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Unscrambling confounded effects of sowing date trials to screen for crop adaptation to high temperature

Victor O. Sadras[a,*], Vincent Vadez[b], R. Purushothaman[b], Lachlan Lake[a], Helen Marrou[c]

[a] South Australian Research and Development Institute, Australia
[b] Crop Physiology Laboratory, ICRISAT, Patancheru 502324, Telangana, India
[c] Montpellier Supagro, UMR System, bât. 27, 2 Place Viala 34060 Montpellier Cedex 02, France

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ABSTRACT

Against the backdrop of climate change, genotypes with improved adaptation to elevated temperature are required; reliable screening methods are therefore important. Sowing date experiments are a practical and inexpensive approach for comparison of large collections of lines. Late-sown crops usually experience hotter conditions and phenotypes thus partially capture this environmental influence. Two sets of confounded factors, however, limit the value of sowing date trials. First, daily mean temperature correlates with both minimum and maximum temperature, photoperiod, radiation and vapour pressure deficit, and it may also correlate with rainfall. Second, temperature alters the genotype-dependent phenology of crops, effectively shifting the timing and duration of critical periods against the background of temperature and other environmental variables.

Here we advance a crop-level framework to unscramble the confounded effects of sowing date experiments; it is based on four physiological concepts: (1) annual crops accommodate environmental variation through seed number rather than seed size; (2) seed number is most responsive to the environment in species-specific critical windows; (3) non-stressful thermal effects affecting seed set through development and canopy size can be integrated in a photothermal quotient relating intercepted photosynthetically active radiation (PAR) and mean temperature during the critical window; (4) stressful temperature reduces yield by disrupting reproduction.

The framework was tested in a factorial experiment combining four chickpea varieties with putatively contrasting adaptation to thermal stress and five environments resulting from the combination of seasons and sowing dates. Yield ranged from 13 to 577 $\mathrm{g\,m^{-2}}$. Shifts in phenology led to contrasting photothermal conditions in the critical window between flowering and 400 °C d after flowering that were specific for each variety–environment combination. The photothermal quotient ranged from 2.72 to 6.85 $\mathrm{MJ\,m^{-2}\,{}^{\circ}C^{-1}}$; it explained 50% of the variation in yield and maximum temperature explained 32% of the remaining variation. Thus, half of the variation in yield was associated with developmental, non-stressful thermal effect and (at most) 16% of the variation was attributable to thermal stress. The photothermal quotient corrected by vapour pressure deficit accounted for by 75% of the variation in yield and provided further insight on photosynthesis-mediated responses to temperature.

Crop adaptation to non-stressful, developmental thermal effects and stressful temperatures disrupting reproduction involve different physiological processes and requires partially different agronomic and breeding solutions. Our analytical approach partially separates these effects, adds value to sowing date trials, and is likely to return more robust rankings of varieties.

1. Introduction

Global warming drives an increasing need to understand, quantify, model and manage crop responses to elevated temperature (Dreccer et al., 2014; van Oort et al., 2014; Asseng et al., 2015; Barlow et al., 2015). It is necessary to separate two aspects of warming and their agronomic consequences: the gradual, long-term increase in ambient temperature ($\sim$0.01 $^{\circ}\mathrm{C\,yr^{-1}}$)

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* Corresponding author at: SARDI, GPO Box 397, Adelaide 5001, Australia. Tel.: +61 8 8303 9661; fax: +61 8303 9717.
E-mail address: victor.sadras@sa.gov.au (V.O. Sadras).

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that primarily shifts phenological development (Menzel et al., 2006; Ellwood et al., 2012) and the changes in frequency, intensity and duration of extreme temperature events that disrupt crop processes, particularly reproduction (Talukder et al., 2013). Developmental shifts and likelihood of extreme temperatures disrupting reproduction are not independent (Anwar et al., 2015) but adaptation to each of these thermal effects involves different physiological processes and requires partially different agronomic and breeding solutions. For example, temperature-driven shifts in phenology and reduced leaf area and biomass at anthesis, similar to the effects of late sowing, can be partially compensated with reduced row spacing and increasing sowing density or by breeding for slightly longer duration cultivars (Vadez et al., 2012) but this would be ineffective to deal with disruptive heat stress.

Bonada and Sadras (2015) made the distinction between indirect and direct approaches to assess the effects of elevated temperature on plant traits. Indirect methods include comparisons in space and time which are useful but are bound to be inconclusive due to confounded effects. Proof of cause and effect requires direct comparison of plants grown under different thermal regimes. Experimental manipulation of temperature ranges from growth chambers and glasshouses that allow for the fine control of temperature at the expense of realism to heating chambers, open-top chambers and chamber-free methods in the field which seek higher agronomic relevance. Sowing date experiments have been used to investigate thermal effects, particularly during reproduction, on crop traits including grain yield (Krishnamurthy et al., 2011; Tiwari et al., 2012; Devasirvatham et al., 2015). This method is practical, inexpensive and allows for comparisons of large collections of lines. However, this approach is indirect and therefore inconclusive; rankings of varieties as a function of the difference in yield between late and early sown crops are likely to be biased. Late-sown crops normally experience hotter conditions and phenotypes thus partially capture this environmental influence. There are, however, two important sets of confounded factors in sowing date trials. First, daily mean temperature correlates with both minimum and maximum temperature, radiation, photoperiod and vapour pressure deficit, and it may also correlate with rainfall (Rodriguez and Sadras, 2007). Sowing date changes the pattern of supply and demand for both water (Gimeno et al., 1989) and nitrogen (Caviglia et al., 2014). Second, temperature alters the genotype-dependent phenological development of crops (Slafer et al., 2015), effectively shifting the timing and duration of critical periods against the background of temperature and other environmental variables (Fig. 1A).

