Agronomy Division, International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, Andhra Pradesh, India

Investigation of Factors Determining Genotypic Differences in Seed Yield of Non-irrigated and Irrigated Chickpeas Using a Physiological Model of Yield Determination

L. Krishnamurthy, C. Johansen and S. C. Sethi

Authors' address: Dr L. Krishnamurthy (corresponding author), Dr C. Johansen and Dr S.C. Sethi, International Crops Research Institute for the Semi-arid Tropics (ICRISAT), Patancheru, A.P. 502 324, India

With 8 figures and 2 tables

Received March 18, 1998; accepted September 12, 1998

Abstract

Physiological attributes determining yield, both under drought and under irrigated conditions, of some advanced chickpea lines of recent origin were investigated over two seasons using a physiological model. Total shoot biomass, grain yield, and vegetative (D_v) and reproductive (D_r) durations were measured and the crop growth rates (C) and the rate of partitioning to seed (p) were estimated. The contribution of model parameters to variations in grain yield were determined by path analysis, and the relationships of the yield determinants with seed yield were obtained by regression techniques. The model was found to be suitable for chickpea, and when the parameters were fitted the model explained 98% of the variation. Irrigation enhanced Dr and C. While C was the major single yield determinant, the combination of C and p in non-irrigated environments explained most of the grain yield variation. D_v and D_r exhibited a negative relationship while C and p exhibited a positive relationship under drought stress and a negative relationship in the irrigated environment. There were indications of the existence of an optimum D, for maximum C among the genotypes, suggesting the need to select for optimum duration genotypes. As high values for p and C in severe drought stress and D_r and C in the irrigated environments are advantageous for high yield, separate breeding strategies are needed for different soil water environments.

Key words: Cicer arietinum L. — chickpea — crop growth rate — drought stress — physiological model — rate of partitioning — soil water environments — yield determinants

Introduction

Chickpea (Cicer arietinum L.) is best adapted to the cool winter temperatures of the semi-arid tropics and the spring to early summer seasons of the Mediterranean region. Temperatures above 30 °C greatly

hasten maturity (Summerfield et al. 1990) and the seasonal patterns of temperature have an important role in determining the duration of the crop, and therefore the yield potential of chickpea in a given environment (Saxena 1984). Also, the rate of evapotranspiration of the stored soil moisture, on which chickpea is usually dependent as it is normally grown in a post-rainy period, depends among other factors on the atmospheric temperature, setting a limit to the growing period (Piara Singh and Virmani 1990). Consequently, under warm short duration environments, such as in peninsular India, chickpea responds well to supplementary irrigation, increasing the productivity 2 to 3 times compared to a crop grown on stored soil moisture alone (Saxena 1984). Most chickpea production on Vertisols in peninsular India relies on residual soil moisture, although production from irrigated chickpea is increasing (Johansen et al. 1994). The need for a separate selection programme in chickpea breeding efforts for target moisture environments was emphasized by the contrasting performance of genotypes in different moisture environments (Johansen et al. 1994). The processes which lead to these contrasting responses must be further evaluated to enable a more directed approach for future breeding efforts. Genotypic variation in functional processes such as C, D, and p was used to explain the grain yield production of short duration pigeonpea in different environments (Chauhan et al. 1995). If these functional attributes are found to be useful, they are simple to measure from any yield trial.

The development of chickpea is controlled largely by genetic attributes and environmental factors such as photoperiod, temperature (Summerfield et al. 10 Krishnamurthy et al.

1990) and soil water. Photoperiod triggers reproductive growth (Roberts and Summerfield 1987), while the rates at which reproductive structures are initiated are determined by temperature (Monteith 1981). Thus, as temperature increases from the base temperature to the optimum, the plant accumulates more thermal time (°Cd) per calendar day and develops faster, although in terms of thermal time, ontogeny occurs at a constant rate (Mohamed et al. 1988). This effect is of particular significance when comparing crop development in contrasting environments.

A model for analysing the processes leading to seed yield determination in groundnuts was proposed by Duncan et al. (1978). This was adapted by Williams and Saxena (1991) to explain the yield differences among chickpea genotypes grown in Hisar in northern India and by Chauhan et al. (1995) for short duration pigeonpea. The model is:

$$Y = C \times D_r \times p, \tag{1}$$

where Y = grain yield, C = mean crop growth rate, $D_r = \text{duration}$ of reproductive growth, and p = mean fraction of crop growth rate partitioned to Y.

