.) and wheat (*Triticum aestivum*) and in 18 species (17 crop species, different genotypes) via the meta-analysis of 72 literature references.
- Lines with tropical or north-temperate origins had common response curves over the whole range of temperature. Conversely, appreciable differences in response curves, including optimum temperatures, were observed between species growing in temperate and tropical areas.
- Therefore, centuries of crop breeding have not impacted on the response of development to short-term changes in temperature, whereas evolution over millions of years has. This slow evolution may be a result of the need for a synchronous shift in the temperature response of all developmental processes, otherwise plants will not be viable. Other possibilities are discussed. This result has important consequences for the breeding and modelling of temperature effects associated with global changes.

Introduction

Lines and species of crop plants have evolved and been selected in different latitudes and altitudes, thereby generating differences in temperature adaptation via a large range of mechanisms (Atkin *et al.*, 2006). Indeed, gradients of latitude are accompanied by gradients of traits, such as the duration of the plant cycle, specific leaf area and survival from heat or cold stresses (Kratsch & Wise, 2000; Atkin *et al.*, 2006; Barnabas *et al.*, 2008; Penfield, 2008). The analysis of the genetic variability of the response of crop plants to temperature is therefore essential in a context in which climate changes increase the risk of yield loss because of high temperatures, without necessarily reducing the risk of exposure to low temperatures (Battisti & Naylor, 2009; Lobell *et al.*, 2011).

The analysis of short-term response curves differs from the study of the irreversible effects at high or low temperature, which require several weeks to become evident (Wise *et al.*, 1983; Bukovnik *et al.*, 2009; Gorsuch *et al.*, 2010). It involves the quantitative analysis of the short-term effects of changes in temperature over a large range, not limited to its low or high ends, in which effects are reproducible for a given line and a given range of conditions, are reversible and not dependent on the temperature history of the plant, and are independent of the intrinsic value of the studied variable measured at a standard temperature. When these conditions are fulfilled, meta-analyses of a series of experiments result in response curves to temperature or other environmental variables that allow the comparison of life kingdoms (Gillooly *et al.*, 2001; Dell *et al.*, 2011) or fitness between species in ecological studies (Poorter *et al.*, 2010). They also allow the study of quantitative genetics based on response parameters (Reymond *et al.*, 2003; Yin *et al.*, 2004) or analysis of the coordination between different mechanisms under fluctuating conditions (Parent *et al.*, 2010b; Tardieu *et al.*, 2011).

Following pioneering studies that compared the temperature responses of phyllochron and leaf elongation rate (LER) (Ong, 1983a,b; Warrington & Kanemasu, 1983a,b), we have shown recently that the germination rate, cell division rate, leaf initiation rate, LER and the reciprocal of the duration of phenological phases follow a common response to temperature after normalization by their absolute rates at 20°C (Parent *et al.*, 2010b). This implies that these processes have similar temperature responses. Conversely, the responses of *in vitro* enzyme activities and of net photosynthesis differ from those mentioned above (Parent *et al.*, 2010b). It is therefore relevant to analyse jointly the temperature responses of rates involved in the progression of plant development or in expansive growth (called 'developmental rates' hereafter), independent of those involved in plant metabolism and biomass production.

The response to temperature of enzyme activities has been described by the equation of Johnson *et al.* (1942), adequately extended to processes as diverse as the growth of bacteria (Johnson & Lewin, 1946), parameters of photosynthesis (Farquhar *et al.*, 1980), insect development (Sharpe & Demichele, 1977), plant development (Feng *et al.*, 1990; Parent *et al.*, 2010b) and 1072 physiological and ecological traits in microbes, animals and plants (Dell *et al.*, 2011).

$$F(T) = \frac{A\,T e^{\left(\frac{-\Delta H_A^{\ddagger}}{RT}\right)}}{1 + e^{\left[\frac{\Delta S_D}{R} - \frac{\Delta H_D}{RT}\right]}} \qquad \text{Eqn 1}$$

(Johnson *et al.*, 1942) ($F(T)$ is the considered rate, T is the temperature (K), $\Delta H_A^{\ddagger}$ (J mol^{-1}) is the enthalpy of activation of the reaction and determines the curvature at low temperature (Supporting Information Fig. S1a), ΔH_D (J mol^{-1}) and ΔS_D (J mol^{-1} K^{-1}) are the enthalpy and entropy of enzyme inactivation at high temperature and A is the trait scaling coefficient). When describing integrated variables instead of enzyme activities, the parameters lose their biochemical nature, and so a more intuitive modified version was preferred:

$$F(T) = \frac{A\,T e^{\left(\frac{-\Delta H_A^{\ddagger}}{RT}\right)}}{1 + \left[e^{\left(\frac{-\Delta H_A^{\ddagger}}{RT}\right)}\right]^{\alpha\left(1 - \frac{T}{T_0}\right)}} \qquad \text{Eqn 2}$$

where α (dimensionless) is the ratio $\Delta H_D/\Delta H_A^{\ddagger}$ in Eqn 1 and determines how sharp is the decrease in rate at high temperature (Fig. S1c). T_0 (K) equals the ratio $\Delta H_D/\Delta S_D$ in Eqn 1. It is the temperature at which half of the system is in an inactive state (Fig. S1b) and determines the temperature at which the rate is at a maximum (T_{opt}, Methods S1). After normalization by the rate at 20°C (to scale different processes and species and to compare them independently of their absolute values; Parent *et al.*, 2010b), parameter A is not free and depends on $\Delta H_A^{\ddagger}$, T_0 and α.

The analysis of the genetic variability of the temperature response of the developmental rates will provide essential elements to understand the thermal adaptation of contrasting genotypes grown in common ranges of temperature. A very low or nonexistent genetic variability between species or lines originating from cold or warm areas may suggest that this relationship is based on an immutable law (Eqn 2) with parameters based on physical constraints. The existence of genetic variability would indicate that mutations on key genes can substantially alter the regulatory pathways that govern the temperature response of developmental rates (McClung & Davis, 2010). Although large-scale comparisons between the temperature responses of different species and life kingdoms have been studied for enzyme activities (Campbell *et al.*, 2007) and metabolic rates (Gillooly *et al.*, 2001), such comparisons are not available for developmental processes. In this study, we performed the following investigations:

- We tested the working hypotheses for the analysis of temperature responses, that is, that these responses are reproducible and reversible without after-effects of previous temperature, and that different developmental processes have similar temperature responses after normalization by their absolute rate at a standard temperature.
- We tested whether lines originating from cold or warm areas have different temperature responses; this was performed for lines of maize (*Zea mays*), wheat (*Triticum aestivum*) and rice (*Oryza*) with diverse breeding histories and ecological origins, from temperate to tropical, by testing whether the parameters of Eqn 2 were common or differed between the lines of one species.
- We extended our analysis to the diversity of responses in 18 species (17 major crop species comprising the 14 most cultivated species in the world (http://faostat.fao.org; Table 1) and *Arabidopsis thaliana*) by compiling literature data. We tested the commonality of response curves by asking whether one or more parameter(s) of Eqn 2 could be considered as common to several species and, within each species, to different genotypes.

Description

Genetic material

Eight maize (*Zea mays* L.) lines were used in the experiments, originating from the Caribbean zone (latitudes 10–20°), tropical areas (lines CML69 and CML444; http://apps.cimmyt.org/english/wps/obtain_seed/cimmytCMLS.htm) or tropical highlands (line F331); the US corn belt (latitudes 30–40°; dent lines B73, A188 and Io); and Canada, grown since then in Europe in latitudes 40–50° (flint lines UH007 and F2). These lines are genetically very distant (Camus-Kulandaivelu *et al.*, 2006; A. Charcosset, pers. comm.) and were bred in different thermal environments (average temperature of 19°C in temperate environments, for example, north USA, or 24°C in tropical environments; Lobell *et al.*, 2011). The hybrid Io × *F2* (Dea) was considered in the same analysis.

