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Physiological Basis of Yield Variation in Short-duration Pigeonpea Grown in Different Environments of the Semi-Arid Tropics[1]

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With 1 figure and 4 tables

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Abstract

Five short-duration pigeonpea (*Cajanus cajan* (L.) Millsp.) genotypes were grown at three plant populations in three locations during the 1986 and 1988 rainy seasons, to determine the physiological basis of observed variations in yield. Significant differences were found in seed yield (Y), crop growth rate (C), and the durations of vegetative (Dv) and reproductive (Dr) growth, and partitioning (P). These were attributable to genotypes and their interactions with environments (except for C). Variation in C, Dr, and P together explained 78 % of the observed variation in Y due to different genotypes and environments. Crop growth rate alone contributed about 71 % of the variation in Y, and reached an optimum value of around 6.5 kg ha^{-1} °Cd^{-1}. Crop growth rates increased with the duration of the vegetative period and with plant population. However, a negative relationship between C and P resulted in plant population having little effect on seed yield. The maximum-yielding genotype, ICPH 8 had the highest C and an intermediate P.

Key words: *Cajanus cajan* L. Millsp., pigeonpea, crop growth rates, partitioning, phenology, yield, biomass

Introduction

Pigeonpea (*Cajanus cajan* (L.) Millsp.) is an important grain legume crop grown in tropical and sub-tropical environments. Most traditional varieties are locally adapted. They are highly photoperiod-sensitive (MCPHERSON et al. 1985) and take 25—40 weeks to mature. This results in their exposure to terminal drought stress at lower latitudes, and to frosts at higher latitudes. In recent years, relatively photoperiod-insensitive, short-duration cultivars and hybrids which take only 18—20 weeks to mature have been developed (SINGH et al. 1990). Their earliness enables them to escape terminal droughts and frosts (PATEL and SHARMA 1989). However, with the avoidance of these particular stresses, other environmental factors may assume importance, and limit the adaptation of short-duration genotypes. A coherent analysis of the response of short-duration pigeonpea to diverse environments is therefore necessary.

As crop responses to environment are usually complex, the use of appropriate crop growth models can help to understand such responses. For example, an analytical model of yield proposed by DUNCAN et al. (1978) has been successfully used to understand the basis of grain

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yield variation among genotypes and environments in chickpea (WILLIAMS and SAXENA 1991) and groundnut (WILLIAMS 1992). This model is described by the equation:

$$Y = C \times Dr \times P$$

where Y = seed yield (t ha^{-1}), C = mean crop growth rate (kg ha^{-1} $°Cd^{-1}$), Dr = duration of crop reproductive growth (°Cd), and P = mean fraction of crop growth partitioned to grain yield. The ability of the model to provide an understanding of the process of yield formation in short-duration pigeonpea in three diverse environments was tested.

Materials and Methods

The experiment was conducted at three locations in India; at ICRISAT Center near Hyderabad (18 °N, 72 °E, and 764 mm annual rainfall), the experiment station of the College of Agriculture, Jawaharlal Krishi Vishwa Vidyalaya, Gwalior (26 °N, 78 °E, and 980 mm annual rainfall) and the experiment station of Haryana Agricultural University, Hisar (29 °N, 75 °E and 447 mm annual rainfall), during the 1986 and 1988 rainy seasons. At ICRISAT Center, the experiment was grown on an Alfisol (Udic Rhodustalf) and a Vertisol (Typic Pellustert) in 1986, and only on an Alfisol in 1988. The experiment at Gwalior was conducted on an Inceptisol (Typic Ustochrepts), and at Hisar on an Entisol (Typic Cambrothids). On Alfisol, Vertisol, and Inceptisol, a basal dose of 100 kg ha^{-1} of diammonium phosphate was incorporated prior to sowing. On the Entisol, only single superphosphate at 125 kg ha^{-1} was applied, since previous experience had shown that there is usually little response to a basal dose of nitrogen in this soil. At all locations, trials were laid out in a split-plot design with genotypes as main plots, and plant populations as sub-plots. There were three replications. The genotypes used in 1986 were UPAS 120, ICPL 87, ICPL 151, ICPL 161, ICPH 8 (a hybrid), and *ms* Prabhat (with 50 % male-sterile plants). In 1988, ICPL 151 was replaced with hybrid ICPH 9. Genotypes UPAS 120, ICPL 161, and ICPH 8 are of indeterminate growth habit, and the remaining genotypes are of determinate growth habit (GUPTA and KAPOOR 1991). The three plant populations used in the experiment were 16, 33, and 66 plants m^{-2}. They were achieved by using a 30 cm row spacing. The gross size of each sub-plot was 4.2 × 4.0 m.