This model uses thermal time as the growing period instead of calendar days and functional processes to explain yield determination. The objective of this paper is to examine, using the above model, (1) the relative importance of physiological processes (C, D_r and p) in determining yield of improved chickpea lines of recent ICRISAT origin in two different soil moisture environments, and (2) the processes which have the largest contributions to seed yield both under non-irrigated and under irrigated conditions.

Materials and Methods

Experiments were conducted in the 1991/92 and 1992/93 post-rainy seasons on a Vertisol field (fine montmorillonitic isohyperthermic typic pallustert) at the ICRI-SAT Center (17°30′ N; 78°16′ E; altitude 549 m) in peninsular India. The soil depth of the field used in 1991/92 was about 1.2 m and in 1992/93 was about 0.9 m. These soils retained about 180 and 120 mm, respectively, of plant available water in the soil profile. The fields were prepared into flat seed beds with a fine tilth after surface application and incorporation of 18 kg N ha⁻¹ and 20 kg P ha⁻¹ as diammonium phosphate.

Nineteen chickpea lines were sown on 31 October 1991 and 40, inclusive of the eight tested in the first year, on 1 November 1992 in a split-plot design with three replications, with soil moisture level in the main plots and chickpea lines in the subplots. The two soil moisture

treatments comprised a non-irrigated and an irrigated treatment. The non-irrigated plots received no irrigation other than a post-sowing irrigation, in order to charge the profile and to ensure complete seedling emergence. The irrigated plots received a further three irrigations during the 1991/92 season, on 9 and 26 December 1991 and 22 January 1992, and four during the 1992/93 season, on 17 December 1992, and 6 January, 21 January and 3 February 1993. The chickpea entries used were mostly advanced breeding lines, recently selected at the ICRI-SAT Center from preliminary and advanced yield trials conducted across varying soil moisture environments along with some cultivars and control genotypes, like Annigeri and ICC 4958. Most of these entries had short and medium durations, generally adapted to the region, and were found to yield better than the control varieties in the preliminary and advanced yield trials conducted across varying moisture environments. For the sake of brevity these entries are collectively referred to as 'chickpea lines' in the rest of this paper. The seeds were manually sown at 30×10 cm spacing with 2 seeds per hill and later thinned to 1. The plot size was 6×4 m in 1991/92 and 4×3 m in 1992/93. Intensive protection against the pod borer (Helicoverpa armigera) was provided and the plots were kept weed-free.

To measure water applied, two rows of plastic buckets were placed between two rows of perforated pipe at a distance of 1 m in each replication. Soil moisture was estimated from soil samples collected gravimetrically at stages before and after each irrigation.

By regular observation, the mean date on which more than 50% of the plants reached flowering was recorded as the 50% flowering time and the date on which 80% of pods dried was recorded as the time of maturity.

At maturity, plants from an area of $19.44 \,\mathrm{m}^2$ in 1991/92 and $8.64 \,\mathrm{m}^2$ in 1992/93 were harvested and dried to constant weight in hot air dryers at $45 \,^{\circ}\mathrm{C}$, shoot dry weights were recorded and the dry weights were adjusted for an estimated 21% loss of dry matter as leaf fall (Saxena 1984, Williams and Saxena 1991). Grain weights were recorded after threshing. For each chickpea line, the preflowering and post-flowering periods were converted to thermal time using temperature observations in the meteorological observatory of the ICRISAT Center. The base temperature (t_b) was taken to be $0\,^{\circ}\mathrm{C}$ (Williams and Saxena 1991, Piara Singh and Virmani 1996) and the equation used for calculating thermal time ($^{\circ}\mathrm{Cd}$) was:

$${}^{o}\mathrm{Cd} = \sum_{i=0}^{n} \left(\frac{t_{max} + t_{min}}{2} - t_{b} \right)$$

The crop growth rate (C) in kg ha⁻¹ °Cd and the partitioning coefficient (p) of each line were estimated using the equations

$$C = (V + Y)/(D_v + D_r)$$

and

$$P = (Y/D_r)/C,$$

where $V = \text{vegetative shoot mass (kg ha}^{-1})$ (adjusted for

leaf fall), Y = grain mass (kg ha⁻¹), D_r = duration of growth after 50% flowering (°Cd), D_v = duration of growth before 50% flowering (°Cd).

