

Differences in temperature responses among phenological processes in diverse Ethiopian sorghum germplasm can affect their specific adaptation to environmental conditions

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Received: 17 October 2022 Returned for revision: 3 January 2023 Editorial decision: 9 January 2023 Accepted: 12 January 2023
Electronically published: 20 January 2023

- **Background and Aims** Main shoot total leaf number (TLN) is a key determinant of plant leaf area and crop adaptation. Environmental factors other than photoperiod can affect TLN in sorghum, implying that leaf appearance rate (LAR) and development rate can differ in response to temperature. The objectives of this study were to determine (1) if temperature effects on TLN can be explained as a consequence of differences in temperature responses across phenological processes and (2) if genotypic differences in these responses can be linked to agroecological adaptation.
- **Methods** Nineteen sorghum genotypes were sown on 12 dates at two locations in Ethiopia with contrasting altitude, creating temperature differences independent of photoperiod. TLN and temperature were recorded in all experiments and LAR for six sowing dates.
- **Key Results** Eleven of the genotypes showed a temperature effect on TLN, which was associated with a significantly higher base temperature (T_{base}) for LAR than for pre-anthesis development rate (DR). In contrast, genotypes with no effect of temperature on TLN had similar T_{base} for LAR and DR. Across genotypes, T_{base} for LAR and DR were highly correlated, but genotypes with low T_{base} had the greatest difference in T_{base} between the two processes. Genotypic differences were associated with racial grouping.
- **Conclusions** Genotypic and racial differences in responses of phenological processes to temperature, in particular in T_{base} , can affect specific adaptation to agroecological zones, as these differences can affect TLN in response to temperature and hence canopy size and the duration of the pre-anthesis period. These can both affect the amount of water used and radiation intercepted pre-anthesis. A multi-disciplinary approach is required to identify genotype \times environment \times management combinations that can best capture the ensuing specific adaptation.

Key words: Agroecological adaptation, base temperature, development rate, leaf appearance rate, leaf number, sorghum race, temperature response.

INTRODUCTION

Phenology is an important aspect of crop adaptation, as the timing of anthesis can play a significant role in minimizing the adverse effects of end-of-season drought stress on crop yields (Messina *et al.*, 2011). This is particularly the case for sorghum (*Sorghum bicolor*), which is usually grown under rainfed conditions in semi-arid tropical and sub-tropical environments, where the timing and severity of drought stress can be highly variable in both space and time (Kholová *et al.*, 2013; Hammer *et al.*, 2014). In sorghum, timing of anthesis is a function of the total leaf number (TLN) produced by the main shoot and the rate at which leaf ligules appear to mark full expansion of a leaf (leaf appearance rate, LAR, leaves $\text{d}^{-1} \text{ } ^\circ\text{C}^{-1}$), which in turn depends on temperature and photoperiod.

TLN in sorghum arises from the four leaf initials present in the seed (Paulson, 1969) and the number of leaf primordia initiated at the apical meristem prior to panicle initiation (PI), when the apical meristem transitions from initiating leaf primordia to initiating reproductive organs. The number of leaf primordia initiated is thus the product of the leaf initiation rate (LIR, leaves $\text{d}^{-1} \text{ } ^\circ\text{C}^{-1}$) and the duration of the period between plant emergence and PI ($^\circ\text{Cd}$), which in turn depends on the pre-anthesis phenological development rate (DR). LIR, LAR and DR (and thus PI) each depend on temperature, and the response is such that rates will be zero when temperature is below a base temperature (T_{base}) or above a maximum temperature (T_{max}) and rates will be highest at the optimum temperature (T_{opt}) (Ong and Monteith, 1985; Hammer *et al.*, 2010). In general, DR, LIR and LAR are assumed to have similar cardinal temperatures

(T_{base} , T_{opt} , T_{max}) (Parent and Tardieu, 2012). Such a common response to temperature means that any change in DR (and hence timing of PI) in response to changes in temperature will be compensated for by a change in LIR, such that the total number of leaves initiated (and hence TLN) will be independent of temperature. This provides a simple model to predict the timing of anthesis of sorghum, based on estimated TLN and the response of LAR to temperature (Hammer et al., 2010).

As sorghum is a short-day crop, the duration ($^{\circ}\text{Cd}$) from emergence to PI will be extended for photoperiod-sensitive genotypes if the photoperiod prior to PI exceeds a threshold (Major et al., 1990; Ravi Kumar et al., 2009). This delayed occurrence of PI will extend the duration of leaf initiation, resulting in increased TLN (Muchow and Carberry, 1990; Ravi Kumar et al., 2009). Although the assumption of common cardinal temperatures for DR, LIR and LAR implies that TLN will only be affected by photoperiod, there are reports for cereals of temperature effects on TLN that are independent of daylength. Increased TLN in response to higher temperature has been reported for sorghum (Caddel and Weibel, 1971; Gerik and Miller, 1984; Craufurd et al., 1998; van Oosterom et al., 2011) and maize (Cooper and Law, 1978; Warrington and Kanemasu, 1983), although there is some evidence that high temperature only increases TLN above a certain temperature threshold (Craufurd et al., 1998). Observations from controlled environments, where temperature during the transition from dark to light affects the timing of PI (Morgan et al., 1987; Ellis et al., 1997), would imply a possible role of night temperature. Temperature effects on TLN that are independent of photoperiod could indicate a difference between LIR and pre-anthesis DR in their response to temperature, such that increased temperature will have different effects on these two processes, potentially increasing the number of leaves that are initiated prior to PI. Because the rate of leaf appearance is a temperature-driven process (Hammer et al., 2010), increased TLN would increase the amount of thermal units required to reach anthesis, and could also increase leaf area production if there is no effect on tillering (van Oosterom et al., 2011). This may increase pre-anthesis water use, thus adversely affecting post-anthesis water availability and hence grain yield in environments with end-of-season drought stress (Borrell et al., 2014; George-Jaeggli et al., 2017). If changes in temperature affect the synchrony of leaf production and life cycle development differently among genotypes, this could have important implications for adaptation to a warming climate.

A previous study (Tirfessa et al., 2020) identified significant genotypic differences in the response of phenology (pre-anthesis DR) to temperature amongst diverse Ethiopian germplasm. Although Parent et al. (2019) warn that such differences could be associated with confounding effects in the analyses, the observation that these differences were associated with differences in the base temperature (T_{base}) that were linked to racial grouping adds veracity to these results. In addition, significant genotypic differences in LAR and in the effect of temperature on TLN have been reported for sorghum genotypes that included germplasm of Ethiopian background (van Oosterom et al., 2011). However, no studies have been conducted that link genotypic differences in the response of TLN to temperature to underpinning genotypic differences in the responses of LAR and DR to temperature. Hence, the objectives of this study were to use a set of diverse Ethiopian sorghum

germplasm to (1) establish the presence of temperature effects on TLN, (2) develop a crop physiological framework that could explain this by determining differences in temperature responses between LAR and pre-anthesis DR, and (3) discuss implications for specific adaptation to agroecological zones and hence breeding.

