Genotype × environment interaction effects on some physiological yield determinants in cowpea (*Vigna unguiculata* (L.) Walp

K. O. MARFO & F. WALIYAR
(K. O. M.: Savanna Agricultural Research Institute, P. O. Box 52, Nyankpala, Tamale, Ghana; F. W.: International Crops Research Institute, B. P. 320, Bamako, Mali)

SUMMARY

A simple crop physiological model was employed to study the yield basis and environmental effects on 31 cowpea genotypes of early, medium and late maturities. The tests were carried out at four sites in northern Ghana between 1992 and 1994. Genotypic variations observed for pod yields (Y), reproductive duration (RD), crop growth rates (CGR) and partitioning coefficients (*p*) were wide. Pod yields averaged 2032, 2170 and 1983 kg ha^{-1} for the early, medium and the late lines, respectively. The interaction effects of years with genotypes were quite substantial for pod yield and all the other physiological parameters. Partitioning coefficient was more stable than pod yields in the medium and late lines as shown by the non-significant interactions of genotype × location effects. Regression of pod yields and partitioning coefficients with their respective environmental means also showed the latter to be more stable. Plant breeders may, therefore, put selection pressure on *p* when developing cowpea varieties for the Guinea and Sudan savanna agro-ecological zones, because of its relative stability compared with pod or grain yields. Pod yields correlated with *p* in all the maturity groups. CGR correlated better with Y for medium and late lines than the early genotypes. This indicates good possibilities for identifying lines which can produce both haulms for livestocks and pods for human consumption in the medium and late lines.

Original scientific paper. Received 25 Jul 96; revised 23 Jan 97.

RÉSUMÉ

MARFO, K. O. & WALIYAR, F. : *Les effets d'interaction de l' environnement de génotype × sur quelques déterminants de rendements physiologiques en dolique* (Vigna unguiculata *(L.) Walp).* Un simple modèle physiologique culturel était employé pour étudier la base de rendement et les effets environnementaux sur 31 génotypes de dolique des maturités précoces, moyennes et tardives. Les essais se sont déroulés à quatre endroits au nord du Ghana entre 1992 et 1994. Les variations génotypiques observées pour les rendements de cosse (Y), la durée reproductive (RD), les proportions de croissance culturelle (CGR), les coefficients de partition (*p*) étaient étendues. Les rendements de cosse avaient la moyenne 2032, 2170 et 1983 kg ha^{-1} respectivement pour les lignes précoces, moyennes et tardives. Les effets d' interaction des années avec les génotypes étaient substantiels pour le rendement de cosse et autres paramètres physiologiques. Le coefficient de partition était plus stable que les rendements de cosse dans les lignes moyennes et tardives comme montrées par les interactions non-significatives des effets de location de génotype ×. La regression de rendements de cosse et les coefficients de partition avec leurs moyens environnementaux respectifs ont également montré le dernier d' être le plus stable. Les phytogénéticiens peuvent donc, mettre une pression de sélection sur lorsqu' ils développent les variétés de dolique pour les zones agro-écologique de la Guinée et de Soudano-savane, à cause de la stabilité relative comparée avec les rendements de cosse ou de grain. Les rendements de cosse corrélaient avec dans tous les groupes de maturité. Les CGR corrélaient mieux avec Y pour les lignes moyennes et tardives que les génotypes précoces. Ceci indique des bonnes possibilités pour l'identification de lignes qui peuvent produire à la fois, les haulms pour les bétails et les cosses pour la consommation humaine dans les lignes moyennes et tardives.

Introduction

Breeding for yield increase in crop plants is likely to be more successful if the physiological basis of variation in yields and how this is affected by the environment is known. However, investigations on the physiological basis of variation in yields

Ghana Jnl agric. Sci. **30**, 15-21 | Accra: National Science & Technology Press

are rarely done because of the time and expense involved. Plant breeders may carry out these investigations if they are simple and less labour intensive, such as the one developed by Duncan *et al.* (1978). This model makes use of simple agronomic data recorded during plant growth and at harvest. The model states that:

$$Y = RD \times CGR \times p$$

where Y = Pod or fruit yield
RD = Reproductive growth duration
CGR = Mean crop growth rate
p = Ratio of pod growth rate to crop growth rate, i.e. partitioning coefficient.

