Modelling possible benefits of root related traits to enhance terminal drought adaptation of chickpea

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Abstract

Chickpea is cultivated at the end of the rain in tropical and sub-tropical regions like in India. Crop growth depends on the soil moisture contained in the soil profile, commonly leading to terminal water deficits. The past three decades of research have focused on improving rooting traits, with a particular focus on the speed of root extension in the soil, making the assumption that this would lead to more water extraction. Here, we used a robust crop simulation model to assess genetic and management modifications that would affect water availability to the crop. Against expectations, increasing the rate of depth of root extension to 30 mm day^{-1} from a baseline of 17 mm day^{-1}, to reflect the characteristics of an existing root trait QTL on linkage group 5 of chickpea, brought about a yield penalty in all situations (4-6%), especially in locations where the in-season rainfall was low (up to a 15% yield penalty). By contrast, modifying soil characteristics by increasing the depth of effective water extraction from 1000 mm to 1200 mm led to yield increases in all situations (8-12%) as a result of greater water available at the end of the growing season. Changing the rate of leaf area development rate associated with the root QTL locus on LG5, had no impact on yield except for a yield increase at the two highest yielding locations. The greatest changes in yield were obtained by irrigating the crop with 30 mm at R5. The average yield gain across all locations was 29% and the high yield benefit was achieved across all yield levels. These results indicated that some benefit would come from growing the crop in soil with a higher depth of effective water extraction, which may require faster root growth in very low rainfall environments, but the greatest yield benefit would result from modest irrigation at R5.

1. Introduction

Terminal drought is a common constraint faced by many crops such as chickpea in climates with highly seasonal rainfall patterns. Improved root characteristics have been suggested as the solution to this problem for a long time (Saxena et al., 1984; Saxena et al., 1996). Some positive relationships between the depth of rooting and seed yield of crops subjected to terminal drought have indeed been shown in chickpea (eg Kashiwagi et al., 2005). Screening methodology for root extension under controlled conditions in cylinders has been developed to identify germplasm with deeper and more profuse roots (Kashiwagi et al., 2006). As a result of their study, major efforts are under way to improve chickpea tolerance to terminal drought by genetically altering rooting characteristics (Gaur et al., 2008).

The assessments of root traits in tall cylinders (Kashiwagi et al., 2005) consisted of measuring the root length density and the maximum rooting depth achieved 35 d after sowing. The soil was watered to 70% field capacity at the beginning of the experiment. Therefore, their assessments were focusing on the speed of rooting depth and the maximum depth of rooting, and not on the contribution of roots to water extraction. Using this method,

a quantitative trait locus (QTL) for root dry weight and for root length density was found on linkage group 5, explaining 33.1% and 33.4% of the phenotypic variation for root dry weight and maximum root depth at marker locus Taa170 (Chandra et al., 2004). However, this locus also co-located a major QTL for shoot dry weight, explaining 56.2% of the phenotypic variation. Therefore, the root QTL identified in chickpea, which is currently used for introgression in popular varieties (Gaur et al., 2008) and considered as a "drought tolerance QTL", is likely to be more appropriately identified a plant-growth-vigor QTL.

A possible consequence of incorporating a vigorous growth trait into plants is that this could result in a rapid use of water during the vegetative stage, leaving the crop with less soil water available for the grain filling period. In fact, we can expect that a vigorous root is a consequence of having a vigorous shoot, the contrary being possible in situations where water is limited. A recent modelling study with soybean indicated that a faster rate of root growth had a negative effect on yield as a result of rapid use of soil water (Sinclair et al., 2010). Recent studies in chickpea (Zaman-Allah et al., 2011a) and groundnut (Ratnakumar et al., 2009) bring experimental evidence to this by showing the importance of temporal patterns of water use rather than root development *per se* and profuse rooting. Zaman-Allah et al. (2011a, b) found that slower shoot growth in chickpea resulted in water saving during vegetative stages (2011b) and this was critical in making water available during grain filling (2011a). Therefore, it appears that the seasonal dynamics of water use are crucial and the question is still open about the benefit of introgression of a QTL for more vigorous root and shoot under terminal drought conditions.

Resolving the benefit of the vigorous-growth trait is experimentally difficult because of the complexity of temporal drought dynamics and the possible trade-offs between the more rapid water use and conservative water use. Clearly, the benefit of the root extension trait, and virtually all drought traits, is dependent on the environments in which the plants are grown. For example, cultivar performance for increased rate of root growth likely depends on the pattern of water use and the depth of water extraction that is permitted by the soil. What is the impact on tolerance to drought stress if the depth and speed of root growth is "de-coupled" from the probable linkage with shoot growth? These issues are multi-factorial questions for which it is improbable, and surely impractical, to obtain sufficient experimental data to resolve. An alternate approach to explore these issues is crop simulation modelling, which offers a convenient and fast way to explore the complexity of the genotype-environment system. Crop modelling has been used to examine these issues for chickpea in the temperate climate of Iran (Soltani et al., 1999, 2000, 2001), but not in tropical regions. The chickpea model of Soltani and Sinclair (2011) presented an improved version of an earlier version of the model (Soltani et al., 1999), based on more recent experimental data and new functions related to yield formation. This model is used here to test the effect of rooting and water use on seed yield across different chickpea growing regions in the monsoonal climate of India. This present study is then set in a different region, with a different cropping cycle for chickpea, and a different focus than earlier works by Soltani and Sinclair (2011). Here, we focus mostly on traits concerning root characteristics. This work is very timely, because intensive work is currently carried out on roots in chickpea, and because chickpea cultivation is currently shifting to South India, where water availability is less and cropping season shorter, with obvious consequences for overall water balance of the crop.

