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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 arietum*)†

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Summary

Mathematical models for yield determination are most commonly used to estimate the probable final crop yield in a given circumstance based on measured physiological parameters but the reverse may be done. Simple models of yield determination may be used to estimate the model parameters associated with a measured final product. One can then obtain a better understanding of the physiological attributes of large numbers of genotypes without the labour intensive destructive measurements usual to interpretive physiology. This approach has been demonstrated using 120 chickpea genotypes.

The total mass, seed yield, vegetative (D_v) and reproductive (D_r) durations were observed and the crop growth rates (C) and partitioning to seed (p) estimated. The contribution of variations in C, D_r, and p to the variations in seed yield were analysed by regression techniques. Contrary to expectations based on other crops, the variations in C were an important source of yield variation, rather than variations in p and D_r. Counteracting relationships existed between the parameters of the yield model; C was inversely related to D_r and p. The influence of these features of chickpea yield determination on genotype by environment interactions and maximising yield are discussed.

Key words: *Cicer arietum*, chickpea, modelling, yield determination, crop growth rate, partitioning, methodology

Introduction

In many breeding programmes the analysis of variation of multi-locational trials shows that the genotype by environment interaction component of variance (G × E) greatly exceeds the genotype component, but little is done to understand the basis of this G × E interaction because of the difficulties in characterising genotypes (in sufficient numbers) in terms of their physiological determinants of yield.

Since chickpea is an indeterminate crop the processes determining yield are conveniently analysed against the model proposed for groundnuts by Duncan, McCloud, McGraw & Boote (1978):-

$$Y = C \times D_r \times p \qquad (1)$$

where Y = yield of fruit or seeds
C = Mean *c*rop growth rate
D_r = *D*uration of reproductive growth
p = mean fraction of crop growth rate *p*artitioned to Y.

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This approach has a number of advantages over the analysis of yield determination by harvest index because it introduces a measure of the extent of indeterminate growth (p), and evaluates the processes rather than final result of these. Determination of the values associated with these parameters for a crop has been traditionally carried out using destructive growth analysis to provide an estimate of the crop growth rate, and the pod or seed growth rate (e.g. Witzenberger, Williams & Lenz, 1988). Duncan *et al.* (1978) utilised linear regressions through the linear phases of crop and pod growth and described p as the ratio of these linear regression coefficients. Although Harris, Matthews, Nageswara Rao & Williams (1988) showed that this approach was only an approximation (p changed progressively throughout the reproductive phase) to reality, it provides a value describing partitioning which is an adequate basis for comparing genotypes.

As in most plants the development of chickpea is controlled largely by genetic attributes and two environmental factors, photoperiod and temperature (Summerfield, Virmani, Roberts & Ellis, 1990). The former is of particular significance in triggering the start of reproductive growth (Roberts & Summerfield, 1987), while the rates at which structures are initiated is determined by temperature (Montieth, 1981). Thus, as temperature increases between the base temperature and the optimum the plant accumulates more thermal time (°Cd) per calendar day and develops faster, although in terms of thermal time, the ontogeny occurs at a constant rate (Mohamed, Clark & Ong, 1988). This effect is of particular significance when comparing crop development in contrasting environments. In spring, as temperatures rise and the rate of crop development accelerates; evaporative demand usually increases leading to a more rapid depletion of the available soil moisture.

Chickpeas are best adapted to the cool temperatures of winter in the semi-arid tropics and spring – early summer seasons of the mediterranean regions. 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 yields of chickpea in any environment (Saxena, 1984).

In this paper we demonstrate that simple non-destructive measurements of plant attributes can be exploited, in combination with simple models, to provide valuable information concerning the functioning of genotypes within a given environment.

Materials and Methods

Chickpea genotypes and cultivation

One hundred and twenty "desi" chickpea genotypes arising from six crosses between cvs Gaurava and Pant G114, were used. These were sown at Hisar (29°N 76°E : altitude 221 m) in north India, on an Entisol (sandy clay loam) with 210 mm available water capacity in the top 1 m. The 120 genotypes were grouped into 12 groups (mainplot) each with 10 genotypes (subplot size 24 m^2) based on the time to first flower. There were three replicates. Sowing was by hand into rows 30 cm apart, at a depth of 5 – 7 cm. Plants were later thinned to leave 10 m^{-1}. To ensure full achievement of genotype potential, pests identified by scouting were controlled by appropriate sprays, and weeds were controlled by hand as necessary.