Additionally, the mean maximum temperatures for the 10 days prior to maturity were computed for each genotype, and termed the 'end temperature'. The direct and indirect contributions of C, $D_{\rm r}$ and p to seed yield were assessed using path analysis. The pairwise relationship among these variables was assessed by regression analyses.

Results

Extent of terminal drought

During the crop growth period, rainfall was recorded on 3 November (1.0 mm) and 16/18 November (2.0 mm) in 1991/92, and on 17/18 November (77.0 mm) in 1992/93. The amount of water applied was 66, 57 and 38 mm in 1991/92 and 67, 58, 61 and 56 mm in 1992/93. The drought stress that resulted when the plots received no irrigation was more severe in the 1992/93 season, despite the heavy November rains, than in the 1991/92 season (Fig. 1) due to the shallow soil depth and poor water-holding capacity of the soil in the field used in 1992/93.

Extent of variation amongst chickpea lines

The variation observed amongst the lines for shoot biomass, grain yield and the three determinants of grain yield in both irrigated and stress environments was large (Table 1). The extent of variation observed with irrigation across all the chickpea lines was equivalent to that observed in the northern Indian environment (Williams and Saxena 1991). The increase in mean shoot dry matter and seed yield with irrigation was substantial, about 2- to 3-fold depending on the drought intensity in the non-irrigated plots. Durations of both the vegetative (D_v) and reproductive (D_r) phases of growth were increased by irrigation, but these enhancements were higher for the reproductive phase than for the vegetative phase. D, increased by about 25% in the first and 50 % in the second year of study. The differences in mean D, between the non-irrigated and irrigated treatments were low as the difference in soil moisture between the irrigation treatments at this stage was also low (Fig. 1). C was substantially increased by irrigation but p was reduced during the first year and appeared to remain unaffected during the second year.

Suitability of the model for chickpea

When the mean yields of chickpea lines under both soil moisture levels in the two seasons were con-

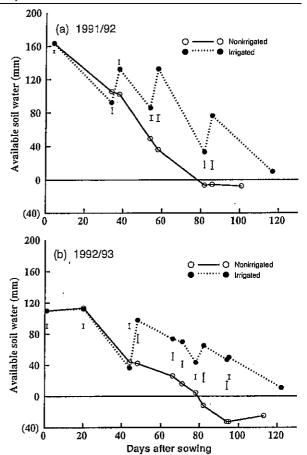


Fig. 1: Changes in total available soil water (mm) with and without irrigation over the crop growing period in the Vertisol fields during (a) 1991/92 and (b) 1992/93 post-rainy seasons. (Vertical bars are standard errors to compare means of available soil moisture between non-irrigated and irrigated treatments during the period of sampling)

sidered together for path analysis, model 1 was found to explain 97.9% of the variation. When the line-by-year variations were considered individually for both non-irrigated and irrigated environments, the variation explained was 99.2% in both the soil moisture environments.

The relationship between yield and model parameters $(C, D_r$ and p)

The relationship between yield and C was positive and very strong (Fig. 2). The direct and indirect contributions of the three yield determinants to seed yield assessed through path analysis are presented in Table 2. These coefficients are proportions to 1. The diagonal elements represent direct effects, the

Table 1: Mean shoot dry matter, grain yield, D_v , D_r , C and p for chickpea advanced breeding lines in the 1991/92 and 1992/93 post-rainy seasons under non-irrigated and irrigated conditions

	Non-irrigated			Irrigated		
	Range	Mean	S.E.	Range	Mean	S.E.
1991/92 post-rainy season (n = 19)					
Shoot dry matter (kg ha ⁻¹)	2528-4129	3722	87.5	5095-7291	6597	135.3
Seed yield (kg ha-1)	1159-1966	1696	56.3	2070-3208	2610	78.0
D, (°Cd)	760-1198	918	26.6	739-1219	932	31.8
D, (°Cd)	866-1126	960	15.8	1005-1374	1200	28.1
C (kg há ⁻¹ °Cd ⁻¹)	1.42-2.25	1.98	0.050	2.56-3.40	3.09	0.058
p	0.77-1.01	0.89	0.014	0.55-0.79	0.71	0.014
$\frac{1}{1992/93}$ post-rainy season (n = 40))					
Shoot dry matter (kg ha ⁻¹)	18022695	2175	36.8	3295-7854	5527	141.2
Seed yield (kg ha ⁻ⁱ)	505-1179	840	32.8	1407-3531	2534	71.0
D, (°Čd)	876-1377	1089	21.7	857-1420	1102	24.5
D _r (°Cd)	813-1119	930	10.2	1141-1594	1393	20.7
C (kg ha ^{-l} °Cd ^{-l})	0.83-1.37	1.08	0.023	1.41-3.06	2.22	0.056
p	0.54-1.07	0.83	0.021	0.62-0.97	0.83	0.010