MATERIALS AND METHODS

Experiment details

Experiments were conducted at two locations in Ethiopia with comparable latitude but contrasting altitude: Melkassa (1046 m, 8 $^{\circ}$ 25'N, 39 $^{\circ}$ 19'E) and Kulumsa (2259 m, 8 $^{\circ}$ 01'N, 39 $^{\circ}$ 09'E), which represent lowland and highland altitudes respectively. The sorghum [*Sorghum bicolor* (L.) Moench] genotypes were sown on 12 different dates in 2013 and 2014, with six sowing dates per year per location. Sowings were conducted at ~3-week intervals, ranging from 24 March to 8 July in 2013 and 12 April to 25 July in 2014. The difference in sowing dates between locations was generally no more than 2 d, with only one occurrence of a 4-d difference (Table 1). Combined with the difference in altitude between locations, this created differences in temperatures that were independent of photoperiod. Daily temperatures at Melkassa ranged from ~15 to 34 $^{\circ}\text{C}$ and at Kulumsa from ~10 to 25 $^{\circ}\text{C}$ (Fig. 1). During the 4 weeks after sowing, which covers most of the period prior to PI, when TLN is determined (van Oosterom et al., 2010), average temperatures at Melkassa were 4.4–8.3 $^{\circ}\text{C}$ higher than at Kulumsa (Table 1).

Each experiment (location \times sowing date) was set up as a randomized complete block design with two replications, with a different randomization for each experiment. Plots consisted of a single row of 5 m length with a row spacing of 0.75 m and 1.5 m distance between blocks. Seeds were manually drilled into the rows and seedlings were thinned to 0.15 m between plants at ~20 d after emergence. Phosphorus fertilizer (46 kg ha $^{-1}$ P $_2$ O $_5$) in the form of di-ammonium phosphate and nitrogen fertilizer (23 kg ha $^{-1}$ nitrogen as urea) were applied at sowing and at 35 d after sowing, respectively. All experiments were well watered.

Genetic material

A set of 19 diverse Ethiopian genotypes that included landraces and improved varieties was evaluated in this study (Table 2). The genotypes represented three major sorghum races and included seven Ethiopian highland *durra* types, five *caudatum* types and four *kafir* types (Table 2). For 12 of these 16 genotypes, at least 99 % of their genome belonged to a single racial group. The four exceptions were Macia (96.9 % *caudatum*), Birmash (94.1 % *kafir*), Jamiyu (91.2 % Ethiopian highland *durra*) and Geremew (80.7 % *kafir*). The last also contained 11.0 % Ethiopian highland *durra* and 7.1 % *caudatum* (Tirfessa et al., 2020). In addition, two of the genotypes were *caudatum*/*guinea* mixed race: Adukura (50 % *caudatum* and 22 % *guinea*) and Bobe red (63 % *caudatum* and 22 % *guinea*). For ESH-2, the racial classification was not available. Racial classification was closely associated with the four major

TABLE 1. Date of sowing and average daily maximum (T_{max}) and minimum (T_{min}) temperature during the 4 weeks¹ following sowing for each of the 12 sowing dates at Melkassa (low altitude) and Kulumsa (high altitude). The last column gives the average difference in daily mean temperature between the two locations, with positive values indicating higher mean daily temperature at Melkassa.

Melkassa			Kulumsa			Difference in mean temp. (°C)
Sowing date	T_{max} (°C)	T_{min} (°C)	Sowing date	T_{max} (°C)	T_{min} (°C)	
24-Mar-13	31.1	16.2	24-Mar-13	25.2	13.4	4.37
15-Apr-13	31.4	16.6	15-Apr-13	24.3	10.8	6.49
07-May-13	32.6	17.1	07-May-13	24.1	9.0	8.29
27-May-13	31.6	17.4	27-May-13	24.2	9.3	7.75
17-Jun-13	28.2	16.1	17-Jun-13	22.1	9.0	6.62
08-Jul-13	25.6	16.2	08-Jul-13	21.1	9.7	5.48
12-Apr-14	32.2	16.7	11-Apr-14	25.7	12.9	5.15
03-May-14	30.9	16.7	02-May-14	24.3	12.5	5.35
23-May-14	32.0	16.3	23-May-14	25.0	12.2	5.52
14-Jun-14	30.9	17.3	16-Jun-14	23.3	11.5	6.67
04-Jul-14	27.5	16.8	08-Jul-14	21.1	10.7	6.24
25-Jul-14	26.6	16.1	25-Jul-14	20.3	11.6	5.45

¹This approximates the period from emergence to panicle initiation, during which total leaf number is determined.

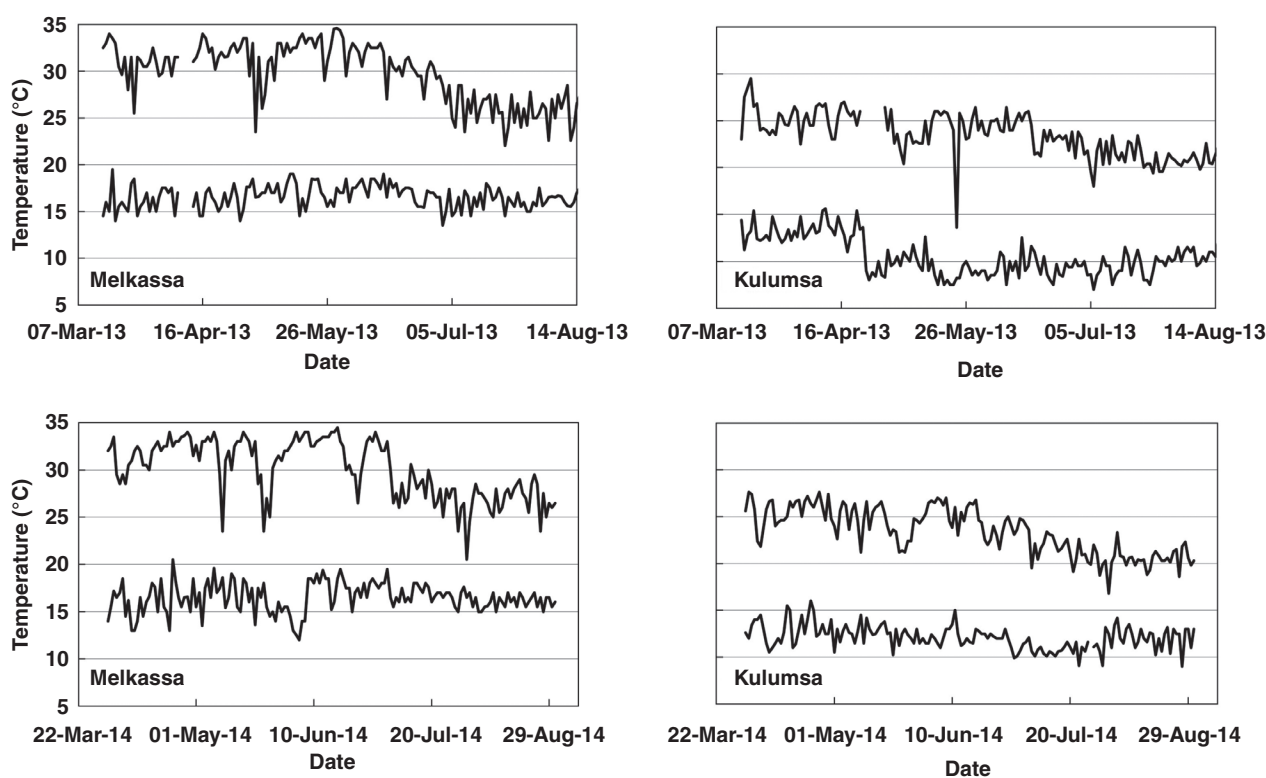


FIG. 1. Daily maximum and minimum temperatures at Melkassa and Kulumsa for the 2013 and 2014 seasons.

