Crop simulation analysis of phenological adaptation of chickpea to different latitudes of India

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ABSTRACT

Plant phenology is a critical component of crop adaptation, especially under environmental conditions that don't allow crop growth for unlimited periods. In chickpea (cicer arietinum L.), which faces terminal drought and increasing temperature at the end of its growing season, it is widely considered that longer duration genotypes are needed for the higher latitudes of India and shorter duration genotypes for lower latitudes. Here, we compare two sets of genotypes bred in two locations varying in latitude (high latitude: Hisar, Haryana, India; low latitude: ICRISAT, Andhra Pradesh, India) for the number of biological days from emergence to flowering (EMR1) and for the grain filling period (R5R7). Biological days referred to days where the phenological development was optimal and therefore provides a measure of thermal time. Using a robust crop simulation model, the optimum EMR1 and R5R7 were determined for various locations. As expected, EMR1 and R5R7 values of genotypes bred for low latitude were lower than those bred for high latitude. However, predicted yields of these two sets of genotypes were similar when simulated for each of the two environments, yields being overall higher at Hisar. Results for the combined set of genotypes at each location predicted a similar optimum EMR1 to achieve maximum yield at each location: 44.3 biological days at Hisar and 43.5 biological days at ICRISAT. Derivation of optimum EMR1 across a total of ten locations in India indicated a wider range (37.2 to 51.8 biological days), although in eight locations the optimum EMR1 was in a narrower range (39.4 to 47.3 biological days). The differences in EMR1 across locations did not

correspond to their latitudinal differences. Instead, rainfall through the growing season was significantly and positively related ($R^2 = 0.55$) to optimum EMR1. These results indicate that the breeding for optimum EMR1 of chickpea in India needs to be focused on expected rainfall for a region, and that an optimum EMR1 of about 43 biological days would likely fit most of the environments.

Key words: Chickpea, Terminal drought, latitude, flowering time, breeding

1. Introduction

Plant phenology is an important aspect of crop adaptation to environmental conditions in order to match optimally the cropping cycle with the seasonal weather pattern. Phenology has particular importance in water-limited situations where the cropping cycle has to match seasonal variability in available soil water. For chickpea cultivation in tropical areas, it is widely assumed that chickpea varieties differing in their duration need to be developed for adaption to different latitudes (Saxena, 1984; Kumar and Abbo, 2001; Berger et al., 2011). In India, where terminal drought is the major limitation to yield, it is then considered that longer duration genotypes are more adapted to higher latitude, whereas shorter duration genotypes are better adapted to lower latitudes (Berger et al., 2006). The rationale is that the higher latitude usually has cooler temperature until at least March, and longer duration cultivars can sustain CO_2 accumulation and fill grain for a longer period before summer temperatures become too high (Saxena et al., 1996; Khanna-Chopra and Sinha, 1987). By contrast, in southern India the chickpea crop duration window is constrained by sowing at the termination of rains (later October) and increasing heat of summer (early March), resulting in a narrow window for shorter duration cultivars. For southern India, breeding for earliness has been widely recommended (Saxena 1984; Kumar and Abbo, 2001; Berger et al., 2004).

The difficulty in adopting the concept of latitude-adapted cultivars is that there is limited experimental evidence in India based on comparisons of short- and long-duration genotypes over a range of latitudes. Often breeding programs from the North India report the testing of their long-duration lines, whereas breeding programs from the South report the testing of their short-duration material (Saxena, 1984). Berger et al. (2006) noticed this major problem and attempted to fill that gap by testing a fairly large set of lines, varying in duration, across a range of locations varying in latitude, in order to assess whether there is specific phenological adaptations of chickpea to different latitudes. Their conclusion, based on analysis of the experimental data, sustained the original hypothesis in selecting cultivar phenology based on latitude.

However, there were at least three limitations in the study of Berger et al. (2006). First, the low-latitude region was represented only by a single location in the South situated at 17ºN, whereas all the other locations were between 23ºN and 29ºN. This is particularly important in the current context since there has been increasing cultivation of chickpea in southern locations (around 17-18ºN latitude). Therefore, the question is whether the conclusion of Berger et al. (2006) was limited by having results from only a single low-latitude location. Also, some of the most northern locations where chickpea is grown (e.g. Amritsar) were not included. Second, the analysis of Berger et al. (2006) was based simply on days to flowering. In comparing phenological development across location it is important to take account of dynamic changes in temperature during development. That is, the rate of phenological development towards flowering for example is highly dependent on the daily temperature environment. Cultivar comparisons across latitudes need to account for the temperature environment and the developmental differences among cultivars in their response to temperature, as recently shown (Berger et al., 2011). Third, there is ambiguity between their main conclusion of the need to select cultivar duration with regards to location latitude, and

their report of a cluster of medium duration genotypes reaching the highest yield across all latitudes (Berger et al., 2006).

The sensitivity of phenology in chickpea as a function of temperature and photoperiod is well documented (Ellis et al., 1994; Soltani et al., 2006a, 2006b). Soltani et al. (2006a) reported for several chickpea cultivars their baseline and optimal temperature for phenological development, as well as critical photoperiod. The critical photoperiod was consistently at 11h indicating for this long-day species that the rate to flowering was delayed at shorter daylengths. While this was an important consideration in the studies of Soltani et al (2006a) in Iran where the critical photoperiod was often exceeded, at the low latitude of India with shorter photoperiod the influence would be less important. In any case, in the higher latitudes in India where temperatures are cooler than in the south and there is the possibility of some daylengths slightly shorter than 11 h, environmental conditions can have a large influence on expression of cultivar phenology. Further, soil water deficit accelerates phenological development in chickpea (Singh 1991; Soltani et al., 2001; Soltani and Sinclair, 2011). Therefore, it is essential to account for these environmental variables when attempting to assess the optimal phenological traits over a range of latitudes.

It is now possible to undertake a phenological comparison across cultivars and latitudes by using crop simulation models. A robust model for chickpea exists that accounts for the influence of temperature, photoperiod, and soil water content on phenological development of individual genotypes (Soltani et al., 1999; Soltani and Sinclair, 2011). The model has successfully been tested using independent data from a wide range of growth and environmental conditions (Soltani and Sinclair, 2011). Vadez et al. (2012) have also successfully tested the model performance in response to water deficit under Indian conditions using the data from three line-source experiments which provided a range of water availability. Soltani et al. (2006a, 2006b) have confirmed the robustness of the phenology

submodel of the chickpea model under a wide range of environmental conditions that influence phenological development.

This model was used to address three objectives. First, evaluate the thermal time requirement of various genotypes in the development rate during specific phenological stages (i.e. EMR1, time from emergence to flowering, and R5R7, duration of seed filling). This was done by determining the cumulative temperature units (often referred to as "degree day" even though time is not an explicit component of this term) for individual genotypes using observations from a northern (Hisar, Haryana, India) and a southern location (Patancheru, Andhra Pradesh). Second, the range of EMR1 and R5R7 values among genotypes was used to assess the sensitivity of yield to variation in these parameters. The range of variation in the optimum values for these two parameters across locations in India was then assessed. Third, having found variation among locations in the optimum EMR1, the environmental variable accounting for the need for differing EMR1 was studied.

2. Material and Method

2.1. Crop model

The chickpea model of Soltani and Sinclair (2011) was used in this study. The model simulates phenological development, leaf development and senescence, mass partitioning, plant nitrogen balance, yield formation and soil water balance. Responses of crop processes to environmental factors of solar radiation, photoperiod, temperature, nitrogen and water availability, and genotype differences were included in the model. The required model inputs include soil information, crop management and daily weather data. The status of the crop is updated in the model using daily time steps. The model has successfully been tested using independent data from a wide range of growth and environmental conditions (Soltani et al.,

2006a; Soltani and Sinclair, 2011). In testing the model, observed days to maturity have been varied from 78 to 228 d and observed grain yield were between 20 and 325 g m^{-2}. In most cases, simulated phenology and grain yield were similar to observed ones.