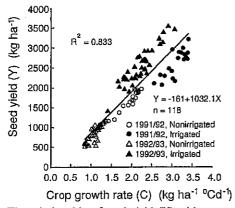


Fig. 2: The relationship of seed yield (Y) with crop growth rate (C) across 19 advanced breeding lines of chickpea during the 1991/92 post-rainy season and across 40 lines during the 1992/93 post-rainy season under non-irrigated and irrigated conditions

off-diagonal elements the indirect effects and the total represents the net effects. For example, in Table 2a, the direct contribution of C to yield is 0.542 (or 54.2%), that through D_r is (0.041 + 0.041) 0.082 and that through p is (0.121 + 0.121) 0.242. The net contribution of C to yield is 0.704. The major source of yield variation was C, contributing 83.4% of the total variation under non-irrigated and 82.3% under irrigated environments across both years (Tables 2e

and f). The D_r of chickpea lines in both the soil moisture environments and years together showed a positive relationship with seed yield (Fig. 3), but chickpea lines did not show any such positive relationship either within soil moisture treatments or within seasons. Nevertheless, an increase in D_r was clearly apparent with increased soil moisture (Fig. 3 and Table 1). The direct contribution of D_r to yield was positive but the indirect contribution through C and p was mostly negative, reducing the net contribution (Table 2). Dr in the irrigated environment across both years made a high (61.6%, Table 2f) direct contribution but in the non-irrigated environment made a low contribution (1.8%, Table 2e). However, the variation in chickpea lines was comparatively low under non-irrigated conditions (Fig. 3). The determinant p was also not directly related to yield when non-irrigated and irrigated treatments were collectively considered. However, p had a close positive relationship with yield in the severely drought-stressed ($r^2 = 0.78$) environment as observed in 1992/93 (Fig. 4). The net contribution of p to yield was positive in both the soil moisture environments and in both years, whereas the contribution of p through D_r was negative (Table 2). However, the net contribution was the highest (52.9%) and the direct contribution was moderately high (35.9%) in the non-irrigated environment of 1992-93 (Table 2c).

Table 2: Direct and indirect contributions of C, D_r and p to seed yield in various soil moisture environments assessed through path analysis (the diagonal elements represent direct effects, and the off-diagonal elements the indirect effects; the totals represent the net effects)

	С	D_r	p	С	D_{r}	р	
(a) 1991–92,	non-irrigated		(b) 1991–92, irrigated				
C	0.542	0.041	0.121	0.397	-0.105	0.208	
D_{r}	0.041	0.228	-0.171	-0.105	0.635	-0.356	
p	0.121	-0.171	0.245	0.208	-0.356	0.470	
Total	0.704	0.098	0.195	0.500	0.174	0.322	
(c) 1992–93,	non-irrigated		(d) 1992-93, irrigated				
Č	0.327	-0.047	0.207	0.853	-0.074	0.067	
D,	-0.047	0.064	-0.037	-0.074	0.266	-0.142	
p	0.207	-0.037	0.359	0.067	-0.142	0.174	
Total	0.487	-0.148	0.529	0.846	0.050	0.099	
(e) Non-irrig	ated (both years)			(f) Irrigated	(both years)		
Ċ	0.732	0.017	0.085	1.793	-0.569	-0.401	
D_r	0.017	0.018	-0.008	-0.569	0.616	-0.006	
p	0.085	-0.008	0.058	-0.401	-0.006	0.523	
Total	0.834	0.027	0.136	0.823	0.041	0.128	
(g) Overall (b	ooth years and irri	igations)	•				
Č	0.525	0.167	-0.030	•			
D _r	0.167	0.189	-0.027				
p	-0.030	-0.027	0.047				
Tota!	0.661	0.329	-0.011				

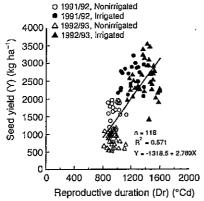
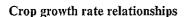