The mean date at which production of pods commenced was established by observation of the plants on three alternate days each week. The date of maturity was fixed as the time when 90% of the plants in a plot had senesced.

At maturity the plants in each plot were harvested, dried and weighed, and the weights were adjusted for an estimated 10% loss of dry matter leaf by senescence (Saxena, 1984). After threshing seed yields were determined. Both weights were expressed on a unit area basis.

For each genotype, the time taken for the the pre-podding and podding phases was converted to thermal time using temperature observations in the meteorological site of Hisar University. As the base temperature (t_b) was assumed to be 0 °C, the equation used was:-

$$°\mathrm{Cd} = \frac{(t_{max} - t_{min})}{2} \qquad (2)$$

The crop growth rate and partitioning coefficient of each genotype were estimated using the equations:

$$C = (V + Y) / (D_v + D_r) \qquad (3)$$
$$p = (Y / D_r) / C \qquad (4)$$

where: V = Total vegetative mass (adjusted for leaf shed)
Y = Seed mass.
D_r = Duration of growth after the start of podding °Cd
D_v = Duration from sowing to start of podding in °Cd.

Additionally the mean maximum temperatures for the 10 days prior to maturity were computed for each genotype, these being termed the 'end temperature'.

Results

There was wide variation amongst the genotypes for total biomass, seed yield and all three determinants of yield (Table 1). The range in p (0.91 to 0.40) was approximately the same observed in the course of varietal improvement in the Florida groundnut breeding program

Table 1. *Mean yield, total shoot mass, D_r, D_v, C, and p for 120 chickpea genotypes*

	Mean	S.E.	Range
Total dry matter (kg ha^{-1})	3914	1045	2157 -6990
Seed yield (kg ha^{-1})	1369	247	833 -2187
D_v (°Cd)	1024	175	792 -1430
D_r (°Cd)	1257	117	999 -1508
C (kg ha^{-1} °Cd)	1.70	0.393	0.98-2.89
p	0.66	0.104	0.42-0.91

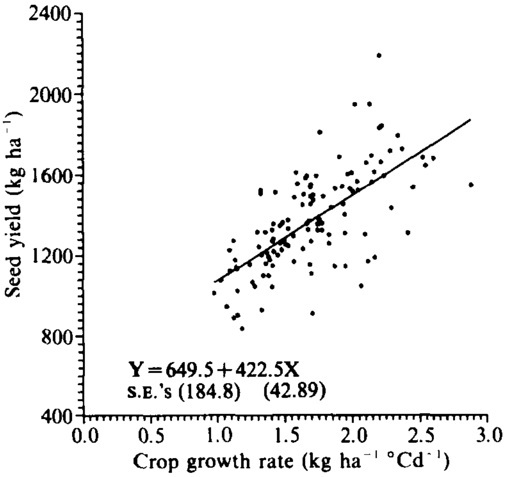

Fig. 1. The relation of seed yield with crop growth rate across 120 chickpea genotypes.

(Duncan *et al.*, 1978). The highest yielding genotype (ICC 50197) had the highest absolute partition coefficient (0.91), and above average values of vegetative duration (1310 °Cd) and C (2.21 kg ha^{-1} °Cd).

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

These differed substantially from those observed for groundnuts by Duncan *et al.* (1978) in that C here was the major source of yield variation accounting for 47% of the variation about the mean (Fig. 1); while p was not directly related ($R = 0.11$) (Fig. 2) to the final yield. There was no direct association with D_r (Fig. 3) despite the considerable range amongst genotypes for these parameters.

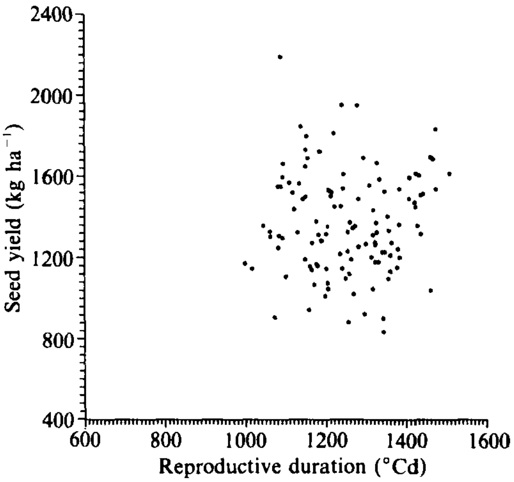

Fig. 2. The seed yield achieved by 120 chickpea genotypes as influenced by the duration of the reproductive phase.