This model accounts for the effects of temperature, photoperiod and water deficit on phenological development of chickpea. The phenological stages of emergence, first-flower (R1), first-pod (R3), beginning seed growth (R5), first-maturity (R7) and full-maturity (R8) are predicted by the model (Soltani et al., 2006a, 2006b). Phenological development is predicted using biological day requirements between stages (Soltani and Sinclair, 2011). Biological day requirement is the minimum calendar days between events under optimal temperature, photoperiod and water conditions. Soil stress indeed hastens phenological development (Singh 1991; Soltani et al., 2001). Optimal temperature is the temperature that allows the maximum phenological development rate. Maximum development rate takes place between a lower and a higher optimum temperature. Below the lower optimum and above the higher optimum temperature, phenological development is less than maximum and is decreased by the appropriate temperature response function described below. Therefore, the concept of biological days refers to a thermal time accumulation and does not equate to a calendar unit. The more familiar cumulative temperature unit for a phenological event is then equal to biological days multiplied by the difference between optimum and base temperatures. Biological days are required in the model for the periods of sowing to emergence, emergence to R1, R1 to R3, R3 to R5, R5 to R7 and R7 to R8. Except for the periods of emergence to R1 (EMR1) and R5 to R7 (R5R7; grain filling period), the biological day requirements are fairly constant among genotypes (Soltani et al., 2006a, 2006b).

Cardinal temperatures were set at 2 ^{o}C for base temperature, 21 ^{o}C for lower optimum temperature, 30 ^{o}C for upper optimum temperature and 40 ^{o}C for ceiling temperature (Soltani et al., 2006a, 2006b). A linear-plateau (2-piece segmented) function is used to account for the

effect of photoperiod on development rate. This function separates photoperiod response of development rate into distinct phases; linear increase in development rate occurs in phase 1 until photoperiod reaches a critical value (critical photoperiod) above which development rate remains at its maximum. The plateau line describes this maximum development rate under photoperiods longer than critical photoperiod. Soltani et al. (2006a) have provided data for chickpea on both functions. The linear-plateau function with constant critical photoperiod of 11 h and photoperiod sensitivity coefficient of 0.143 was used for Indian genotypes as reported by Singh and Virmani (1996). The biological days requirements for phenophases were also obtained from Singh and Virmani (1996), but they were corrected for different cardinal temperatures used in the chickpea model of this study. The critical photoperiod of 11 h is obviously lower than values of 15 to 21 h reported for non-Indian chickpea cultivars (Ellis et al., 1994; Roberts et al., 1980; Soltani et al., 2006a).

2.2. Model testing

Following Soltani et al (2006a, 2006b), the phenology submodel was further tested for Indian conditions. Model predicted phenological stages of R1, R3, R5 and R8 are compared with recorded days to these stages. For this purpose, data from four experiments conducted in ICRISAT, Patancheru (17° 30' N; 78° 16' E; altitude 549 m asl, India) and described by Singh and Virmani (1996) were used. The experiments were conducted under both irrigated and rainfed conditions in 1985, 1987, 1992 and 1993. The 1985 experiment was conducted to study the response to various severities of water deficit at different phenological stages in the chickpea cultivar Annigeri using the line-source irrigation technique. There were 12 treatments with irrigation water ranging from 45 to 227 mm during the growth period. Non-irrigated treatment received 45 mm irrigation water to ensure crop establishment. For the purpose of this test, days to different phenological stages under both irrigated and non-

irrigated treatments were used. The 1987 experiment was a similar design and had the same treatments as in the 1985 experiment. However, the cultivar was JG 74 and it was sown on 28 October 1987. The amounts of irrigation applied to various treatments ranged from 25 to 247 mm and rainfall received during the growing season was 241 mm. The 1992 experiment was a split-plot experiment consisting of irrigated and non-irrigated treatments in the main plots, and six cultivars (ICCV 88202, Annigeri, ICCC 32, ICCC 42, ICCV 2 and ICCV 10) in sub-plots. The 1993 experiment was conducted during 1993 post-rainy season, starting in November. Six cultivars of chickpea (ICCV 88202, Annigeri, ICCC 32, ICCC 42, ICCV 2 and ICCV 10) were grown under rainfed conditions after an initial irrigation of 55 mm at sowing to facilitate crop emergence. Phenological data of Annigeri from the 1992 and 1993 experiments were used here for model testing.

2.3. Field experiments and genotypes

Deriving genotype parameters from trials in Hisar and ICRISAT: The genotypes tested in Hisar and ICRISAT are listed in Table 1. In both places the set of genotypes that were used represented either released or advanced breeding lines bred in Indian institutions, or local landraces (e.g. Annigeri), except for the inclusion of P1329, a longer duration line from the north in the ICRISAT trial. Two trials were carried out at ICRISAT and one trial in Hisar. Here we used the phenological data to parameterize the EMR1 and R5R7 values of these different genotypes in both locations.

In ICRISAT, eight genotypes were chosen from an original set of sixteen chickpea varieties (Annigeri, K 850, JG-74, P1329, ICC7684, ICC10985, ICCL82001, ICC10991, ICC4958, ICC10428, ICC11051, ICC10448, ICCC22, ICCC33, ICCC37, ICCC41). The eight entries were chosen to cover the range of observed number of days to flowering. These genotypes were evaluated in two regular crop growing seasons (1986-87 and 1987-88) in Vertisols (fine

montmorillonitic isohyperthermic typic pallustert) at ICRISAT, Patancheru (17° 30' N; 78° 16' E; altitude 549 m) in south India. The soil depth of the fields used in the three seasons was ≥1.2 m and these soils retained about 230 mm of plant available water in the 120-cm (maximum rooting depth) soil profile. The fields were prepared into broad bed and furrows with 1.2-m wide beds flanked by 0.3-m wide furrows in both years. Surface application and incorporation of 18 kg N ha^{-1} and 20 kg P ha^{-1} as di-ammonium phosphate was carried out in all the experiments. The plot size was 3.0 m x 4.0 m in both years. The experiments were conducted with two irrigation levels as main plot treatments (i.e. drought stressed, which was non-irrigated except for a post-sowing irrigation, and irrigated) in a split plot design with three replications. Seeds were treated with 0.5% Benlate® (E.I. DuPont India Ltd., Gurgaon, India) + Thiram® (Sudhama Chemicals Pvt. Ltd. Gujarat, India) mixture in both the seasons. All the experiments were hand sown at the first opportunity after the cessation of the rains in the fourth week of Oct 1987 and Oct 1988. The sowing was in rows 30-cm apart with 10 cm between plants at 3-5 cm depth with two seeds per hill, which was later thinned to one plant. Phenological stages were recorded on a daily basis.

In Hisar, a similar procedure was used in which eight genotypes were selected for parameterization from the original set of sixteen different varieties (G 24, BG 209, G 543, C 235, K 468, H 208, C 104, S 26, L 144, C 214, GL 769, K 850, GAURAV, Pant G 114, G 130 and L 550) to cover the entire spectrum of observed numbers of days to flowering. These genotypes were evaluated in field conditions at Haryana Agricultural University Farm, Hisar in the 1986-87 post rainy season. Hisar (29° N; 76° E; altitude 221 m) is situated in north India and the soils were Entisols (sandy clay loam) with 210 mm available water capacity in the top 1.0 m soil depth. This crop was sown in a flat bed and the rest of the crop management remained the same as at ICRISAT. By regular observation, the date when 50% or more of the plants in a plot flowered was recorded as the flowering date for the plot. Similarly,

when 80% of the pods in a plot were dried the date was recorded as the time of maturity for each plot.