sorghum agroecological growing areas in Ethiopia. These areas differ in altitude (metres above sea level, m asl), rainfall (mm) and duration of the growing period (d), and comprise the highlands (>1900 m asl, 800 mm, 170–200 d), intermediate zone (1600–1900 m asl, >1000 mm, 150–180 d), wet lowlands

(<1600 m asl, >1000 mm, 110–150 d) and dry lowlands (<1600 m asl, <600 mm, 90–130 d) (Ayana and Bekele, 2000). The four highland genotypes were all *durra*, the four genotypes grown at intermediate altitude were all *kafra*, the two genotypes from the wet lowlands were both *caudatum/guinea*, whereas

TABLE 2. Mean, minimum and maximum values for total leaf number at Melkassa and Kulumsa plus the average difference between the two locations across 12 sowing dates for the 19 Ethiopian (ETH) genotypes. Significance relates to the difference in average leaf number between the two sites. Within each of the two response patterns, genotypes have been grouped by race and germplasm type.

Genotype	Race	Germplasm type	Agroecology	Total leaf number		Difference ²
				Melkassa	Kulumsa	
				Mean (range)	Mean (range)	
Genotypes with significantly greater leaf number at Melkassa than at Kulumsa						
Chiro	ETH highland <i>durra</i>	Improved landrace	Highland	27.1 (24.8–30.7)	23.3 (21.7–26.5)	3.76***
Chelenko	ETH highland <i>durra</i>	Improved landrace	Highland	26.7 (23.3–29.8)	23.4 (21.3–25.5)	3.31***
ETS2752	ETH highland <i>durra</i>	Improved landrace	Highland	26.0 (23.2–31.0)	23.0 (20.3–26.0)	3.05***
Alemaya70	ETH highland <i>durra</i>	Improved landrace	Highland	24.5 (21.7–28.2)	22.5 (19.3–25.8)	1.99**
Jamiyu	ETH highland <i>durra</i>	Landrace	Dry lowland	21.6 (19.2–24.3)	18.8 (17.2–21.2)	2.81***
Degalit	ETH highland <i>durra</i>	Landrace	Dry lowland	23.4 (20.8–27.0)	21.8 (20.3–23.8)	1.68*
ESH2	NA ¹	Released	Dry lowland	15.2 (12.3–17.0)	13.2 (11.3–14.3)	2.29***
Adukara	<i>caudatum/guinea</i>	Landrace	Wet lowland	26.7 (22.1–31.7)	25.2 (19.3–29.2)	1.58**
Gambella1107	<i>caudatum</i>	Released	Dry lowland	18.0 (15.8–20.2)	16.2 (15.0–17.8)	1.88***
Melkam	<i>caudatum</i>	Released	Dry lowland	16.3 (14.0–18.5)	14.8 (12.7–19.2)	1.55*
Teshale	<i>caudatum</i>	Released	Dry lowland	15.8 (13.5–17.5)	14.3 (13.0–15.8)	1.47**
Genotypes with leaf number at Melkassa not greater than at Kulumsa						
Jigurti	ETH highland <i>durra</i>	Landrace	Dry lowland	20.0 (17.3–22.5)	19.0 (17.7–20.7)	0.99 n.s.
Bobbe red	<i>caudatum/guinea</i>	Landrace	Wet lowland	24.9 (19.5–29.9)	23.9 (18.5–26.3)	1.07 n.s.
Macia	<i>caudatum</i>	Released	Dry lowland	16.2 (14.0–18.2)	15.6 (14.3–17.8)	0.61 n.s.
Meko	<i>caudatum</i>	Released	Dry lowland	15.0 (12.7–17.0)	15.1 (13.0–19.5)	–0.10 n.s.
Geremew	<i>kafir</i>	Released	Intermediate	20.9 (18.7–23.3)	19.8 (17.7–21.7)	1.06 n.s.
Birmash	<i>kafir</i>	Released	Intermediate	19.7 (17.7–22.3)	19.8 (17.5–21.0)	–0.16 n.s.
IS9302	<i>kafir</i>	Released	Intermediate	19.3 (16.0–21.8)	19.7 (18.0–21.3)	–0.36 n.s.
Dagem	<i>kafir</i>	Released	Intermediate	20.5 (16.8–24.2)	21.4 (18.7–23.8)	–0.98*
Race means ²	Race	No. of genotypes				
	ETH highland <i>durra</i>	7				2.51 a
	<i>caudatum/guinea</i>	2				1.33 ab
	<i>caudatum</i>	5				1.08 b
	<i>kafir</i>	4				–0.11 b

¹NA, not available.

²Racial means followed by a different letter differ significantly ($P < 0.05$) according to a t -test using the pooled method for equal variances.

Asterisks indicate significance at * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$. n.s., not significant.

the dry lowland genotypes were either *durra* or *caudatum* (Table 2).

Observations

In each experiment, observations were conducted on three plants per plot that were tagged when about five leaves had fully expanded. Main shoot TLN was recorded in all experiments once the flag leaf was fully expanded. In addition, the number of fully expanded main shoot leaves throughout the vegetative period was counted at regular intervals in all experiments in 2014. A leaf was considered as fully expanded when its ligule became visible above the enclosing sheath of the previous leaf (Hammer *et al.*, 1993). Leaf counts were done up to twice a week in the first sowing dates, but at lower frequencies

in later sowing dates. Weather data (daily maximum and minimum temperature) were collected from a weather station that was located in close proximity to the experiment.