Therefore, the objectives of the work were to examine specific plant traits that have been proposed for improving chickpea yields for growth conditions across India. A chickpea model was used to simulate crop growth and yield at 14 locations and for at least 14 years at each location. The studied traits were (i) changed rate of increase in depth of water extraction, i.e. root extension, (ii) changes in soil characteristics, i.e. the maximum depth of water extraction, and (iii) alteration in rate of leaf area development. For comparison, the model was also used to simulate yield response to a single 30-mm irrigation at the beginning of seed fill.

2. Material and methods

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 model needs readily available weather and soil information and operates on daily time steps. The model has successfully been tested using independent data from a wide range of growth and environmental conditions (Soltani and Sinclair, 2011).

Root depth is increased linearly in the simulations from emergence to the beginning of seed growth. In the version used in this study (Soltani and Sinclair, 2011), a constant daily rate of root penetration per calendar day (17 mm per day; Brown et al., 1989) was used. Root extension started at emergence and terminated at the beginning of seed growth like the original model (Soltani et al., 1999). Therefore, the model "grows" roots at a set rate, and then considers that on any given day the water available for transpiration is the amount contained in the volume of soil accessed by the roots on that day, i.e. depth of rooting (mm) multiplied by volumetric extractable soil water.

The model also fixes a maximum depth up to which water can be extracted. This is set by soil impedence or chemical factor impeding root growth such as aluminum. Daily rate of root penetration in the soil is then calculated until this maximum effective depth of water extraction, i.e. the soil depth above which it is considered that all available water can be used, is reached. Therefore, the final depth to which water can be extracted is either determined by rooting capacity of the plant, i.e.,by the crop phenology (the time when seed growth begins), or by the soil through mechanical or chemical impediment to root growth. IIncreasing the depth of the extraction front based on the daily downward root extension was a simple way of representing the increase in volume of soil that became accessible for transpiration every day. While roots likely don't grow this way - the extraction front may be more like a conical shape - the model provided a simple representation that can allow comparisons. This approach resulted in the simulation ofessentially two types of situations: (i) the final rooting depth achieved by the plants was less than the maximum depth of water extraction set by the soil characteristic, and in this case, the reservoir of water available for transpiration was set by the

volume of soil that the roots had reached; (ii) the rooting depth capacity of the plants was greater than the maximum depth of water extraction (most cases, see below) and in this case, the reservoir of water available for transpiration was limited by this maximum soil depth of water extraction. (The model can readily distinguish both factors and allow to combine the effect of both plant and soil traits.) Therefore the simulations allowed tests of the consequences of having roots quickly reaching that effective depth of water extraction, in other words to have made earlier full access to the water reservoir available for transpiration.

This model accounts for the effects of temperature, photoperiod and water deficit on phenological development of chickpea, being a long-day plant. 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., 2006). A linear-plateau (2-piece segmented) function accounted for the effect of photoperiod on development rate. This modification was based on Singh and Virmani (1996) to simulate response of Indian genotypes to photoperiod; a 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) (development was decreased by this coefficient in situation when the photoperiod was shorter than 11h).

The model was further tested specifically for Indian conditions. For this purpose, data from three line-source irrigation experiments conducted in ICRISAT (Patancheru, Andhra Pradesh, India, 17° 30' N; 78° 16' E; altitude 549 m), and described by Singh (1991) and Singh and Virmani (1996) were used. The procedure they used in their experiments provided a wide range of water availability during different phenological stages. In brief, the first experiment was conducted in 1985 using cv. Annigeri with a total of 12 watering treatments. The experiment consisted of 4 main × 3 sub-treatments. The main treatments were: (1) gradient irrigation during all phenological stages, (2) gradient irrigation during emergence to flowering and uniform irrigation during other stages, (3) gradient irrigation from 50% flowering to beginning of pod-fill and uniform irrigation during other stages and (4) gradient irrigation from beginning pod-fill to physiological maturity and uniform irrigation during other stages. Each main plot was further divided into three equal size subplots to define three moisture regimes in decreasing order of irrigation amount received. Uniform irrigation was given to the crop using perforated pipes. The 1986 and 1987 experiments had the same treatments (total = 12) and the experimental design as the 1985 experiment, except for using cultivar JG 74. In total, there were 36 combinations of year-cultivar-irrigation. Measured and simulated grain yield and crop mass at maturity for the 36 combinations were compared to model output to test model robustness. Simulated values of crop mass at maturity were multiplied by 0.77 to account for senesced leaves and petiole mass. This adjustment was based on the results of Saxena (1984) who found that the apparent harvest index in chickpea is about 0.1 lower than the biological harvest index.

2.2. Simulation analysis

Simulations were performed at fourteen locations in India (Table 1), which were selected because of the availability of long-term daily weather data (14 to 33 years) and their distribution across the spectrum of chickpea growing environments. Seven locations are in

the southern part of India, which is gaining increasing importance as a major chickpea production region. Five locations are in northern India and represent the traditional chickpea growing areas. The remaining two locations are in central India.

Initially the model was run for all locations and years for the standard chickpea cultivar using the baseline parameters described by Soltani and Sinclair (2011). Then, the model was run for modified drought traits for all locations and years with a change in individual baseline parameters. The percent change in mean yield at each location between the yield simulated for the revised parameter and the baseline parameter was the basis for assessing the impact of the changed trait on crop performance.