2.4. Simulation analysis

2.4.1. Simulating ICRISAT and Hisar lines

To simulate yields of ICRISAT and Hisar, the biological day requirements for the phenological stages were needed for each line. An iterative procedure was used to obtain biological day requirements for EMR1 and R5R7 so that simulated predictions of the biological day durations for these two stages matched phenological field observations for each genotype. Requirements of biological day for other phenological stages mentioned in section 2.1 were kept constant. Unfortunately, there was no overlap in cultivars between the two locations so the phenological parameters were determined for each genotype for the location at which it was grown.

The derived EMR1 and R5R7 values were then used as input parameters to simulate for each genotype their phenological stages and seed yield across 28 years of weather data at Hisar (1973-2002) and 33 years of weather data at ICRISAT-Patancheru (1977-2010). The eight genotypes selected for study from each location were combined and simulations were done for all 16 genotypes at each location. All other input parameters were held constant across simulations. Except for the biological day parameters, all other parameters were those described by Soltani and Sinclair (2011). Seed yields are presented on a dry weight basis, adjusted for seed moisture (15%).

For the simulation of chickpea phenological response, a standard soil depth of 1200 mm, a depth of effective water extraction of 1000 mm and a rate of daily root growth of 17 mm day^{-1} were used. The model made one run for each season, independently of previous season's

run or previous crop, and considered that the profile was fully charged with water at the time of sowing in each season. A uniform sowing date (1 November), and a uniform plant density of 25 plants m^{-2} were simulated. Daily minimum and maximum temperatures, solar radiation, and precipitation needed for the model were obtained from local weather stations. All simulations were performed assuming no irrigation so the crops only received observed amounts of rainfall. Seasonal rainfall was then the cumulated rain received during the cropping season determined by the model.

Mean yield for each genotype was calculated from simulations across all years for all genotypes at both Hisar and ICRISAT—Patancheru. A plot was generated for each location from the mean yield of each genotype graphed against the biological days of EMR1 for that genotype. Therefore, the simulation results provided mean yield estimates of all 16 genotypes. The results for each location were then analyzed by a third-order regression to determine the EMR1 value resulting in the maximum yield. A procedure identical to that done with EMR1 was done for the R5R7 stage. That is, mean yield for each of the 16 genotypes at each location was plotted against the biological days for R5R7.

2.4.2. Simulating optimal EMR1 and R5R7 across locations

Simulations were done to determine if there was widespread consistency for optimal EMR1 and R5R7. Eight additional locations were studied covering the latitude spectrum in which chickpea is cultivated in India. The selection of these locations required at least 15 years of weather data (the range of number of years available was 18-33 years) and offered a wide range of latitudes. Therefore, a total of ten locations were simulated: four locations were taken from south India (Bangalore, Annigeri, Gulbarga, ICRISAT, with latitude of 12.97, 15.13, 17.35, 17.88 ^{o}N respectively), two from central India (Indore, Jabalpur, with latitude

of 22.72, 23.20 ºN), and four from north India (Jaipur, Delhi, Hisar, Amritsar, with latitude of 26.82, 28.66, 29.16, 31.60 ºN, respectively) (Fig. 1). For these simulations, all other parameters were kept constant, in particular soil characteristics such as depth, to allow comparison to ICRISAT and Hisar.

An optimum EMR1 was explored at each of the ten locations. A R5R7 duration was fixed at 35 biological days for this test. A series of simulations were done to determine mean yield resulting from various assumed values of EMR1. Simulations were done assuming values of EMR1 ranging from 25 to 70 biological days at 5 d intervals. At each of the ten locations, mean simulated grain yield was plotted vs. EMR1 and fitted using a third-order polynomial from which the optimum EMR1 for each location was obtained.

3. Results and Discussion

3.1. Model testing

Figure 2 shows a direct comparison of simulated versus recorded days to different phenological stages of R1, R3, R5 and R8 for the four experiments conducted at ICRISAT. Recorded days to the R1, R3, R5, and R8 stages ranged from 38 to 50, 44 to 57, 48 to 71, and 89 to 114 days, while simulated days ranged from 34 to 44, 44 to 57, 51 to 68, and 89 to 114 days, respectively for R1, R3, R5, and R8. Means of recorded and simulated days for R1, R3, R5, and R8 were 44 and 38, 49 and 48, 62 and 58, and 101 and 89, respectively. On average across the different stages, the mean observed and predicted number of days was 64 and 58 days. Differences here were mostly due to an underestimation of R8 under irrigated conditions. The model gave good predictions of stages of R1, R3 and R5 which are critical phenological stages in crop yield formation. Nearly all model predictions for these stages were within 15% lines of discrepancy. The model also provided very good predictions of R8

under rainfed conditions, but underestimated days to R8 under irrigated conditions. However, all model predictions for non-irrigated conditions, which were our focus in this study, were close to a 1:1 line.

Since the overall root mean square of error (RMSE) of the predictions was 6 days, about 11% of the recorded mean, it was concluded that the model is robust for simulating phenological development of chickpea in India. These results confirmed a similar robustness shown in Iran (Soltani et al., 2006). Parallel study also showed the robustness of the model to predict crop yield under rainfed conditions in India (Vadez et al., 2012, unpublished).

3.2. Parameterization of genotypes

A large range among genotypes at ICRISAT and Hisar was found in their biological days for EMR1 and the duration of R5R7 (Table 1). The values for EMR1 ranged from 27 biological days for ICC4958 at ICRISAT to 65 biological days for BG209 at Hisar. There was a clear distinction between the genotypes grown at ICRISAT where the average biological days for EMR1 was 38.9 biological days as compared to an average of 56.3 biological days for genotypes grown at Hisar. This analysis clearly indicates that breeding for chickpea genotypes at each region selected genotypes with quite different phenotypic development, i.e. a short EMR1 at ICRISAT and a long EMR1 at Hisar.

The difference among genotypes for the duration of the R5R7 period was somewhat less than for EMR1, although there was substantial variability (Table 1). The total range of R5R7 was from 27 biological days for ICC10985 and ICC109911 at ICRISAT to 52 biological days for Gaurav at Hisar. The average biological days for the duration of R5R7 for the two locations were 30.3 at ICRISAT and 43.8 at Hisar. Again, breeding has resulted in faster phenological development at ICRISAT as compared to Hisar.

3.3. Simulating phenology and yield of ICRISAT and Hisar lines

Phenological development and yield was simulated for all 16 genotypes for all years at both locations. Given the difference in inherent biological days for EMR1 and R5R7, it is not surprising that differences in the phenological development for the genotypes developed for each region were apparent in the simulation results at each location. That is, the genotypes developed for the low latitude were simulated to have substantial more rapid development than those from the high latitudes at both ICRISAT and Hisar (Table 2). The average difference in the number of days to maturity between the two groups of genotypes was 23 d when simulated at ICRISAT and 25 d when simulated at Hisar. The simulated number of days to maturity for these genotypes (87 and 148 days at ICRISAT and Hisar, respectively) were also close to the observed average time to maturity of the ICRISAT and Hisar genotypes at their respective location (92 and 145 days, respectively).

In contrast to the large phenology differences among the lower and higher latitude genotypes, there was no difference between the two groups in average simulated yield (Table 2). Indeed, at both locations, the difference in average yield of the two groups of genotypes was less than 2 g m^{-2}. That is, the genotypes developed for a particular latitude did not out-yield those genotypes from another latitude when placed in the same environment. No yield advantage was simulated at either location for either a short-season or long-season phenological development. There were, however, substantial yield differences simulated for the two locations (Table 2). Average simulated yield across all genotypes of 83.8 g m^{-2} at ICRISAT was much less than 139.4 g m^{-2} at Hisar.