At ICRISAT Center in 1986, crops were sown on 17 June on the Alfisol (A 86) and 19 June on the Vertisol (V 86), and on 17 June 1988 on the Alfisol (A 88). At Gwalior, sowings were completed on 3 July 1986 (G 86) and 4 July 1988 (G 88). At Hisar they were sown on 9 July 1986 (H 86) and 29 June 1988 (H 88).

At ICRISAT Center, weeds were controlled by a pre-emergence herbicide containing a mixture of fluchloralin at 0.75 kg a.i. ha^{-1} and prometryn at 2.0 kg a.i. ha^{-1}. Additional hand weedings were done as necessary. At the other locations, weeds were controlled by 2—3 hand weedings. The crop was protected from pod borer (*Helicoverpa armigera*) attack during the reproductive phase by 2—4 sprays of 0.07 % endosulfan (35 EC). The crops grown on Alfisols, Inceptisols, and Entisols were irrigated during the dry periods in 1986. No irrigation was necessary on the Vertisols in 1986, or on any of the soils in 1988 as the crops did not exhibit any drought stress symptoms.

Days to 50 % flowering and 75 % maturity were recorded in all experiments. Samples for growth analysis were taken at about 15-day intervals, with the first sampling at 20 days after sowing (DAS). In 1986, the samples were taken from all the plant populations. In 1988, samples were taken from the 33 plants m^{-2} population treatment, for which an additional area (12 m^2) area was grown adjacent to the area for yield estimation. At maturity, a 6 m^2 area was harvested from each plot for the estimation of total (above-ground) dry matter (TDM) and seed yield. The measured TDM did not include fallen plant parts, which amounted to about 15 % of the total biomass produced (estimated from 18 samples only). Times (days) taken for 50 % flowering and 75 % maturity were converted into thermal time using daily maximum (t_{max}) and minimum temperature (t_{min}) observations for that period. To determine thermal time, the following equation was used, assuming a base temperature for pigeonpea of 10 °C (DE JABRUN et al. 1981):

$$°Cd = \Sigma(((t_{max} + t_{min})/2) - 10)$$

The crop growth rate and partitioning coefficient for each genotype were calculated according to the following equations described by WILLIAMS and SAXENA (1991):

$$C = TDM/(Dv + Dr)$$
$$P = Y/(Dr \times C)$$

where C = crop growth rate, TDM = total above-ground recoverable dry matter, Dv = duration of vegetative growth phase (°Cd), Dr = duration of reproductive growth phase (°Cd), Y = seed yield, and P = partitioning coefficient.

Analysis of variance was performed on Y, C, Dv, Dr, and P using the GENSTAT package. ICPL 151 and ICPH 9 were excluded from the combined analysis as they were not planted in both years. The performance of these two genotypes, however, was not distinctly different from the general trend among genotypes. The relationship of C, Dv, Dr, and P with Y and among themselves was further analysed using regression analysis. The linear relationship between the C estimated from sequential samplings (as slope values of linear regression of dry matter accumulation over time) and that from final biomass was also determined.

Results

At all locations, more rain fell during the 1988 growing season than in 1986 (Table 1). There were considerable differences in both maximum and minimum temperatures among the different locations during the early stages of crop growth, with Hisar being the warmest and ICRISAT Center the coolest (Table 1).

The main effects of environment and genotype were significant for Y and Dv, and the three physiological determinants, C, Dr, and P (Table 2). Genotype × environment interactions were significant for Y, Dv, Dr, and P, but not for C. Only C and P were significantly affected by plant population. The sums of squares accounted for by environments were 41 % for Y, 78 % for C, 62 % for Dv, 55 % for Dr, and 47 % for P. C derived from the TDM at harvest was highly correlated ($r = 0.91^{**}$, $n = 35$) with that derived as a slope of linear regression of C estimated from growth analysis, indicating the reliability of the C derived from TDM at harvest.