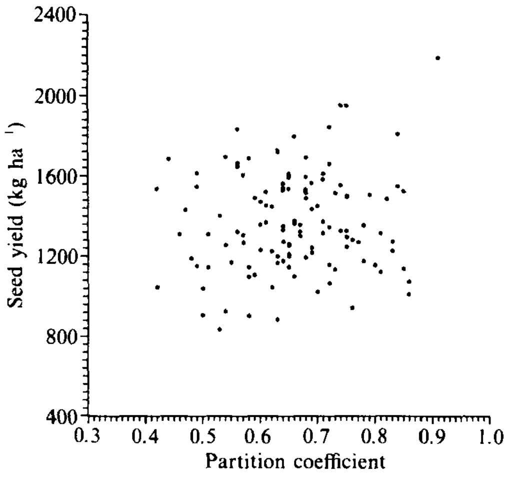

Fig. 3. The relation between seed yield and partitioning for 120 genotypes of chickpea.

While the highest individual yield was associated with high partitioning, this was not essential to achieve high yield; apparently because genotypes with low p values may compensate by having high C, long D_r, or both. The lack of direct relationships between seed yields and p and/or D_r to account for the remaining variation in yield are due to interactions between the components of the equations (Table 2), and these with the environment.

Total dry mass (TDM) was determined by C and crop duration (D), and these were almost equally associated ($R^2 = 0.53$ and $R^2 = 0.48$, respectively) with the variations in TDM between genotypes.

Crop growth rate relationships

C was inversely related ($R^2 = 0.32$) to p (Fig. 4*a*); but positively related to D_v ($R^2 = 0.38$) (Fig. 4*b*). These counteracting effects are understandable, since high p would be likely to limit canopy and root expansion after the start of seed growth, while a long D_v would allow these to take place before pod filling. However, in a multiple regression of seed yield on C with p and D_r they were both significantly and positively correlated with seed yield and in combination with C accounted for 95% of the variation in seed yields.

Table 2. *Correlation matrix between seed yield and growth parameters in 120 chickpea genotypes*

Parameter	SEEDWT	C	D_r	p	D_v	ENDTEMP
SEEDWT	1.000	0.671**	0.039	0.117	0.280*	0.392**
C	0.671**	1.000	−0.214	−0.520**	0.573**	0.558**
D_r	0.039	−0.214	1.000	−0.231	−0.724**	−0.156
P	0.117	−0.520**	−0.231	1.000	−0.081	−0.260*
D_v	0.280*	0.573**	−0.724**	−0.081	1.000	0.741**
ENDTEMP	0.392**	0.558**	−0.156	−0.260*	0.741**	1.000

N = 120. 2-tailed significance: * −0.01, ** −0.001.