2.2.1. Rate of increase in rooting depth

The potential amount of water that is available for uptake by the crop is calculated based on the extraction depth of the roots (see 2.2.2) and the extractable volumetric soil water content. In these simulations the extractable volumetric water content was held constant at 0.13 cm^{-3} cm^{-3}, and the depth of water extraction was increased daily based on the rate of increase in depth of rooting. Therefore, a more rapid rate of increase in depth of root extension will result in a more rapid availability to the crop of the soil water. In the studies of Kashiwagi et al (2005), there were genetic differences in the depth reached by chickpea roots in 35 d. Some genotypes had roots at a depth 1260 mm indicating an average root extension rate of 36 mm day^{-1} (= 1260/35). In the simulation analysis, two rates of increase in the rate of rooting depth were simulated. In the baseline scenario, the rate of rooting depth was set equal to 17 mm day^{-1}. A faster rate of rooting depth was set at 30 mm day^{-1}, i.e. a rate nearly double of that in the baseline scenario. The baseline value for chickpea is based on observations of Brown et al. (1989) and in line with more recent observations of Serraj et al. (2004). We recognize that these absolute rates of root growth may not be achieved in poorly structured soil. However, the existence of genetic variation for that rate of root growth justified the relevance of testing how these differences would influence seed yield.

2.2.2. Maximum effective depth of water extraction

It was assumed that the soil had been fully filled with water by the time of chickpea sowing. Therefore, the maximum extraction depth, taken as a soil characteristic, directly defines the total amount of soil water ultimately available to the crop, provided that the rate of root growth and phenological phases (beginning of seed growth corresponding to termination of root growth) allow the roots to reach that depth. Even at a modest rate of root growth and in short duration environments, with beginning of seed growth reached in about 60 biological days, the root system could reach the maximum depth of effective water extraction set here in the baseline simulations at 1000mm. Therefore, reaching the maximum effective depth of water extraction in the baseline case did not depend on a quicker rate of root growth. Two variations in the maximum soil depth for water extraction were simulated: 800 and 1200 mm. The simulation results for the shallower depth can also be interpreted as resulting from a shallower soil where physical or chemical barriers prevent deeper penetration of roots.

Recent results using a lysimetric system also indicated that genotypes vary by more than 20% in the quantity of water that can be extracted from a same soil profile, and that there was no significant relationship between the root length density in any of the layers and the total water extracted (Zaman-Allah et al., 2011a). Therefore a shallower depth of water extraction also simulates such cases in which there is an incomplete water extraction above a depth where these is insufficient RLD to fully extract water.

2.2.3. Leaf area development rate

It has been shown in chickpea that deeper and faster root development is physiological and / or genetically associated with faster shoot development (Serraj et al., 2004) and that the root QTL on LG5 of chickpea also explained more than 50% of the variations in shoot weight (Chandra et al., 2004). Therefore, a faster leaf area development during vegetative growth was also included in the study to evaluate the consequence of this linkage. In the model, leaf number on main stem was first estimated based on the phyllochron concept. Then, plant leaf area is calculated from main stem leaf number using an allometric equation (as $y = x^b$). To simulate a faster leaf area development trait, i.e. greater early plant "vigor", the coefficient b in the allometric relationship was increased by 15% from its standard value of 2.14.

An important component of the water balance is the rate of leaf area development since the rate of crop water use depends on crop leaf area. Faster leaf area development can enhance water use early in the growing season, but this necessarily means less water would be available later in the season during grain filling. Data for chickpea indicated that genotypes having tolerance to terminal drought tend to have smaller leaf area (Zaman-Allah et al., 2011b), which allowed these genotypes to use soil water at a slower rate than those genotypes with a larger leaf area. However, faster leaf area development trait might have a positive impact in wet seasons or locations when water is not limiting because there would also be an increase in radiation interception, likely resulting in a yield increase as compared with the slower leaf area development (Sinclair et al., 2010).

2.2.4. Irrigation

A final set of simulations were done to test directly the sensitivity to providing additional water on crop yield. This test was done simply be including a 30-mm irrigation to the crop at the beginning of seed growth (stage R5).

3. Results and Discussion

3.1. Model testing

A plot of simulated versus measured crop mass at maturity in the line-source experiments is presented in Fig. 1a. Measured crop mass ranged from 151 to 586 g m^{-2}, and simulated crop mass varied from 148 to 465 g m^{-2}. Means of observed and simulated crop mass were 383 and 377 g m^{-2}, respectively. The model generally provided good agreements of crop mass with RMSE of 52 g m^{-2} which is 14% of the measured mean.

Fig. 1b shows simulated and measured grain yield for the line-source experiments. Simulated yield varied from 93 to 208 g m^{-2} and measured yield from 84 to 219 g m^{-2}, and the means were 173 and 171 g m^{-2}, respectively. Correlation coefficient between measured and simulated yields was 0.82. The model provided good estimates of crop yield with majority of simulated yields having less than 18% discrepancy with observed yields and with a RMSE of 20 g m^{-2} which is 12% of the observed yield.

Line-source experiments provided a wide range of crop yields as a result of drought and watering during different phenological stages. Still, the crop model provided very close predictions across the irrigation treatments. Therefore, it was concluded that the model predictions were robust for Indian conditions and suitable for simulating the effect of rooting and soil depth traits on chickpea yield.

3.2. Baseline yields

Average yields among the 14 locations varied from only 80 g m^{-2} at Annigeri to 227 g m^{-2} at Ludhiana (Table 1). Much of the variation in yield was associated with differences in the in-season rainfall (Fig. 2; $R^2 = 0.59$). Increased rainfall resulted in a trend of increasing yield. However, there was considerable scatter in this relationship. The dynamics of rainfall and water use through the season are important in influencing the ultimate impact on yield. Hence, it is necessary to use the mechanistic-based model to account for the water-use dynamics to understand the sensitivity on crop yield of modification of individual plant traits.

