



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



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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 g m⁻². Shifts in phenology led to contrasting photothermal conditions in the critical window between flowering and 400 °Cd after flowering that were specific for each variety–environment combination. The photothermal quotient ranged from 2.72 to 6.85 MJ m⁻² °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.

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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 (~0.01 °C yr⁻¹)

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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 (Rodríguez 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 m² samples were taken to determine yield and its components.

PAR interception was measured with a ceptometer (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 °Cd after flowering (Lake and Sadras, 2014);

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