The aim of this paper is to advance and test a crop-level framework to unscramble the confounded effects of sowing date experiments. The framework, outlined in Fig. 1B, is based on four physiological concepts: (1) annual crops accommodate environmental variation through seed number rather than seed size (Sadras, 2007; Sadras and Slafer, 2012; Slafer et al., 2014); (2) seed number is most responsive to the environment in species-specific developmental windows (Fischer, 1985; Andrade et al., 2005; Arisnabarreta and Miralles, 2008; Sandaña and Calderini, 2012; Lake and Sadras, 2014); (3) non-stressful thermal effects on seed set mediated by development, canopy size and radiation interception can be integrated in a photothermal quotient relating intercepted photosynthetically active radiation (PAR) and mean temperature during the critical window (Fischer, 1985); (4) stressful temperature reduces yield by disrupting reproduction (Devasirvatham et al., 2012; Kaushal et al., 2013; Dreccer et al., 2014). The framework was tested in a factorial experiment combining four chickpea varieties with putatively contrasting adaptation to heat stress and five environments resulting from the combination of seasons and sowing dates.

2. Methods

2.1. Experimental design and crop husbandry

Crops were grown on a vertisol (fine montmorillonitic isohyperthermic typic pallustert) at ICRISAT, India (17° 30′ N; 78° 16′ E; altitude 549 m) during two seasons, 2012/2013 and 2013/2014. A factorial experiment combined four chickpea lines and five environments corresponding to two sowing dates (1/11/12 and 1/1/2013) in season 1 and three sowing dates (2/11/2013, 22/11/2013, and 20/12/2013) in season 2. Two heat-tolerant chickpeas ICCV 92944 and ICC 1205 were compared with two sensitive lines, ICC 4567 and ICC 5912. The putative difference in thermal adaptation of these lines was derived from the screening of a large collection of chickpea germplasm in sowing-date trials in the field (Krishnamurthy et al., 2011; Devasirvatham et al., 2015).

The experimental design was a randomised complete block design, with sowing date as the main block and genotypes randomised three times within each block. Plots were 6 m long and consisted of 4 rows with 0.3 m distance between rows and 0.1 m between plants. During field preparation, di-ammonium phosphate was applied as basal fertilizer at a rate of 100 kg ha^{-1}. Soil was land formed into 1.2-m-broad beds and a 0.3-m furrow between beds. Sowing rows were marked at the time of preparing the beds and sowing was done manually. A 20 mm irrigation was applied immediately after sowing to induce germination. The crop was fully furrow-irrigated throughout the experiment; frequency of irrigation was based on crop needs, usually every 2–3 weeks. Crops were weeded by inter-row cultivation before 4 weeks after sowing. Preventive insecticide spraying maintained crops free of *Helicoverpa* spp.

Daily maximum and minimum temperature, relative humidity at 7 am and 2 pm, and solar radiation were recorded in a meteorological station 500 m from the experiment. PAR was calculated as 0.5 × solar radiation. Vapour pressure deficit (VPD) was calculated from saturation vapour pressure ($e_{s(T)}$) and relative humidity at 2 pm with

$$e_{s(T)} = a \exp\left[b\frac{T}{c-T}\right]$$

where T is maximum temperature in °C and $a = 613.75$, $b = 17.502$ and $c = 240.97$ (Jones, 1992).

2.2. Crop traits

Phenology was recorded twice a week; we focused on the time of 50% flowering and physiological maturity assessed as change in pod colour to yellow–brown (Berger et al., 2006). At maturity, 3.0 m^2 samples were taken to determine yield and its components.

PAR interception was measured with a ceptomer (Accupar LP-80, Decagon Services, Pullman, Washington, USA) three times each week in each replicate. Polynomials were fitted to characterise the dynamics of PAR interception during the growing season and used to derive daily PAR interception, cumulative PAR interception during the critical period of yield determination and cumulative seasonal PAR interception. Radiation use efficiency, a measure of crop-level photosynthesis (Sinclair and Muchow, 1999), was calculated as the ratio of shoot biomass at maturity and seasonal PAR interception.