3.3. Rate of increase in depth of soil water extraction

A higher daily rate of increase in depth of soil water extraction had a consistent, negative impact on yield at all locations. Yield was decreased in all locations as a result of a greater rate of increase in depth of water extraction (Fig. 3). The mean yield loss was 5% (Table 2) averaged across locations and the greatest yield decrease was 10-12%. The greatest percentage losses in yield were in the lowest yield locations, i.e. at low rainfall locations. In the higher yield locations, the loss in yield as a result of a negative of a high rate of increase in extraction depth was small.

The yield loss with an increased rate of root extension was a consequence of a more rapid consumption of soil water at depth, resulting in a greater soil-water deficiency late in the season during seed filling period. These results are in full agreement with experimental water extraction data obtained from lysimeters, where faster water extraction at vegetative stage correlated negatively with grain yield (Zaman-Allah et al., 2011a). For these terminally stressed crops, it was essential to conserve soil water so that the grain growth could be maximized. If a key consequence of the root QTL at marker loci Taa170 on LG5 in chickpea (Chandra et al., 2004) is an increased rate of increase in depth of soil water extraction, this QTL carries the burden of a negative impact on yield.

3.4. Maximum water extraction soil depth

Maximum effective extraction depth, taken as a soil characteristic, was varied from the 1000 mm baseline to 800 mm and 1200mm. As expected, the decrease in maximum extraction depth resulted in a large decrease in yield (Fig. 4). The mean yield decrease was approximately 26% (Table 2) in all locations except the two locations with the highest yield where the loss was still 20%. Clearly, a soil restriction in achieving water extraction in deeper layers resulted in a severe loss of yield.

Increased maximum rooting depth from 1000 mm to 1200 mm resulted in a mean yield increase at all locations (7.5%). However, the yield increase at the four lowest yielding environments was quite small (< 3%). This was related to the fact that in these short duration environments, a baseline rate of root growth would not have allowed the roots to reach the 1200 mm depth of effective water extraction. In about half of the locations, yield increase was slightly greater than 10%, and no negative effect was detected in any location (Fig. 4). Therefore, the cultivation of chickpea is soil allowing a greater depth of effective water extraction is advised. Studies on other crops and environments also show that increasing the depth of effective water extraction has positive consequence in terms of crop yield (e.g. Sinclair and Muchow, 2001; Manschadi et al., 2006; Ludwig and Asseng, 2010), and is related to a higher water-capturing capacity during the grain filling period, when the roots have reached these depths (Ludlow and Muchow, 1990).

Simulations were done in which combining different rates of root growth as a plant trait and maximum depths of water extraction as a soil characteristic were combined. In all cases of an 800-mm maximum depth of water extraction, an increased rate of rooting depth further decreased yield (Fig. 4). The additional decrease in yield was similar to what was obtained in the 1000-mm maximum depth simulations (Fig. 3) (5%). The increase in yield obtained from the combination of a greater soil depth of water extraction (1200 mm) and a faster rate in rooting depth was similar to the yield obtained from the 1200-mm maximum depth of water extraction alone (6.5% vs 7.5%) (Fig. 4). However, the four locations with the lowest baseline yields actually had a small increase in yield with a greater rate of increase in extraction rate. This corroborated our interpretation above that, in these short duration environments the baseline rate of root growth may not have allowed the roots to reach the maximum depth of effective water extraction and therefore these environments may require a faster rate of root growth to reap the benefit of a deeper effective depth of water extraction. Overall, these results still indicated that the increased rate in rooting depth was a negative trait in situation of shallow extraction depths and had virtually no effect at higher extraction depth, except small effects in short duration environments. Thus, a key finding of this study was that faster rooting generally decreased the benefits due to an increased soil depth for water extraction, except in short duration environments.

3.5 Leaf area development rate

It has been reported that faster rooting is physiologically and genetically associated with faster leaf area development during the early growing season (early plant vigour) in several

crops including chickpea, and indeed the root QTL in LG5 of chickpea also increased shoot dry weight (Chandra et al., 2004). Simulation results for a faster leaf area development trait itself indicated that this trait led to non-significant yield increases across locations (Table 2; Fig. 5). These non-significant effects on the mean yield change across environments were related to the fact that faster leaf growth led to a wide range of effects, from negative (-10 to -15 g m^{-2}) to very positive (+40 to +50 g m^{-2}), on the seed yield. For instance in two locations with highest baseline yields, Ludhiana and Amritsar, faster leaf growth led to yield increases of 24% and 19%, respectively. The faster leaf growth did bring a slight negative effect in several low yielding environments, which agrees with the hypothesis that faster soil water depletion can lead to negative effects. Also, the coefficient we used to increase leaf area growth was quite conservative and may not have reflected the variation available in the germplasm. Work is on-going to obtain estimates of that range in the chickpea germplasm. In higher yielding environments, with more in-season rainfall, as expected, there was a benefit of faster leaf growth, and the more so in high rainfall/long season environments. In sum, "early plant vigor" as reflected in rate of increase in leaf area development is of little or no benefit in most locations. This trait needs to be targeted specifically to the high rainfall, high yield locations.

Experimental assessment of the value of increased plant early vigor in crops under water-limited conditions has been contradictory, and positive and negative effects have been reported. Positive effects have been reported as a result of reducing soil evaporation, inhibition of weeds and the greater CO_2 fixation per unit of water transpired (e.g. Lopez-Castaneda et al., 1996; Elhafid et al., 1998; Rebetzke and Richards, 1999). Negative effects have been reported mainly due to early soil water depletion as a result of a greater canopy growth, where the crop is mainly dependent to stored soil water (e.g. Soltani and Galeshi, 2002). Similarly, in chickpea contradictory results have been reported (e.g. Sabaghpour et al., 2003; Toker and Canci, 2007; Gaur et al., 2008; Zaman-Allah et al., 2011b). Therefore, it can be concluded that optimal plant leaf area development depends on environment under consideration and its water availability pattern.