This model has advantage over yield analysis with harvest index since p measures the extent of indeterminate growth. Additionally, Duncan *et al.* (1978) model evaluates crop and pod growth processes and their output instead of only the output in harvest index.

Greenberg, Williams & Ndunguru (1992) and Ndunguru *et al.* (1992) employed this model to study the differences in yield among some groundnut lines under high temperatures and drought. They attributed the yield differences observed to variation in partitioning coefficient, since p was the only trait which strongly correlated with Y. Ntare & Williams (1993) interpreted the performance of some cowpea genotypes grown during the cool season in the Sahel with this model. In another study on the response of cowpea in inter-crop with millet at different planting dates with phosphorus, Ntare, Williams & Batiano (1993) observed that CGR and p accounted for the variations in grain yields. Williams & Saxena (1991) also identified CGR to be the most important source of grain yield differences in chickpea (*Cicer arietinum*). Duncan *et al.* (1978) attributed differences in groundnut yield mainly to p, since no significant differences were observed among the lines for CGR. The influence of daylength was critically analyzed by Witzenberger, Williams & Lenz (1988) in groundnut by using this non-destructive sampling technique of Duncan *et al.* (1978).

In the present study, early, medium and late maturing cowpea breeding lines were tested at four locations for 3 years in northern Ghana. The aim was to determine the physiological basis of the variation in their yields and how these yield components are influenced by the environment.

Materials and methods

Between 1992 and 1994, 11 early, 12 medium and 10 late maturing cowpea lines were tested in the major ecological zones of northern Ghana. The test locations were Nyankpala in the Guinea savanna, Manga in the Sudan savanna, Wa in the transition between Guinea and Sudan savanna , and Damongo in a transition between Guinea and woodland savanna. Some of these lines were originally developed at the International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria, whilst others were derivatives from heat-tolerant parents bred at the University of California, Riverside, USA. After land preparation by chisel or disc plowing, 45 kg $P_2 0_5$ ha^{-1} as single super phosphate was applied. Seeds were treated with Thiram[R], dust at 5 g.a.i. kg^{-1} seed to prevent seedling mortality. Each plot was made up of four rows, 4 m in length. The rows were 60 cm apart with distance of 20 cm between hills at two plants per hill. The experimental design was randomized complete blocks with four replications. However, in 1994 as a result of inadequate seeds, only three replications were used for the early maturing lines. Weeds were controlled by hand weeding as and when necessary. Insect pests such as pod sucking bugs and borers were controlled by the application of 12.5 g.a.i. ha^{-1} Karate[R] insecticide, a synthetic pyrethroid. Spraying was done on three occasions beginning from floral bud initiation. This was to ensure that any differences observed within the performance of the lines was not attributed to their reactions to insects or diseases.

The number of days from sowing to 50 per cent flowering and full maturity were recorded. At maturity (between 65 and 83 days after planting), plants in the two innermost rows of each plot were harvested. Pod and haulm weights were noted after thorough sun drying for about 3 weeks to a moisture level of about 5 per cent measured with a moisture meter. The model of Duncan *et al.* (1978), which approximates plant growth as a linear function, was used to compute the following parameters:

DFF	=	Number of days from sowing to 50 per cent flowering
DH	=	Number of days from sowing to maturity
RD	=	DH-DFF
Y	=	Pod weight for the two inner harvested rows
H	=	Crop residue weight or haulm weight for the two innner rows including shed leaves on the ground
T	=	Total biomass = Y+H
CGR	=	T/DH in kg ha^{-1} day^{-1}
PGR	=	Pod growth rate in kg ha^{-1} day^{-1} = Y/RD
p	=	PGR/CGR

Pod yields and the physiological parameters were subjected to analysis of variance by using GENSTAT 5 Release 3.1[R]. Correlation analysis was performed between pod yield and other yield components such as RD, CGR and p to determine how they were related. The relative stabilities of the various genotypes were compared by regressing pod yields and partitioning coefficients over their respective environmental indices (Finlay & Wilkinson, 1963).

