

Importance of Canopy Attributes in Determining Dry Matter Accumulation of Pigeonpea under Contrasting Moisture Regimes

N. H. Nam, G. V. Subbarao, Y. S. Chauhan, and C. Johansen*

ABSTRACT

Variability in the yield of extra-short-duration (ESD) pigeonpea [*Cajanus cajan* (L.) Huth.] genotypes in drought environments is related to variation in crop growth rate (CGR) and total dry matter (TDM) production. Our investigation was aimed at assessing the importance of canopy attributes in determining the growth of ESD pigeonpea under contrasting moisture regimes. Using two automated rain-out shelters (ROS), six genotypes were grown under well watered conditions or with water deficit imposed from flowering until maturity. Water deficit significantly decreased the cumulative intercepted photosynthetically active radiation (CIR). The relationship between biomass accumulation and CIR was linear and water deficit affected the slope of the relationship (i.e., radiation use efficiency, RUE) ($b = 1.92 \text{ g MJ}^{-1}$ for well watered vs. 1.43 g MJ^{-1} for water deficit). Genotypes differed in RUE under well watered (1.70 to 2.19 g MJ^{-1}) and moisture deficit (1.30 to 1.66 g MJ^{-1}) conditions. Genotypic variation in canopy attributes was significant. Leaf area duration (LAD) significantly correlated with CGR only under well watered conditions. Cumulative intercepted radiation and RUE accounted for nearly 99% of the genotypic variation in CGR under both moisture regimes, of which RUE alone contributed nearly 90%. Variation among genotypes in CIR alone did not explain the differences in dry matter accumulation under either moisture regime. Only RUE explained more than 90% of the genotypic variation in CGR and 70% in TDM under both moisture regimes. The results indicated that RUE is critical in determining pigeonpea productivity under well watered and moisture-deficit regimes.

CROP GROWTH can be considered as the product of incoming solar radiation, the fraction of that intercepted by the crop as determined by the leaf area index

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(LAI), and the efficiency with which the intercepted radiation is used to produce biomass, i.e., RUE. The dry matter productivity of many crops has been closely linked with light interception (LI), and RUE is generally considered constant for a given crop species (Monteith, 1977; Muchow and Sinclair, 1994). Matching canopy size and duration to the seasonal moisture and irradiance patterns either through agronomic or genetic means is one of the main tasks of crop improvement. This enables the production in a target environment to be optimized (Monteith and Elston, 1983). Pigeonpea is an important grain legume in the semiarid tropics. The recently developed ESD pigeonpea genotypes mature in <110 d and have yield potentials similar to short- and medium-duration cultivars when grown under adequate moisture supply (Chauhan et al., 1992; Nam et al., 1993). However, ESD genotypes are poorly adapted to rainfed conditions because their shallow rooting behavior makes them susceptible to drought stress, particularly during flowering and pod-filling, resulting in severe yield losses (Nam et al., 1993).

There is very limited information on canopy development, canopy geometry, and RUE under different moisture environments for ESD pigeonpea. Earlier studies using a large number of genotypes in this maturity class have indicated substantial differences in their dry matter accumulation and yielding abilities under both nonlimiting and moisture-deficit environments (Chauhan et al., 1992; Nam et al., 1993). The limited phenotypic plasticity of the ESD genotypes could severely limit yield potential during moisture deficits. The present investigation was designed to assess the relative contribution of can-

Abbreviations: CGR, crop growth rate; CIR, cumulative intercepted photosynthetically active radiation; DAS, days after sowing; ESD, extra-short-duration; LAD, leaf area duration; LAI, leaf area index; LI, light interception; PAR, photosynthetically active radiation; PM, physiological maturity; ROS, rain-out shelter; RUE, radiation use efficiency; TDM, total dry matter. *,** Significant at the 0.05 and 0.01 probability levels, respectively.

opy attributes such as LAI, canopy extinction coefficient (k), LAD, and RUE in determining dry matter production under contrasting moisture regimes.