Additional simulations were done to evaluate the impact of faster rooting accompanied by a faster leaf area development trait. This exercise was performed to simulate the apparent combination of traits resulting from the observed "plant vigor" of QTL at marker locus Taa170 (Chandra et al., 2004). The increased rate of rooting decreased the yields simulated for the increase in leaf area development by itself (-6% compared to faster leaf development alone). Certainly these results indicated the coupling these two traits was not a desirable modification. However, the penalty of the increased rate of rooting was not severe in the two locations where the increased leaf area development was advantageous (Fig. 5). Therefore, the "vigor" QTL is still appropriate for the highest yield environments.

Simulations were done to explore the combined effect of increased leaf area development and the benefit of an increased soil depth for maximum water extraction. Combining these two traits gave an increase in yield for all but the two lowest-yield locations where the yield change was slightly negative (Fig. 6). Average yield over all locations was increased by 14% by increasing the leaf area development and increasing soil depth (Table 2). Interestingly, there was a positive trend of increasing yield for these two combined plant and soil traits with

increasing baseline yield ($R^2 = 0.66$). Therefore, selection for faster leaf area development (early plant vigor) would have greatest benefit for situations where soil is deep, especially in higher rainfall environments.

A multiple combination of increased leaf area development, rate of increase in rooting depth, as plant traits, and maximum effective depth of water extraction as a soil characteristic, were also simulated. Across locations, the addition of a greater rate of increase rooting depth did not change the yield benefit from a faster leaf development and deeper soil. Again, the locations with the lowest baseline yields exhibited a small increase in yield as a result of the multiple combinations of plant and soil traits as compared to the baseline yield. Therefore, it can be concluded that faster rooting is not a desired plant trait for chickpea in drought-prone environments of India, except in cases in low yielding environments where the maximum depth of water extraction is higher, and is likely to bring little benefit in breeding programs.

3.5. Irrigation at R5

Modifications of plant traits resulting in increased yields were generally modest. Except three high-yielding environments where the combination of increased leaf area development and maximum depth of water extraction resulted in yield increases of 25% to 34%, yield increases were only 15% and less. Commonly, yield gains were about 10%. Simulations were done using the baseline model to simply add 30-mm water by irrigation (with an efficiency of 100%) at the R5 stage. Such simulation results offer a context in which to judge the possible yield gains anticipated from genetic traits as compared to improved management of irrigation.

The single irrigation in the simulations resulted in average yield gain across of all locations of 29%. The range in yield gain was 20 and 40%, with no trend relating yield benefit to baseline yield at locations (Fig. 7). These results clearly indicated that if possible, irrigation is a direct approach to substantial yield increase in all environments.

4. Conclusions

These simulation studies highlighted the importance of maximum depth of soil water extraction by roots, as a soil characteristic, is the critical component of terminal drought adaptation (8-12% yield benefit). On the other hand, a faster rate of increase in rooting depth, for which a QTL exists and is being introgressed into chickpea, conferred a yield penalty in all situations (5-10% yield decrease). In particular, the penalty was greatest when faster root growth was not de-coupled from faster leaf area development. This analysis also highlighted that irrigating with 30 mm at the beginning of seed growth would increase yield by about 30%, which is approximately three times greater than the yield commonly achieved with the best genetic options identified here. Besides showing the criticality of having water available to the crop at a key stages, here the beginning of seed growth, the yield response to irrigation showed that improving chickpea yield under terminal drought would benefit more from irrigation than from genetic options, and that both need to be applied to maximize yield.

References

Brown, S.C., Gregory, P.J., Cooper, P.J.M., Keatinge, J.D.H., 1989. Root and shoot growth and water use of chickpea (*Cicer arietinum*) grown in dryland conditions: effects of sowing date and genotype. *J. Agric. Sci. (Cambridge)* **113**, 41–49.

Chandra S, Buhariwalla HK, Kashiwagi J, Harikrishna S, Sridevi KR, Krishnamurthy L, Serraj R and Crouch JH 2004. Identifying QTL-linked Markers in marker-deficient Crops. Proceedings of the 4th International Crop Science Congress Brisbane, Australia, 26 September – 1 October 2004, T Fisher (ed.), The Regional Institute Ltd (Publisher), Gosford New South Wales, Australia

Elhafid, R.R., Smith, D.H., Karrou, M., Samir, K., 1998. Root and shoot growth, water use and water use efficiency of spring durum wheat under early season droughts. Agronomie 18, 181-195.

Gaur, P.M., Krishnamurphy, L., Kashiwagi, J., 2008. Improving drought-avoidance root traits in chickpea (Cicer arietinum L.)- current status of research at ICRISAT. Plant Prod. Sci. 11(1), 3-11.

Kashiwagi, J., Krishnamurthy, L., Crouch, J.H., Serraj, R., 2006. Variability of root characteristics and their contributions to seed yield in chickpea (*Cicer arietinum* L.) under terminal drought stress. Field Crops Res. 95, 171–181.

Kashiwagi, J., Krishnamurthy, L., Upadhyaya, H.D., Krishna, H., Chandra, S., Vadez, V., Serraj, R., 2005. Genetic variability of drought-avoidance root traits in the mini-core germplasm collection of chickpea (*Cicer arietinum* L.). Euphytica 146, 213–222.

Lopez-Castaneda, C., Richards, R.A., Farquhar, D.G., Williamson, R.E., 1996. Seed and seedling characteristics contributing to variation in early vigor among temperate cereals. Crop Sci. 36, 1257-1266.

Ludlow, M.M., Muchow, R.C., 1990. A critical evaluation of traits for improving crop yields in water limited environments. Adv. Agron., 43, 107-153.