Results and discussion

Early maturing lines

Genotypic variations were large for pod yields, biomass production, CGR, PGR and p. Pod yields were high, ranging between 1768 and 2265 kg ha^{-1} with an average of 2032 kg ha^{-1}. All the genotypes had partitioning coefficients exceeding 1.0 (Table 1), indicating how efficient they were in diverting photosynthates towards the development of fruits.

The first order (lines × years, lines × locations, and locations × years) and second order (lines × years × locations) interaction effects on pod yields and other components of the model were significant (Table 2). This indicates they require further evaluations before they are released as varieties; or specific lines would have to be recommended for cultivation in specific agro-ecological zones. However, there were a few lines which combined high pod yields with stability in performance across the sites and years of evaluations. They included Val × BB2, a material in pre-release stage in Ghana; and the line, IT 87D-1951 (Table 6). These genotypes had slopes close to 1.0 for both p and Y. A comparison of the stabilities of pod yields and partitioning indicated marked deviations from unity for pod yields than p, emphasizing the relative stability of the latter. Reproductive duration and crop growth rate did not have any direct effects on pod yields (Table 5) which were similar to observations made by Williams & Saxena (1991) in chickpea. Pod yields, however, strongly correlated with partitioning coefficient, indicating the possibility of simultaneously selecting for both traits.

Medium maturing lines

Pod yield in the medium maturing lines averaged 2170 kg ha^{-1}. The amount of photosynthetic assimilates partitioned to the reproductive sinks was higher compared with the photosynthetic assimilates deposited at the reproductive sources for all the lines. This resulted in all the medium lines having p values greater than 1.0 (Table 1).

Strong interaction effects were observed within location× years; lines × years, and location × years × lines for pod yield and most of the traits (Table 3). However, locations did not change genotypic ranking with respect to RD and p. This means one representative test site would be adequate if RD and p were to be the selection criteria. The genotype KV × 396-4-5, a *Striga* resistant line, proved to be not only among the top grain producers but also the most stable (Table 5) with slopes for p and Y very close to 1.0. Partitioning coefficients, in general, appeared to be more stable than pod yields as shown by the deviations of the latter from a slope of 1.0.