Data analysis

Total leaf number (TLN). An analysis of variance (ANOVA) for TLN was conducted to determine if there were any effects of location and genotype on TLN across pairs of experiments with common sowing dates. Hence, the 24 experiments (2 locations \times 12 sowing dates across two seasons) were analysed in terms of sowing date (11 d.f.) and location within sowing date (12 d.f.). The presence of significant genotype and location effects on TLN was subsequently analysed in more detail using a paired-sample t -test for TLN across all 12 sowing dates for

TABLE 3. Analysis of variance for total leaf number for 19 genotypes, grown in 24 experiments that comprised 12 sowing dates (sow) \times two locations (loc), with near-similar sowing dates across locations. The experimental effect was analysed in terms of sowing date and location within sowing date. Each experiment (location \times sowing date) was set up as a randomized complete block design with two replications, with a different randomization for each experiment

Source	d.f.	Sum of squares	F value	P value
genotype	18	13 026	683.15	<0.0001
exp	23	1771	72.68	<0.0001
sow	11	952	81.72	<0.0001
loc(sow)	12	819	68.22	<0.0001
geno \times exp	410	1663	3.83	<0.0001
geno \times sow	198	992	4.73	<0.0001
geno \times loc(sow)	212	671	3.17	<0.0001
rep(experiment)	24	31	1.23	0.2119

each individual genotype, to identify genotypes with a significant location effect on TLN. The TLN data were analysed using the ANOVA and TTEST procedures in SAS Enterprise Guide 9.4 (SAS, 2013).

Leaf appearance rate (LAR). For each genotype in each of the 12 experiments in 2014, the average number of fully expanded leaves was plotted against the number of days after sowing (DAS). Leaf number was the average value across the two replications for each experiment (six plants per genotype). For the period during which leaf number was linearly related to DAS, the slope of the regression was taken as the LAR (leaves d^{-1}). Because temperatures were relatively constant for large periods of time during the growing season (Fig. 1), a single regression generally sufficed for most of the period of leaf appearance (see Results). Observations close to maximum TLN were excluded from the regression, as these leaf counts could potentially have been biased by some of the plants having reached flag leaf. The first observation(s) were also excluded from the regression in cases where these early leaf counts had a disproportionate effect on the slope of the regression (LAR, leaves d^{-1}). For some early-flowering genotypes, the number of observations was too limited in some experiments to reliably determine LAR. For situations with LAR data, weather data were then used to calculate the average daily temperature for the period during which leaf number was linearly related to DAS. The data for LAR and mean daily temperature that were thus obtained for each genotype in each experiment were then plotted against each other in order to determine the response of LAR (leaves d^{-1}) to mean daily temperature. Each regression had up to 12 data points (2 locations \times 6 sowing dates). The intercept of the regression with the x-axis was considered to be the base temperature (T_{base}) for LAR and represented the average daily temperature at which LAR is zero. The slope of the regression (leaves $d^{-1} \text{ } ^\circ\text{C}^{-1}$) represents the increase in LAR (leaves d^{-1}) for each degree increase in average daily temperature. To determine if genotypes differed in T_{base} , the slope of the regression or both, the following fixed effect non-linear model was fitted:

$$LAR_{ijk} = b(T_{ijk} - T_{base}) + \varepsilon_{ijk} \quad (1)$$

where b is the slope of the relationship, $T_{base} = \alpha/\beta$, with α and β the intercept and slope respectively for the simple linear expression of LAR on T_{av} , and $\varepsilon_{ijk} \sim N(0, \sigma^2)$. Analyses were done in R version 4.05 (R Core Team, 2021) using the non-linear least squares (*nls*) function (Ritz and Streibig, 2008) to estimate the parameters. Equation (1) was fitted with and without genotype-specific values for T_{base} and the slope of the temperature response, and the significance of genotype-specific parameter values was determined through model comparisons.

The T_{base} for LAR was also compared with the T_{base} for pre-anthesis DR (Tirfessa et al., 2020) to determine if differences between the two processes for individual genotypes could account for genotypic differences in the response of TLN to location (Melkassa vs. Kulumsa). A higher T_{base} and responsiveness to temperature for LAR than for DR could indicate that an increase in temperature would have a relatively larger effect on LAR than on rate of development. As LAR is associated with LIR (Padilla and Otegui, 2005), this could result in more leaves being initiated at higher temperatures, resulting in greater TLN. All regressions were conducted using the REG and NLIN procedures in SAS Enterprise Guide 9.4 (SAS, 2013).

RESULTS

Location effect on TLN in some genotypes

Genotypic differences in TLN were highly significant (Table 3). Average TLN at Melkassa ranged from 15.0 (Meko) to 27.1 (Chiro) and at Kulumsa from 13.2 (ESH2) to 25.2 (Adukara) (Table 2). In general, TLN at Melkassa exceeded TLN at Kulumsa, particularly for the first three sowing dates in each year (Fig. 2). The sowing date and location within sowing date each captured around half of the total sum of squares across the 24 experiments and both effects were highly significant ($P < 0.0001$; Table 3). Genotypes differed in their response of TLN to location (daily mean temperature), as indicated by the highly significant ($P < 0.0001$) genotype \times experiment interaction and in particular the highly significant ($P < 0.0001$) genotype \times location (sowing date) interaction (Table 3).

To explore the genotypic differences in the response of TLN to location in more detail, a pairwise *t*-test across the 12 sowing

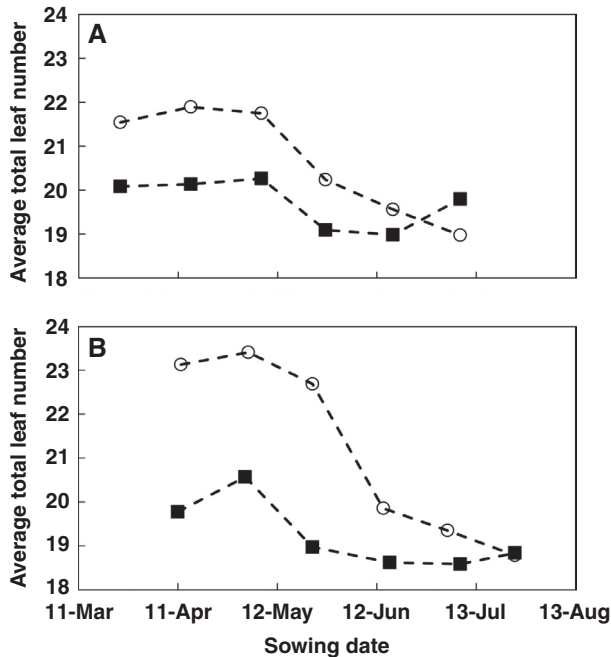


FIG. 2. Average total leaf number (TLN) vs. sowing date at Melkassa (○) and Kulumsa (■) in (A) 2013 and (B) 2014.

dates was conducted for each genotype. The results showed that 11 genotypes had significantly greater TLN at Melkassa than at Kulumsa (Table 2). Among the remaining eight genotypes, seven had no significant location effect, whereas Dagem had significantly lower TLN at Melkassa than at Kulumsa. The response of TLN to location (temperature) had some association with racial background. Six of the seven highland *durra* genotypes produced significantly greater TLN in the warmer conditions of Melkassa compared to the cooler conditions of Kulumsa, with three of these (Chiro, Chelenko and ETS2752) on average producing >3 more leaves at Melkassa than at Kulumsa (Table 2). In contrast, none of the four *kafir* genotypes showed such a response. The difference in the location effect on TLN between the *durra* and *kafir* groups was highly significant ($P < 0.01$) according to a *t*-test. However, the seven *caudatum* and *caudatum/guinea* genotypes were more evenly distributed between the two groups (Table 2).