2.3. Data analysis

We calculated a photothermal quotient PTQ (Fischer, 1985) as the ratio between intercepted PAR and mean temperature for the critical window of yield determination between flowering and 400 °C d after flowering (Lake and Sadras, 2014);

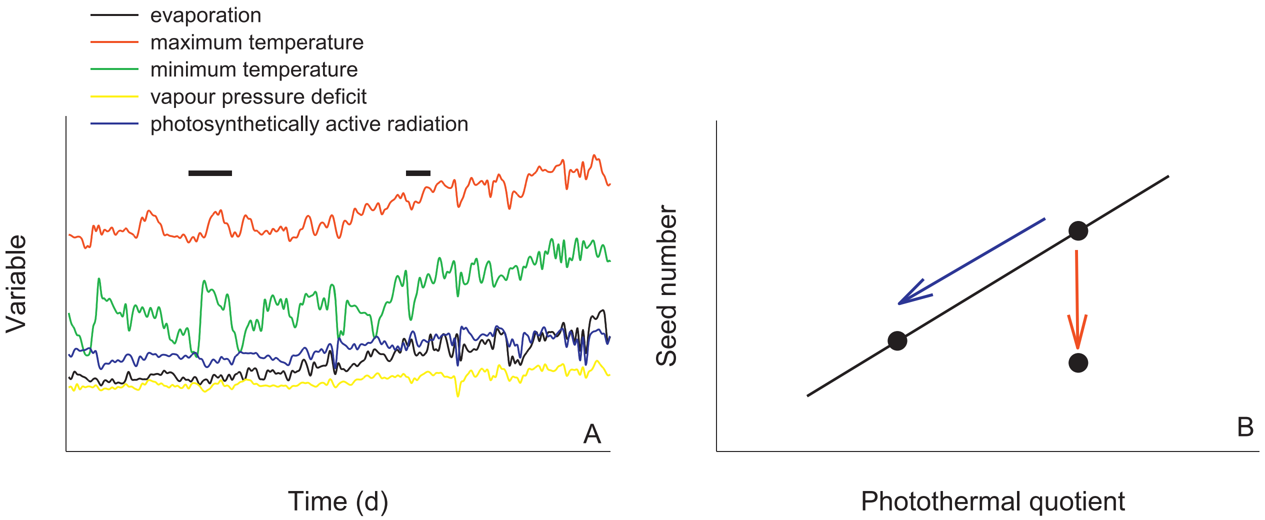

Fig. 1. (A) Sowing date experiments shift and change the duration of the critical period of yield determination (black segments) and confound stressful and non-stressful thermal effects and other factors. (B) Framework to unscramble two types of thermal effects: non-stressful, primarily mediated by development including phenology and canopy size (blue arrow) and stressful, mediated by reduced photosynthesis per unit intercepted radiation, reproductive failure or both (red arrow). Seed number, the main component of yield, is defined in a species-specific critical window. The photothermal quotient is the ratio between photosynthetically active radiation intercepted by the canopy and mean ambient temperature in the critical period. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

base temperature = 0 °C was assumed (Soltani and Sinclair, 2011). A photothermal quotient corrected by vapour pressure deficit PTQvpd was calculated as the ratio between PTQ and mean VPD during the critical period (Rodriguez and Sadras, 2007). In the present study, crops were grown in a single location during the dry season where variation in fraction of diffuse radiation was considered to be minor compared to the variation in VPD, hence we did not include a correction by fraction of diffuse radiation that may be important to account for latitudinal gradients as in the study of Rodriguez and Sadras (2007).

To test our conceptual model (Fig. 1B) we fitted linear regressions: yield versus PTQ and yield versus PTQvpd. Residuals were analysed to test for effects of maximum temperature as an indicator of thermal stress, variety, environment and other crop traits. We used IRENE (Fila et al., 2003) to fit Model II (reduced major axis) regressions where both x and y were measured with error and Model I (least squares) where the error in x is negligible relative to the error in y (Niklas, 1994; Ludbrook, 2012).

Analysis of variance was used to assess the effects of variety, environment and their interaction on crop traits. Environments were defined as the nominal combination of season and sowing date.

3. Results

3.1. Phenology and photothermal regime

Fig. 2A–E outlines the dynamics of temperature and PAR against the patterns of phenological development of the four varieties grown in five environments and Table 1 summarises growing conditions in the critical window of yield determination. All three sources of variation, that is variety, environment and their interaction, influenced time of flowering and time of maturity (all $P < 0.0001$). Averaged across environments, ICC1205 and ICC5912 reached anthesis at 53 days after sowing (DAS), ICC4567 at 49 DAS and ICCV92944 at 40 DAS (Fig. 1A–E). In relation to the first sowing, time to flowering and maturity were shortened in the second sowing of season 1, and the third sowing of season 2. The interaction is illustrated in the 4-d reduction in time to flowering for ICCV92944 between the first and second sowing in season 1, in comparison to the negligible change for ICC5912 (Fig. 2A vs. B).

Across sowing dates, seasons and varieties, maximum/minimum temperature averaged 28.9/14.1 °C before flowering and 30.7/16.2 °C after flowering. PAR averaged 7.8 MJ m^{-2} d^{-1} before and 8.5 MJ m^{-2} d^{-1} after flowering. Sowing date had a small effect on the photothermal environment of the crops before flowering, with more marked effects after flowering. Crops sown in the second and third dates grew under higher maximum and minimum temperatures, particularly after flowering, than their counterparts sown in the first date. Sowing date did not change the average PAR before flowering, whereas post-flowering PAR increased from 7.8 MJ m^{-2} d^{-1} in the first sowing to 8.8 MJ m^{-2} d^{-1} in the second and third sowing.