The results of these simulations were used to determine the optimum EMR1 at ICRISAT and Hisar to maximize yields. Plots of simulated yield vs. biological days for EMR1 clearly

indicated an optimum value for EMR1 (Fig. 3). At both locations the results were well represented by a third-order polynomial: r^2 of 0.92 at ICRISAT and 0.89 at Hisar. Interestingly at both locations there was a tendency for the lower-latitude genotypes to have EMR1 shorter than the optimum and the higher-latitude genotypes to have EMR1 longer than the optimum. The optimum EMR1 for maximum yield derived from the polynomial equation was 43.5 biological days in ICRISAT and 44.3 biological days in Hisar. That is, the effort to breed for genotypes with EMR1 appropriate for these two locations was not rewarded with a yield advantage. As illustrated in Fig. 3, a single cultivar with EMR1 of about 44 biological days seemed best for both locations. Therefore, there seemed to be no justification to breed for latitude specific genotypes, at least from the point of view of maximizing the cropping duration. The only reason to breed for longer duration genotypes in Hisar would be to avoid chilling stress early in the season, but this is usually avoided by sowing later in the higher latitudes. While Berger et al. (2006) concluded that genotypes with specific phenology had specific adaptation to different latitudes, these authors also mentioned that one cluster of genotypes having medium duration (cluster 1 in their study) had the highest yield across locations, which fully agrees with our findings.

The simulated yields were also compared to the biological days for R5R7 of the genotypes when grown at ICRISAT and Hisar (Fig. 4). In both locations, genotypes developed for ICRISAT were well represented by the second-order polynomial equation, indicating that in both locations there was an optimum R5R7. Again, the optimum value for the two locations did not differ with the optimum R5R7 at ICRISAT equal to 29.8 biological days and at Hisar it was equal to 30.2 biological days. However, the results for simulations of genotypes developed for Hisar did not show an optimum R5R7 period at either location. Instead, the yields of the Hisar genotypes were described by a weak, but significant, positive linear relationship with duration of the R5R7 period. That is, for the genotypes developed for the

higher latitudes a lengthening of the R5R7 appears to be slightly advantageous among these genotypes.

Since the previous analysis of the dependency of yield on the duration of R5R7 included a variable EMR1 for each genotype, a more detailed analysis of R5R7 was made to determine an R5R7 when EMR1 was held constant at the previously determined optimum biological days for EMR1 at each location. Simulations were carried out with a wider range of assumed R5R7 values from 20 to 60 days at approximately five biological day intervals. In this case, a 2-piece segmented function, i.e. a linear-plateau function, was required to obtain optimal R5R7 value which results in maximum crop yield. The function includes a sloping line which describes increase in crop yield due to increase in R5R7 and a plateau line that defines maximum crop yield when R5R7 is higher than a critical value (x_o). The function is:

$$y = a + b\,x \qquad \textit{if} \qquad x < x_o \qquad (1)$$

$$y = a + b\,x_o \qquad \textit{if} \qquad x > x_o$$

where y is the crop yield, x the value of R5R7, a the intercept with the vertical axis ($x = 0$), b the rate of linear increase in crop yield with increase in R5R7, x_o the minimum value of R5R7 that results in maximum crop yield. Clearly, the outcome of that analysis is that there was no yield advantage in increasing the R5R7 duration greater than about 30 biological days (Fig. 5).

3.4. Optimizing phenology across ten locations

The unexpected conclusion that there was little variation in the optimum EMR1 for maximum yield between ICRISAT and Hisar stimulated an exploration of this result for additional locations over a range of latitudes. Based on the previous results and to avoid confounding variability, the R5R7 was held constant at 35 biological days for all locations. The plots of yield vs. EMR1, which was varied from 25 to 70 biological days, were well described by third-order polynomial at all locations. The regression for all locations resulted in a r^2 greater than 0.95 (Fig. 6). Across the ten locations EMR1 was clearly not constant (Fig. 6). The optimum EMR1 obtained from the regressions varied from 37.2 biological days at Annigeri to 51.8 biological days at Bangalore. Nevertheless the original estimates of optimum EMR1 at ICRISAT and Hisar remained equal between the two locations and in this re-analysis optimum EMR1 was only slightly shorter than the original estimate at about 43 biological days. The optimum EMR1 for ICRISAT and Hisar in this comparison of locations is approximately the median value among all locations. Also, eight out of the ten locations had an optimum EMR1 fitting in a narrow range (39.4 to 47.3 biological days in Indore and Ludhiana, respectively), and five location were within one biological day of a median value of 43 biological days (Fig. 6). Additional locations were tested and showed similar results (data not shown). Therefore, despite the variation in the optimum EMR1 across locations, there appeared to be a median EMR1 value around 43 biological days to which a majority of locations appeared to be fitting. This result would fit the fact that a cluster of medium duration lines, appeared to have wide adaptation and yielded the most across Indian locations (cluster 1 in this study) (Berger et al., 2006).

A similar analysis was made for R5R7 for all ten locations. Similar to the case of Hisar and ICRISAT (Fig. 5), an increase in yield was observed with increasing R5R7 at low R5R7, but yield reached a plateau at higher R5R7 (data not shown). Based on estimation from Eq. (1), the criterion of the lowest R5R7 to achieve maximum yield, the average across location of

R5R7 was 32.1 biological days, and none of the optimal R5R7 of the ten locations was different from 32.1. This recommended R5R7 is consistent with the optimum R5R7 obtained from the ICRISAT genotypes. Also, this R5R7 is consistent with the lack of yield variation among the higher-latitude genotypes above 35 biological days.

Since the optimum EMR1 varied among locations, a critical issue in breeding chickpea is the environmental variable that caused variation in the optimum EMR1. In other words, in selecting EMR1 for a specific location, what environmental variable determines the desirable EMR1? A common assumption is that EMR1 should be matched to latitude for high latitude locations based on an assumed sensitivity to photoperiod. However, the impact of chickpea photoperiod sensitivity in the comparatively low latitudes of India is hypothetically small (Soltani et al., 2006a). A plot of the optimum EMR1 for each of the ten locations vs. their latitude failed to show a significant correlation (Fig. 7a). This analysis leads to the unexpected conclusion that latitude is not a determining factor in the optimization of EMR1 for any specific location.

On the other hand, a plot of optimum EMR1 vs. the seasonal rainfall at each location gave a positive correlation (r^2=0.55, P<0.01, Fig. 7b), while R5R7 had no significant relationship with rainfall. Locations with increasing rainfall required cultivars with longer optimum EMR1. These results show that EMR1 needs to be adjusted for each location, but the basis for selecting EMR1 is the rainfall that is anticipated for that location.

Interestingly, the average seasonal rainfall at ICRISAT was 41 mm and at Hisar was 44 mm. Nearly identical amounts of rainfall at these geographically divergent locations explained the basis for the nearly identical optimum EMR1 values obtained in the initial analysis. Even though the two locations were quite different latitudes, their common amount of rainfall resulted in the prediction of a common EMR1.

4. Conclusions

The parameterization of EMR1 and R5R7 using a phenology model showed considerable variation among chickpea genotypes. Genotypes developed in lower latitudes for locations such as ICRISAT had distinctively shorter development stages than the genotypes developed for the northern latitude of Hisar. Unexpectedly, using the parameters of these 16 genotypes in simulations of yield in these two locations resulted in a common optimum EMR1 of about 44 biological days for maximum chickpea yield in both locations.

When optimum EMR1 for chickpea was determined across ten divergent locations in India, a wider range of values were determined, although a majority of the locations were close to a median value of about 43 biological days. Unexpectedly the variation in the optimum EMR1 for each location did not correspond with the latitude of the location, but rather with rainfall. The results of this simulation analysis indicates that breeding of future chickpea cultivars in specific regions should strongly consider matching plant phenology traits with the amount of rainfall expected in the target region. Locations with similar in-season rainfall around 30-40 mm, which represents a majority of cases, would all have optimum performance of genotypes having an EMR1 of about 43 biological days. In locations with high in-season rainfall, genotypes with higher EMR1 than 43 biological days will be needed, since the number of biological days for optimum EMR1 increases with increasing rainfall.