The range of variation in TDM, Y, C, Dr, and P was greater among environments than among genotypes (Table 3). Environments caused up to a 4.5 fold difference in C, a similar difference in TDM (4.8 fold), a 2.7 fold difference in P, and a corresponding 2.4 fold difference in Y. There was also a 1.4 fold difference in Dv and a 1.7 fold difference in Dr caused by the environments. Among the genotypes, ICPH 8 had highest Y, TDM, and C, whereas Dv was maximum in ICPL 161, Dr in *ms* Prabhat and P in ICPL 87. Maximum C (5.2 kg ha^{-1} $°Cd^{-1}$) was observed at the highest plant population, whereas P was maximum at the lowest plant population.

Of the three determinants of seed yield, C, Dr, and P, only C had a significant positive association with Y (Table 4). These three determinants together accounted for about 78 % of the variation in grain yield. Crop growth rate alone contributed 71 % of the observed variation in yield. Yield increased with C up to about 6.5 kg ha^{-1} $°Cd^{-1}$, and then declined (Fig. 1a). The 5 data points representing a decline in yield were from the H 86 environment; but a significant positive linear relationship was evident when these points were excluded. Similarly the correlation between P and Y was not significant (Table 4). But when the data points of the H 86 environment were excluded, a significant negative linear relationship was evident (Fig. 1b). Crop growth rate was negatively related to P, but positively associated with Dv (Table 4). Dr had a significant negative relationship with Dv and P a similar relationship with Dr (Table 4).

Discussion

The locations selected for this study include both sub-tropical and tropical latitudes. The weather conditions during the crop growth period varied sufficiently among locations and seasons to cause large differences in yield, and all of its three physiological determinants evaluated. Generally, higher yields were obtained in the sub-tropical environments, which were characterized by high temperatures during the early part of the growing season. The significant positive association of grain yield with thermal time accumulated during the vegetative phase (Dv), and not with that accumulated during the reproductive phase (Dr), suggests that the climatic conditions prevailing in the early part of the growing season may be important to the adaptation of short-duration pigeonpea.

The genotypes included in the study also differed significantly in grain yield. Although the range of variation was not so great as that caused by different environments, the differences were significant at all locations. The hybrid ICPH 8 gave the highest mean yield across the environments, followed by ICPL 87, and *ms* Prabhat was the lowest-yielding genotype. The genotype × environment (G × E) interaction was significant, but it accounted for only a relatively minor (3 %) variation in grain yield. This suggests that the performance of short-duration genotypes need only be evaluated at a few contrasting locations, and that large-scale multilocational testing may not be necessary. However, highly significant G × E interactions have also been reported (KATYAR and SARIAL 1987, JAG SHORAN et al. 1981) and genotypes that are superior in specific environments have been identified. The environments tested in those studies were not so diverse as those in the present study, but

Table 1. Monthly rainfall and mean daily maximum and minimum temperature data for ICRISAT Center(I), Gwalior(G) and Hisar(H) sites during 1986 and 1988 rainy seasons

Environment	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total (Jun—Sep)
				Rainfall (mm)				
I 86	118.2	131.2	230.9	57.3	0.4	36.8	6.3	536.7
G 86	182.1	145.5	101.9	66.7	1.5	0.0	0.0	496.2
H 86	126.9	62.1	126.6	50.0	6.6	0.0	0.0	363.4
I 88	122.1	255.7	273.1	247.0	2.3	0.0	6.7	897.9
G 88	76.5	189.0	272.6	273.1	0.0	0.0	0.0	811.2
H 88	74.3	139.4	143.6	313.6	0.0	0.0	2.3	670.9
				Mean daily maximum/minimum temperature (°C)				
I 86	33.6/23.9	30.9/22.8	28.6/21.7	32.0/22.2	32.6/19.4	29.9/17.7	28.5/15.3	
G 86	40.1/26.9	33.3/24.5	33.5/23.9	34.8/21.9	33.8/16.2	30.5/10.0	23.8/4.5	
H 86	40.2/26.0	35.1/25.2	35.5/24.2	35.1/20.8	32.3/16.1	28.3/10.0	21.2/3.7	
I 88	34.7/24.4	24.4/23.0	28.8/22.6	29.4/22.2	30.4/18.1	29.0/14.2	27.2/13.4	
G 88	39.1/25.0	33.9/24.4	32.4/23.2	34.7/23.2	33.9/-[1]	28.9/-[1]	24.8/5.6	
H 88	39.4/26.7	34.6/26.9	33.8/25.3	33.6/22.6	32.3/15.3	27.6/9.5	22.6/6.6	

[1] Correct data not available due to weather station defect (but can be assumed to be similar to G 86 values)