The environment-driven, genotype-dependent shifts in phenology led to weather conditions in the critical window that were different for each variety–environment combination (Table 1). For example, in the first sowing of season 1, ICC 5912 intercepted less PAR and experienced higher minimum and maximum temperature and higher VPD than ICCV 92944. This was captured in PTQvpd of 0.94 MJ m^{-2} $°C^{-1}$ kPa^{-1} for ICC5912 compared to 1.56 MJ m^{-2} $°C^{-1}$ kPa^{-1} for ICCV92944. Thus, even in the absence of stressful temperature, these differences in photothermal conditions during the critical period would lead to differences in yield as shown in Section 3.3. In the second sowing of season 2, ICC 5912 and ICCV 92944 were exposed to similar temperatures and VPD and intercepted similar amounts of PAR during the critical window; this led to similar PTQ and PTQvpd between these varieties, further highlighting the complex interactions between variety and environment mediated by shifts in phenology.

3.2. Yield and its components

Yield ranged from 13 to 577 g m^{-2} and was affected by all three sources of variation: variety, environment and their interaction (all $P < 0.0001$). Across sources of variation, yield was closely related to biomass and unrelated to harvest index, more closely related to seed number than to seed weight, tightly related to radiation use efficiency and unrelated to seasonal PAR interception (Table 2). It was unrelated to days to flowering, days to maturity and duration

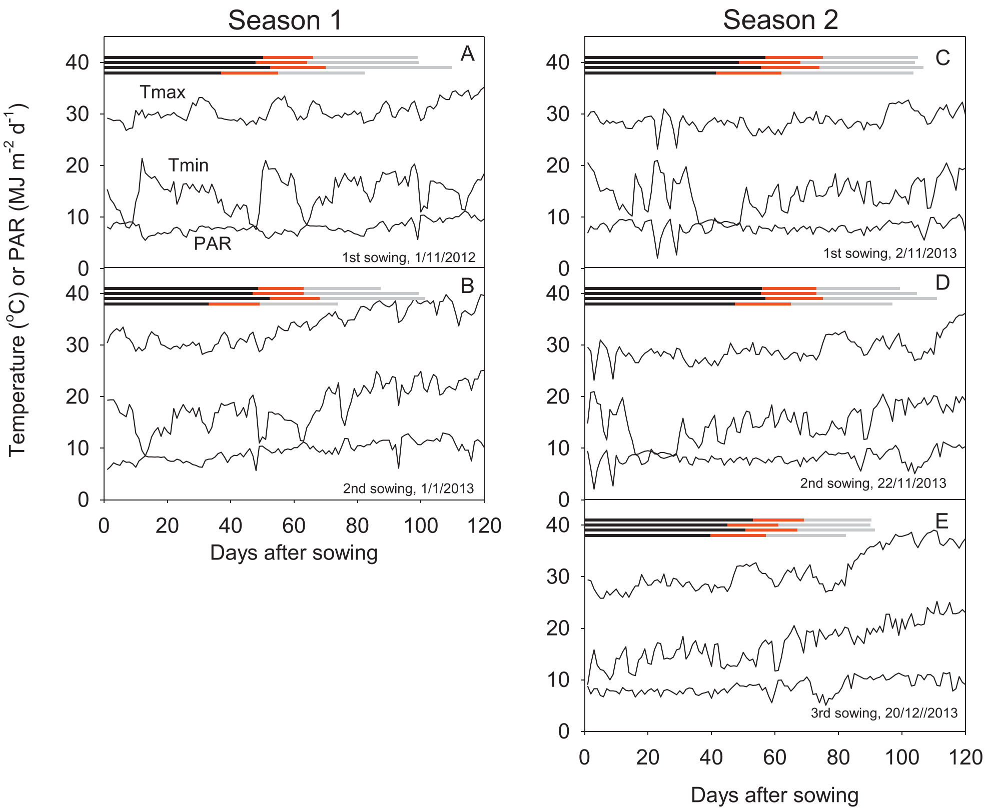

Fig. 2. (A–E) Seasonal dynamics of photosynthetically active radiation (PAR), maximum (T_{max}), and minimum temperature (T_{min}) in five environments resulting from the combination of seasons and sowing dates. Bars are time from sowing to flowering (black), flowering to 400 °C d after flowering (red) and flowering to maturity (grey) for four chickpea varieties; from top to bottom: ICC 1205, ICC 4567, ICC 5912, ICCV 92944.

of post-flowering period expressed as days or percentage of season duration. Seed number was strongly associated with pod number and weakly associated with seeds per pod (Table 2).

3.3. *Unscrambling confounded effects of sowing date on yield*

The photothermal quotient during the critical period, PTQ, accounted for half and the PTQvpd for three quarters of the variation in yield (Fig. 3A and B). Seed number explained the variation in yield in response to PTQ and PTQvpd as expected from theory (Fig. 3C and D).