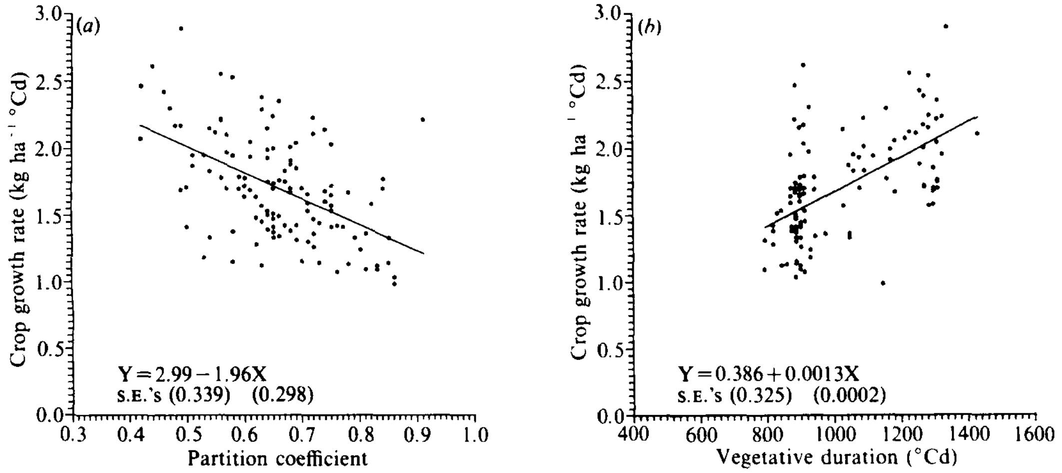

Fig. 4. The relation between partitioning and crop growth rate (*a*) and between the duration of the vegetative phase and crop growth rates (*b*) in 120 chickpea genotypes.

Vegetative and reproductive duration effects

There was considerable variation in D_v; however, as D_v was inversely related to D_r (Fig. 5*a*), (since a long D_v limited the duration of reproductive growth by exposing the variety to high end-temperatures (Fig. 5*b*)) the benefits of a long D_v (high C) were not realised in terms of seed yield because these were associated with short D_r.

The chickpea has an indeterminate growth habit with limited flower production from each node; sustained flowering depends on continued vegetative growth providing new nodes to be initiated. Since seed growth competes with the initiation of further fruiting nodes for the available assimilate, the concept that D_r may be limited by high partitioning was tested by plotting D_r against p (Fig. 6). Although there was a trend for D_r to decrease as p increased, this too was a small effect ($R^2 = 0.05$) within this data set and in this environment, possibly because of the stronger environmental effect on D_r.

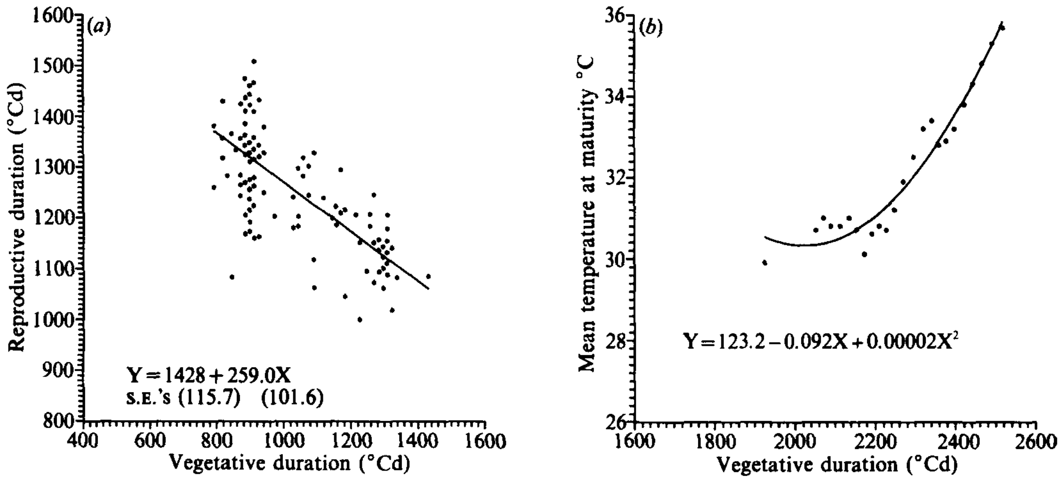

Fig. 5. The relationship between the duration of vegetative and reproductive phases of 120 chickpea genotypes (*a*) and the effect of vegetative duration on the maximum temperatures experienced at the time of maturity (*b*).

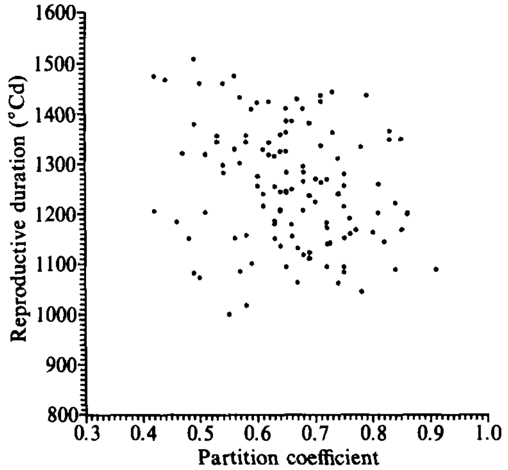

Fig. 6. The relation between partitioning and the duration of the reproductive phase for 120 chickpea genotypes.