Ludwig, F., Asseng, S., 2010. Potential benefits of early vigor and changes in phenology in wheat to adapt to warmer and drier climates. Agric. Syst. 103, 127-136.

Manschadi, A.M., Christopher, J., deVoil, P., Hammer, G.L., 2006. The role of root architectural traits in adaptation of wheat to water-limited environments. Func.Plant Bio. 33, 823–837.

Ratnakumar P, Vadez V, Nigam SN & Krishnamurthy L 2009. Assessment of transpiration efficiency in peanut (*Arachis hypogaea* L.) under drought by lysimetric system. Plant Biology 11, 124-130

Rebetzke, G.J., Richards, R.A., 1999. Genetic improvement of early vigor in wheat. Aust. J. Agric. Res. 50, 291-301.

Sabaghpour, S.H., Kumar, J., Rao, T.N., 2003. Inheritance of growth vigor and its association with other characters in chickpea. Plant Breed. 122, 542–544.

Saxena NP 1984. Chickpea. In: GoldsworthyPR and Fisher NM (Eds) The Physiology of Tropical Field Crops, Wiley, New York pp 207-232.

Saxena, N.P., Saxena, M.C., Johansen, C., Virmani, S.M., Harris, H., 1996. Future research priorities for chickpea in WANA and SAT. In: Saxena, N.P., Saxena, M.C., Johansen, C., Virmani, S.M., Harris, H. (Eds), Adaptation of chickpea in the west Asia and north Africa region. ICARDA, Aleppo, Syria, pp. 257-263.

Serraj, R., Krishnamurthy, L., Kashiwagi, K., Kumar, J., Chandra, S., Crouch, J.H., 2004. Variation in root traits of chickpea (*Cicer arietinum* L.) grown under terminal drought. Field Crop Res. 88, 115–127.

Sinclair, T.R., Messina, C.D., Beatty, A., Samples, M., 2010. Assessment across the United States of the benefits of altered soybean drought traits. Agron. J. 102, 475-482

Sinclair, T.R., Muchow, R.C., 2001. System analysis of plant traits to increase grain yield on limited water supplies. Agronomy Journal 93, 263–270.

Singh P 1991. Influence of water-defitis on phenology, growth and dry matter allocation in chickpea (*Cicer arietinum*). Field Crops Research 28, 1-15.

Singh P and Virmani SM 1996. Modelling growth and yield of chickpea (*Cicer arietinum L.*). Field Crops Research 46, 41-59.

Soltani, A., Galeshi, G., 2002. Importance of rapid canopy closure for wheat production in a temperate sub-humid environment: Experimentaion and simulation. Field Crops Res. 77, 17-30.

Soltani, A., Ghassemi-Golezani, K., Khooie, F.R., Moghaddam, M., 1999. A simple model for chickpea growth and yield. Field Crops Res. 62, 213–224.

Soltani, A., Khooie, F.R., Ghassemi-Golezani, K., Moghaddam, M., 2000. Thresholds for chickpea leaf expansion and transpiration response to soil water deficit. Field Crops Res. 68: 205-210.

Soltani, A., Khooie, F.R., Ghassemi-Golezani, K., Moghaddam, M., 2001. A simulation study of chickpea crop response to limited irrigation in a semiarid environment. Agric. Water Manag. 49: 225-237.

Soltani A., Hammer, G.L., Torabi, B., Robertson, M.J., Zeinali, E., 2006. Modeling chickpea growth and development: phenological development. Field Crops Res. 99: 1-13.

Soltani, A., Sinclair, T.R., 2011. A simple model for chickpea development, growth and yield. Field Crop Res. (In Press).

Toker, C., Canci, H., 2005. Selection for drought and heat resistance in chickpea under terminal drought conditions. In: Kharkwal, M. C. (Ed.) Food Legumes for Nutritional Security and Sustainable Agriculture, Indian Society of Genetics and Plant Breeding, New Delhi.

Zaman-Allah M, Jenkinson D, and Vadez V 2011a. A conservative pattern of water use, rather than deep or profuse rooting, is critical for the terminal drought tolerance of chickpea. Journal of Experimental Botany doi: 10.1093/jxb/err139

Zaman-Allah M, Jenkinson D, and Vadez V 2011b. Chickpea genotypes contrasting for seed yield under terminal drought stress in the field differ for traits related to the control of water use. Functional Plant Biology 38, 270-281

Table 1. Main characteristics of locations (latitude, number of year of weather data available, in-season rainfalls, optimum time to flowering in degree-days to achieve the highest predicted yield) and baseline days to flowering and maturity, yield estimations at fourteen different locations of India. Yield predictions at each location have been done using a standard genotype with phenological characteristics (flowering time) leading to maximum baseline yield at each location.

Locations	Latitude	Years	Optimum R1	Days to flower	Days to maturity	Yield (g/m2)	Season rainfall
Bangalore	12.97	25	45.8	52	96	141	87
Annigeri	15.13	24	35.3	43	85	80	40
Dharwad	15.43	21	37.9	44	87	102	36
Bijapur	16.82	14	40.5	47	90	118	37
Gulbarga	17.35	23	37.9	44	87	104	35
Solapur	17.67	23	37.9	44	87	89	33
ICRISAT	17.9	33	40.5	48	91	104	35
Indore	22.72	24	37.9	46	96	103	23
Jabalpur	23.2	29	37.9	48	103	126	59
Jaipur	26.82	29	37.9	48	108	149	28
Delhi	28.66	24	37.9	58	125	182	62
Hisar	29.2	29	43.2	64	135	161	40
Ludhiana	29.6	18	48.4	78	143	227	99
Amritsar	31.6	18	43.2	76	146	193	99

Table 2. Simulated mean (g m^{-2}), standard error (SE, g m^{-2}) and coefficient of variation (CV, %) of grain yield across 14 locations and yield increase as mean (g m^{-2}) and percentage decrease (%) and the number of locations (#, out of 14) with positive yield increase as a result of the modified plant trait (root and leaf development), soil trait (depth of water extraction), or agronomic management (irrigation)..

