Field-screening for crop adaptation to heat stress: untangling confounded effects of sowing date trials

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Abstract
We need reliable methods to screen genotypes adapted to elevated temperature. Sowing date experiments are practical and inexpensive but confounded factors limit their value. First, 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. Our aim is to advance a framework to untangle the confounded effects of sowing date experiments; it is based on four physiological concepts: (1) annuals accommodate environmental variation through seed number; (2) seed number is determined in species-specific developmental windows; (3) non-stressful thermal effects affecting seed set through development and canopy size can be integrated in a photothermal quotient (PTQ), (4) stressful temperature reduces yield by disrupting reproduction. The framework was tested in a factorial experiment combining four chickpea varieties and five environments resulting from the combination of seasons and sowing dates. The environment-driven, genotype-dependent shifts in phenology led to different conditions in the critical window (between flowering and 400oCd after flowering) for each variety-environment combination. Yield ranged from 13 to 577 g m-2. The PTQ explained 50% of yield variation and maximum temperature for 32% of the remaining variation. Thus, half of the variation in yield was associated with developmental, non-stressful photothermal effect and (at most) 16% of the variation was attributable to thermal stress. The PTQ corrected by vapour pressure deficit explained 75% of the variation in yield and provides further insight on photosynthesis-mediated responses to temperature.

Keywords
Chickpea, radiation use efficiency, vapour pressure deficit, phenology, breeding

Introduction
Sowing date experiments have been used to investigate thermal effects on crop traits including grain yield. 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. Sowing date changes the pattern of supply and demand for both water and nitrogen. Second, temperature alters the genotype-dependent phenological development of crops, effectively shifting the timing and duration of critical periods against the background of temperature and other environmental variables (Fig. 1A).

Here we 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; (2) seed number is most responsive to the environment in species-specific developmental windows; (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 #519}; (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 heat stress and five environments resulting from the combination of seasons and sowing dates.

Method

Fully irrigated crops were grown on a vertisol at ICRISAT, India during two seasons, 2012/13 and 2013/14. 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.

Phenology was recorded twice a week. At maturity, 3.0 m2 samples were taken to determine yield and its components. PAR interception was measured with a ceptomer 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 was calculated as the ratio of shoot biomass at maturity and seasonal PAR interception.

We calculated a photothermal quotient PTQ (J Agric Sci 105: 447-461) as the ratio between intercepted PAR and mean temperature for the critical window of yield determination between flowering and 400 oC d after flowering (Field Crops Res 168:1-7); base temperature = 0 oC was assumed. A photothermal quotient corrected by vapour pressure deficit PTQvpd was calculated as the ratio between PTQ and mean VPD during the critical period. 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.

To test our conceptual model (Fig. 1B) we fitted linear regressions: yield vs PTQ and yield vs PTQvpd. Residuals were analysed to test for effects of maximum temperature as an indicator of thermal stress, variety, environment and other crop traits.

Results

All three sources of variation, i.e. variety, environment and their interaction, influenced time of flowering and time of maturity (all $P < 0.0001$). The environment-driven, genotype-dependent shifts in phenology led to weather conditions in the critical window that were different for each variety-environment combination.

Yield ranged from 13 to 577 g m-2 and was affected by all three sources of variation: variety, environment and their interaction (all $P<0.0001$). The photothermal quotient during the critical period, PTQ, accounted for half and the PTQvpd for three quarters of the variation in yield (Fig. 1AB). Seed number explained the variation in yield in response to PTQ and PTQvpd as expected from theory (Fig. 1CD).

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. 1EF). Hence, vapour pressure deficit and maximum temperature may have contributed to the reduction in scatter of the relationship between PTQvpd and seed number (Fig. 1 C vs D) and yield (Fig. 1 A vs B) in comparison to PTQ.

Residuals of the relationship between yield and PTQvpd increased with individual seed weight (Fig. 2A). This is consistent with the dominant role of seed number and the secondary role of seed weight in yield determination. Importantly, the association in Fig. 2A reinforces the notion that yield residuals are physiologically meaningful. If heat stress contributed to departures from the general relationship yield vs PTQvpd, we could expect, but did not find, correlation between yield residuals and maximum temperature during the critical period (Fig. 3B). 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. 3C).

The expected decline in yield with late sowing was verified (Fig. 3D) but seasonal and sowing date effects disappeared after accounting for PTQvpd (Fig. 3E). 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. 3F).

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

Conclusion

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.

Acknowledgements

Our research was funded by the GRDC, the Australia–India Strategic Research Fund, and the CGIAR Research Program (CRP) on Grain Legumes. This paper is a summary of full paper published in Field Crops Research (2015).

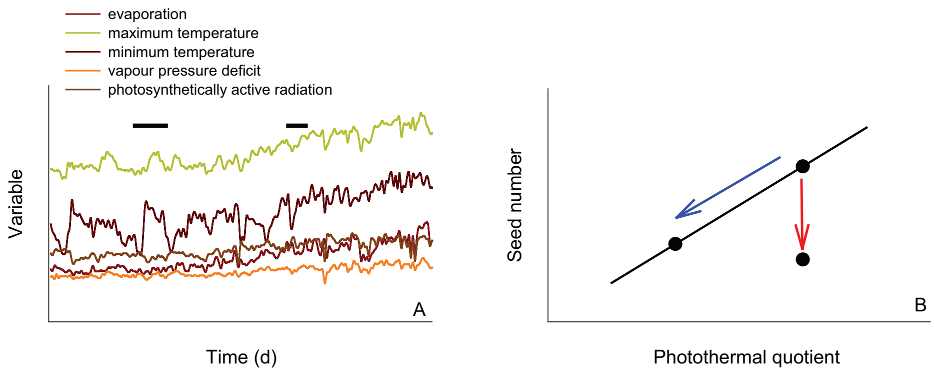

Figure 1. (A) Sowing date experiments shift and change the duration of the critical period of yield determination (black segments) and confound stressful and non-stressful thermal effects and other factors. (B) Framework to unscramble two types of thermal effects: non-stressful, mediated by phenology and canopy size (blue arrow) and stressful, mediated by reduced photosynthesis per unit intercepted radiation, reproductive failure or both (red arrow).