The seven studied rice lines belonged to two species, *Oryza glaberrima* Steud. (CG14) and *Oryza sativa* L. (other cultivars), and three subfamilies of *Oryza sativa*: temperate *japonica* (Nipponbare), tropical *japonica* (Azucena, Moroberekan) and *indica* (Apo, Vandana and IR64). They originated from temperate (Nipponbare; Koumura, 1972) or tropical (others) regions. They therefore experienced different thermal environments during their breeding history, from nearly constant high temperatures in tropical areas (23–31°C in the Philippines; Peng *et al.*, 2004) to large temperature amplitudes (5–30°C in Japan; http://www.knowledgebank.irri.org). These lines also differ in their year of release, from traditional cultivars (Azucena), cultivars developed during the green revolution (IR64) in the 1980s (Moroberekan) and recently released cultivars (Vandana, Apo).

Seven wheat (*Triticum aestivum* L.) lines were analysed (Drysdale, Gladius, Kukri, Excalibur, RAC875, Chinese Spring and Bob White). Chinese Spring is a Chinese landrace, selected in a cool climate (average temperature *c.* 10°C; Lobell *et al.*, 2011), whereas South Australian lines were selected under high thermal

Table 1 Origin of the data for the different processes in 18 species

Species	Origin of data	Process
Maize	New data	Leaf elongation
	Database	Leaf elongation
	Parent *et al.* (2010b)	Germination
	Barlow & Boersma (1972)	Seedling elongation
	Ben-Haj-Salah & Tardieu (1995)	Cell division
	Blacklow (1972)	Shoot initiation
		Shoot elongation
		Radicle elongation
		Radicle initiation
	Hesketh & Warrington (1989)	Development (primordium–tip)
		Development (tip–ligule)
		Growth duration^{-1}
		Leaf elongation
		Leaf appearance
	Lehenbauer (1914)	Seedling elongation
	Tollenaar *et al.* (1979)	Leaf appearance
	Warrington & Kanemasu (1983a)	Development (sowing–anthesis)
		Development (sowing–tassel initiation)
		Emergence
	Warrington & Kanemasu (1983b)	Leaf appearance
		Leaf initiation
	Weaich *et al.* (1996)	Coleoptyl elongation
		Internode elongation
Rice	New data	Leaf elongation
	Database	Leaf elongation
	Parent *et al.* (2010b)	Germination
	Summerfield *et al.* (1992)	Development (sowing–flowering)
	Yin & Kropff (1996)	Leaf appearance (f5–f6)
	Yin *et al.* (1996)	Development (sowing–flowering)
Wheat	New data	Emergence
		Seedling elongation
		Germination
	Addae & Pearson (1992)	Emergence
		Germination
	Cutforth *et al.* (1992)	Emergence
	Dejong & Best (1979)	Emergence
		Coleoptyl elongation
		Internode elongation
	Gallagher *et al.* (1979)a	Leaf elongation
	Kemp & Blacklow (1982)	Leaf elongation
	Lafond & Baker (1986)	Germination
	Lafond & Fowler (1989)	Germination
	Lindstrom *et al.* (1976)	Emergence
Arabidopsis thaliana	Parent *et al.* (2010b)	Germination
	Granier *et al.* (2002)	Growth duration^{-1}
		Leaf expansion
		Leaf initiation
	Orbovic & Poff (2007)	Seedling elongation
Soybean	Covell *et al.* (1986)	Germination
	Hesketh *et al.* (1973)	Development (3rd trifoliate–flower)
		Development (planting–trifoliate)
		Development (unifoliate–trifoliate)
		Trifoliate production
	Lawn & Hume (1985)	Node production
		Pod production
Sorghum	Lafarge *et al.* (1998)	Leaf elongation
	Lawlor *et al.* (1990)	Germination
	Wade *et al.* (1993)	Germination
Millet	Garciahuidobro *et al.* (1982)	Germination
	Mohamed *et al.* (1988a)	Germination
	Mohamed *et al.* (1988b)	Leaf elongation
	Ong & Monteith (1985)	Root elongation
	Ong (1983a)	Leaf appearance
	Ong (1983b)	Leaf elongation
	Pearson (1975)	Leaf appearance
Cotton	Arndt (1945)	Cotyledon emergence
		Hypocotyl elongation
		Primary root elongation
	Hesketh *et al.* (1972)	Development (flower–boll)
		Development (square–flower)
		Relative leaf growth
		Plastochrons (flower, square, leaf)
	Mutsaers (1983)	Relative growth
	Reddy *et al.* (1997)	Relative internode expansion
		Relative leaf expansion
		Leaf unfolding
Canola	Marshall & Squire (1996)	Germination
	Morrison *et al.* (1989)	Development (sowing–maturity)
	Singh *et al.* (2008)	Pollen tube elongation
		Pollen germination
	Vigil *et al.* (1997)	Emergence
Sunflower	Chimenti *et al.* (2001)	Embryo growth
	Gay *et al.* (1991)	Hypocotyl elongation
		Root growth
		Germination
	Villablobos & Ritchie (1992)	Leaf appearance
Peanut	Kakani *et al.* (2002)	Pollen tube elongation
	Mohamed *et al.* (1988a)	Germination
	Prasad *et al.* (2006)	Development (sowing–V2 stage)
		Emergence
Sugar cane	Campbell *et al.* (1998)	Node production
	Inmanbamber (1994)	Plant expansion
	Mongelar & Mimura (1972)	Spindel elongation
Cassava	Akparobi *et al.* (2000)	Growth duration^{-1}
		Leaf initiation
		Leaf opening
	Keating & Evenson (1979)	Emergence
Potato	Benoit *et al.* (1986)	Stem elongation
	Fleisher & Timlin (2006)	Cell expansion and division
		Growth
	Fleisher *et al.* (2006)	Leaf appearance
	Kirk & Marshall (1992)	Leaf elongation
		Leaf appearance
Cowpea	Covell *et al.* (1986)	Germination
	Craufurd *et al.* (1996a)	Emergence
		Germination
	Craufurd *et al.* (1996b)	Development (sowing–flowering)
	Craufurd *et al.* (1996c)	Development (sowing–flowering)
	Craufurd *et al.* (1997)	Leaf appearance
	Hadley *et al.* (1983)	Development (sowing–flowering)

Table 1 (Continued)

Species	Origin of data	Process	Species	Origin of data	Process
Barley	New data	Emergence			Development (sowing–ripe pods)
		Seedling elongation			Development (sowing–visible bud)
		Germination	Common bean	Moss & Mullett (1982)	Seedling elongation
	Ellis *et al.* (1987)	Germination		Scully & Waines (1987)	Germination
	Gallagher & Biscoe (1979)	Leaf elongation		White & Montes (1993)	Germination
			Cauliflower	Olesen & Grevsen (1997)	Leaf area expansion
				Wurr *et al.* (1990)	Curd growth

Information on exact processes, materials and methods, and genotypes is available in the original papers.

amplitude (RAC875, Excalibur, Gladius, temperature from 3 to 40°C, average temperature *c.* 16°C, records from ACPFG weather stations). Excalibur and RAC875 are considered as heat tolerant and Kukri as heat sensitive (Izanloo *et al.*, 2008; Bukovnik *et al.*, 2009). Lines differ in their year of selection, from the old cultivars Chinese Spring (1940) and Bob White (1970) to recent varieties Drysdale (2002) and Gladius (2008). A barley line (Golden Promise) was added to this series to analyse the behaviour of another species from the Triticeae tribe.

LER in maize and rice subjected to short-term temperature changes

All measurements of LER were performed during the night, under well-watered conditions with wet air (air vapour pressure deficit maintained under 0.8 kPa) to avoid confusion between the effects of temperature and of evaporative demand (Ben-Haj-Salah & Tardieu, 1997). Data presented in this study are the result of a meta-analysis of several independent experiments with similar protocols.