Fig. 3: The relationship of seed yield (Y) with reproductive duration (D_r) across 19 advanced breeding lines of chickpea during the 1991/92 post-rainy season and across 40 lines during the 1992/93 post-rainy season under non-irrigated and irrigated conditions



Under non-irrigated conditions in 1992/93, C was positively related to p whereas under irrigated con-

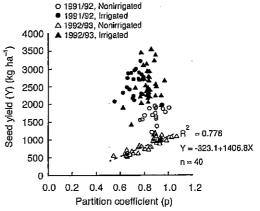


Fig. 4: The relationship of seed yield (Y) with partitioning coefficient (p) across 19 advanced breeding lines of chickpea during the 1991/92 post-rainy season and across 40 lines during the 1992/93 post-rainy season under non-irrigated and irrigated conditions

ditions, when both the years were considered together, it was negatively related (Fig. 5). Further, C was negatively related to D_v under non-irrigated

14 Krishnamurthy et al.

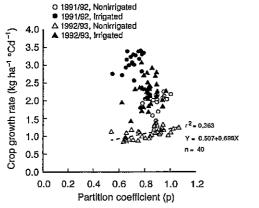


Fig. 5: The relation between partitioning coefficient (p) and crop growth rate (C) across 19 advanced breeding lines of chickpea during the 1991/92 post-rainy season and across 40 lines during the 1992/93 post-rainy season under non-irrigated and irrigated conditions

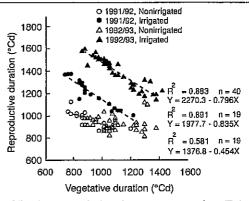


Fig. 7: The inverse relation between vegetative (D_{ν}) and reproductive durations (D_{r}) across 19 advanced breeding lines of chickpea during the 1991/92 post-rainy season and across 40 lines during the 1992/93 post-rainy season under non-irrigated and irrigated conditions

O 1991/92, Nonirrigated

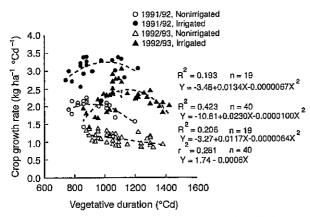


Fig. 6: The relation between vegetative duration (D_{ν}) and crop growth rate (C) across 19 advanced breeding lines of chickpea during the 1991/92 post-rainy season and across 40 lines during the 1992/93 post-rainy season under non-irrigated and irrigated conditions

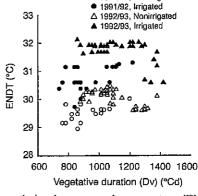


Fig. 8: The relation between end temperature (ENDT) and vegetative duration (D_v) across 19 advanced breeding lines of chickpea during the 1991/92 post-rainy season and across 40 lines during the 1992/93 post-rainy season under non-irrigated and irrigated conditions

conditions in the 1992/93 season, whereas this relationship was quadratic in 1991/92 and under irrigated conditions in both seasons (Fig. 6). These interacting effects can be easily explained. Under receding soil moisture conditions, the major part of the exponential growth phase of relatively late duration lines occurs when moisture availability is low, thereby adversely affecting the overall C. In such a situation, an early duration chickpea line tends to have a higher C with relatively more soil water left at the water extraction front at the reproductive stage of the crop, enabling a higher p. When the drought effects were ameliorated by periodic irrigation, the biomass production of the relatively late duration lines also continued unhindered and

the adverse effects on C were reduced. Nevertheless, the increasing imbalance in enhanced water requirement due to continuously increasing atmospheric evaporative demand and reducing soil moisture supply at later stages adversely affects the partitioning. This effect has been clearly shown by the inverse relationship between D_v and D_r (Fig. 7). Longer D_v reduced D_r, particularly under irrigated conditions. The test entries used in this study were more or less in the adapted range of duration, i.e. 85-100 days to maturity. Such an adverse effect would have been much more pronounced in the event of inclusion of late duration lines (Saxena 1984). There was no clear-cut relationship between the length of D_v of the chickpea lines and the end temperature (Fig. 8), in contrast to the observations made at Hisar in

northern India (Williams and Saxena 1991). However, the end temperature prevailing at the time of maturity of the irrigated treatment was higher (about 32 °C) than that of the non-irrigated treatment (about 30 °C). The rise in temperature at the approach of summer in peninsular India is gradual compared to the abrupt rise in northern India.