Table 2. Mean sums of squares from analyses of variance for seed yield (Y), crop growth rates (C), durations of vegetative (Dv) and reproductive (Dr) growth periods, and partitioning (P)

Source	df	Y	C	Dv	Dr	P
Environment (E)	6	8.85***	370.63***	1622018***	781479***	1.14***
Residual	14	0.80	9.59	8412	5059	0.05
Genotype (G)	4	3.31***	14.39***	705759***	169820***	0.20***
G × E	24	0.82**	3.26	111879***	103747***	0.69**
Residual	55	0.36	2.27	7999	8215	0.03
Population (N_p)	2	0.11	5.58***	479	870	0.50***
E × N_p	12	0.08	7.18***	308	750	0.27**
G × N_p	8	0.16*	0.72	181	516	0.29**
E × G × N_p	48	0.87	0.50	251	576	0.14
Residual	134	0.75	0.56	238	463	0.11

*, ** and *** significant at $P < 0.05$, 0.01, and 0.001, respectively

Table 3. Effect of environment, genotype, and plant population on total dry matter (TDM), seed yield (Y), crop growth rates (C), durations of vegetative (Dv) and reproductive (Dr) growth periods, and partitioning (P)

Factor	TDM (t ha^{-1})	Y (t ha^{-1})	Dv (°Cd)	Dr (°Cd)	C (kg ha^{-1} °Cd^{-1})	P
Environment						
V 86	4.44	0.91	1213	761	2.24	0.56
A 86	4.82	1.19	1223	725	2.47	0.68
G 86	10.62	1.87	1419	952	4.48	0.44
H 86	21.26	1.78	1366	703	10.29	0.26
A 88	5.45	1.31	1203	811	2.68	0.60
G 88	7.83	1.42	1515	570	3.76	0.71
H 88	14.27	2.19	1715	584	6.20	0.66
SE	±0.941	±0.133	±13.7	±10.6	±0.461	±0.034
Genotype						
UPAS 170	8.77	1.53	1274	777	4.20	0.54
ICPL 87	9.90	1.69	1427	716	4.53	0.63
ICPL 161	10.83	1.42	1516	661	4.93	0.57
ICPH 8	11.09	1.78	1408	707	5.21	0.58
ms Prabhat	8.47	1.19	1271	786	4.07	0.47
SE	±0.409	±0.075	±11.3	±11.4	±0.190	±0.022
Plant Population m^{-2}						
16	8.37	1.51	1381	728	3.90	0.63
33	9.96	1.56	1377	733	4.65	0.55
66	11.10	1.50	1379	727	5.21	0.50
SE	±0.162	±0.027	±1.5	±2.1	±0.073	±0.010

Table 4. Correlation matrix among seed yield (Y), crop growth rates (C), durations of vegetative (Dv) and reproductive (Dr) growth periods, and partitioning (P)

Dr	−0.650**			
P	0.276	−0.471**		
C	0.388**	−0.211	−0.577*	
Y	0.537**	−0.067	−0.045	0.619**
	Dv	Dr	P	C

the significance of the G × E component also depends on the genotypes tested.

The cause of the variation in grain yield was analysed in terms of its physiological determinants, C, P, and Dr. Only C was significantly related to yield although the effects of environment and genotype were significant for all the three components in this study. The model of DUNCAN et al. (1978) explained a large proportion of the variation in seed yield due to genotype, environment, and their interaction. The model also indicated that changes in C accounted for much more variation in grain yield than changes in P or Dr. In chickpea, changes in C accounted for 47 % of the variation in grain yield (WILLIAMS and SAXENA 1991). By contrast, changes in C accounted for a much smaller variation in yield in groundnut than changes in P (DUNCAN et al. 1978, WILLIAMS 1992). In groundnut, yield improvement in genotypes over the years has been attributed to improvement of P (DUNCAN et al. 1978). In the present study, high yield was associated with a high C and low P. A positive association of grain yield with C observed in the present study suggests that genotypes with high C should be selected to improve the yield of short-duration pigeonpea. A particular example is hybrid ICPH 8, which had the highest C and also the highest yield. A highly positive correlation between C measured by sequential sampling, and that estimated from above-ground biomass at maturity could be used to select genotypes with high C, thus obviating the need for cumbersome sequential samplings. Variation in C among genotypes could occur because of the differences in the duration of their vegetative phases, as indicated by a positive correlation between Dv and C. Genotypes with a larger Dv develop more canopy, intercept a greater amount of light, and thus grow faster. A high C could also be the result of higher efficiency of conversion of intercepted radiation to biomass, although it is considered to be a conservative trait (SQUIRE 1990). The extent of genetic variation in this characteristic is not known in pigeonpea, although values ranging between typical of C_3 ($1.3\ g\ MJ^{-1}$) and that of C_4 ($2.2\ g\ MJ^{-1}$) have been quoted in the literature (LAWN and TROEDSON 1990). About 30 % of the genetic variation in radiation use efficiency has been reported in a limited number of groundnut cultivars (MATTHEWS et al. 1988) suggesting the possible existence of similar variation in other legumes.