Maize and rice plants were grown in polyvinylchloride (PVC) columns in a glasshouse with temperature fluctuating in the range 18–32°C, light in the range 10–20 mol d^{-1} m^{-2} and air vapour pressure deficit in the range 1–2.5 kPa. Soil was maintained at a water potential above − 0.05 MPa via irrigation with a 1/10 Hoagland-type nutrient solution controlled by individual pot weight (http://bioweb.supagro.inra.fr/phenodyn/). Temperatures taken into account in this article are the meristem temperatures, measured with thermocouples inserted near the meristem of at least five plants (http://bioweb.supagro.inra.fr/phenodyn). Meristem temperatures were averaged every 15 min and stored in the database PhenodynDB (http://bioweb.supagro.inra.fr/phenodyn), together with air temperature, irradiance, air vapour pressure deficit and soil water content. At the six-leaf stage, plants were transferred to the growth chamber under different temperature conditions. Environmental conditions were measured using the same methods as in the glasshouse. Typical temperature scenarios are presented in Fig. 1(c). They were intentionally varied between days and plants to avoid any confounding effect of sequences of temperature (e.g. the step at 16°C that would systematically follow a step at 28°C). In 10 plants of lines B73, CML444, A188, F-2 and UH007, LER was measured at 20°C after periods of 4 h at 6 or 35°C in order to test the possible after-effect of low or high temperature.

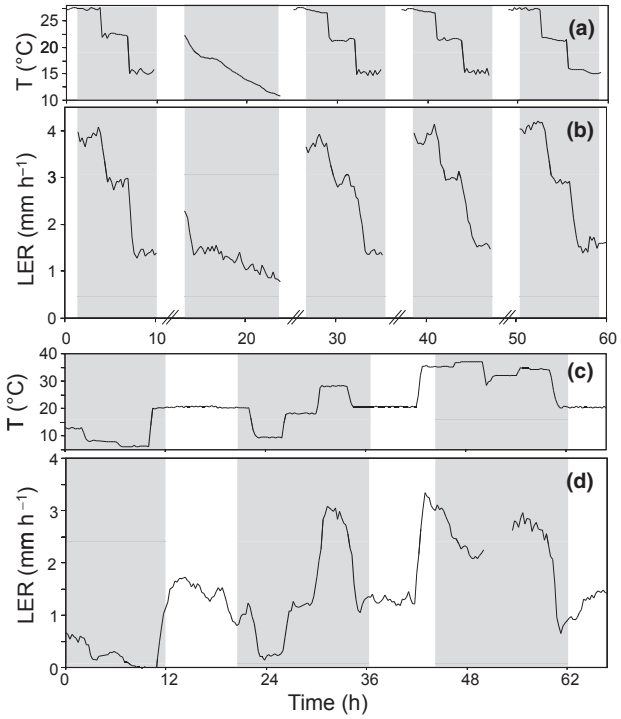

Fig. 1 Time courses of meristem temperature (*T*) and leaf elongation rate (LER) of the maize (*Zea mays*) line CML444. Grey panels indicate night periods. (a,b) Plants were placed in the growth chamber under a controlled environment, transferred to the glasshouse for a cold night (second night) and then transferred back to the growth chamber (third night) under a similar temperature scenario. (c,d) Plants were placed in the growth chamber under a wide range of temperatures from 6 to 37°C. It should be noted that temperature scenarios changed every day.

The temperature control of the growth chamber was based on the meristem temperature. Relative humidity, light intensity and air temperature were measured as in Parent *et al.* (2010b). The night temperature varied in steps of 3–4 h (Fig. 1c). LER was measured in leaf 6 with rotating displacement transducers (http://bioweb.supagro.inra.fr/phenodyn/) during the period with linear elongation (i.e. 2 d after leaf appearance in rice, Parent *et al.*, 2009; 5–6 d in maize, Sadok *et al.*, 2007), and after stabilization of temperature and LER (usually the last 2 h of each temperature step). A cloud of points of LER vs temperature, corresponding to one line in one experiment, can be seen in Fig. S2(a).

In addition, glasshouse experiments with maize or rice were included in the dataset, in particular that presented in Fig. 1(a) in maize. During the latter experiment, plants were transferred between the growth chamber and the glasshouse in order to test the after-effect of a cold night with continuously decreasing temperature. Each data point for regression is a coupled value of the meristem temperature and LER for 3 h. A cloud of points corresponding to one line in several experiments can be seen in Fig. S2b. A total of 2630 coupled values of LER and temperature were collected for maize and 598 for rice in growth chamber and glasshouse experiments. Finally, a dataset was added, for hybrid Dea only, comprising measurements of the cell division rate in leaves (Ben-Haj-Salah & Tardieu, 1995).

Germination rate at constant temperature in wheat, barley, maize and rice

The germination rate was measured under constant temperature in the seven above-mentioned wheat lines, one barley line (Golden Promise), one maize hybrid (Dea) and two rice lines (Azucena and IR64). Seeds were sown in Petri dishes (100 seeds per Petri dish) lined with saturated Whatman filter paper and placed under different temperatures (4, 9, 15.5, 20, 24.5, 28 and 35°C). Germination was scored every 8 h (6 h in rice and maize) for 2 d, every 12 h for the next 3 d, and every 1 d after that. The appearance of a radicle was scored as a germinated seed. The time for 50% cumulative germination was determined by regression on the progression curves. Data points were not taken into account when fewer than 50% of seeds germinated.

Emergence rate and seedling elongation rate at constant temperature in wheat and barley

Seedling elongation rate was measured in the wheat and barley lines presented above. Twelve seeds per line and per tested temperature were sown at a depth of 1 cm in pots filled with coco peat. Pots were placed in trays with 1 cm of free water and kept in the dark, with saturated soil and air. The appearance of coleoptiles at the soil surface was scored, and the length of the emerged coleoptiles was measured every 12 h during 5 d, and every 1 d thereafter. The time for 50% cumulative emergence was determined by regression on the progression curves. Data points were not taken into account when fewer than 50% of the initial number of seeds emerged. The coleoptile elongation rate was calculated by linear regression between 10 and 100 mm length for wheat (common linear phase in all lines) and between 10 and 60 mm length for barley.

Meta-analysis of lines originating from our database

Normalization and pooling of data Each process rate (e.g. LER, germination rate, etc.) was normalized by its mean value at 20°C (Parent *et al.*, 2010b), thereby allowing joint analysis for different processes, regardless of dimensions, units or absolute values. The normalization at 20°C was chosen because data at 20°C are available in most publications, species and processes. The rate at 20°C was determined via a linear regression performed in the vicinity of 20°C (e.g. from 18 to 22°C). Because information criteria for model comparison are sensitive to the number of data points, analyses were performed after pooling data points in 15–16 groups (example in Fig. S2c).

Test of differences in model parameters The model presented in Eqn 2 has three parameters (because A depends on $\Delta H_A^{\ddagger}$, T_0 and α, Methods S2). In order to determine which parameters are common/differ between lines, the model with three parameters (called M.3 hereafter) was compared with seven models in which one, two or three parameters were common to the studied lines (Table 2). Three models had two free parameters (M.2a, M.2b and M.2c) and one parameter common to the studied lines. Three models (M.1a, M.1b and M.1c) had one free parameter and two parameters common to the studied lines. Finally, one model (M.0) had no free parameter, thereby resulting in a common temperature response for all lines.

Calculation of model parameters Parameters of individual response curves were calculated using the nonlinear regression function *nls* of the R language (R Development Core Team, 2005). Depending on the number of free/fixed parameters, different procedures were used to ensure convergence in the fitting procedure (Fig. S3).