The numerator of PTQ accounts for intercepted radiation but variation in crop photosynthesis per unit intercepted radiation may contribute to the scatter of the relationship between yield or seed number and PTQ. Radiation use efficiency was inversely related to vapour pressure deficit and maximum temperature (Fig. 3E and

Table 1
Average (T_{av}, °C), minimum (T_{min}, °C) and maximum temperature (T_{max}, °C), vapour pressure deficit (VPD, kPa), intercepted PAR (PARi, MJ m^{-2}), photothermal quotient (PTQ, MJ m^{-2} °C^{-1}) and photothermal quotient corrected by VPD (PTQvpd, MJ m^{-2} °C^{-1} kPa^{-1}) during the critical window of yield determination in chickpea crops resulting from the combination of seasons, sowing dates and varieties.

Season	Sowing	Variety	T_{av}	T_{min}	T_{max}	VPD	PARi	PTQ	PTQvpd
1	1	ICC 1205	23.1	15.7	30.9	2.62	86	3.71	1.42
		ICC 4567	23.0	15.5	30.6	2.53	84	3.64	1.44
		ICC 5912	22.9	14.5	31.2	2.89	62	2.72	0.94
		ICCV 92944	21.5	13.5	29.5	2.42	81	3.76	1.56
	2	ICC 1205	23.7	15.0	32.3	3.45	107	4.52	1.31
		ICC 4567	23.7	15.5	32.1	3.36	114	4.80	1.43
		ICC 5912	24.3	15.4	33.3	3.80	96	3.95	1.04
		ICCV 92944	23.8	17.0	30.6	2.84	82	3.45	1.22
2	1	ICC 1205	21.1	14.0	28.1	2.16	131	6.20	2.87
		ICC 4567	20.2	12.9	27.5	2.07	133	6.62	3.20
		ICC 5912	20.9	13.8	28.0	2.15	127	6.07	2.83
		ICCV 92944	19.4	11.3	27.4	2.18	133	6.85	3.14
	2	ICC 1205	21.7	15.2	28.2	2.16	118	5.44	2.51
		ICC 4567	21.7	15.2	28.2	2.16	119	5.49	2.54
		ICC 5912	21.6	15.0	28.3	2.21	129	5.96	2.70
		ICCV 92944	22.0	15.4	28.6	2.24	107	4.88	2.18
	3	ICC 1205	23.3	16.3	30.4	2.81	117	5.03	1.79
		ICC 4567	22.4	14.3	30.5	3.04	106	4.74	1.56
		ICC 5912	23.3	16.0	30.6	2.95	111	4.74	1.61
		ICCV 92944	22.2	14.2	30.2	2.92	131	5.89	2.02

The critical window spans from flowering to 400 °C d after flowering.

Table 2
Correlation matrix of crop traits in a factorial experiment combining four chickpea varieties and five environments.

Trait (range)	Shoot biomass	HI	Seed number	Seed weight	PARi	RUE	Pod number	Seeds per pod	Time to flowering	Time to maturity	Postflowering duration (d)	Postflowering duration (%)
Yield (13–577 g m^{-2})	***0.86***	0.35	***0.89***	**0.61**	−0.18	***0.92***	***0.85***	*0.48*	0.16	0.36	0.39	0.16
Shoot biomass (274–2044 g m^{-2})		−0.08	***0.87***	0.26	0.18	***0.94***	***0.84***	0.16	0.37	*0.53*	0.43	0.01
HI (0.02–0.53)			0.23	***0.74***	−***0.74***	0.16	0.14	***0.75***	−*0.46*	−0.39	−0.11	0.32
Seed number (300–3297 m^{-2})				0.34	−0.03	***0.86***	***0.90***	*0.47*	0.41	*0.45*	0.26	−0.13
Seed weight (35–239 mg)					−**0.64**	*0.49*	0.33	**0.64**	−*0.54*	−0.17	0.30	***0.67***
PARi (284–1099 MJ m^{-2})						−0.12	−0.16	−0.43	0.41	0.12	−0.25	−*0.54*
RUE (0.5–3.6 g MJ^{-1})							***0.86***	0.28	0.20	*0.45*	*0.50*	0.21
Pod number (410–2583 m^{-2})								0.22	0.43	**0.61**	*0.50*	0.04
Seeds per pod (0.3–1.3)									−0.18	−0.25	−0.20	0.01
Time to flowering (33–57 d)										***0.77***	0.14	−**0.70**
Time to maturity (74–111 d)											***0.74***	−0.09
Post-flowering duration (37–62 d)												***0.60***

P values are indicated in italics ($P < 0.05$), bold ($P < 0.01$) and bold + italics ($P < 0.001$). HI is harvest index, PARi is seasonal interception of photosynthetically active radiation, RUE is radiation use efficiency. Time to flowering and maturity are from sowing.