Response of LAR to temperature

The relationship between fully expanded leaf number and days after sowing was generally linear until close to full flag leaf appearance for most of the genotype \times experiment combinations. This is illustrated in Fig. 3A for Jigurte and Bobe red, sown at Melkassa on 12 April, 2014. The only exception was Adukara, for which a bilinear relationship generally gave a significantly better fit than a linear relationship (Fig. 3B). Because Adukara was one of the genotypes that produced most leaves (Table 2) and was amongst the latest to reach anthesis (Tirfessa et al., 2020), it is possible that this bilinear relationship reflected a delayed onset of stem elongation, where the first slope represented the period when the growing point was still below the soil surface. Hence, to facilitate comparisons

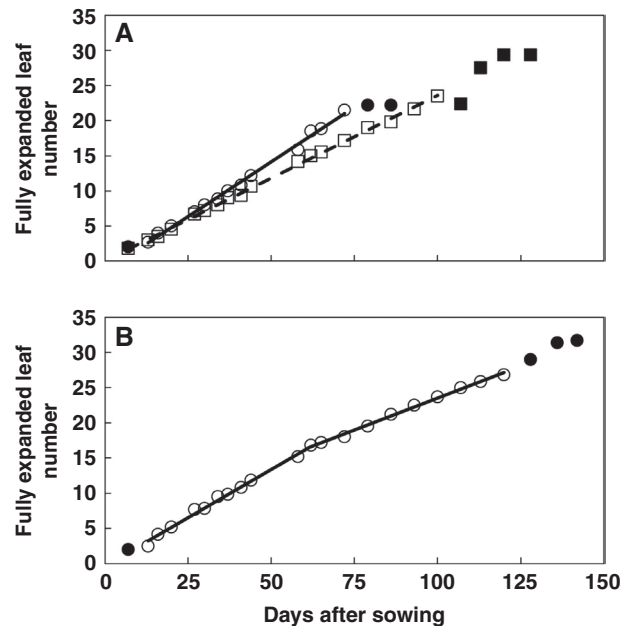


FIG. 3. Fully expanded leaf number (FEL) vs. days after sowing (DAS) for sowing 1 at Melkassa in 2014 for (A) Jigurte (○—○) and Bobe red (□ - - □) and (B) Adukara (○—○). Data are averaged across two replications (six plants). Closed symbols have been excluded from the regressions. Equations:

$$\text{Jigurte} : FEL = 0.0754 + 0.2355 * DAS; n = 18; R^2 = 0.998$$

$$\text{Bobe red} : FEL = 1.3992 + 0.2243 * DAS; n = 20; R^2 = 0.988$$

$$\text{Adukara} : FEL = -0.3264 + 0.2743 *$$

$$DAS \text{ if } DAS < 61.5; \text{ else } FEL = 5.4069 + 0.1811 * DAS; n = 20; R^2 = 0.998.$$

with other genotypes, the second slope was used for further analyses. Across all genotype \times experiment combinations, the average number of observations in each regression used to derive LAR was 9.08 (range 3–23) and the average R^2 was 0.995 (range 0.965–1.000). Across all experiments, the average daily temperature ranged from ~16.0 to 24.1 °C, although the range was slightly lower for Adukara (16.0–22.9 °C), where only data for the second slope (Fig. 3B) were used.

An ANOVA showed that for the relationship between LAR and daily average temperature, genotypes differed significantly for both slope and T_{base} . A model that assumed a genotype-specific slope but common T_{base} across genotypes (eqn 1) gave a significantly ($P < 0.0001$) better fit than a common regression across all genotypes. Similar results were obtained with a model that assumed a genotype-specific T_{base} but a common slope across genotypes. Importantly, however, in both cases, the model improved significantly ($P < 0.05$) if genotype-specific values for both slope and T_{base} were used. Moreover, a common T_{base} of 11 °C, commonly used as the T_{base} of phenological processes for Australian sorghum (Hammer et al., 1993), gave a fit that was significantly worse ($P < 0.0001$) than that of using genotype-specific values. This indicates that it was appropriate to fit separate slopes and T_{base} in eqn (1) for each genotype (Table 4).

TABLE 4. Statistics for the regression of leaf appearance rate (LAR, leaves d^{-1}) on average daily temperature for key Ethiopian (ETH) sorghum germplasm. Statistics include the number of experiments (n , sowing date \times location) for which LAR could be estimated reliably, goodness of fit (R^2), slope of the response (leaves $d^{-1} \text{ } ^\circ\text{C}^{-1}$) \pm s.e., estimated base temperature (T_{base}) \pm s.e. for LAR, and estimated LAR at 24 $^\circ\text{C}$. The final two columns indicate estimated T_{base} for pre-anthesis development rate (DR) (Tirfessa et al., 2020) and the difference in T_{base} between LAR and DR. Genotypes have been classified according to whether leaf number at Melkassa was significantly greater than at Kulumsa (Table 2).