Model comparison We used several indicators to compare nonlinear models, including the root-mean-square error (RMSE) and the coefficient of variation of the RMSE (CV_{RMSE}). We also used indicators that add a penalty to the number of estimated parameters, thereby avoiding overfitting, namely the Akaike information criterion (AIC; Akaike, 1974; function *AIC*() in R software) and the Bayesian information criterion (BIC; Schwarz, 1978; function *BIC*()). The best model according to these indicators is that with the lowest values of BIC and AIC. The Akaike weights (Akaike, 1978) indicate the probability for one model to be the best model given the dataset. Here, we calculated these weights for BIC values (w_{BIC}).

Table 2 Number of free/fixed parameters in each of the eight studied models

Model	No. of free parameters	$\Delta H_A^{\ddagger}$	T_0	α
M.3 (Eqn 2)	3	Free	Free	Free
M.2a	2	Fixed	Free	Free
M.2b	2	Free	Free	Fixed
M.2c	2	Free	Fixed	Free
M.1a	1	Fixed	Free	Fixed
M.1b	1	Fixed	Fixed	Free
M.1c	1	Free	Fixed	Fixed
M.0	0	Fixed	Fixed	Fixed

The three parameters are those of Eqn 2. In each model, a free parameter is calculated individually for each genotype or species. A fixed parameter is common to all considered genotypes or species.

For an easier interpretation of these criteria, we compared model indicators with that of model M.3. ΔCV is the difference between CV_{RMSE} of one model and that of model M.3, and is interpreted as the additional error when fixing parameters. With regard to experimental errors and the difference targeted between lines, an additional error of 5% was accepted for models with fewer parameters. ΔAIC and ΔBIC are the differences in values between the considered model and model M.3. ΔAIC and ΔBIC of < 5 were accepted for models with fewer parameters compared with model M.3.

Sensitivity analysis on model comparison The sensitivity of statistical indicators to changes in the temperature response was tested using the procedure described in Fig. S4. New datasets were created by modifying that of maize. To test a shift in the whole response curve, including T_{opt}, all temperatures in the original dataset were shifted by a step of 1°C between − 2 to + 2°C in relation to the original values (for example, the temperature was lowered by −1°C for each coupled value of rate/temperature; Fig. S4c,d). To test a difference in the sensitivity of rates to high temperature, rates above the optimum temperature were lowered or increased by a step of 5% from − 20% to + 20% in relation to the original values (e.g. for + 10%, all data points above 30.8°C were multiplied by 1.1; Fig. S4a,b). Each new dataset was compared with the original by calculating ΔBIC and ΔCV between model M.3 and model M.0.

Comparison of four species from our database Normalized data corresponding to different lines were pooled within each of the four tested species (maize, rice, wheat and *Arabidopsis thaliana*). We used a similar procedure to that explained above to compare lines, taking into account 13–20 groups of data per species. Parameter calculation and model comparison were carried out as described above for lines. To confirm the results of model comparison obtained with the Bayesian approach, a cascade of *F*-tests was carried out on the nested models (R function anova.nls()). The simplest model was accepted unless the test was significant ($P < 0.05$).

Comparison of 18 species from our database or from the literature

All other data were collected from the literature (Table 1), from tables or figures of the original papers. The positions of data points were recorded in figures by image analysis (software ImageJ (http://rsbweb.nih.gov/ij/)). In Covell *et al.* (1986) and Ellis *et al.* (1987), only the 50% germination rates were retained in the analysis. For the germination rates taken from Scully & Waines (1987), only the crop species were analysed. In Hadley *et al.* (1983), only the photoperiod insensitive lines were analysed. In Weaich *et al.* (1996), the coleoptile elongation rate was calculated as the reciprocal of the duration to reach a length of 15 mm. The internode elongation rate was calculated as the reciprocal of the duration to reach a length of 25 mm. In Summerfield *et al.* (1992), Yin & Kropff (1996) and Yin *et al.* (1996), only data obtained under constant temperature were used in the analysis.

Each dataset was normalized by the corresponding value at 20°C using the procedure described above. A pooling of the data resulted in 13–20 groups per species. For each model, the fixed parameter values were those of the four species analysed. Parameter values and model criteria were calculated as in the line analysis.

The optimum temperature T_{opt}, at which the rate is at a maximum, was calculated from model parameters (Methods S1):

$$\frac{1}{T_{opt}} = \frac{1}{T_0} + \frac{R}{\alpha \Delta H_A^{\ddagger}} \log\left(\frac{(\alpha - 1)\Delta H_A^{\ddagger} - R * 303}{\Delta H_A^{\ddagger} + R * 303}\right) \qquad \text{Eqn 3}$$

Confidence intervals of model parameters and T_{opt} were calculated by bootstrapping (1000 replicates).

Results

The working hypotheses for the analysis of temperature responses were fulfilled

The first condition mentioned in the Introduction is that a trait has a unique response to temperature over a large range of conditions for a given line of the studied species. This was the case when either similar or different temperature scenarios were applied on several days (Fig. 1a,b, days 1, 3, 4, 5, and Fig. S2a). Similar results were found in rice (Parent *et al.*, 2010b).

Second, the establishment of response curves requires that the temperature effect is reversible, that is, the rate at a given temperature is independent of previous temperatures during the experiment. This was the case for durations of exposure ranging from hours to days. Exposures to 6 or 34°C for 4 h (the duration of a typical peak of temperature in natural conditions) had no significant effect on LER at 20°C ($P = 0.6$; Figs 1c,d, S5a,b). In the same way, LER was unaffected by a previous long night at low temperature (Fig. 1a,b, night 2). This resulted in a unique response curve per line, regardless of plant, experiment and thermal history, even though absolute rates at a given temperature differed between lines (Fig. S2). Lines of rice showed a similar behaviour in this respect (data not shown).

The domain of validity of the response covered a large range of developmental processes. After normalization by the rate at 20°C, which allows one to scale different processes that have different units, the response to temperature in one line was common between several developmental processes in maize (hybrid Dea; Fig. 2a), rice (line Azucena; Fig. 2r) and wheat (variety Drysdale; Fig. 2j). A meta-analysis of 21 sources of information (Table 1) extended this conclusion to traits referring to leaves, roots or seedlings, growth rates, cell division rate, germination rate or reciprocal of duration of phenological phases. This led to a common response curve for all of these processes, exemplified in Fig. 3(b) for maize. It is noteworthy that processes associated with response times of a few days (e.g. phyllochron) showed similar response curves to those having a response time of minutes (e.g. elongation rates; Figs 2a, 3b), indicating that the responses of the processes studied here were essentially time independent in the range 6–37°C.