MATERIALS AND METHODS

Location

This experiment was conducted on an Alfisol (a clayey-skeletal, mixed iso-hyperthermic Udic Rhodustalf) field at ICRISAT Asia Center, India (17° N, 78° E; 500-m elevation) in the rainy season of 1993 under an automatic ROS which excluded rain from an experimental area of 50 by 25 m. The soil has a maximum plant-available water-holding capacity of ≈ 100 mm to a depth of ≈ 90 cm. A split-plot design with four replications was used. The main plots consisted of two watering regimes (well watered and water deficit imposed from 36 d after sowing [DAS] until maturity by withholding irrigation) and the subplots were ESD pigeonpea genotypes [ICPL 83015 DT (determinate type), ICPL 84023 DT, ICPL 85010 DT, ICPL 88032 IDT (indeterminate type), ICPL 88039 IDT, and ICPL 89002 IDT]. Plants were in the vegetative growth stage at 36 DAS. Each subplot consisted of six rows 4.5 m long spaced at 0.3 m. Irrigated and unirrigated plots were separated by 1 m to prevent seepage between them. All experimental plots were covered by the automatic ROS during rainfall events.

Field Preparation and Cultural Details

The field was surface tilled incorporating a basal dose of 100 kg ha^{-1} $(\text{NH}_4)_2\text{HPO}_4$ (18% N and 20% P) and 60-cm ridges were established. Seeds were treated with thiram (bis [dimethylthiocarbamoyl] disulfide) and metalaxyl (N -[2,6-dimethylphenyl]- N -[methoxyacetyl]-DL-alanine methyl ester) (750 g kg^{-1}) at the rate of 3 g kg^{-1} of seed before sowing to control soil-borne fungal diseases. Sowing was done in shallow furrows on both sides of 60-cm ridges with 30-cm interrow

and 10-cm intrarow spacings. Two seeds per hill were sown and plants were thinned to one per hill at 20 to 25 DAS to give a plant density of 33 plants m^{-2} . A preemergence herbicide mixture containing fluchloralin (N -[2-chloroethyl]-2,6-dinitro- N -propyl-4-[trifluoromethyl] alanine) (450 g kg^{-1}) at 1.5 kg ha^{-1} with prometryn (N,N' -bis [1-methylethyl]-6-methylthio-1,3,5-triazine-2,4-diamine) (500 g kg^{-1}) at 1.5 kg ha^{-1} and paraquat (1,1'-dimethyl-4,4'-bipyridinium ion) (2.5 g kg^{-1}) at 4.0 kg ha^{-1} was applied 1 d after sowing. Three additional hand weedings were done at 20-d intervals. Different pesticides were used including endosulfan (1,4,5,6,7,7-hexachloro-5-norbornene-2,3-dimethanol cyclic sulfite) (350 g kg^{-1}) at 2 kg ha^{-1} or monotoxophos (3-[dimethoxyphosphinyloxy]- N -methyl-*cis*-crotonamide) (360 g kg^{-1}) at 1.0 kg ha^{-1} during the flowering stage and quinalphos (O,O -diethyl- O -2-quinoxalinyloxy phosphorothioate) (250 g kg^{-1}) or methomyl (S -methyl- N -[(methylcarbomoyl)oxy]thioacetimidate) (240 g kg^{-1}) at 2 kg ha^{-1} during the pod-filling stage to control pod borer [*Helicoverpa armigera* (Hübner)] and spotted borer [*Maruca testulalis* (Geyer)]. Metalaxyl (750 g kg^{-1}) at 1.0 to 2.0 kg ha^{-1} was also sprayed twice during the growing period to control *Phytophthora* blight (*Phytophthora dreschleri* Tucker f. sp. *cajani*).