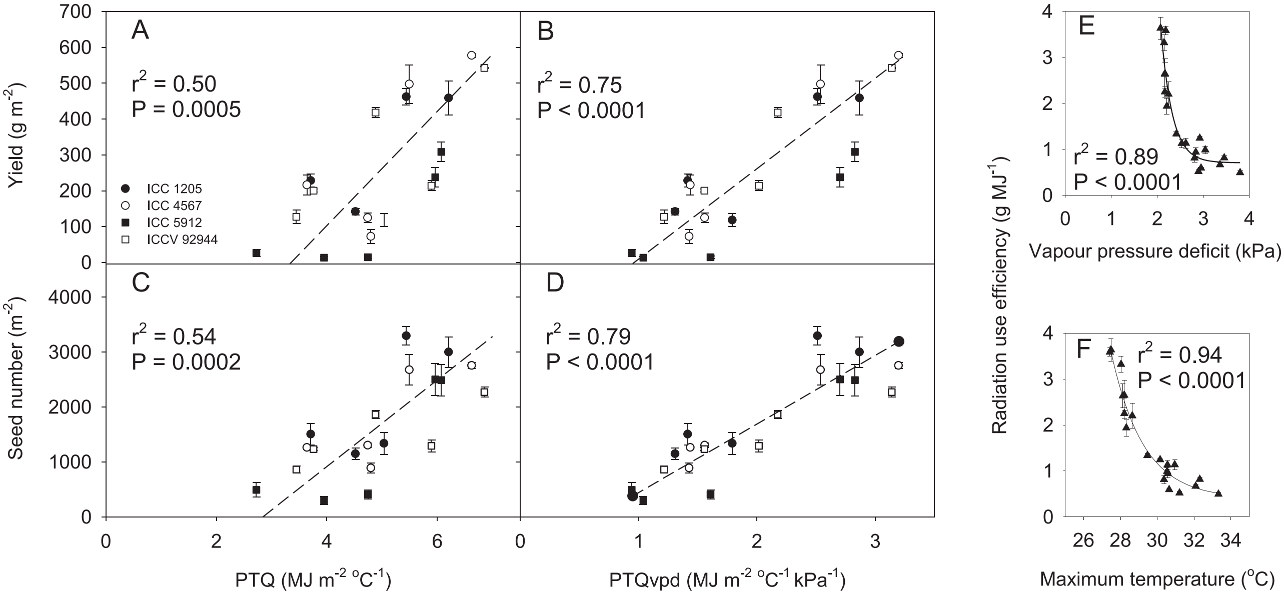

Fig. 3. (A–D) Yield and seed number of chickpea crops as a function of photothermal quotient PTQ and photothermal quotient corrected for vapour pressure deficit PTQvpd. Each point is a cultivar, according to key in A, grown under five environmental conditions resulting from combination of seasons and sowing dates. Dashed lines are model II regressions (reduced major axis). Relationship between crop radiation use efficiency and (E) vapour pressure deficit and (F) maximum temperature for the pooled data set; each point is a combination of variety and season/sowing date. Error bars are two standard errors of the mean.

F). Hence, vapour pressure deficit and maximum temperature may have contributed to the reduction in scatter of the relationship between PTQvpd and seed number (Fig. 3C vs. D) and yield (Fig. 3A vs. B) in comparison to PTQ.

Residuals of the relationship between yield and PTQvpd increased with individual seed weight (Fig. 4A). This is consistent with the dominant role of seed number and the secondary role of seed weight in yield determination (Table 2). Importantly, the association in Fig. 4A reinforces the notion that yield residuals are physiologically meaningful. If heat stress contributed to departures from the general relationship yield versus PTQvpd, we could expect, but did not found, correlation between yield residuals and maximum temperature during the critical period (Fig. 4B). However, PTQvpd already incorporates maximum temperature in the calculation of vapour pressure deficit. In contrast, residuals of the relationship between yield and PTQ declined with increasing maximum temperature (Fig. 4C).

The expected decline in yield with late sowing was verified (Fig. 4D) but seasonal and sowing date effects disappeared after accounting for PTQvpd (Fig. 4E). The average residuals of the relationship between yield and PTQvpd differed among varieties with ICC5912 showing negative residuals indicating lower yield at the same PTQvpd (Fig. 4F).

Seed weight declined with increasing minimum temperature during grain fill and was unrelated to maximum temperature in this period (Fig. 5).

4. Discussion

The phenotypic variance of crop yield comprises genetic, environmental and interaction components. The environment is the largest source of variation in most cases and yet it is often characterised superficially, for example in nominal terms of site and season (Gauch et al., 2011; Chenu, 2015) or early versus late sowing (Krishnamurthy et al., 2011; Tiwari et al., 2012; Devasirvatham et al., 2015). Significant progress has been made in the quantification of water regimes (Chenu, 2015) but quantification of thermal regimes separating stressful and non-stressful aspects of temperature has received less attention. Indirect methods to establish relationships between crop traits and temperature are in the same category of epidemiological studies; they are useful to guide direct