TABLE 1

Mean Performance of Eleven Early Cowpea Lines Between 1992 and 1994

Lines/years/locations	*Pod yield (Y) kg ha⁻¹*	*Reproductive duration (RD) in days*	*Total biomass (T) kg ha⁻¹ day⁻¹*	*Crop growth rate (CGR) kg ha⁻¹ day⁻¹*	*Pod growth rate (PGR) kg ha⁻¹ day⁻¹*	*Partitioning coefficient (p)*
Lines			*Early maturing*			
IT 86 D - 2020	2015	20	4676	74.98	100.75	1.34
IT 89 KD - 374	2265	20	5205	83.45	113.25	1.36
Val × BBI	2202	20	4717	76.51	110.10	1.44
IT 86 D - 957	2184	21	4979	80.05	104.00	1.30
Val × BB2	2166	20	4668	76.17	108.30	1.42
Val × BE	1923	20	4730	76.93	96.15	1.25
Bengpla (check)	1852	19	4664	78.97	97.47	1.23
IT 86 D - 879 - 1	1895	20	4682	76.46	94.75	1.24
IT 87 D - 829 - 5	2114	21	4680	74.94	100.67	1.34
IT 87 D - 1951	1974	21	4696	75.36	94.00	1.25
IT 87 D - 611	1768	19	4731	77.54	93.05	1.20
Mean	2032	20	4766	77.40	101.60	1.31
SE	80	0.4	148	2.43	4.9	0.05
CV (per cent)	27	13	21	22	32	25
Lines			*Medium maturing*			
IT 87 S - 1462	2246	24	4592	69.00	93.58	1.36
Brown eye (check)	2399	24	5050	75.18	99.96	1.32
IT 85 D - 3577	2198	22	4926	74.81	99.91	1.34
IT 88 DM - 363	2521	25	5279	77.88	100.84	1.30
IT 86 D - 719	2177	26	4684	69.42	83.73	1.21
IT 86 D - 715	2188	24	4831	72.11	91.17	1.26
KV × 396 - 4 - 5	2244	25	4864	70.82	89.76	1.27
IT 87 D - 1627	2204	23	4782	70.79	95.83	1.35
IT 87 D - 1952	1821	24	4438	65.43	75.88	1.16
IT 87 D - 871	1774	25	4503	64.67	70.96	1.10
Sul 518 - 2	2195	24	4773	70.78	91.46	1.29
IT × 148 - 1	2070	25	4777	70.83	82.80	1.17
Mean	2170	24	4791	70.98	90.42	1.27
SE	82	0.4	146	2.21	3.9	0.04
CV (per cent)	26	12	21	22	29	21
Lines			*Late maturing*			
Sul × 148 - 2 - 7	2091	29	5062	70.78	72.10	1.02
Sumbrisogla	2110	29	4929	69.32	72.76	1.05
KV × - 250 - 57 - 18	1907	28	4805	67.27	68.11	1.01
CR - 06 - 05	2104	29	5185	71.88	72.55	1.01
Sul × 148 - 1	2107	29	5014	68.27	72.66	1.06
KV × 396 - 4 - 15	2099	30	5153	69.17	69.96	1.01
Sawla (check)	1854	30	4811	65.01	61.80	0.95
KV × - 30 - 305 - 39	1850	30	4751	65.53	61.67	0.94
Sul × 148 - 5	1854	29	4724	65.67	63..93	0.97
IT 86 D - 534	1858	28	4654	62.86	66.36	1.06
Mean	1983	29	4909	67.58	68.38	1.01
SE	85	0.6	159	2.36	4.5	0.045
CV (percent)	29	15	22	24	33	29

TABLE 2

ANOVA Table for Pod Yield and Other Physiological Traits of Early Maturing Cowpea Lines, 1992-1994

Source of variation	DF	MS				
		Pod yield (Y)	Reproductive duration (RD)	Crop growth rate (CGR)	Pod growth rate (PGR)	Partitioning coefficient (p)
Reps	3	1101000	4.41	783.6	2265**	0.02
Years	2	9272000**	96.50**	1957.20**	1392.12	3.61**
Locations	3	341100000**	1573.84**	111378.12**	246490.13**	3.01**
Lines	10	12770000**	23.93**	314.70	2945.22**	0.32**
Locations & years	6	125900000**	42.21**	28649.30**	52742.24**	3.62**
Years & lines	20	19430000**	62.99**	934.92**	6002.54**	0.32**
Locations & lines	30	20460000**	23.18**	626.63**	3212.23**	0.24**
Years & locations & lines	60	39600000**	25.09**	769.12**	3480.22**	0.25**
Residual	349 (44+)	107500000	7.25	284.04	1153.12	0.13
Total	483 (44+)					
CV (per cent)		27	13	22	32	25

*, ** Significantly different at 5 and 1 per cent levels of probability, respectively.
\+ Figures in brackets are treated as missing values.