Genotype	Race	n^1	R^2	Slope (leaves $d^{-1} \text{ } ^\circ\text{C}^{-1}$)	T_{base} LAR ($^\circ\text{C}$)	LAR at 24 $^\circ\text{C}$ (leaves d^{-1})	T_{base} DR ($^\circ\text{C}$)	T_{base} difference ($^\circ\text{C}$)
Genotypes with significantly greater leaf number at Melkassa than at Kulumsa								
Chiro	ETH highland <i>durra</i>	12	0.87	0.0143 \pm 0.0018	4.0 \pm 2.0	0.286	1.5	2.5
Chelenko	ETH highland <i>durra</i>	12	0.83	0.0145 \pm 0.0018	4.0 \pm 1.9	0.290	0.1	3.9
ETS2752	ETH highland <i>durra</i>	12	0.86	0.0146 \pm 0.0017	4.1 \pm 1.9	0.292	0.0	4.1
Alemaya 70	ETH highland <i>durra</i>	12	0.91	0.0145 \pm 0.0017	3.9 \pm 1.9	0.293	3.4	0.5
Jamiyu	ETH highland <i>durra</i>	12	0.82	0.0164 \pm 0.0017	5.8 \pm 1.5	0.300	5.4	0.4
Degalit	ETH highland <i>durra</i>	11	0.91	0.0174 \pm 0.0018	6.1 \pm 1.4	0.311	5.5	0.6
ESH2	NA ²	11	0.88	0.0140 \pm 0.0017	3.7 \pm 2.0	0.284	0.4	3.3
Adukara	<i>caudatum/guinea</i>	12	0.84	0.0144 \pm 0.0019	9.1 \pm 1.3	0.214	8.9	0.2
Gambella 1107	<i>caudatum</i>	11	0.84	0.0147 \pm 0.0018	4.0 \pm 2.0	0.294	0.9	3.1
Melkam	<i>caudatum</i>	12	0.91	0.0114 \pm 0.0017	1.8 \pm 2.7	0.252	0.0	1.8
Teshale	<i>caudatum</i>	11	0.97	0.0155 \pm 0.0017	5.5 \pm 1.6	0.286	1.3	4.2
Average³				0.0147*	4.72*	0.282 n.s.	2.49***	2.23***
Genotypes with leaf number at Melkassa not greater than at Kulumsa								
Jigurti	ETH highland <i>durra</i>	12	0.85	0.0172 \pm 0.0016	5.7 \pm 1.4	0.315	6.6	-0.9
Bobé red	<i>caudatum/guinea</i>	10	0.93	0.0154 \pm 0.0018	6.9 \pm 1.5	0.263	7.3	-0.4
Macia	<i>caudatum</i>	11	0.91	0.0155 \pm 0.0017	5.3 \pm 1.6	0.291	4.1	1.2
Meko	<i>caudatum</i>	11	0.91	0.0158 \pm 0.0017	5.2 \pm 1.6	0.296	6.0	-0.8
Geremew	<i>kafir</i>	12	0.95	0.0144 \pm 0.0017	6.2 \pm 1.6	0.256	7.2	-1.0
Birmash	<i>kafir</i>	12	0.93	0.0181 \pm 0.0017	7.7 \pm 1.1	0.294	9.8	-2.1
IS9302	<i>kafir</i>	12	0.96	0.0213 \pm 0.0017	9.2 \pm 0.8	0.315	9.4	-0.2
Dagem	<i>kafir</i>	12	0.93	0.0191 \pm 0.0017	8.6 \pm 1.0	0.294	9.0	-0.4
Average				0.0171	6.86	0.290	7.43	-0.56
Race means⁴								
	ETH highland <i>durra</i>	7		0.0156 a	4.79 b	0.298 a	3.21 b	1.57 a
	<i>caudatum</i>	5		0.0146 a	4.36 b	0.284 ab	2.46 b	1.90 a
	<i>caudatum/guinea</i>	2		0.0149 a	8.01 a	0.238 b	8.10 a	-0.09 ab
	<i>kafir</i>	4		0.0182 a	7.93 a	0.290 ab	8.85 a	-0.92 b

¹Leaf counts to estimate LAR were only conducted in 2014, giving a maximum of 12 data points (6 sowing dates \times 2 locations). For some of the early genotypes, one or two experiments had insufficient data points to reliably estimate LAR.

²NA, not available.

³Asterisks indicate significance at $*P < 0.05$ and $***P < 0.001$ in the comparison of the average values for the two groups of genotypes. n.s., not significant.

⁴Means followed by a different letter differ significantly ($P < 0.05$) according to a t -test using the pooled method for equal variances.

The response of LAR (leaves d^{-1}) to average daily temperature was strongly linear across experiments (Fig. 4), with R^2 ranging from 0.82–0.83 for Jamiyu and Chelenko to 0.96–0.97 for IS9302 and Teshale respectively (Table 4). The estimated T_{base} for LAR ranged from 1.8 $^\circ\text{C}$ for Melkam to 9.2 $^\circ\text{C}$ for IS9302 (Table 4). The *kafir* and *caudatum/guinea* genotypes consistently had an estimated $T_{\text{base}} \geq 6.2 \text{ } ^\circ\text{C}$, whereas the *caudatum* and highland *durra* genotypes all had an estimated $T_{\text{base}} \leq 6.1 \text{ } ^\circ\text{C}$ (Table 4). As a consequence, the average T_{base}

of the *caudatum* and highland *durra* races was significantly lower than that of the *kafir* and *caudatum/guinea* races. The slope of the relationship between LAR and daily average temperature ranged from 0.0114 leaves $d^{-1} \text{ } ^\circ\text{C}^{-1}$ for Melkam to 0.0213 leaves $d^{-1} \text{ } ^\circ\text{C}^{-1}$ for IS9302 (Table 4). With the exclusion of Adukara, T_{base} and slope were highly positively correlated ($R^2 = 0.83$, $n = 18$), such that genotypes with high T_{base} increased the LAR quickest with increasing temperature. Hence, the three genotypes with the greatest slope all

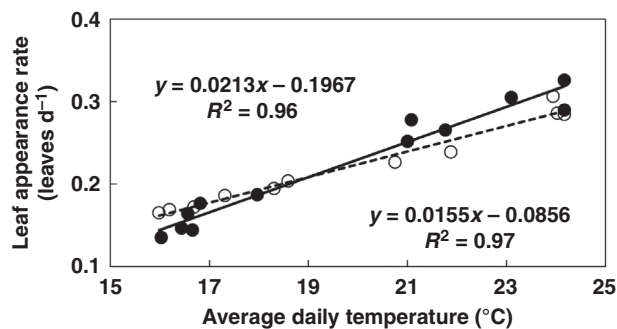


FIG. 4. Leaf appearance rate (LAR, leaves d^{-1}) vs. average daily temperature ($^{\circ}C$) for Teshale (○ - - ○) and IS9302 (● - ●). Each data point in this figure represents the LAR of one experiment, as determined from data illustrated in Fig. 3.

belonged to the *kafir* race with high T_{base} . Nonetheless, there were no significant differences in the average slope among racial groups (Table 4). The estimated LAR at 24 $^{\circ}C$ ranged from 0.214 leaves d^{-1} (Adukara) to 0.315 leaves d^{-1} (Jigurti, IS9302). The two *caudatum/guinea* genotypes both had low LAR at this temperature and the average of this group was significantly lower than that of the highland *durra* genotypes (Table 4).

Difference in base temperature between LAR and DR is linked to a location effect on TLN

The veracity of the genotypic differences in T_{base} for LAR was supported by the observation that across all genotypes, T_{base} for LAR was significantly positively associated with the T_{base} for pre-anthesis DR ($R^2 = 0.81$, $n = 19$, $P < 0.0001$, Fig. 5). The 11 genotypes with a significant temperature (location) effect on TLN on average had significantly lower T_{base} for both LAR ($P < 0.05$) and DR ($P < 0.001$) than the eight with no temperature effect on TLN (Table 4). Importantly, however, for the former group of 11 genotypes, T_{base} for LAR was on average 2.2 $^{\circ}C$ higher than T_{base} for DR (Table 4) and this value was significantly ($P < 0.05$) greater than zero based on a t -test for pairwise comparisons. In contrast, for the other eight genotypes T_{base} for LAR was, with the exception of Macia (Table 4), slightly lower than T_{base} for DR. Importantly, the average difference of 0.6 $^{\circ}C$ was not significantly different from zero. These differences in T_{base} between LAR and DR were partly associated with racial grouping. The four *kafir* genotypes, which had significantly higher T_{base} for both LAR and DR than the highland *durra* and *caudatum* genotypes, also had a significantly smaller difference in T_{base} between these two processes than the *durra* and *caudatum* groups (Table 4). Across all 19 genotypes, the difference in TLN between Melkassa and Kulumsa was positively associated with the difference in T_{base} between LAR and DR ($R^2 = 0.47$, $n = 19$, $P < 0.01$, Fig. 6). These results thus indicate that genotypes with a significant response of TLN to temperature (as indicated by the location effect on TLN) had a greater difference in T_{base} between LAR and DR than genotypes with no difference in TLN between Melkassa and Kulumsa.