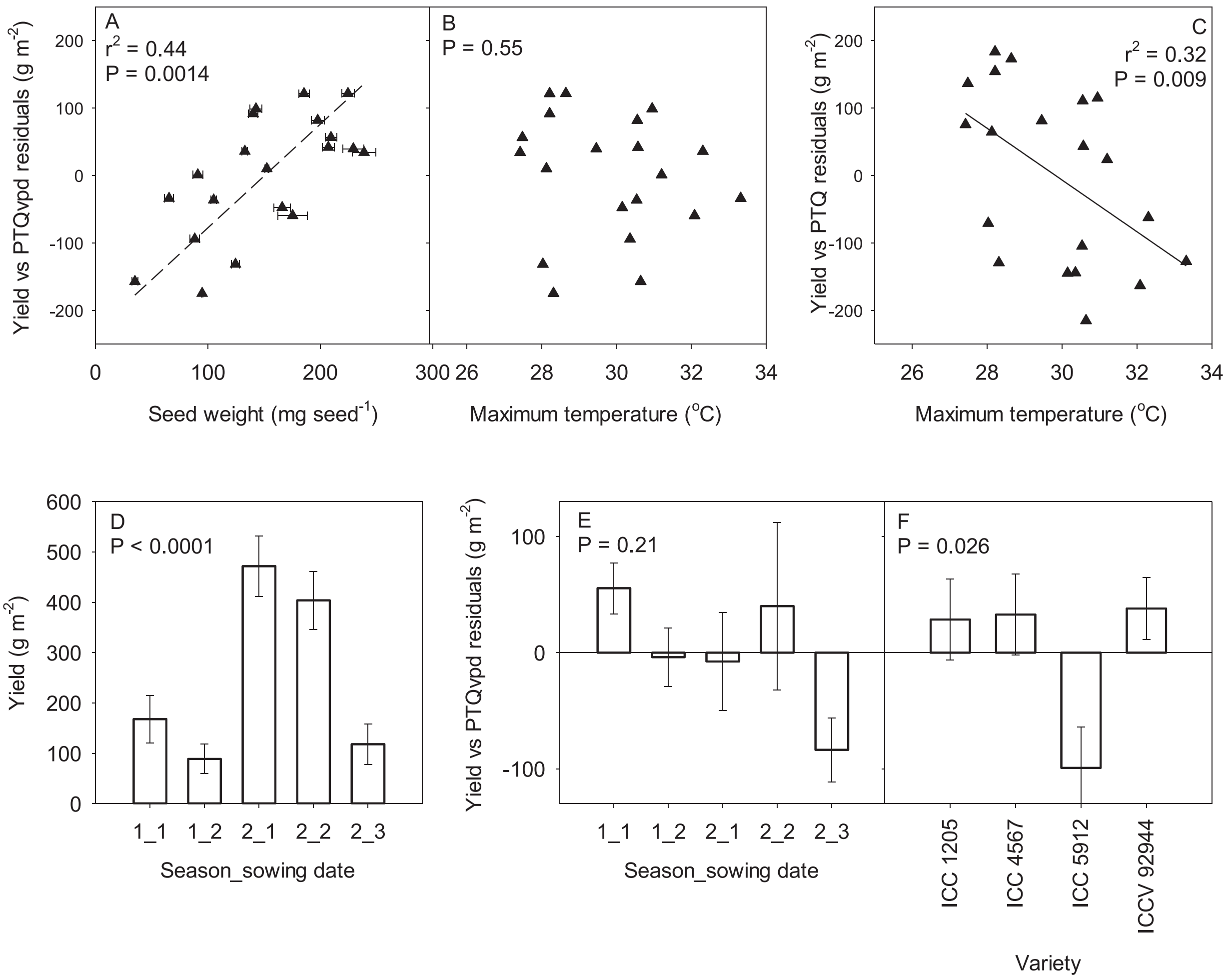

Fig. 4. Residuals of the relationship yield versus PTQvpd in chickpea crops grown in five environments as a function of (A) seed weight and (B) maximum temperature during the critical period. (C) Residuals of the relationship yield versus PTQ as a function of maximum temperature during the critical period. (D) Yield and (E) average residuals of the relationship yield versus PTQvpd in five environments defined from combination of season and sowing date. (F) Average residuals of the relationship yield versus PTQvpd of four varieties. Data are pooled across varieties (D and E) or environments (F). In (A) the dashed line is model II regression (reduced major axis) and in (C) the solid line is model I regression (least squares). Error bars are two standard errors of the mean.

experimental work necessary to prove cause and effect but inconclusive and often biased (Bonada and Sadras, 2015).

Sowing date experiments are indirect and therefore inconclusive but provide a practical approach to test large number of lines in field conditions and help to establish testable hypotheses. Confounded factors are an obstacle in the interpretation of this type of experiments. Rankings of varieties that do not account for the specific weather conditions experienced by each variety in its critical developmental window are likely to be biased. Hence our objective of advancing a conceptual framework to untangle these confounded factors and to account for genotype and environment specific conditions. In the semiarid tropics of India where we established our trials some of these confounded factors are minor; photoperiod is relatively stable at low latitude and a distinct dry season minimises the confounding effects of rainfall which was further diminished with irrigation. Stressful and non-stressful aspects of temperature and their mode (average, minimum, maximum), vapour pressure deficit and radiation remained confounded. Data analysis in terms of nominal treatments is uninformative (Fig. 4D) and indices of heat tolerance based on yield differences between early and late sowing need to be interpreted with caution (Tiwari et al., 2012; Devasirvatham et al., 2015).