TABLE 3

ANOVA Table for Pod Yield and Other Yield Components in the Medium Cowpea Lines 1992-1994

Source of variation	DF	MS				
		Pod yield (Y)	Reproductive duration (RD)	Crop growth rate (CGR)	Pod growth rate (PGR)	Partitioning coefficient (p)
Reps	3	733900	12.47*	161.92	642.6	0.14
Years	2	14870000**	1033.51**	52878.94**	22343.44**	14.70**
Locations	3	47000000**	1690.82**	11522.52**	75961.55**	5.17**
Lines	11	2089000**	46.12**	690.54**	4623.60**	0.32**
Locations & years	6	57200000	78.04**	29229.31**	74021.02**	3.07**
Years & lines	22	1128000**	21.33**	322.92	2048.82**	0.24**
Locations & lines	33	961100**	9.91	470.82**	2360.23**	0.14
Years & locations & lines	66	535100**	19.12**	279.04	1293.41**	0.15*
Residual	429	323900**	7.8	235.33	713.14	0.07
Total	575					
CV (per cent)		26	12	22	29	21

*,** Significantly different at 5 and 1 per cent levels of probability, respectively.

In the medium lines strong associations were observed between pod yields on one hand; and CGR and p on the other (Table 6). This indicates it is feasible to breed genotypes which can combine high crop residue production for livestocks with high pod yields for human consumption.

Late maturing lines

Variations within the lines for pod yields and all the physiological parameters were high (Table 1). The mean pod yield (1983 kg/ha) and the range of pod yields (1850 to 2110 kg/ha) were lower than the early and medium lines. Pod yield was highly influenced by the combined effects of lines × years, and lines × years × locations (Table 4). This was not so with partitioning coefficient which appeared to be unaffected by environmental effects. The relative stability of *p* is further confirmed when its slopes are compared with those for grain yields in regressions with their environmental means (Table 6). The values for *p* were very close to unity. Highly significant correlations were observed between pod yields with CGR and *p*, with *r* values of 0.880 and 0.715, respectively (Table 5). It is, therefore, feasible to select for "dual purpose", genotypes which combine high biomass with high pod yields to serve as grain for human consumption and foliage for livestock in the late materials.

TABLE 4

ANOVA Table for Pod Yield and Other Physiological Traits in the Late Maturing Cowpea Lines 1992-1994

Source of variation	DF	MS				
		Pod yield (Y)	Reproductive duration (RD)	Crop growth rate (CGR)	Pod growth rate (PGR)	Partitioning coefficient (p)
Reps	3	8406000**	19.04	155.7	2286.8*	0.28
Locations	3	51360000**	156.55**	7342.61**	66799.23**	3.56**
Years	2	12260000**	2299.29**	14403.42**	21194.12**	4.51**
Lines	9	767100**	19.48	381.50	2029.04*	0.15
Locations & years	6	17870000**	292.77**	9011.13**	27492.91**	2.86**
Years & lines	27	397500	31.92*	180.91	530.12	0.08
Locations & lines	18	583400*	27.47	486.52**	1780.40*	0.11
Years & locations & lines	54	593200**	31.45*	377.44*	1734.44*	0.10
Residual	357	347300	19.22	266.83	972.51	0.09
Total	479					
CV (per cent)		29	15	24	33	29

*,** Significantly different at 5 and 1 per cent levels of probability, respectively.

TABLE 5

Correlation Matrix Between Pod Yield and Other Physiological Parameters of Cowpea, 1992-1994

(a) *Early maturing lines*

	Y	RD	CGR	P
Y				
RD	0.536			
CGR	0.312	-0.102		
P	0.793**	0.034	0.167	

(b) *Medium maturing lines*

Y	-0.052			
CGR	0.894**	-0.196		
P	0.644*	-0.689*	0.561	

(c) *Late maturing lines*

Y	-0.064	-		
CGR	0.880**	-0.009	-	
P	0.715*	-0.584	0.602	-

*,** Significantly different at 5 and 1 per cent levels of probability, respectively.