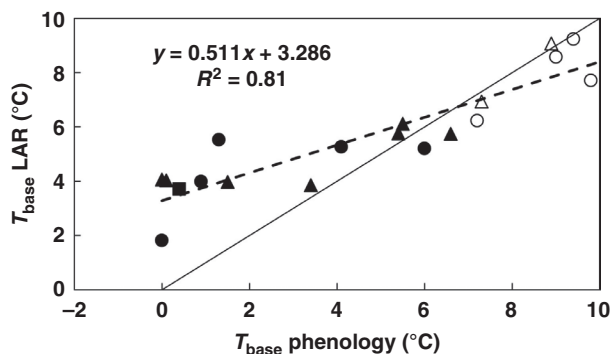


FIG. 5. Base temperature (T_{base} , $^{\circ}C$) for leaf appearance rate (LAR) vs. base temperature for pre-anthesis development rate (DR) for the 19 genotypes representing the *caudatum* (●), highland *durra* (▲), *kafir* (○) and *caudatum/guinea* (Δ) races. ESH-2, for which the race was unknown, is represented by ■. The solid line is the 1:1 line.

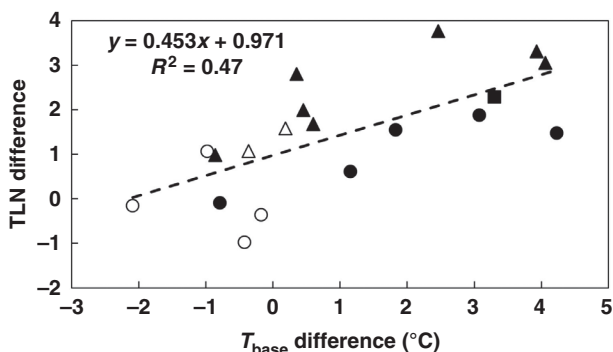


FIG. 6. Association between average difference in total leaf number (TLN) at Melkassa and Kulumsa across 12 sowing dates vs. differences in base temperature (T_{base} , $^{\circ}C$) between leaf appearance rate and pre-anthesis development rate for the 19 genotypes representing the *caudatum* (●), highland *durra* (▲), *kafir* (○) and *caudatum/guinea* (Δ) races. ESH-2, for which the race was unknown, is represented by ■.

DISCUSSION

Genotypes differed in base temperature for response of leaf appearance rate to temperature

Genotypes differed significantly in the response of LAR to temperature. Genotypic differences in LAR have been reported previously in C_4 cereals, including maize (Padilla and Otegui, 2005) and sorghum (Major et al., 1990; van Oosterom et al., 2011). For sorghum, Major et al. (1990) found that genotypic differences in LAR were associated with interactions among the sorghum maturity genes (Ma_1 , Ma_2 , Ma_3), with Ma_3 having greater phyllochron (lower LAR) than ma_3 if ma_2 is recessive, but not if Ma_2 is dominant, whereas Ma_1 had greater phyllochron than ma_1 if Ma_2 is dominant, but not if ma_2 is recessive. For maize, Padilla and Otegui (2005) related genotypic differences in LAR to differences in T_{base} , but no such information is available for sorghum. The current analyses indicated that genotypic differences in the response of LAR to temperature were associated with genotypic differences in both T_{base} and the slope of the response, even though the two factors were highly correlated.

The analyses also indicated that the T_{base} of 11 °C that has been derived in Australia (Hammer *et al.*, 1993) was significantly greater than values obtained in the current analyses. In addition, there were significant differences amongst racial groups in the T_{base} for LAR (Table 4). Moreover, across the 19 genotypes, the T_{base} for LAR was significantly correlated with the T_{base} for pre-anthesis DR (Fig. 5), which was determined concomitantly (Tirfessa *et al.*, 2020). This high correlation between the T_{base} of these two processes would support the view of Parent and Tardieu (2012) that temperature responses of different processes may have shifted synchronously throughout evolution. Hence, the current analyses support the hypothesis that the significant genotypic differences in the response of LAR to temperature were at least partly associated with genotypic differences in the T_{base} for LAR.

The racial differences in T_{base} for LAR were very distinct, with *caudatum* and highland *durra* genotypes consistently having lower T_{base} than the *kafir* and *caudatum/guinea* genotypes, resulting in highly significant differences in average T_{base} across these racial groups (Table 4). The low T_{base} of *durra* genotypes would explain the significantly greater LAR of hybrids based on the Ethiopian *durra* inbred line ATx642 compared to AQL39 hybrids when LAR is expressed in leaves d^{-1} (van Oosterom *et al.*, 2011). The low T_{base} of these genotypes allows LAR to proceed at higher rates under low temperatures. Because temperatures tend to decline with altitude (Fig. 1) this provides specific adaptation to the agroecological zone of adaptation of these highland *durra* genotypes. Conversely, the high T_{base} of the two *caudatum/guinea* genotypes (Table 4) potentially provides adaptation to the agroecology of the wet lowlands (Table 2), where, in the absence of drought, biomass accumulation is likely to be radiation-limited rather than water-limited. A high T_{base} for LAR could potentially slow LAR, which would in turn extend the time to full flag leaf appearance and hence increase radiation interception to increase biomass accumulation and hence grain yield. This consistency between racial differences in T_{base} for LAR and their agroecological adaptation lends further veracity to the observed differences in T_{base} for LAR.

Temperature effects on leaf number were related to differences in base temperature between leaf appearance and development

Significantly greater TLN under the high temperatures at Melkassa compared to lower temperatures at Kulumsa for similar sowing dates indicated a temperature effect on TLN that was independent of photoperiod. Similar increases in TLN under higher temperatures during the period following emergence have been observed previously in maize (Cooper and Law, 1978) and sorghum (Quinby *et al.*, 1973; Gerik and Miller, 1984; van Oosterom *et al.*, 2011). Initiation of new leaf primordia in the meristem ceases at PI, the timing of which depends on photoperiod and temperature (Hammer *et al.*, 2010). The number of leaves initiated depends on the duration of the period until PI and on LIR. If daily temperature increases, the accelerated DR towards PI will be offset by an accelerated LIR, such that if the two processes have similar T_{base} , then TLN will be independent of daily temperature. However, if T_{base} for LIR exceeds T_{base} for DR and if the slope of the response to temperature for the two processes is comparable (e.g. both are linear)

for a particular genotype, then an increase in average daily temperature will result in a relatively larger change in thermal units (°Cd) for LIR compared with DR. This will increase LIR to a relatively larger extent than DR, which in turn will increase the number of leaves that are initiated at the apical meristem prior to PI, resulting in greater TLN.