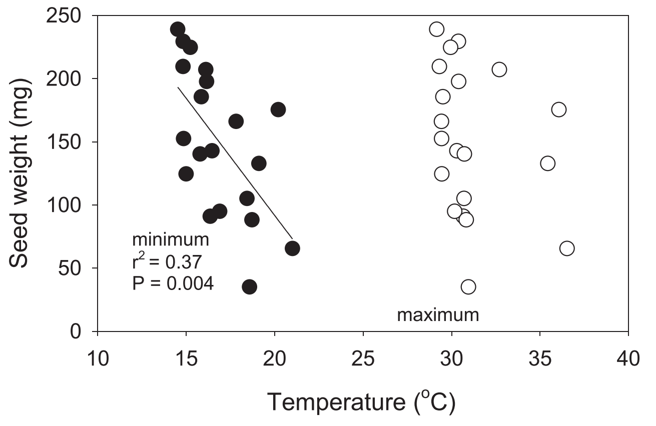

Fig. 5. Seed weight as a function of minimum and maximum temperature (average from the end of the critical period to maturity) in four chickpea varieties grown under five photothermal regimes. Solid line is model I (least squares) regression.

A simple and robust framework based on physiological principles allowed for deeper insight and partial unscrambling of confounded effects. Half of the variation in yield was accounted for by the photothermal quotient (Fig. 3A and C). We are confident this can be interpreted as a mostly developmental, non-stressful effect. The photothermal quotient corrected by vapour pressure deficit accounted for by 75% of the variation in yield and the residuals of this relationship were unrelated to both maximum temperature and nominal environment (Fig. 4B and E). The vapour pressure deficit correction could be capturing (i) a detrimental effect of high vapour pressure deficit on crop photosynthesis, (ii) a detrimental effect of high maximum temperature on crop photosynthesis, and (iii) a direct effect of maximum temperature on reproduction. Alternatives (i) and (ii) are supported by evidence for casual and non-casual (i.e., temperature-mediated) effects of vapour pressure deficit on radiation use efficiency (Rodriguez and Sadras, 2007; Stockle and Kemanian, 2009). Stomata-mediated reduction in chickpea transpiration under high VPD (Zaman-Allah et al., 2011) further supports a direct link between vapour pressure deficit and photosynthesis, that is hypothesis (i). Irrespective of the actual driver, we can expect that disruption of photosynthesis would cause deviations from the maximum yield versus PTQ relationship and that these can be captured with vapour pressure deficit or maximum temperature. The third interpretation, that is a direct effect of maximum temperature on reproduction is also possible. With maximum temperatures over 30 °C (Figs. 3F and 4C) reproductive damage is likely in chickpea (Devasirvatham et al., 2012). These three interpretations are not mutually exclusive. The simplest model based on photothermal quotient indicates a non-stressful effect of temperature accounting for 50% of the variation in yield (Fig. 3A) and a maximum of 16% variation in yield associated with stressful temperature (Fig. 4C where maximum temperature accounts for 32% of the remaining 50% variation). The model based on corrected photothermal quotient links impaired photosynthesis at high temperature and reproductive damage; this link has been demonstrated mostly at plant level in controlled environments (Kaushal et al., 2013; Dreccer et al., 2014; Wang et al., 2015). Dreccer et al. (2014) proposed a conceptual model which implicitly separates non-stressful thermal effects on development and stressful effects on reproduction mediated by finer aspects of the carbon economy of the plant including current assimilation, reserves and partitioning.

Previous work based on sowing date trials classified chickpea ICCV 92944 and ICC 1205 as heat-tolerant and ICC 4567 and ICC 5912 as sensitive. After accounting for the photothermal quotient under our experimental conditions (Fig. 2 and Table 1), ICC 4567 fell in the same category of ICCV 92944 and ICC 1205 (Fig. 4F) indicating that the low yield of this variety in late-sown crops is not necessarily an indication of sensitivity to heat stress but rather a developmental response to non-stressful high temperature. Previous studies on sowing date could be re-analysed and new studies could benefit from this approach. An important aspect of the photothermal quotient is the need to quantify intercepted, rather than total PAR in the critical period (Fischer, 1985). For large collections of germplasm, PAR interception could be estimated as a function of canopy size using remote sensing (Foulkes and Reynolds, 2015).

Seed weight is a secondary source of variation in yield but can have implications for commercial quality. Our framework could be expanded to incorporate thermal effects on grain weight that are mediated by the responses of rate and duration of seed growth (Sofield et al., 1977). Experiments are required to separate the effects of minimum and maximum temperature, as suggested by correlations (Fig. 5).

Crop adaptation to non-stressful, developmental thermal effects and stressful temperature disrupting reproduction involve different physiological processes and requires different agronomic and breeding solutions. Our analytical approach partially separates these effects on the basis of strong physiological principles, adds value to sowing date trials, and is likely to return more meaningful rankings of varieties. This approach could also be used to test the adaptive value of agronomic practices.

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