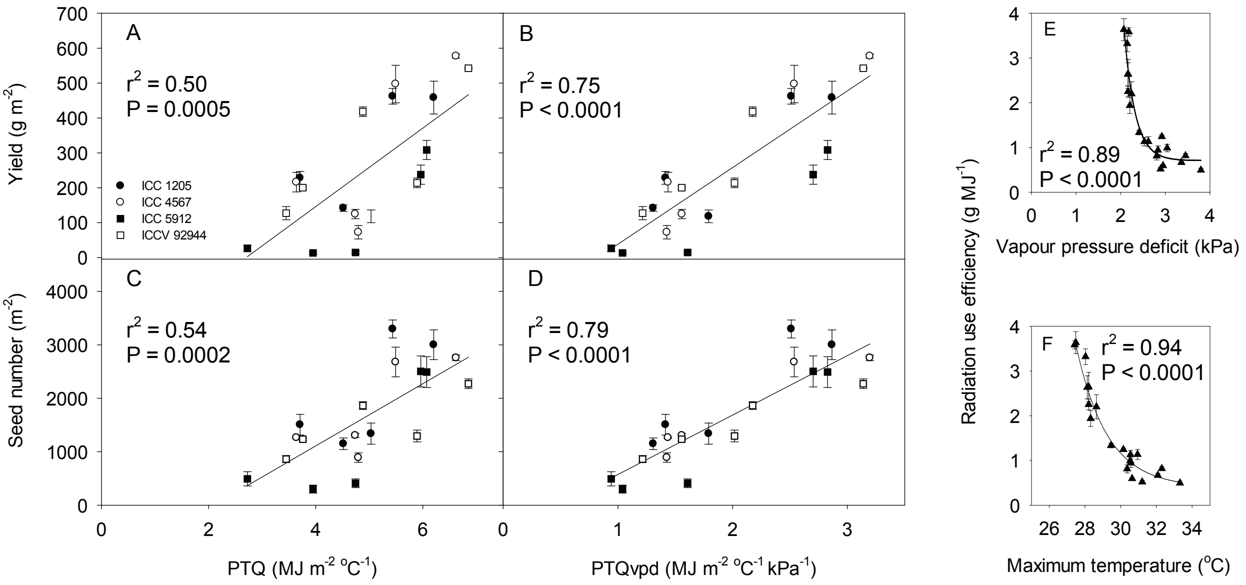

Figure 2 (A-D) Yield and seed number of chickpea crops as a function of photothermal quotient PTQ and photothermal quotient corrected for vapour pressure deficit PTQvpd. Each point is a cultivar, according to key in A, grown under five environmental conditions resulting from combination of seasons and 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.

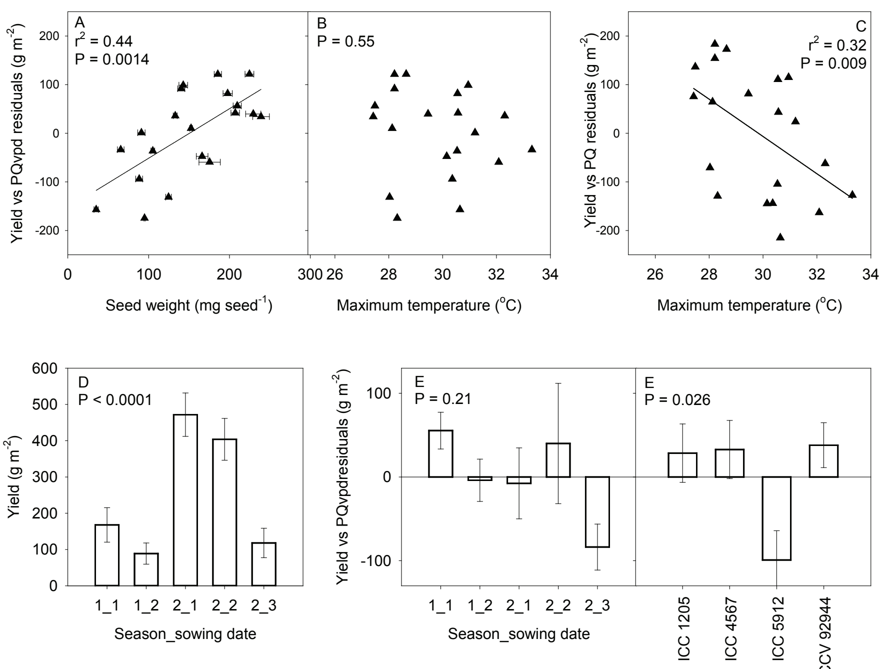

Figure 3. Residuals of the relationship yield vs PTQvpd in chickpea crops grown in five environments as a function of (A) seed weight and (B) maximum temperature during the critical period. (C) Residuals of the relationship yield vs PTQ as a function of maximum temperature during the critical period. (D) Yield and (E) average residuals of the relationship yield vs PTQvpd in five environments defined from combination of season and sowing date. (F) Average residuals of the relationship yield vs PTQvpd of four varieties. Data are pooled across varieties (D,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.