The very strong effect of environment and plant population on C suggests that it could be manipulated agronomically. For example, sowing time could be advanced to take advantage of warmer growing conditions (to increase Dv) wherever feasible. Summer sowing of short-duration pigeonpea is already being recommended in the irrigated tract of northern India in an attempt to increase grain and fuel wood yield (SINGH et al. 1985). In the present study, C increased with plant population from 16 to 66 plants m^{-2}. However, this did not result in increased yield, due to a proportionate reduction in P. There appeared to be an optimum level of C, beyond which yield tended to decline. This was probably caused by increased mutual shading. This lack of effect of C on yield beyond a certain level could also be attributed to profuse growth preventing adequate insect control. For subtropical environments where C is at high levels by flowering, improvement in P should be given priority.

Genotypes differed significantly for P. This parameter is an indicator of indeterminateness, which increases as P decreases (WILLIAMS 1992). Genotype ICPL 87 that had the highest P is of determinate growth habit. The other determinate genotype, *ms* Prabhat, had the lowest P values. This may be due to inadequate

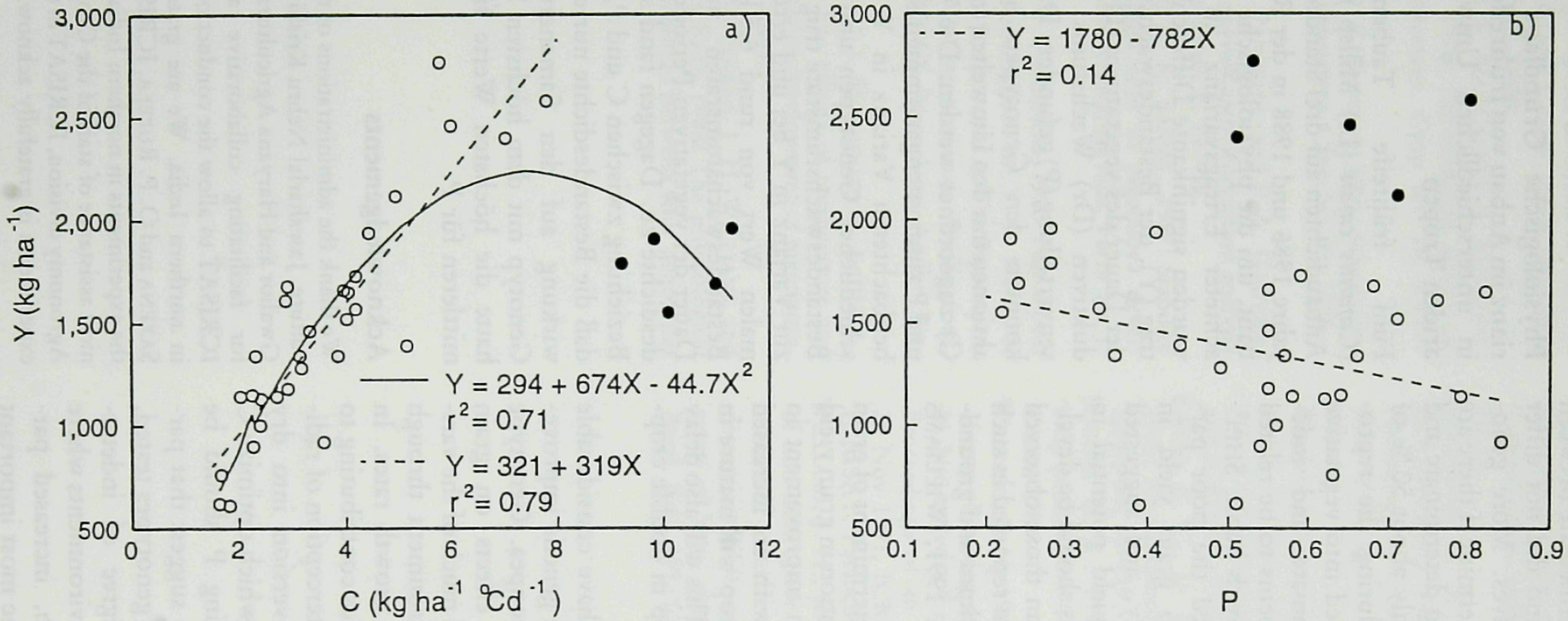

Fig. 1. Relationship of grain yield with crop growth rates (a) and partitioning coefficient (b). Symbols represent observations and the lines are the fitted regressions. Dark symbols represent the data points of an extreme environment (H 86) and the broken lines are the fitted regression after excluding these points from the analysis

cross-fertilization in the male-sterile plants that constituted about 50 % of the population. The three indeterminate genotypes ICPH 8, ICPL 161, and UPAS 120 were intermediate between ICPL 87 and *ms* Prabhat, and did not differ significantly among themselves. More genotypes need to be tested to determine if there are subtle differences in P among determinate and indeterminate genotypes. Only about 50 % of the dry matter produced during the reproductive period was partitioned into vegetative structures in both determinate and indeterminate genotypes. This seems to be related to pigeonpea's perennial growth habit. SHELDRAKE (1984) also attributed the poor partitioning of dry matter to grain yield in pigeonpea to its perenniality, and suggested that in order to improve yield potential in pigeonpea, annual plant types should be developed. Values of P higher than those observed in the present study have been reported in such other annual legumes, as chickpea and groundnut (WILLIAMS and SAXENA 1991, WILLIAMS 1992).