	Yield (g m^{-2})			Yield increase		
Modified trait	Mean	SE	CV	g m^{-2}	%	#
Baseline yield	134.2	11.6	32.3	-		-
Faster root	127.2	11.7	34.3	-7.0 **	-5.2	0
Faster leaf	141.1	15.3	40.5	6.9 ns	5.1	9
Faster root and leaf	133.0	15.5	43.7	-1.2 ns	-0.9	2
Decreased Depth of water extraction	99.1	10.5	39.5	-35.1 **	-26.2	0
Decreased Depth of water extraction + faster root	92.4	10.5	42.4	-41.9 **	-31.2	0
Increased Depth of water extraction	144.2	12.8	33.3	10.0 **	7.5	14
Increased Depth of water extraction + faster root	143.0	12.0	31.4	8.8 **	6.5	14
Increase Depth of water extraction + faster leaf	153.3	17.0	41.6	19.1 **	14.2	12
Increase Depth of water extraction + faster leaf + faster root	153.0	15.9	39.0	18.8 **	14.0	14
Irrigation at R5 (30 mm)	168.2	13.3	29.7	34.0 **	25.3	14

Figure Captions

Figure 1. Simulated versus measured total crop mass at maturity (a) and crop yield (b) for line-source experiments. The 18% ranges of discrepancy between simulated and measured are indicated by dashed lines. Solid line is 1:1 line. Simulated values of crop mass at maturity were multiplied by 0.77 to account for senesced leaves and petiols' mass.

Figure 2. Relationship between the predicted yield at fourteen Indian locations and the in-season rainfall received on average on each location (18 to 33 years of weather data depending on location). The baseline uses an effective depth of water extraction of 1000 mm and a standard rate of root growth of 17 mm day^{-1}. These settings are those used in subsequent figures if no specification is provided.

Figure 3. Simulated yield increase, in percentage of the baseline yield in Table 1, at fourteen Indian locations in response to a faster root growth (from 17 to 30 mm day^{-1}, open circle).

Figure 4. Simulated yield increase, in percentage of the baseline yield in Table 1, at fourteen Indian locations in response to a factorial of plant (rate of root growth) and soil (effective depth of water extraction) traits: (i) a decrease in the effective depth of water extraction (from 1000mm to 800mm, closed circle); (ii) a decrease in the effective depth of water extraction (from 1000mm to 800mm) combined to a faster root growth (from 17 to 30 mm day^{-1}, open circle); (iii) an increase in the effective depth of water extraction (from 1000mm to 1200mm, closed square); (iv) an increase in the effective depth of water extraction (from 1000mm to 1200mm) combined to a faster root growth (from 17 to 30 mm day^{-1}, open square).

Figure 5. Simulated yield increase, in percentage of the baseline yield in Table 1, at fourteen Indian locations, using a fixed 1000 mm soil depth of water extraction, in response to the development of a larger leaf area (closed triangle), and to the combination of the development of a larger leaf area and a faster root growth (from 17 to 30 mm day^{-1}, open triangle).

Figure 6. Simulated yield increase, in percentage of the baseline yield in Table 1, at fourteen Indian locations, using a combination of plant (rate of root growth and development of a larger leaf area) and soil (depth of water extraction) traits: (i) development of a larger leaf area combined to an increase in the depth of water extraction (from 1000mm to 1200mm, closed square), and (ii) development of a larger leaf area and faster root growth (from 17 to 30 mm day^{-1}) combined to an increase in the depth of water extraction (from 1000mm to 1200mm)(open square).