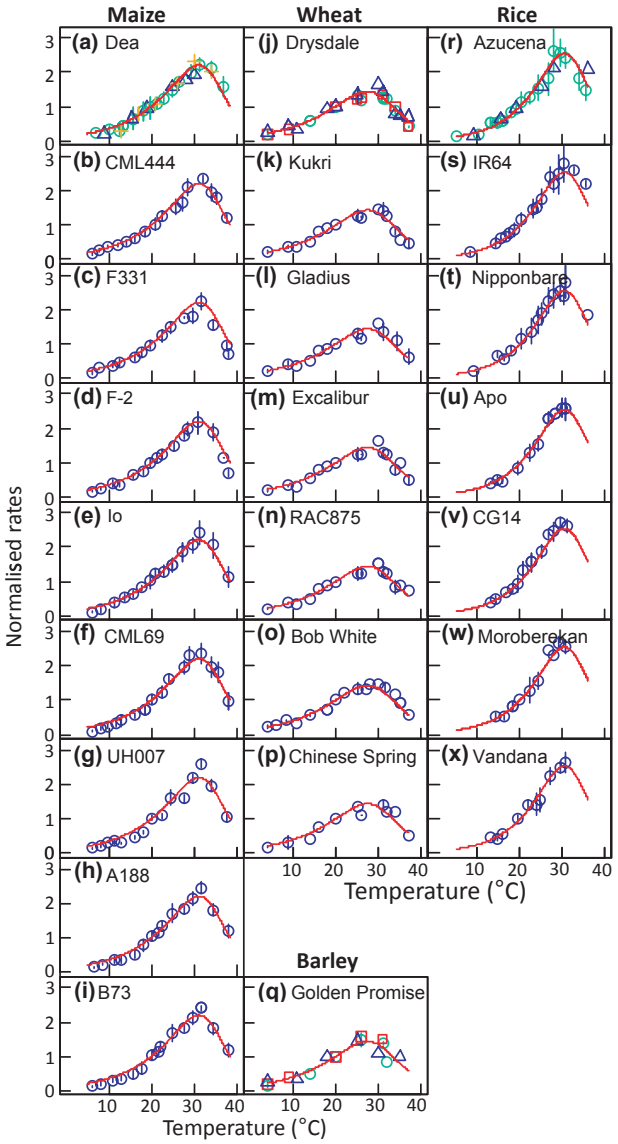

Fig. 2 Response curves to temperature of several rates involved in plant development in lines of maize (a–i), wheat (j–p), barley (q) and rice (r–x). Rates are normalized by their mean value at 20°C, set to unity. For each species, the red line corresponds to a common model for all genotypes (model M.0, Table 2). A common model applies to barley (q) and wheat (j–p). (a,j,r,q) The normalized responses to temperature of several developmental processes presented on the same graph. Green circles, leaf (a,r) or seedling (j,q) elongation rate; red squares, reciprocal of the duration from sowing to emergence; blue triangles, germination rate; orange circles, cell division rate. In all panels, blue circles represent the average of all studied processes. Other panels present the response of leaf elongation rate (maize and rice) or germination and seedling elongation (wheat). Error bars indicate standard deviation (SD).

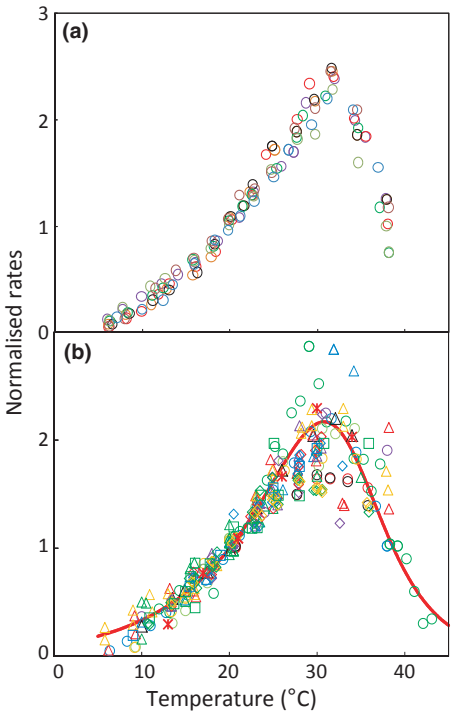

Fig. 3 Response curve to temperature of leaf elongation rate for nine maize (*Zea mays*) lines (a) and of several processes in a meta-analysis of literature data (b). Each process is normalized by its corresponding value at 20°C. The red line represents a common model for all processes and genotypes (M.0, Table 2). Regression parameters are summarized in Table 3. (a) Leaf elongation rate for genotypes: CML444, purple; CML69, red; B73, orange; A188, black; F2, cyan; F331, green; Io, brown; Dea, deep blue. (b) Temperature dependence of several developmental processes. Circles represent expansion processes: leaf elongation, new data (blue); coleoptile elongation from Weaich *et al.* (1996) (red); seedling elongation from Lehenbauer (1914) (cyan) and Barlow & Boersma (1972) (purple); internode elongation from Weaich *et al.* (1996) (black); shoot elongation from Blacklow (1972) (green); radicle elongation from Blacklow (1972) (yellow). Triangles represent organ initiation and appearance: radicle initiation from Blacklow (1972) (black); shoot initiation from Blacklow (1972) (blue); leaf initiation from Warrington & Kanemasu (1983b) (red); leaf appearance from Hesketh & Warrington (1989) (purple); leaf appearance from Warrington & Kanemasu (1983b) (yellow); leaf appearance from Tollenaar *et al.* (1979) (cyan). Diamonds represent development rate between two events: leaf primordium to leaf tip appearance from Hesketh & Warrington (1989) (purple); leaf tip appearance to ligulation from Hesketh & Warrington (1989) (red); growth duration from Hesketh & Warrington (1989) (blue); sowing to tassel initiation from Warrington & Kanemasu (1983a) (cyan); sowing to anthesis from Warrington & Kanemasu (1983a) (yellow). Squares represent germination and emergence: germination from Parent *et al.* (2010b) (blue); emergence from Warrington & Kanemasu (1983a) (turquoise). Stars represent cell division from Ben-Haj-Salah & Tardieu (1995).

Hence, response curves were established hereafter by considering data points originating from different thermal scenarios, different developmental processes and from our own experiments or from the literature. In the experiments presented below, most comparisons between lines were performed on the temperature response of LER.

The genetic variability was very low between lines originating from tropical or temperate regions, from different breeding generations and with different heat tolerances

In maize, the nine studied lines originating from various regions and climates (Caribbean zone, tropical highlands, US corn belt and temperate regions of Canada and Europe) were associated

with similar response curves (Fig. 2), almost indistinguishable over the whole range of temperature when plotted together (Fig. 3a). To identify putative differences between these curves, we tested whether one or more parameters of Eqn 2 could be considered as common to all lines. A model with three free parameters (model M.3, three parameters differing between lines) was compared with seven models with zero, one or two free parameters (Table 2). Statistical criteria indicated that the best model was model M.0, which considers that all three parameters are common to the nine studied lines (Fig. 4a,b and Table S1). Furthermore, CVs of errors increased by 2% only in model M.0 compared with the others, far from the 5% error that was considered as the limit in view of experimental errors (Fig. 4b). A sensitivity analysis showed that this procedure was able to detect a 1°C shift in the whole response curve towards higher or lower temperature (Fig. 4c,d). It also showed that we could detect a difference in rate of ± 10% in the range above T_{opt}, where precision was lower than in the range below T_{opt} (Fig. 4a,b). It can therefore be concluded that a unique response curve applied to maize lines with very different origins, to hybrid as well as to inbred lines. This conclusion can be extended to 23 lines described in the literature, with different origins and dates of release, including one line released in 1914 (Table 1, Fig. 3b). All lines had a response curve with common parameters to those calculated with our data (Fig. 3b).

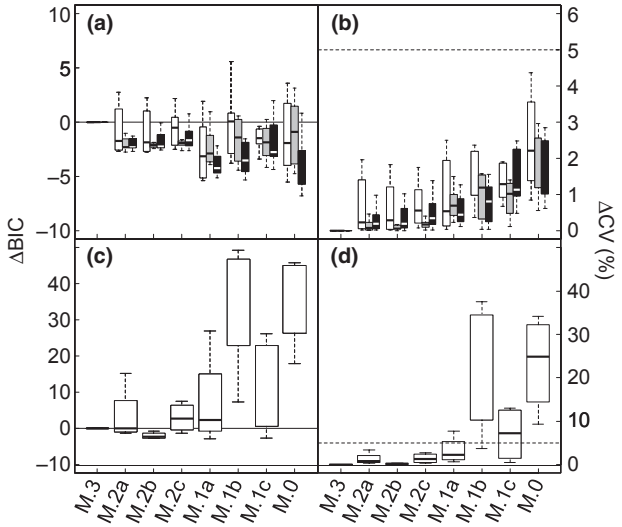

Fig. 4 Comparison of models presented in Table 2. (a,b) Comparison of models assuming that zero to three parameters differ between genotypes of each species. (a) Box-plot of the differences in the Bayesian information criterion (ΔBIC) between model M.3 and the seven other models for genotypes of maize (white), rice (grey) and wheat (black). The lowest values of ΔBIC indicate the best models. (b) Difference in coefficient of variation of the error (ΔCV, in % of CV of model M3) between model M.3 and the seven other models for genotypes of the three species. Lowest values of ΔCV indicate the best models. The horizontal line represents the threshold of tolerance of 5% of additional error compared with model M.3. (c,d) Comparison of models assuming that zero to three parameters differ between four species (maize, wheat, rice and *Arabidopsis thaliana*). (c) Box-plot of ΔBIC between model M.3 and the seven other models for the four species. (d) ΔCV between model M.3 and the seven other models for the four species. Line in (d) as in (b). Other model selection criteria are presented in Supporting Information Table S1.