Discussion

Chickpea is a grain legume well adapted to the mediterranean and to the cool season in the semi-arid tropics. In these environments the crop is most commonly grown on moisture stored in the soil profile at the time of sowing, although in some circumstances this may be supplemented by rain or irrigation. This dependence on stored soil moisture sets a limit to productivity because the total growth of any crop is closely related to cumulative transpiration (Piara Singh & Virmani, 1990). Providing that the soil profile is fully recharged prior to sowing, the amount of water available for crop growth should be relatively stable across years, but may be more variable across sites because of differences in depth and water holding capacities of the soil.

Several aspects of this analysis have relevance to maximising yields of chickpeas by management and choice of appropriate genotypes. Because of the conservative nature of light use efficiency, a high C most probably reflected high energy interception, which may also be achieved by manipulating plant population density, and/or fertility to improve the C of those varieties with high partitioning. The effects of D_v on C can again be explained by the effect of duration of canopy growth on energy interception, and of p on C by either the competition between canopy and reproductive growth, or due to high partitioning limiting sustained root growth and thereby causing variations in water relations amongst genotypes. While the reasons for the wide variation in C need to be firmly established by more intensive crop physiological research it is possible to point to other management and selection issues deserving of research.

The data demonstrate that high yield can be achieved by contrasting strategies. The first strategy is based on establishing the vegetative frame necessary for resource capture (high C) and a large reproductive node number before flowering, and then the partitioning of most subsequent growth to seeds; as in ICC50197 which produced 2187 kg ha^{-1}, having a C of 2.21 kg ha^{-1} $°Cd^{-1}$, D_r of 1088 °Cd and a p of 0.9. In the second strategy (as exemplified by ICC50735, yield 1831 kg ha^{-1}) genotypes may initiate flowering early resulting in a longer D_r (1474 °Cd) but a lower C (1.61 kg ha^{-1} $°Cd^{-1}$) simultaneously developing their reproductive yield and expanding their vegetative framework, this being associated with (and possibly dependent on) a lower p (0.56).

The first strategy would appear to be most appropriate in many chickpea environments, being that of both the highest yielding genotype in this study (ICC 50197) and that of the widely grown cv. Annigeri (peninsular India) and cv. H208 (northern India) (N. P. Saxena, unpublished data). There are a number of reasons for this. Firstly, reproductive growth is often prevented by cold temperatures (Saxena, 1980). Secondly, where the available water is determined by the available soil depth so that the amount of water stored is relatively constant from year to year it is desirable to establish the canopy and root system to exploit this environment, and then partition most subsequent growth into pods. However, this approach must present some problem when soil moisture (depth across sites, fallow management and seasonal rainfall within sites) varies substantially. Depending on the amount of water available a cultivar may, or not, have the right D_v to maximise C and still leave enough water for the grain to mature. Given this basis for yield determination, the cultivator must expect to (and the breeder does) observe large G × E interactions. In this case no single genotype will provide high yields every year. To consistently maximise seed yields at a given site, a cultivar with the appropriate D_v (to maximise C) needs be chosen from a 'portfolio' of cultivars with different vegetative durations (but with high partitioning), according to the amount of water present at time of planting. Given the conflicting requirements it does not seem possible for a single genotype to overcome this source of year and site yield variation.

However, working on the assumption that differences in C other than those due to D_v can be manipulated by appropriate agronomy (population density), genotype selection within a breeding programme can be refined by taking the observations used in this study, and basing selection on the parameters p and D_v.

The strategy of an early start to reproductive growth, combined with relatively low partitioning to allow the crop to continue vegetative growth, is probably suited to those environments where the chickpea grows vigorously because of good fertility, and renewable (or very favourable) soil water resources. Here the growth potential of the crop is such that the plant may do well to utilise some fraction of its growth for pods from an early stage and thus prevent excessive canopy development. Research to confirm this strategy, and to identify the model coefficients needed to maximise yields for different fertility and water environments is needed. Once this knowledge is achieved, the breeder should have little difficulty identifying genotypes with the partitioning attributes needed to maximise yield for described environments, using the methods described here.

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