Figure 7. Simulated yield increase, in percentage of the baseline yield in Table 1, at fourteen Indian locations, using a 1000 mm effective depth of water extraction, the standard development of leaf area, and a standard rate of root growth (17 mm day^{-1}) in response to an irrigation of 30 mm at R5 stage (beginning of seed growth) (closed square).
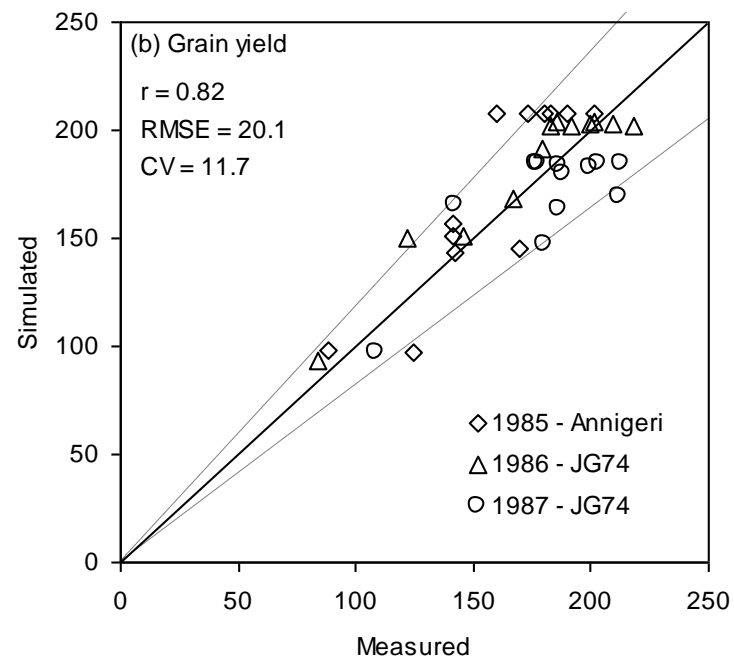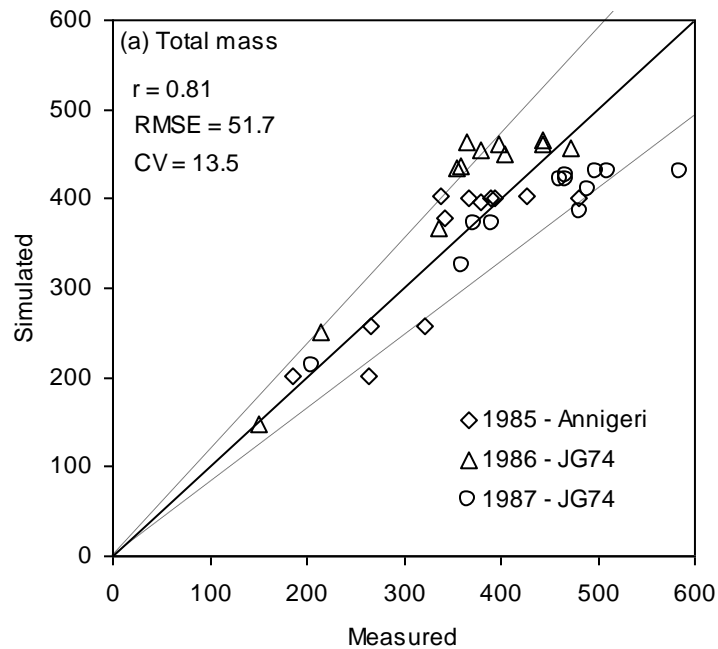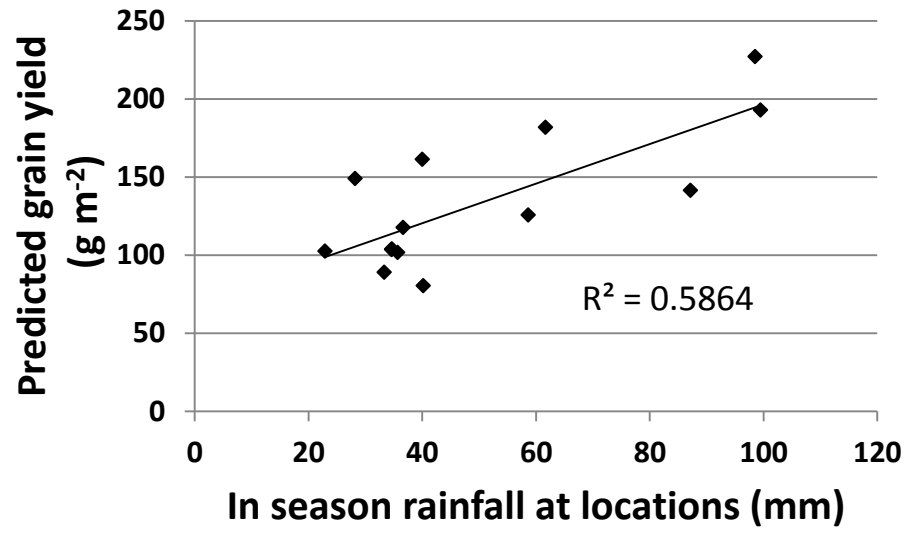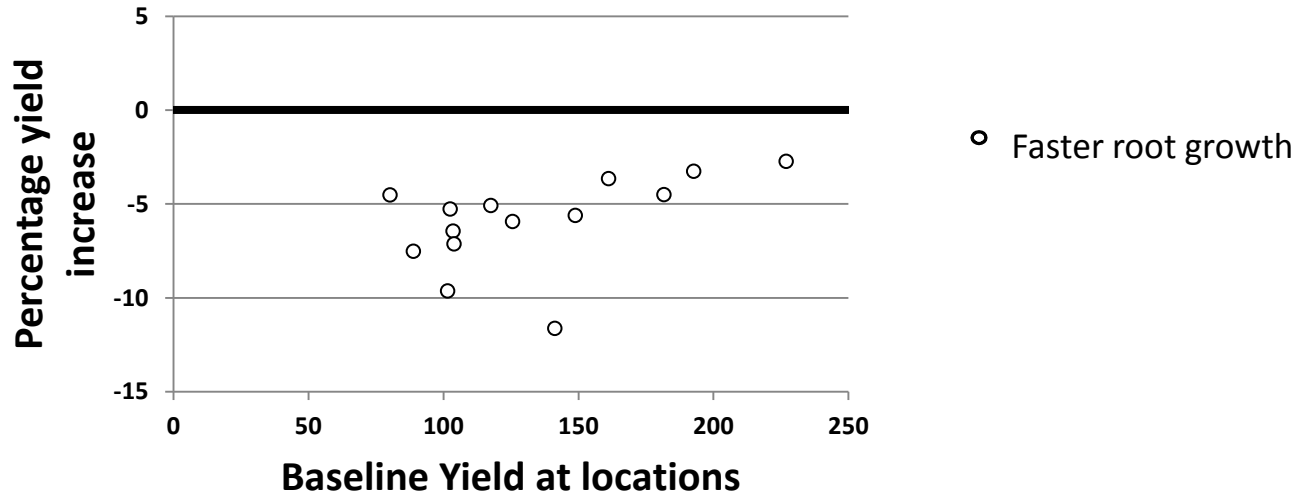
Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6

Legend:

■ Increased leaf area
+ Increased depth of water extraction

□ Increased leaf area
+ Increased depth of water extraction
+ Faster root growth

Figure 7