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Table 1. Phenology coefficient of a group of genotypes tested at Hisar (Latitude = 29.166 degrees N) and ICRISAT Patancheru (Latitude = 17.86 degrees N) determined in biological days by crop simulation. Phenological stages that were iterated to match model outputs and field observations were the number of biological days from emergence to flowering (EMR1) and the duration of grain filling (R5R7).

Hisar			**ICRISAT**		
Genotype	**EMR1**	**R5R7**	**Genotype**	**EMR1**	**R5R7**
Gaurav	48	52	ICC4958	27	35
C214	50	50	Annigeri	30	33
G543	53	50	ICC10991	34	27
K850	55	38	ICC10985	35	27
C235	57	40	JG74	37	27.6
L550	60	35	P1329	45	30
PG114	62	40	ICCC33	49	32
BG209	65	45	ICCC41	54	31
Range	48-65	35-52		26-54	26-35
Mean	56.3	43.8		38.9	30.3
SE	2.1	2.3		3.3	1.1

Table 2. Predicted number of days to flowering and maturity and grain yield (g m^{-2}) in Hisar (latitude = 29.16 degrees N) and ICRISAT-Patancheru (latitude = 17.88 degrees N) in genotypes that have been bred in Hisar (top eight genotypes) and bred in ICRISAT (bottom eight genotypes except P1329).

	Hisar predictions				ICRISAT predictions		
	Flowering	Maturity	Yield		Flowering	Maturity	Yield
Genotype	**Mean**	**Mean**	**Mean**	**Genotype**	**Mean**	**Mean**	**Mean**
Gaurav	72	150	**150**	Gaurav	55	111	**91**
C214	76	149	**148**	C214	57	110	**89**
G543	81	151	**145**	G543	60	112	**85**
K850	84	142	**141**	K850	62	104	**83**
C235	88	145	**139**	C235	64	107	**82**
L550	92	143	**134**	L550	67	106	**80**
PG114	95	149	**133**	PG114	68	111	**78**
BG209	99	154	**131**	BG209	71	117	**76**
Mean	**85.9**	**147.8**	**140.0**		**63.2**	**109.7**	**82.9**
SE	**3.3**	**1.5**	**2.5**		**1.9**	**1.4**	**1.8**
ICC4958	38	117	**125**	ICC4958	33	81	**74**
Annigeri	43	118	**136**	Annigeri	37	82	**82**
ICC10991	48	115	**134**	ICC10991	41	81	**82**
ICC10985	50	116	**137**	ICC10985	42	82	**85**
JG74	53	119	**141**	JG74	44	84	**90**
P1329	67	128	**148**	P1329	52	91	**93**
ICCC33	74	133	**147**	ICCC33	56	96	**89**
ICCC41	83	135	**141**	ICCC41	61	98	**84**
Mean	**56.9**	**122.5**	**138.7**		**45.7**	**86.8**	**84.8**
SE	**5.6**	**2.9**	**2.7**		**3.5**	**2.5**	**2.1**

Figure captions

Figure 1. Map representing the location which were assessed in this study.

Figure 2. Simulated versus observed number of calendar days from emergence to phenological stages of EMR1 (first flower), R3 (first pod), R5 (beginning seed growth) and R8 (full maturity) during four different growing season under irrigated and rainfed conditions of Patancheru, India. The 15% ranges of discrepancy between simulated and measured are indicated by dashed lines. Solid line is the 1:1 line.

Figure 3. Relationship between the number of biological days to reach flowering in a range of genotypes bred respectively for the ICRISAT (a) or Hisar (b) environments, and the predicted yield (g m^{-2}) of these genotypes across 33 years of weather at ICRISAT (top) and 28 years of weather at Hisar (bottom). Arrows indicate optimum EMR1 (43.5 for ICRISAT and 44.3 for Hisar).

Figure 4. Relationship between the number of biological days between R5 and R7 in a range of genotypes bred respectively for for the ICRISAT (a) or Hisar (b) environments, and the predicted yield of these genotypes across 33 years of weather at ICRISAT (top) and 28 years of weather at Hisar (bottom). Arrows indicate optimum R5R7, when available (29.8 for ICRISAT and 30.2 for Hisar).

Figure 5. Relationship between the number of biological between R5 and R7 and the predicted yield (g m^{-2}) of genotypes having a fixed optimum time to flowering, based on Fig. 1, i.e. 43.5 biological days (ICRISAT), and 44.3 biological days (Hisar). The predictions were made using ICRISAT (closed symbols) and Hisar (open symbols) weather data.

Figure 6. Relationship between the number of biological days to reach EMR1 and the predicted yield in ten locations varying in latitude, i,e, four locations of low latitude in Southern India (Bangalore, Annigeri, Patancheru, Gulbarga), two locations with intermediate latitude (Jabalpur, Indore), and four locations of high latitude in Northern India (Jaipur, Delhi, Hisar, Amritsar). In each case, the number of biological days from R5 to R7 was fixed to 35 days.

Figure 7. Relationship between the optimum number of biological days to reach EMR1 (flowering) and the latitude (a) and the incoming rainfall during the cropping season (b). Data for the optimum days to EMR1 at each location were derived from Fig. 5 whereas incoming rainfall during the chickpea season was the mean of 18-33 years, depending on locations.

A robust crop simulation model was used to test whether an optimal phenology is needed for chickpea adaptation across latitudes

There was no simulated yield advantage of breeding latitude-specific genotypes

A medium duration thermal time duration of 43 biological days until flowering (R1) fitted most latitudes

A grain filling period (R5R7) of 30-35 biological days was optimal for all locations

Variations in the thermal time to flowering were closely related to rainfall received at each location, but not to latitude