In rice, the seven studied lines belonged to different species and subspecies (*O. glaberrima*, *O. sativa* ssp. *indica* and *japonica)* from tropical or temperate regions of Asia or Africa. As in maize, the comparison of the different statistical criteria led to the conclusion that the model with common parameters for all lines was acceptable (Fig. 4a and Table S1), with an added error lower than the 5% threshold compared with models specific to each line (2.0% on average; Fig. 4b and Table S1). This indicated that differences between rice lines with regard to the response curve and T_{opt} corresponded, if they existed, to a shift lower than 1°C (Fig S4). Lines originating from different ecological areas and from different species or subspecies therefore had a common temperature–rate relationship. There was no trend for an effect of breeding between lines that were traditional (Azucena, Moroberekan), developed during the green revolution (IR64) or recently released (Vandana, Apo).

In wheat, we compared several lines selected in cool or warm climates, tolerant or sensitive to heat stress and released from the 1940s until recently. As above, a common model applied to the whole dataset (Fig. 2), with no significant differences between lines, as shown by the statistical criteria comparing models (Fig. 4a), as well as by the low additional error obtained when considering that the three parameters were common to all lines (ΔCV = 1.4% on average; Fig. 4b and Table S1). It can be concluded that any difference between lines would involve a shift of < 1°C (Fig S4c,d). The response was also common for a barley line (*Hordeum vulgare* cv. Golden Promise), which, like wheat, belongs to the Triticeae tribe (Fig. 2q), with an increase in error of < 2% when considering a unique model compared with separate models for each species (not shown).

The responses of developmental processes differed in 18 species with a trend between cool-/warm-adapted species

The variability of the temperature response was explored in 18 species (17 crop species comprising the 14 most cultivated species worldwide and *Arabidopsis thaliana*). Results were collected from either our own database or the literature, with 42 variables, 73 references and 122 experiments (Table 1). The variables analysed in this study involved different genotypes for each species and developmental processes as different as the expansion rates of several organs (pollen tube, roots, leaves and embryo), the reciprocal of durations of phases, the cell division rate and germination rate.

In order to select the model that best suited the comparison between species, the analysis was first restricted to four species in which we had access to well-controlled datasets obtained by our groups (dataset of Fig. 2 in maize, rice and wheat, and the *Arabidopsis thaliana* dataset presented in Parent *et al.*, 2010b). When comparing the eight models of Table 2, statistical indicators showed that the response curves differed between species, because a unique model for different species (M.0) was not acceptable (ΔBIC = + 40 and ΔCV = 25%, far from the thresholds of + 5 and + 5%, respectively; Fig. 4c,d and Table S1). An *F*-test procedure resulted in a similar conclusion (Fig. S6). The model M.2b, with a common α for all species, was the best model (ΔBIC = − 2.2; Fig. 4c, Table S1, Fig. S4), with 0.1% of

additional error compared with the model with three parameters. The other models, in particular those assuming that T_0 was common between species, were rejected. We therefore compared the 18 species using model M.2b, in which species differ by two parameters of Eqn 2, namely the characteristic temperature T_0 and activation enthalpy $\Delta H_A^{\ddagger}$.

Response curves corresponding to the 18 studied species followed similar patterns with different parameters (Fig. 5). The model M.2b applied to all species, with r^2 ranging from 0.92 to 0.98 (Table 3). Its two parameters, $\Delta H_A^{\ddagger}$ and T_0, are presented for each species in Table 3 and in spreadsheet format in Table S2. They were independent (Fig. S7a), confirming the two degrees of freedom of this model. In the following paragraph, we have transformed them into two more intuitive characteristics of response curves for each species, namely the optimum temperature T_{opt}, for which rates are at a maximum (related to T_0; Eqn 3; Figs S1b, S7b), and the range of temperature in which the considered rate is higher than 50% of the maximum rate ($range_{50\%}$), related to $\Delta H_A^{\ddagger}$ (Figs 5, 6 and Table 3).

Species originating from cool areas, such as canola (*Brassica napus* L.) and cauliflower (*Brassica oleracea*), showed the lowest values for T_{opt} (23.1 ± 0.7 and 21.6 ± 1.2°C; Table 3 and Fig. 6). Species adapted to warm climates, such as pearl millet (*Pennisetum glaucum*), peanut (*Arachis hypogaea*), cotton (*Gossypium*), sorghum (*Sorghum bicolor*) and cowpea (*Vigna unguiculata*), showed high values of T_{opt} (from 32.4 ± 0.5 to 34.1 ± 1.5°C). This climatic effect applied within families of species, for instance in Poaceae species, in which T_{opt} ranged from relatively low to high values in wheat and sorghum (27.7 ± 0.2 and 34.1 ± 1.5°C, respectively).