Irrigation and Stress Treatments

After sowing, the field was uniformly irrigated to field capacity using perforated pipes to ensure optimum seed germination and even plant establishment. The automated ROS was activated from 10 DAS until harvest and further water was applied to the main plots by a drip irrigation system at 3- to 5-d intervals, depending on the dryness of the soil surface. The amount of irrigation water applied was equal to pan-evaporation.

Measurements

Meteorological data including maximum and minimum air temperature, and incident solar radiation (wavelength range

Table 1. Weekly mean weather† data for 1993 at ICRISAT, Patancheru, India.

Standard week‡	Rainfall	Evaporation	Temperature		Relative humidity		Wind	Sunshine	Solar radiation
			Max.	Min.	at 0700h	at 1400h			
	mm		°C		%		km h ⁻¹	h	MJ m ⁻² d ⁻¹
22	44	84	38.6	24.4	67	29	15.2	9.2	11.2
23	0	82	38.1	26.1	66	31	11.2	9.4	10.7
24	31	72	34.5	23.9	78	49	20.8	6.1	8.8
25	1	78	35.0	24.1	77	43	24.0	7.2	8.7
26	67	62	34.4	23.6	82	46	17.4	5.9	9.1
27	23	52	32.3	23.8	83	52	13.8	6.0	8.5
28	34	49	30.6	23.1	85	62	21.5	1.8	6.2
29	4	44	32.0	23.0	82	57	12.2	7.1	9.3
30	107	31	29.5	22.0	90	72	12.9	2.5	6.4
31	51	24	28.1	22.4	94	77	15.5	1.4	5.4
32	1	36	29.9	22.4	86	61	13.2	5.0	8.2
33	37	29	29.5	21.7	92	70	12.0	4.2	7.4
34	28	38	29.3	21.9	92	68	11.0	5.1	7.4
35	80	30	29.6	22.1	96	73	5.6	4.0	7.3
36	25	29	28.8	21.6	92	74	9.9	4.0	7.2
37	0	40	31.0	21.5	86	53	8.3	9.1	10.2
38	81	34	30.4	21.6	96	69	6.7	5.8	8.5
39	0	34	30.2	21.8	91	66	8.4	7.8	8.7
40	0	35	31.9	21.1	93	53	5.0	8.0	9.0
41	27	25	29.1	22.4	95	71	8.0	6.1	6.8
42	94	33	29.8	21.2	95	65	6.4	7.4	7.7
43	49	30	30.1	19.1	96	54	3.9	8.9	8.4
44	0	36	29.4	17.0	88	51	5.2	9.1	8.1
45	0	35	29.1	17.6	90	45	6.8	9.1	8.2
46	0	34	29.1	16.5	91	48	4.5	8.4	7.7
47	0	34	29.6	14.8	93	38	4.4	9.5	7.9
48	0	32	28.1	9.9	90	27	4.3	9.4	8.3

† Rainfall and evaporation data are totals and not means.

‡ Standard week 1 = January 1 to January 7.

0.4–3 μm) were recorded daily, and the weekly means for the growing season are given in Table 1. Biomass accumulation was determined by sampling 3 plants in each subplot at 7- to 10-d intervals; the first two plants in a row were left, and the next three plants were used for sampling to minimize border effects. Total dry matter and grain yield were determined at maturity by harvesting 3.6 m² (1.2 by 3.0 m). Plants were cut at the base of the stem, transferred to the laboratory in polyethylene bags and kept in a cold room at 5°C until separation into component plant parts (leaves, stem, pods, and flowers), which was completed on the day of sampling. Total dry matter was determined by drying samples at 70°C in a forced-air oven for 48 h, with subsequent dry weight determination. To determine grain yield, all pods of a plot were picked, and seeds were dried in sunlight and threshed to recover seed containing ≈70 g kg⁻¹ moisture content. Total dry matter and grain yield were calculated on a gram per square meter basis.