Discussion

Chickpea growing areas in peninsular India are characterized by a short, warm growing period, generally devoid of rains. As a consequence, productivity is low. Chickpea growing areas on Vertisols in this region include soils with residual soil moisture and optimum irrigation (Johansen et al. 1994). This diversification in soil moisture regimes of chickpea growing areas necessitates development of management practices and selection of appropriate chickpea genotypes specific to these environments.

Phenology

Improved soil moisture increased the thermal time (°Cd) needed to attain various developmental stages (Table 1), similar to observations on soybean (Desclaux and Roumet 1996). Irrigation helps to maintain a low maximum soil temperature, at least 10 °C lower than without irrigation (Reddy et al. 1989), and a low shoot temperature; in sorghum, this is reduced by > 3 °C (Chaudhuri and Kanemasu 1982), in chickpea by about 2 °C (Yadav et al. 1994) and in wheat by up to 2.5 °C (Kumar et al. 1986), at any given time. In South Asia, flowering in chickpea coincides with the occurrence of the coolest ambient temperature of the year, and this cooling would therefore slow down the temperaturedriven metabolic changes affecting developmental processes and aging. Also, irrigation appears to encourage surface rooting, thereby enhancing mineral nitrogen extraction and biological nitrogen fixation (Hebblethwaite 1982) and alleviating nitrogen deficiency in plants. This is expected to delay senescence in plants.

Most of the high-yielding chickpea lines had < 1000 °Cd (data not shown) vegetative and < 950 °Cd reproductive durations under non-irrigated conditions in 1992/93. These values for 1991/92 were < 900 °Cd and < 1000 °Cd, respectively (data not shown). However, under irrigation these values were < 1100 and < 1450 °Cd during 1992/93 and < 900 and < 1300 °Cd during 1991/92.

Yield determinants

The fact that this model was able to explain 97.9% of the variation in grain yield of chickpea lines with or without irrigation confirms the general principle that the three physiological processes, C, D, and p, adequately explain the variation in grain yield of chickpea. Among these three, C was the major determinant of seed yield in chickpea. Using path analysis to find the combination of processes with the largest contribution to yield, the net contribution of C and D_r to yield (67.4% in 1991/92, 89.6% in 1992/93) was found to be closer to the contribution of C and p (82.2% in 1991/92, 94.5% in 1992/93) in the irrigated treatment. However, the net contribution of C and p (89.9% in 1991/92, 100% in 1992/93) was higher than that of C and D_r (80.2% in 1991/92, 33.9% in 1992/93) in the non-irrigated treatment of 1992/93. Also, under non-irrigated conditions, p had a strong positive relationship with grain yield and C and p together accounted for almost all the yield variability. These relationships indicate that at high levels of drought stress, as in 1992/93 season, a high partitioning rate and a high crop growth rate have the largest contributions to high grain yield. In this environment, with a mean yield of 840 kg ha⁻¹, chickpea lines ICCV 90049, ICCV 90008, ICCV 90040 and ICC 4958 yielded $> 1100 \,\mathrm{kg} \,\mathrm{ha}^{-1}$. These lines had the highest C, average D, and above-average p values. A high rate of seed accumulation was found to be advantageous under adverse soil moisture conditions, as in ICC 4958 (ICRISAT 1992). Under extreme soil moisture stress, partitioning is the major determinant of grain yield, as is also found in spring-sown chickpea of the Mediterranean region (Silim and Saxena 1993).

However, under irrigated conditions, as in 1992/93, high C with relatively long D_r seems to favour high yields. In this environment, with a mean yield of 2534 kg ha⁻¹, lines ICCV 89244, ICCV 90009, ICCV 90140 and ICCV 90141 yielded > 3200 kg ha⁻¹. These had the highest C, average D_r and average p. The average D_r in this environment was much higher than that under the non-irrigated treatment. In a similar experiment considering shoot biomass and harvest index in spring-sown chickpea, shoot biomass was found to be positively associated with high grain yield in low drought-stress years, whereas harvest index was most strongly associated with yield in severe drought-stress years (Silim and Saxena 1993).