Figure 1

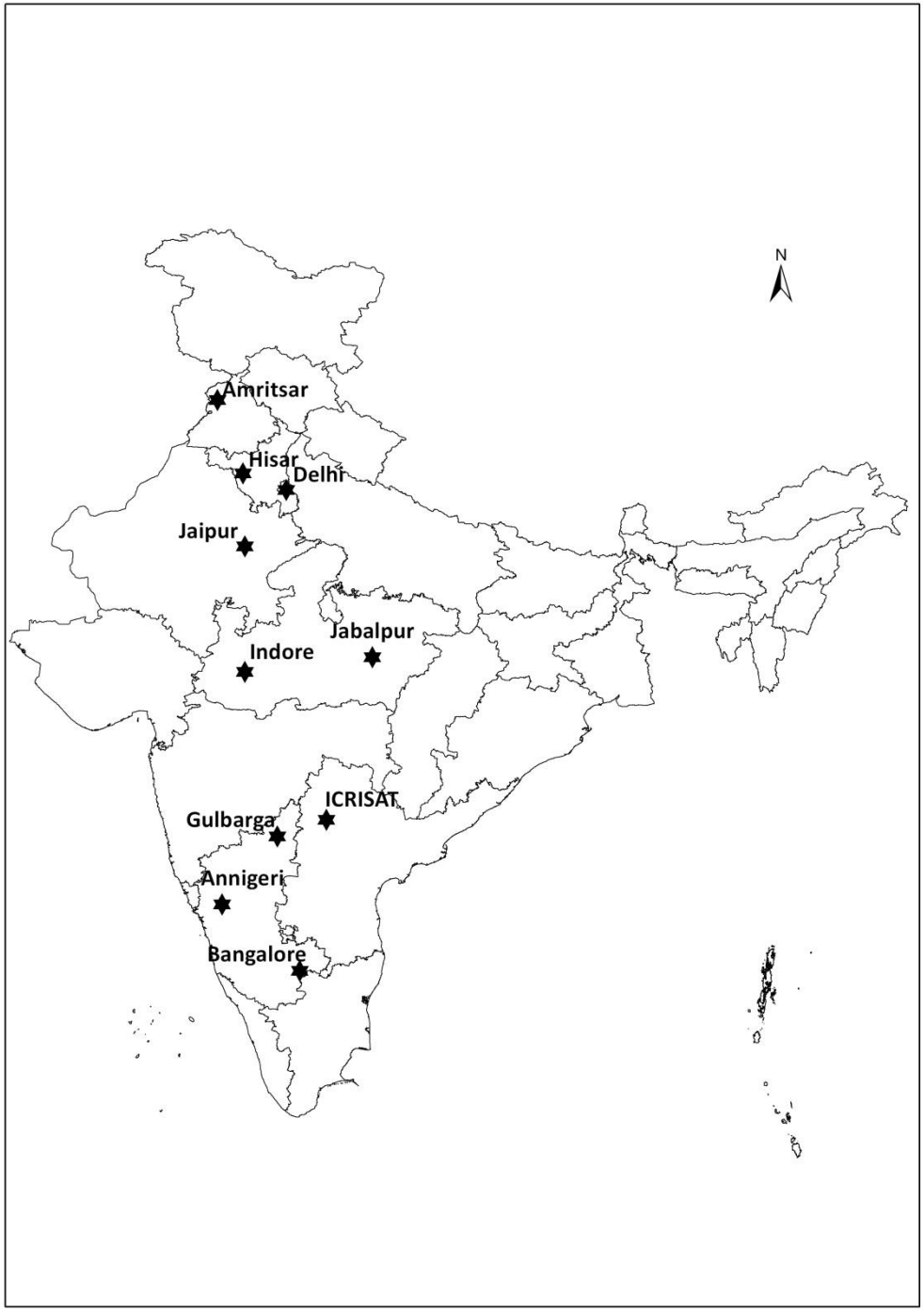

N
Amritsar
Hisar
Delhi
Jaipur
Jabalpur
Indore
ICRISAT
Gulbarga
Annigeri
Bangalore

Figure 2

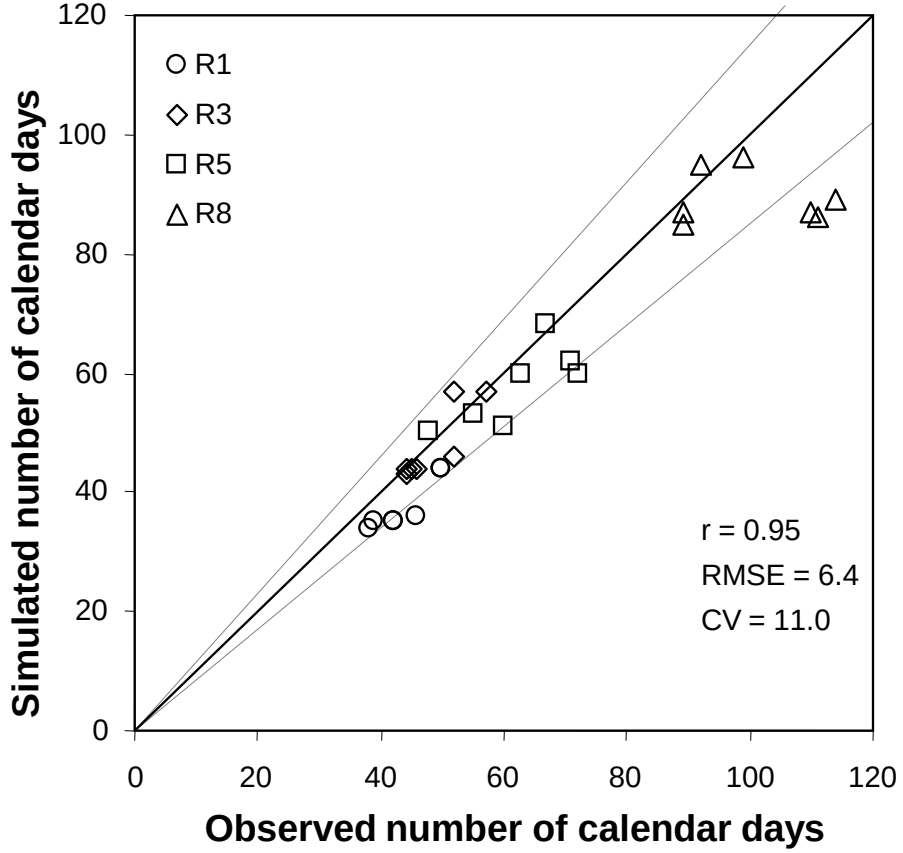

R1
R3
R5
R8
r = 0.95
RMSE = 6.4
CV = 11.0
Simulated number of calendar days
Observed number of calendar days
0
20
40
60
80
100
120

Figure 3

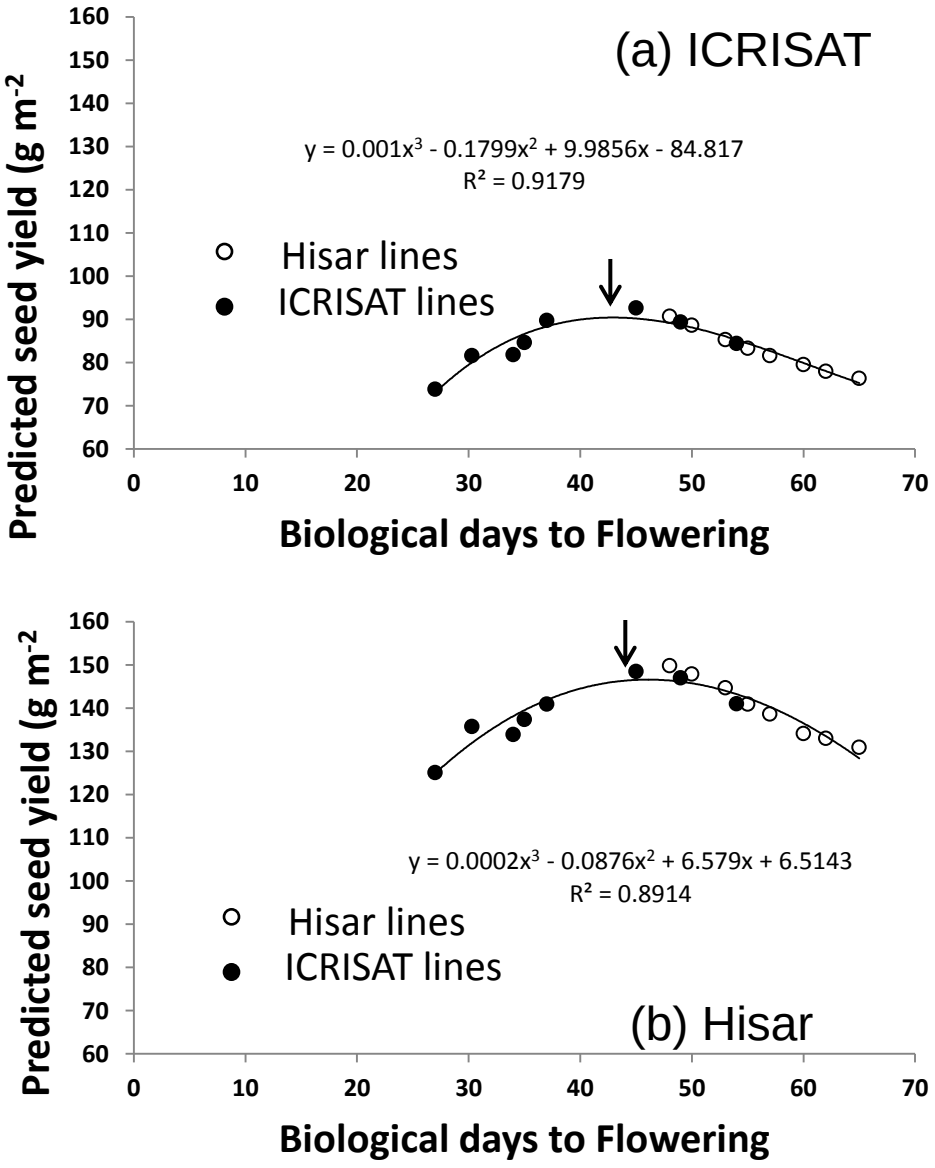

(a) ICRISAT
y = 0.001x³ - 0.1799x² + 9.9856x - 84.817
R² = 0.9179
Hisar lines
ICRISAT lines
Predicted seed yield (g m-2
Biological days to Flowering
y = 0.0002x³ - 0.0876x² + 6.579x + 6.5143
R² = 0.8914
Hisar lines
ICRISAT lines
(b) Hisar
Predicted seed yield (g m-2
Biological days to Flowering