Conclusion

The application of the model of Duncan *et al.* (1978) has assisted in a better understanding of the effects of environment on cowpea in a multilocational test. From the studies it appears placing selection pressure on *p* may be more reliable than on Y or CGR due to the relative stability of *p* as shown by the magnitudes of their significant interactions with years and locations. Stability analysis by regressing pod yields and partitioning coefficient over their environmental means also revealed that partitioning coefficient

TABLE 6

Relative Stabilities of Cowpea Genotypes based on Pod Yield and Partitioning Coefficients regressed over their Respective Environmental Means of Four Locations Between 1992 and 1994

Lines	*Pod yield (slope)*	*Partitioning Coefficient (slope)*
	Early lines	
IT 86D - 2020	2.12	0.18
IT 89KD - 374	0.32	1.29
Val × BB1	0.29	0.82
IT 86D - 957	0.26	1.70
Val × BB2	0.85	1.14
Val × BE	1.32	2.11
Bengpla (Check)	0.04	1.25
IT 86D -879 - 1	0.40	1.24
IT 87D - 829 - 5	0.42	0.99
IT 87D - 1951	1.28	1.08
IT 87D - 611	2.10	0.66
SE	1.16	0.54
	Medium lines	
IT 86D - 719	0.49	1.36
IT 87S - 1462	1.33	0.79
Brown eye (Check)	0.95	0.19
IT 85D - 3577	0.87	0.76
IT 88DM - 363	1.21	0.66
IT 86D - 715	0.12	0.78
KVx 396 - 4 - 5	0.93	1.24
IT 87D - 1627	1.66	0.98
IT 87D - 1952	1.14	0.69
IT 87D - 871	1.84	1.16
Sul 518 - 2	0.77	1.71
IT × 148 - 1	0.98	1.09
SE	0.72	0.46
	Late lines	
Sul × 148 - 2 - 7	0.96	0.83
Sumbrisogla	1.15	1.14
KVx - 250 -57 - 18	0.28	0.47
CR - 06 - 05	1.19	1.56
Sul × 148 - 1	1.84	1.45
KVx 396 - 4 - 15	0.94	0.97
Sawla (Check)	0.49	1.23
KVx - 30 - 305 - 39	1.53	0.72
Sul × 148 - 5	0.98	0.88
IT 86D - 534	0.45	1.26
SE	0.62	0.28

was more stable than grain yields. High pod yields were closely associated with partitioning coefficient in all the maturity groups. Since Y correlated strongly with CGR only in the medium and late lines, it implies that "dual purpose" genes, which are desirable for producing high grains for human consumption and foliage for livestock in a single genetic background, are only common in these two maturity groups.

REFERENCES

Duncan, W. G., McCloud, D. E., McGraw, R. L. & Boote, K. J. (1978) Physiological aspects of peanut yield improvement. *Crop Sci.* **18**, 1015-1020.

Finlay, K. W. & Wilkinson, G. N. (1963) The analysis of adaptation in plant breeding programs. *Aust. J. agric. Res.* **14**, 742-754.

Greenberg, D. C., Williams, J.H. & Ndunguru, B. J. (1992) Differences in yield determining processes of groundnut genotypes in varied drought environments. *Ann. appl. Biol.* **120**, 557-566.

Ndunguru, B. J., Williams, J. H., Stern, R. D. & Ntare, B. R. (1992) Physiological models and agronomic data applied to experimental analysis and interpretation. *Paper presented at the Fifth Regional Groundnut Workshop for Southern Africa. Lilongwe, Malawi, 9-12 March 1992.*

Ntare, B. R. & Williams, J. H. (1993) Selection of cowpea cultivars for cool season production in the Sahel. *Fld Crops Res.* **32**, 27-39.

Ntare, B. R., Williams, J. H. & Batiano, A. (1993) Physiological determinants of cowpea seed yield as affected by phosphorus fertilizer and sowing dates in inter-crop with millet. *Fld Crops Res.* **35**, 151-158.

Williams, J. H. & Saxena., N. P. (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 arietum*). *Ann. appl. Biol.* **119**, 105-112.

Witzenberger, A., Williams, J. H. & Lenz, F. (1988) The influence of daylength on yield determining processes in six groundnut cultivars (*Arachis hypogaea* L.) *Fld Crops Res.* **18**, 89-100.