The yield ranks of chickpea genotypes were reported not to correspond well in contrasting soil moisture environments (Johansen et al. 1994). Such

Krishnamurthy et al.

poor correlations were also evident in the present study, with the correlation between the seed yields of the 40 chickpea lines obtained in the two soil moisture treatments in 1992/93 being low (r = 0.151; data not shown). These relationships clearly indicate that the genotypes with high C and p have maximum advantage under a high intensity of drought stress, whereas a high coefficient of p can be a disadvantage under situations of adequate moisture. However, those genotypes with a high degree of developmental plasticity, for example ICCV 10, can be expected to give high yield across a wide range of soil moisture conditions (Fig. 4; Johansen et al. 1994). The fact that high C is associated with high grain yield in both environments emphasizes the need for chickpea improvement efforts to incorporate this parameter as a trait for selection to achieve higher and more stable yields. Similar conclusions were drawn by Williams and Saxena (1991) and by Wallace et al. (1993). Wallace et al. (1993) cautioned that the current selection methods, exclusively for yield without considering biomass production, are inefficient. To evaluate C together with yield, biomass production from postselection yield trials must be measured. Large genotypic variation for early growth vigour is available in chickpea germplasm (ICRISAT 1990), indicating scope for improving C.

Conclusion

Under peninsular Indian environments, high crop growth rate leads to high seed yield, irrespective of soil moisture regimes. The importance of a high partitioning rate in determining maximum seed yield increases as drought stress increases. Therefore, breeding and selection approaches for droughtprone rain-fed environments need to incorporate a high partitioning rate in addition to a high crop growth rate for maximum seed yield. About half of the chickpea lines considered for this test possessed coefficients of C and p either marginally higher than or comparable to that of the well-adapted chickpea genotype Annigeri, indicating that chickpea breeding efforts are progressing in this direction. However, identification of sources for high coefficients of C and p and a conscious incorporation of these selective processes in breeding efforts should accelerate progress. Breeding efforts need to be targeted separately for irrigated and rainfed environments to increase yield and improve adaptation in these contrasting soil moisture environments.

Zusammenfassung

Untersuchungen von Faktoren unter Verwendung eines physiologischen Modells der Ertragsdefinition genotypischer Differenzen im Samenertrag von nichtbewässerten und bewässerten Kichererbsen

Physiologische Eigenschaften, die den Ertrag bestimmen, wurden unter Trocken- und Bewässerungsbedingungen bei einigen kürzlich entwickelten verbesserten Linien von Kichererbsen über zwei Anbausaisons unter Verwendung eines physiologischen Modells untersucht. Die gesamte Sproßbiomasse, Kornertrag, vegetative (D_v) und reproduktive (Dr) Phasendauer wurden bestimmt und die Bestandeswachstumsraten (C) und die Rate der Assimilatzutelung zu den Samens (p) gemessen. Der Anteil der Parameter an der Variation im Kornertrag wurde mit Hilfe einer Pfadanalyse berechnet und die Beziehung zwischen den Ertragskomponenten zum Samenertrag mit Hilfe einer Regressionstechnik bestimmt. Das Modell erwies sich als geeignet für Kichererbsen, und die Parameter im Modell konnten 98 % der Variation erklären. Die Bewässerung vergrößerte D, und C. Während C die Hauptkomponente des Ertrages war, konnte die Kombination von C und p unter Nichtbewässerungsbedingungen in wesentlichen die Kornertragsvaration erklären. D. und D, zeigten eine negative Beziehung, während C und p eine positive Beziehung under Dürrestress und eine negative Beziehung unter Bewässerungsbedingungen aufwiesen. Es fanden sich Hinweise des Vorhandenseins einer optimalen D, für maximales C innerhalb der Genotypen, was die Notwendigkeit einer Selektion von Genotypen mit optimaler Phasendauer bestätigen würde. Da hohe Werte für p und C unter strengen Dürrestressbedingungen und D, und C unter Bewässerungsbedingungen vorteilhaft für hohen Ertrag sind, werden eigenständige Zuchtstrategien für unterschiedliche Bodenwasserverhältnisse benötigt.

Acknowledgements

Helpful comments on the manuscript, and suggestions for its improvement, by Dr N. P. Saxena of ICRISAT and Professor D. H. Wallace, Emeritus Professor, Cornell University, USA, are gratefully acknowledged, and the chickpea physiology staff of the Agronomy Division at the ICRISAT Center, Patancheru, are thanked for their careful work in assisting with the experiments. This paper has been submitted as J.A. no. 2213 by the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT).

References

Chaudhuri, U. N., and E. T. Kanemasu, 1982: Effect of water gradient on sorghum growth, water relations and yield. Can. J. Plant Sci. 62, 599—607.