Figure 4

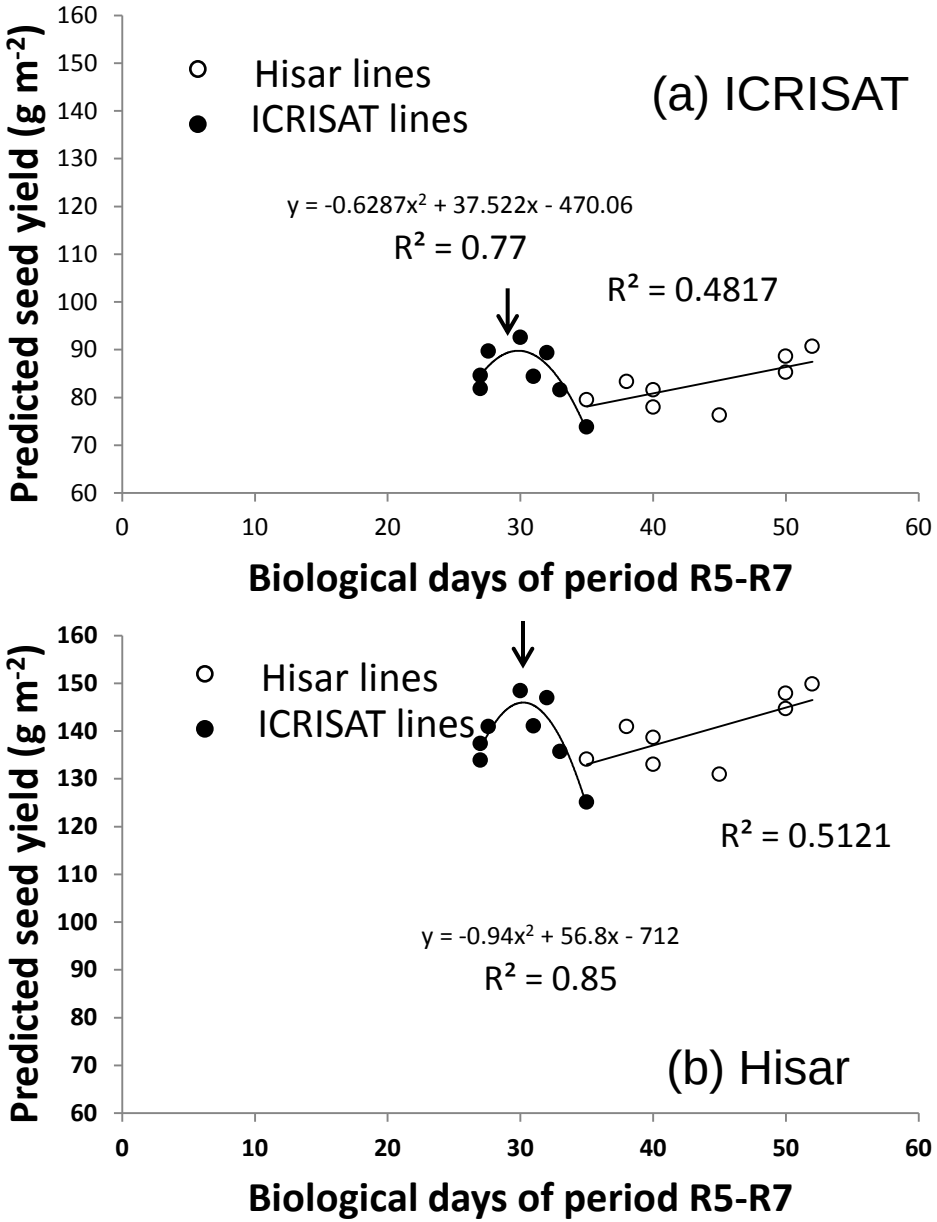

Predicted seed yield (g m-2)
Hisar lines
ICRISAT lines
(a) ICRISAT
y = -0.6287x2 + 37.522x - 470.06
R² = 0.77
R² = 0.4817
Biological days of period R5-R7
Predicted seed yield (g m-2)
Hisar lines
ICRISAT lines
R² = 0.5121
y = -0.94x2 + 56.8x - 712
R² = 0.85
(b) Hisar
Biological days of period R5-R7

Figure 5

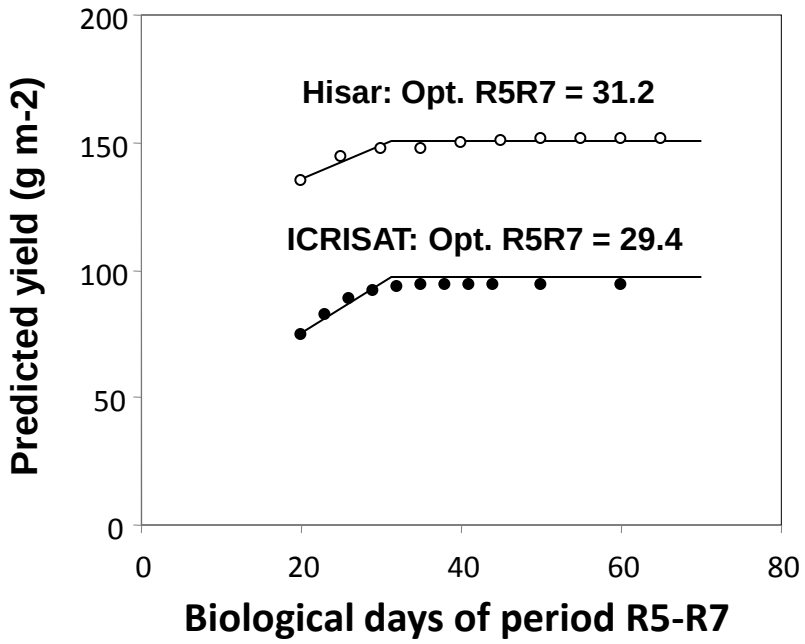

Predicted yield (g m-2)
200
150
100
50
0
Hisar: Opt. R5R7 = 31.2
ICRISAT: Opt. R5R7 = 29.4
0
20
40
60
80
Biological days of period R5-R7