Although the current study estimated T_{base} for LAR, rather than for LIR, genotypic differences in the response of LAR and LIR to temperature are highly coordinated prior to PI, as observed for maize (Padilla and Otegui, 2005). Similarly, in sorghum, genotypic differences in LAR were reflected by differences in LIR (van Oosterom *et al.*, 2011). In rice, the *pl1* gene that accelerates LIR was phenotypically identified through accelerated LAR (Miyoshi *et al.*, 2004). Hence, there is ample evidence across cereals that differences in the temperature response of LAR do represent differences in the response of LIR, which is a biological necessity to ensure plants can respond in a coordinated manner to environmental cues (Parent *et al.*, 2019).

The current results (Table 4) showed significant differences in T_{base} across phenological processes, as the average difference in T_{base} between LAR and DR of 2.2 °C for the 11 genotypes with a significant temperature effect on TLN was significantly greater than zero. This implies that at low temperatures, development will progress more rapidly than leaf appearance and leaf initiation. This would reduce the number of leaf primordia initiated prior to PI, which would explain the significantly lower TLN of these genotypes at Kulumsa compared to Melkassa (Table 2; Fig. 6). This is consistent with the theory that TLN increases with higher temperature for the period prior to PI (which is around 4 weeks from emergence; van Oosterom *et al.*, 2010) if T_{base} for LAR exceeds T_{base} for DR.

To our knowledge, this is the first report for sorghum that links significant genotypic differences in T_{base} across phenological processes to the emergent consequence of a temperature effect on TLN. Significantly, this response was linked to racial grouping. Compared with *kafir* genotypes, highland *durra* genotypes on average had significantly lower T_{base} for both LAR and DR, significantly greater difference in T_{base} , and significantly greater response of TLN to temperature (Tables 2 and 4). This would explain the relatively strong response of TLN to temperature observed by van Oosterom *et al.* (2011) for hybrids based on ATx642 (formerly known as B35), which is derived from IS12555, a *durra* landrace from Ethiopia (Borrell *et al.*, 2000). However, the effect of differences in T_{base} on the response of TLN to temperature was not uniform, as *caudatum* genotypes on average had a T_{base} for both LAR and DR that was comparable with that of highland *durra* genotypes (Table 4), but the ensuing temperature effect on TLN was significantly less (Table 2). As a consequence, in the regression of Fig. 6, *caudatum* genotypes were consistently located on or below the regression line and highland *durra* genotypes on or above the regression line. The reason for this distinct behaviour is unclear. The consistent racial effect on T_{base} for LAR and DR, and on the difference in T_{base} between these two processes (Table 4), contradicts the observation of Parent and Tardieu (2012) that a general lack of genetic variability in temperature responses exists within species. Rather, the location (temperature) effect on TLN in this study indicates that sorghum genotypes can

have different temperature responses across these two phenological processes.

Implications for plant breeding and environmental adaptation

The analyses showed that significant genotypic differences in the response of LAR to temperature exist for sorghum, and that individual genotypes can have different temperature responses across processes, resulting in a response of TLN to the temperature environment. Although the study was conducted with Ethiopian germplasm, the association between temperature response and racial groups indicates generic associations that would facilitate incorporation of the current insights into any sorghum breeding programme through selection of targeted racial groups.

Genotypic differences in T_{base} for LAR and pre-anthesis DR can potentially affect adaptation to post-anthesis drought. A lower T_{base} for LAR would accelerate leaf appearance. Increased LAR can increase early vigour of the main shoot, and the resulting shift in carbon supply–demand balance of the plant can reduce tillering (van Oosterom *et al.*, 2011; Alam *et al.*, 2014). This can reduce canopy size, which in turn can reduce pre-anthesis water use (Borrell *et al.*, 2014; George-Jaeggli *et al.*, 2017). A lower T_{base} for DR could accelerate progress to anthesis, which can also reduce pre-anthesis water use (van Oosterom *et al.*, 2011). In environments where post-anthesis drought is likely, such savings in pre-anthesis water use can increase grain yield, which is highly correlated with post-anthesis water availability (Turner, 2004; Hammer, 2006; Borrell *et al.*, 2014). However, the trade-off of a reduced canopy size is that in well-watered conditions, where productivity is radiation-limited, this is likely to reduce intercepted radiation and hence productivity (Hammer *et al.*, 2010). Considered in isolation, a low T_{base} for either LAR or DR could thus be beneficial to adaptation to post-anthesis drought stress.

However, the observation that genotypes with low T_{base} values had the greatest difference in T_{base} between processes (Fig. 5) can complicate the consequences of low T_{base} on adaptation to drought, particularly under high temperatures. Because of the association between LAR and LIR (Padilla and Otegui, 2005), a low T_{base} for LAR will probably result in the initiation of more leaves prior to PI, although the extent of that will depend on the slope of the response of LAR to temperature. Any effect on TLN will be exacerbated under high temperatures, as the genotypes with low T_{base} for LAR and DR tend to have the greatest difference in T_{base} between these two processes and are thus most likely to increase TLN if temperatures increase (Tables 2 and 4; Fig. 6). An increase in TLN can potentially increase canopy size (if there is no associated reduction in tillering) and is likely to delay flowering if there is no effect on LAR. Both these effects would offset the water saving resulting from low T_{base} per se. Interestingly, there appeared to be some racial differences in this response, as *caudatum* genotypes generally had a smaller increase in TLN for a given difference in T_{base} between LAR and DR than highland *durra* and *caudatum/guinea* genotypes (Fig. 6). This could provide some genetic means to mitigate any increases in TLN and hence canopy size. As TLN is determined at PI, which in sorghum

typically occurs around 4 weeks after emergence, any potential effects of increased temperature on TLN could also be mitigated by earlier sowing in spring, which would be facilitated by the lower T_{base} . However, the consequences of such changes in agronomy on grain yield, particularly across cropping regions with variable timing and intensity of drought and heat stress, can be complex and would require targeted simulation studies to unravel any interactions (Hammer *et al.*, 2014). Hence, the multi-disciplinary approach to crop improvement advocated by Chenu *et al.* (2018), which integrates trait dissection such as described in the current study with crop growth modelling and molecular genetics to elucidate quantitative trait loci for the relevant underpinning traits, would be ideally suited to identify superior genotype \times management \times environment combinations that could exploit the potential benefits of specific adaptation of the current results.

ACKNOWLEDGEMENTS

This research was financially supported by the Bill and Melinda Gates Foundation (BMGF) and the Australian Centre for International Agricultural Research (ACIAR) through the ‘i-Mashalla’ project on ‘A targeted approach to sorghum improvement in moisture stress areas of Ethiopia’. Staff of the Ethiopian Institute of Agricultural Research at Melkassa and Kulumsa provided invaluable help in management of the experiments and in data collection.

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