Chauhan, Y. S., C. Johansen, and K. B. Saxena, 1995: Physiological basis of yield variation in short-duration pigeonpea grown in different environments of the semiarid tropics. J. Agron. Crop Sci. 174, 163—171.

- Desclaux, D., and P. Roumet, 1996: Impact of drought stress on the phenology of two soybean (Glycine max L. Merr) cultivars. Field Crops Res. 46, 61—70.
- Duncan, W. G., D. E. McCloud, R. McGraw, and K. J. Boote, 1978: Physiological aspects of peanut yield improvement. Crop Sci. 18, 1015—1020.
- Hebblethwaite, P. D., 1982: The effects of water stress on the growth, development and yield of *Vicia faba L. In:* G. Hawtin and C. Webb (eds), Faba Bean Improvement, pp. 165—175. Martinus Nijhoff/Junk, The Hague.
- ICRISAT (International Crops Research Institute for the Semi-Arid Tropics), 1990: Chickpea. In: Annual Report 1989, pp. 83—104. ICRISAT, Patancheru, India.
- —, 1992: ICC 4958, a drought resistant chickpea. In: Plant Material Description no. 33, pp. 1—4. ICRISAT, Patancheru, India.
- Johansen, C., L. Krishnamurthy, N. P. Saxena, and S. C. Sethi, 1994: Genotypic variation in moisture response grown under line-source sprinklers in a semi-arid tropical environment. Field Crops Res. 37, 103—112.
- Kumar, A., S. D. Dhiman, and S. K. Yadav, 1986: Stomatal frequency and distribution, water relations and micro environment of wheat genotypes under irrigated and unirrigated conditions. Indian J. Ecol. 13, 256—265.
- Mohamed, H. A., J. A. Clark, and C. K. Ong, 1988: Genotypic differences in the temperature responses of tropical crops. I. Germination responses. J. Exp. Bot. 39, 1121—1128.
- Monteith, J. L., 1981: Climatic variation and the growth of crops. Quart. J. Royal Meteorol. Soc. 107, 749—774. Piara Singh, and S. M. Virmani, 1990: Evapotranspiration and yield of irrigated chickpea. Agric.
- Forest Meteor. **52**, 333—345.

 —, and —, 1996: Modeling growth and yield of chickpea (*Cicer arietinum* L.). Field Crops Res. **46**, 41—59.

- Reddy, P. V., K. B. Reddy, and G. N. S. N. Rao, 1989: Influence of soil moisture content on pod zone temperatures in groundnut. International Arachis Newsletter 6, 9—10.
- Roberts, E. H., and R. J. Summerfield, 1987: Measurement and Prediction of Flowering in Annual Crops. In: J. G. Atherton (ed.), Manipulation of Flowering. Proc. of the 45th Easter School, Faculty of Agricultural Science, University of Nottingham, pp. 17—50. Butterworths, London.
- Saxena, N. P., 1984: Chickpea. In: P. R. Goldsworthy and N. M. Fisher (eds), The Physiology of Tropical Field Crops, pp. 419—452. Wiley, New York.
- Silim, S. N., and M. C. Saxena, 1993: Adaptation of spring-sown chickpea to the Mediterranean basin. II. Factors influencing yield under drought. Field Crops Res. 34, 137—146.
- Summerfield, R. J., S. M. Virmani, E. H. Roberts, and R. H. Ellis, 1990: Adaptation of chickpea to agroclimatic constraints. In: H. A. van Rheenen and M. C. Saxena (eds), Chickpea in the Nineties, pp. 61—72. ICRISAT, Patancheru, India.
- Wallace, D. H., J. P. Baudoin, J. S. Beaver, D. P. Coyne,
 D. E. Halseth, P. N. Masaya, H. M. Munger, J. R.
 Myers, M. Silbernagel, K. S. Yourstone, and R. W.
 Zobel, 1993: Improving efficiency of breeding for higher crop yield. Theor. Appl. Genet. 86, 27—40.
- Williams, J. H., and N. P. Saxena, 1991: The use of non-destructive measurement and physiological models of yield determination to investigate factors determining differences in seed yield between genotypes of 'desi' chickpeas (*Cicer arietinum*). Ann. App. Biol. 119, 105—112.
- Yadav, S. K., K. Chander, and A. Kumar, 1994: Response of late-sown gram (*Cicer arietinum*) to irrigation and phosphorus. Indian J. Agric. Sci. 64, 24—28