Figure 6

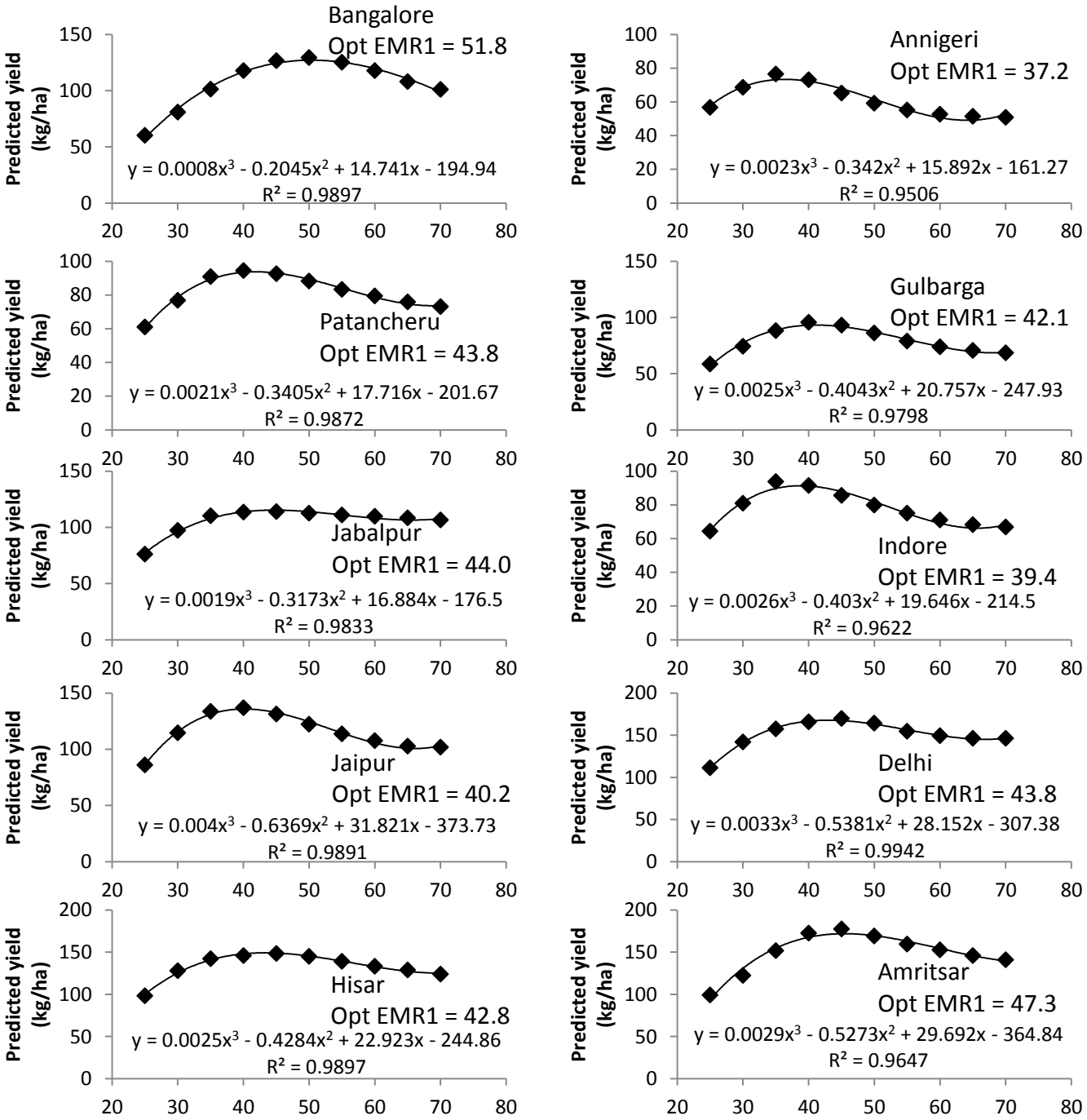
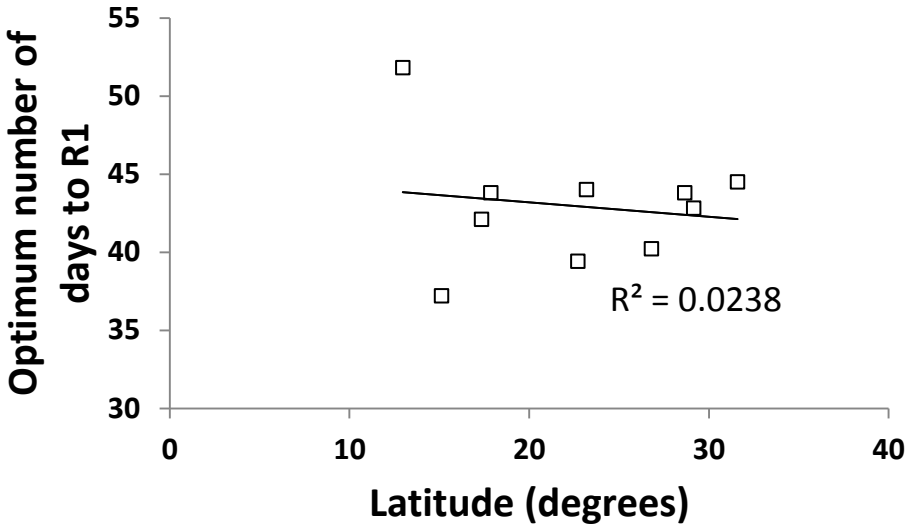
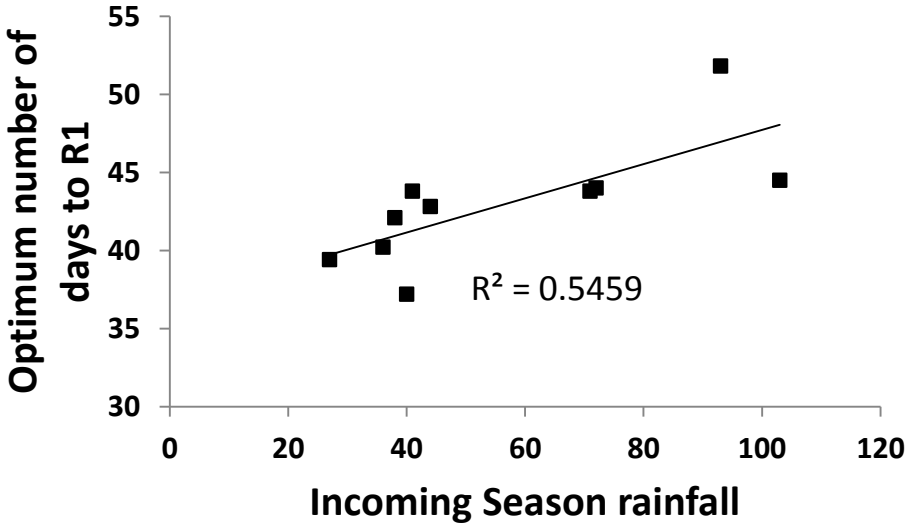

Bangalore
Opt EMR1 = 51.8
y = 0.0008x³ - 0.2045x² + 14.741x - 194.94
R² = 0.9897
Annigeri
Opt EMR1 = 37.2
y = 0.0023x³ - 0.342x² + 15.892x - 161.27
R² = 0.9506
Patancheru
Opt EMR1 = 43.8
y = 0.0021x³ - 0.3405x² + 17.716x - 201.67
R² = 0.9872
Gulbarga
Opt EMR1 = 42.1
y = 0.0025x³ - 0.4043x² + 20.757x - 247.93
R² = 0.9798
Jabalpur
Opt EMR1 = 44.0
y = 0.0019x³ - 0.3173x² + 16.884x - 176.5
R² = 0.9833
Indore
Opt EMR1 = 39.4
y = 0.0026x³ - 0.403x² + 19.646x - 214.5
R² = 0.9622
Jaipur
Opt EMR1 = 40.2
y = 0.004x³ - 0.6369x² + 31.821x - 373.73
R² = 0.9891
Delhi
Opt EMR1 = 43.8
y = 0.0033x³ - 0.5381x² + 28.152x - 307.38
R² = 0.9942
Hisar
Opt EMR1 = 42.8
y = 0.0025x³ - 0.4284x² + 22.923x - 244.86
R² = 0.9897
Amritsar
Opt EMR1 = 47.3
y = 0.0029x³ - 0.5273x² + 29.692x - 364.84
R² = 0.9647
Predicted yield (kg/ha)
Biological days to flowering

Figure 7


Optimum number of days to R1
55
50
45
40
35
30
0
10
20
30
40
Latitude (degrees)
R² = 0.0238

a


Optimum number of days to R1
55
50
45
40
35
30
0
20
40
60
80
100
120
Incoming Season rainfall
R² = 0.5459

b