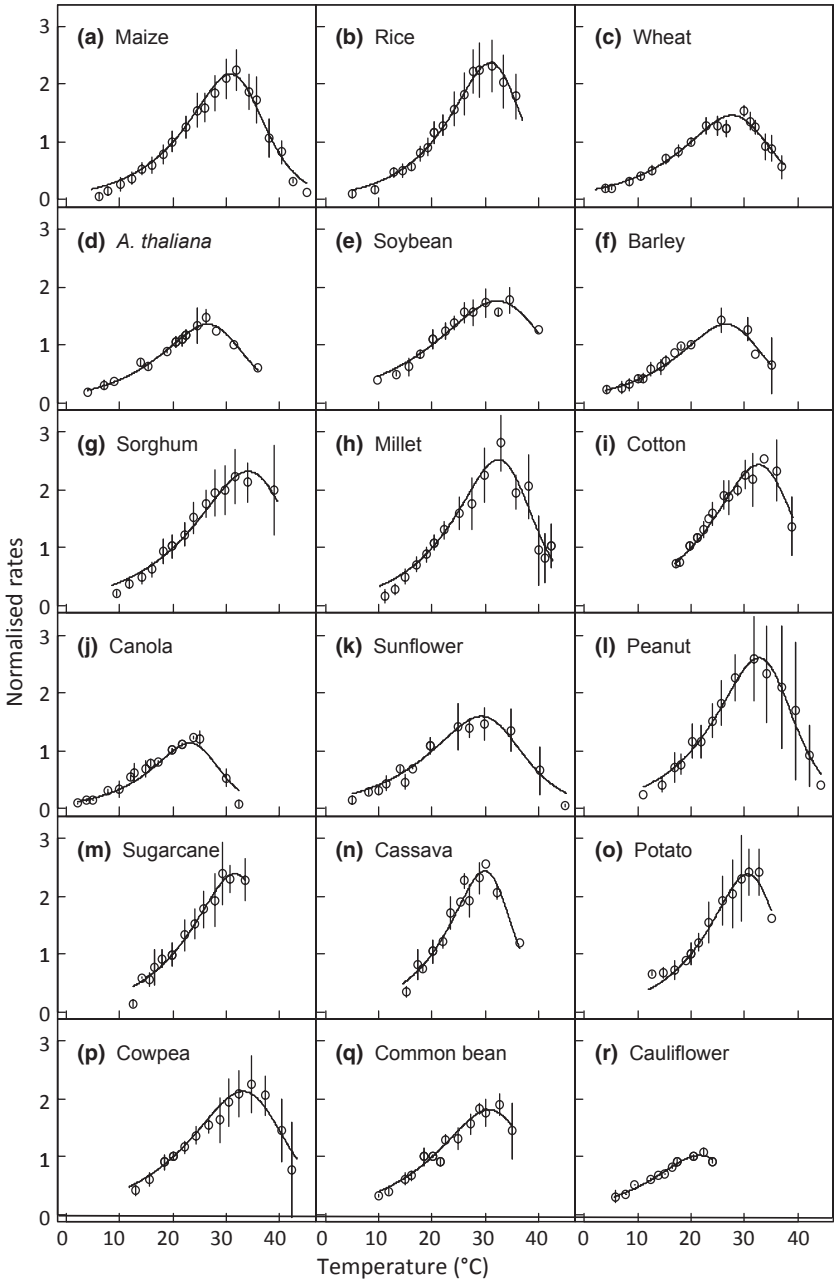

Fig. 5 Response curve to temperature of developmental processes in 18 species. Each variable is normalized by its corresponding value at 20°C. Lines represent models for the considered species (model 2b). The origin of the data is given in Table 1. Model parameters are shown in Table 3 and Supporting Information Table S2.

Table 3 Parameter values and quality of regression for the 18 studied species (model M.2b)

	Model M.2b					
Species	R^2	$\Delta H_A^{\ddagger}$ (kJ mol^{-1})	T_0 (°C)	T_{opt} (°C)	$Range_{50\%}$ (°C)	$Rate_{max}$
Arabidopsis thaliana	0.98	65.1 ± 3.5	29.3 ± 0.4	26.5 ± 0.5	15.6–34.7	1.35
Barley	0.95	65.1 ± 3.5	29.4 ± 0.9	26.5 ± 0.9	15.6–34.7	1.36
Canola	0.94	80 ± 6	25.4 ± 0.8	23.1 ± 0.7	15.0–29.6	1.13
Cassava	0.95	89.6 ± 5.5	32 ± 0.6	29.9 ± 0.6	21.6–35.9	2.43
Cauliflower	0.98	63.6 ± 4.3	24.4 ± 1.2	21.6 ± 1.2	15.0–29.7	1.02
Common bean	0.96	61.7 ± 3.8	33.8 ± 1.2	30.7 ± 1	18.9–39.6	1.81
Cotton	0.95	70.3 ± 3.7	35.4 ± 0.9	32.6 ± 0.7	22.1–40.5	2.44
Cowpea	0.93	60 ± 3.5	36.3 ± 1.1	33.1 ± 0.9	20.8–42.4	2.13
Maize	0.98	73.9 ± 2.1	33.4 ± 0.2	30.8 ± 0.2	20.8–38.2	2.17
Millet	0.92	73.6 ± 4.3	35.1 ± 0.5	32.4 ± 0.5	22.3–39.9	2.53
Peanut	0.97	73.9 ± 2.9	35.3 ± 0.4	32.7 ± 0.3	22.6–40.2	2.61
Potato	0.97	81.7 ± 4	33 ± 1.4	30.6 ± 0.9	21.6–37.3	2.38
Rice	0.99	78.9 ± 3.1	33.4 ± 0.5	30.9 ± 0.5	21.6–37.8	2.36
Sorghum	0.98	60.6 ± 6	37.3 ± 1.7	34.1 ± 1.5	21.8–43.3	2.32
Soybean	0.97	52.3 ± 4.7	35.8 ± 1.2	32.2 ± 1	18.3–42.9	1.76
Sugarcane	0.98	75.2 ± 6	34.2 ± 1.2	31.6 ± 1.3	21.7–38.9	2.39
Sunflower	0.94	60.4 ± 5.8	32.4 ± 1.1	29.3 ± 0.9	17.3–38.3	1.60
Wheat	0.97	63.3 ± 3.6	30.6 ± 0.3	27.7 ± 0.2	16.4–36.2	1.46

R^2, coefficient of determination of the regression between fitted and observed values; $\Delta H_A^{\ddagger}$, T_0 and α are the three parameters of Eqn 2. In model M.2b, α was common to all species (α = 3.5). T_{opt} (optimum temperature) is the temperature at which the development rate is at a maximum. $Range_{50\%}$ is the temperature range within which the development rate reaches 50% of its maximum value. $Rate_{max}$ is the maximum rate in proportion to the value at 20°C. Parameter values are given ± SE calculated by bootstrapping.

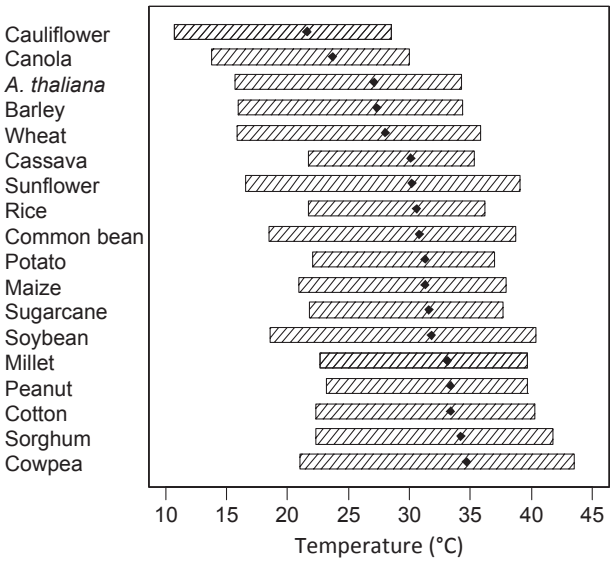

Fig. 6 Temperature at which rates are at a maximum (T_{opt}, black dots) and range of temperature for which the rate of development is at least 50% of its maximum (horizontal bars) in 18 species. Species are ranked by values of T_{opt}, also representing a gradient from temperate to tropical species.

Discussion

Coordination between developmental processes and absence of acclimation of temperature responses

The results presented here confirm and extend to a larger range of processes and species those observations recorded earlier on the coordination of developmental processes via a common response curve to temperature (Ong, 1983a,b; Warrington & Kanemasu, 1983a,b; Parent *et al.*, 2010b). By contrast, photosynthesis and enzyme activities have response curves that differ markedly from those presented here (Campbell *et al.*, 2007; Sage *et al.*, 2008; Parent *et al.*, 2010b). Furthermore, they have nonunique temperature responses because they acclimate to changes in temperature within a few days (Sage & Kubien, 2007).

The absence of acclimation of the temperature response of developmental processes is not in contradiction with plant adaptation to low or high temperatures. Marked differences in the duration of the plant cycle (e.g. number of days after sowing at a given temperature) are observed following selection over several generations in plants, but without modification of the temperature response of this duration (Craufurd *et al.*, 1999). We show here that the response to temperature of these durations was common to all lines within a cultivated species. Morphological or anatomical adaptations to low or high temperature occur over periods of weeks (Gorsuch *et al.*, 2010). For example, changes in anatomy are still small after 6 d at 5°C, are noticeable after 30 d and become dramatic in new leaves developing under cold temperatures (Gorsuch *et al.*, 2010). The same conclusion applies to trees grown in different environments (Rehfeldt *et al.*, 2002).

Morphological changes linked to temperature may be an emerging property generated by the difference in behaviour between metabolic processes, with changes in response to temperature after acclimation, and developmental processes which do not acclimate. This would cause changes in carbon accumulation and specific leaf area (Tardieu *et al.*, 1999), observed experimentally by several groups (Loveys *et al.*, 2002; Shahba & Bauerle, 2009; Atkinson *et al.*, 2010; Fajardo & Piper, 2011).