Even though Dr is also a determinant of grain yield, its contribution to variation in grain yield was small. The scope for an improvement in Dr seems limited because with an increased reproductive duration, the crop will mature in increasingly cooler weather. This will also delay planting of a subsequent crop in double cropping systems.

The results of this study have considerable practical implications for the genetic improvement of short-duration pigeonpea. Genotype × environment interaction effects on grain yield are relatively small, and much of the variation is caused by the environment through its influence on mean crop growth rates. In addition to crop characteristics contributing to a high C such as increased interception of radiation and possibly its conversion into dry matter, agronomic practices which optimize C without substantially affecting P should be identified. These results also suggest that partitioning was very low in the genotypes tested, emphasizing their high degree of indeterminateness. In subtropical environments where crop growth rates are high, increased partitioning to grain becomes the most important consideration for yield improvement. Whether genotypes with a determinate growth habit have higher partitioning could not be clearly established in this study, and a larger number of genotypes need to be tested to confirm this.

Zusammenfassung

Physiologische Grundlage der Ertragsvarianz im Anbau von frühreifen Taubenerbsen in unterschiedlichen Umwelten der semiariden Tropen

Fünf frühreife Taubenerbsengenotypen (*Cajanus cajan* (L.) Millsp.) wurden in drei Anbaudichten auf drei Standorten während der Jahre 1986 und 1988 in der Regensaison angebaut, um die physiologische Grundlage beobachteter Ertragsvarianz zu bestimmen. Es wurden signifikante Differenzen im Samenertrag (Y), der Bestandeswachstumsrate (C) und der Dauer des vegetativen (Dv) und des reproduktiven (Dr) Wachstums sowie der Massenverteilung (P) gefunden. Diese Unterschiede konnten den Genotypen und ihren Interaktionen mit den Umwelten (mit Ausnahme für C) zugeordnet werden. Die Varianz in C, Dr und P zusammengenommen erklärten 78 % der beobachteten Varianz in Y als Folge unterschiedlicher Genotypen und Umwelten. Die Bestandeswachstumsrate trug allein etwa 71 % zur Varianz in Y bei und erreichte einen optimalen Wert von rund 6,5 kg/ha/ °Cd. Die Bestandeswachstumsraten nahmen mit der Dauer der vegetativen Periode und der Bestandesdichte zu. Dagegen fand sich eine negative Beziehung zwischen C und P, die dazu führte, daß die Bestandesdichte nur eine geringe Auswirkung auf den Samenertrag hatte. Der Genotyp mit dem höchsten Ertrag, ICPH 8, hatte die höchsten Werte für C und einen mittleren für P.

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