A similar view has been proposed recently for the response to water deficit (Tardieu *et al.*, 2011).

An absence of genetic variability of responses within the most common species

A different choice of lines within each species is unlikely to have yielded a different conclusion with regard to the genetic variability within species. In maize, the set of studied lines included tropical lines at very large genetic distances from the temperate lines (Camus-Kulandaivelu *et al.*, 2006). Data originating from the literature confirm this conclusion (Fig. 3b). Furthermore, no quantitative trait loci were detected for the temperature response of LER over a shorter range of temperature in three mapping populations (Reymond *et al.*, 2003; Sadok *et al.*, 2007; Welcker *et al.*, 2007), confirming the absence of a structured genetic variability. In the same way, the diversity tested in rice was large, with different species or subspecies, origins and generations of selection. The same result applied to wheat lines with different stress tolerances, suggesting that differences in heat tolerance involve the lowest and highest temperatures for which response curves can be established, but not the response curves themselves. It is noteworthy that, in the panels of lines tested here or in mapping populations derived from them, other traits showed a large genetic variability and clear quantitative trait loci (Reymond *et al.*, 2003; Chardon *et al.*, 2004; Izanloo *et al.*, 2008; Parent *et al.*, 2010a; Welcker *et al.*, 2011). Hence, the lack of genetic variability on the temperature response observed here was not a consequence of a poor choice of lines. It was probably not the result of a low power of statistical tests either, because our sensitivity analysis showed that we could identify a shift of < 1°C when comparing response curves of lines or species. Finally, the conclusion with regard to the absence of genetic variability can be extended to the other crop species presented in Table 1, which were analysed on at least three genotypes each (except barley, two genotypes).

A shift in temperature response probably requires millennia under very contrasting climates

The above paragraph shows that breeding in climates involving either high or low temperature has not affected the response of developmental processes to temperature, in particular T_{opt}. Centuries of mutations and selection are therefore not sufficient to affect this response within each species, contrary to most other traits that have responded to breeding. We therefore propose that a shift in temperature response requires two conditions. First, it requires millennia, i.e. at least the period during which most species have been bred. The second proposed condition is a marked contrast of climate. *Triticum* and *Hordeum* genera that genetically diverged more than 10 million yr (My) ago (Feuillet *et al.*, 2008) still have response curves with common parameters, probably because they grew under similar climatic conditions. This may apply to rice species and subspecies that have diverged for a longer period than that of agriculture (*c.* 11 000 years). No significant difference was observed between the subspecies *indica* and *japonica*, which diverged 0.4 My ago, or between the species *O. sativa* and *O. glaberrima*, which diverged 0.6 My ago (Ma & Bennetzen, 2004). This is probably also the case for sorghum and sugarcane, which diverged 5 My ago (Ming *et al.*, 1998), and sorghum and maize, which diverged 10 My ago (Ramakrishna *et al.*, 2002). Differences were only observed in the case of very ancient divergence and very different climates, as in the contrast between Triticeae species and tropical grasses, such as sorghum, maize, millet or sugarcane, which diverged 50 My ago (Gale & Devos, 1998) and grew for a long period in different climates.

Hypotheses for very slow evolution

A first hypothesis is that the evolution of temperature responses has been slowed down by the necessity for a synchronous shift in the responses of several processes. What would happen if a mutation changed the temperature response of one developmental process but not of the others? Simple computer simulations (not shown) suggest that a plant which loses the coordination between developmental processes because of a mutation would have highly disturbed performances, with, for example, a reproductive development occurring too early in comparison with vegetative development, or a disturbed aspect because of the lack of coordination between processes involved in the control of growth. We can therefore hypothesize that natural and breeder's selection has eliminated mutations that affect temperature responses of one process only, thereby requiring a very long time to obtain the response of all processes to shift simultaneously.

A second hypothesis is based on the fact that even the diversity found in the 18 tested species is low when compared with the six-fold differences in activation enthalpy found in different traits and life kingdoms (Dell *et al.*, 2011). The theory of 'thermodynamic constraint' (or 'warmer is better'), developed in animal studies (Huey & Kingsolver, 1989; Frazier *et al.*, 2006), argues that low temperatures slow down all biochemical reactions and that adaptation cannot change this rule. Because maximum rates occur at low temperature in cold-adapted plant species, such species would have lower maximum rates and performances than warm-adapted species, for which maximum rates occur at higher temperature, with higher rates of all biochemical reactions. By focusing mainly on plant performance, breeding may have selected lines and species with high optimum temperatures regardless of the ecological area. In our results, T_{opt} was generally higher than the mean temperature during the crop cycle. Eleven of the 17 studied crop species had optimum temperatures above 30°C, higher than those commonly observed in their growing regions. In these species, the temperature response may have reached a final equilibrium between a broad adaptation to a range of climate and maximum growth.

Consequences for breeding and modelling

Our study suggests that there is little chance that breeding can substantially affect the temperature responses of the developmental rates analysed here, because of a nonexistent source of genetic

variability in crop species. This does not rule out several possibilities related to genetic adaptations of other traits related to temperature responses. First, the duration of the plant cycle has a considerable genetic variability, in particular between tropical and temperate materials. We therefore argue here that, although durations or rates have a large genetic variability, the change with temperature in these durations or rates does not vary between tropical and temperate lines. One way to avoid a decrease in yield with increasing temperature is to use lines with a longer crop cycle (Lobell *et al.*, 2008). Manipulating the respective durations of crop phases would also improve the yield potential in cereals (Borràs *et al.*, 2010). Second, a genetic gain has been obtained by breeding for the range of temperatures in which plant metabolism is not damaged under prolonged high or low temperature. For instance, the wheat line Excalibur used here tolerates high temperatures that cannot be tolerated by Kukri (Bukovnik *et al.*, 2009). This implies that the responses observed here, which apply to nonstressed ranges, are largely independent of tolerance to cold or heat stress. Third, high temperatures usually occur together with high evaporative demand, which has a considerable effect on gas exchange and growth, with a large genetic variability of this effect (Sadok *et al.*, 2007; Welcker *et al.*, 2007).

Our results also simplify the modelling of the effects of global changes, because lines grown in 50 or 100 yr will probably have a response to temperature similar to that of current lines. Existing crop models (Brisson *et al.*, 2003; Hammer *et al.*, 2010) already implicitly assume a common response of developmental processes, which is confirmed here. The response to temperature of a large range of species can be characterized by two traits that are relatively easy to measure, namely T_{opt} and the ratio between the rate at T_{opt} and that at 20°C. The parameters of Eqn 2 can be derived from these two traits (Eqn 3). Furthermore, because of the similar values of species in a given ecological area or not too distant genetically, modelling can be performed using the values of related species.

Acknowledgements

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Supporting Information

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

Fig. S1 Sensitivity analysis of the model M.3.

Fig. S2 Data handling, example of genotype CML444.

Fig. S3 Calculation of parameter values for models M.3, M.2b and M.0 in the maize hybrid 'Dea'.

Fig. S4 Analysis of the sensitivity of the information criterion (ΔBIC, a,c) and supplemental error (ΔCV, b,d) to changes in the temperature response. BIC, Bayesian information criterion; CV, coefficient of variation.

Fig. S5 Effect of previous high or low temperature on leaf elongation rate at 20°C.

Fig. S6 *F*-test between the different nested models in four species.

Fig. S7 Correlation between model parameters and the optimum temperature in 18 species.

Table S1 Goodness-of-fit evaluation of the different models considering one species (maize, rice or wheat) or four species

Table S2 Spreadsheet with parameters and temperature response functions for the 17 crop species and *Arabidopsis thaliana*

Methods S1 Calculation of optimum temperature from parameters of Eqn 2.

Methods S2 Fitting version of Eqn 2 after normalization at 20°C.

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