Crop growth rate between 38 and 90 DAS was determined by regression analysis of total dry weight against time (Hunt and Parsons, 1981). Coefficients of determination (*r*²) for CGR ranged from 0.61 to 0.98. Using these relationships, the dry matter accumulations for various samplings were estimated, and subsequently used for establishing relationships with other parameters. Canopy photosynthetically active radiation (PAR) interception was measured at midday (1200h) at different growth stages with a line quantum sensor (LI-COR, Inc., Lincoln, NE) and a quantum sensor (LI-COR, Inc.). Two measurements per plot were made, one with interrow placement and another with intrarow placement. The line quantum sensor was placed below the canopy to measure the transmitted light, *I*₀, with *I* being the total radiation reaching the top of the canopy. The output of both the sensors was simultaneously recorded using a polycorder (Omnidata Int., Inc., Logan, UT). Fractional LI *f* was calculated using the following equation,

$$f = (I - I_0)/I \quad [1]$$

Canopy light extinction coefficients (*k*) were determined (based on LAI, and LI from the sequential sampling) according to Monsi and Saeki (1953), with least square regression used to calculate the slope of the relationship between ln(1 - *f*) and LAI. Cumulative intercepted photosynthetically active radiation was calculated by multiplying the daily incoming PAR (MJ m² d⁻¹, calculated by multiplying daily solar

radiation by 0.45) by *f* for each day after sowing. Radiation use efficiency was calculated by regressing dry matter accumulated on CIR and the slopes (*b*) are used as RUE (Kiniry et al., 1989). The experimental data were analyzed using the GENSTAT statistical package (Genstat Manual, 1983). Comparison of regression lines among genotypes was done as described by Snedecor and Cochran (1967).

Leaf area of the harvested plants was determined by using an automatic leaf area meter (Delta-T Devices Limited, Cambridge, England). Leaf area duration at each sampling was calculated by taking the mean leaf area between the two samplings and multiplying it by the number of days between samplings. Total LAD was calculated by summing the LAD of the individual samplings (*n*), viz.:

$$\text{Total LAD} \sum_n [(LAI_{n-1} + LAI_n)/2](t_n - t_{n-1}) \quad [2]$$

where LAI_{*n*} = LAI at sampling time, *t*_{*n*}, and LAI_{*n-1*} = LAI at sampling time, *t*_{*n-1*}.

RESULTS

Canopy Development and Interception of Incident Photosynthetically Active Radiation

Plants reached the 50% flowering stage, and maximum LAI (4.71 and 3.37 in irrigated and drought treatments, respectively) between 50 and 60 DAS. The LAI remained stable until 80 DAS in most of the genotypes under irrigated conditions, except in ICPL 88039 in which LAI declined from 60 DAS (from 5.83 to 3.21). The highest LAI was attained in genotypes ICPL 83015 and ICPL 88039 where it was between 5 and 6 (Table 2). Genotype ICPL 84023 had the lowest LAI under both moisture regimes. Under drought, LAI did not increase from 60 DAS except for ICPL 85010 in which LAI continued to increase until 66 DAS (LAI reached 3.11) before it declined. Leaf area duration, which is a measure of assimilatory capacity, declined significantly (*P* ≤ 0.01) because of moisture deficit. The LAD varied significantly (*P* ≤ 0.01) among genotypes under irrigated and drought treatments (Table 2). There were no clear patterns in LAD among genotypes under either

Table 2. Leaf area duration (LAD), and cumulative intercepted photosynthetically active radiation (PAR) of pigeonpea under contrasting moisture regimes (field experiment conducted in a rain-out shelter in 1993).

Parameter	Genotype						SE ±
	ICPL 83015	ICPL 84023	LCPL 85010	ICPL 88032	ICPL 88039	ICPL 89002	
Total LAD (d) (0–90 d after sowing, DAS)							
Irrigated	278	190	220	230	244	231	9.4
Drought	167	140	132	161	155	163	
LAD during stress (d) (50–90 DAS)							
Irrigated	208	137	159	182	183	167	6.4
Drought	112	93	87	107	105	109	
LAD during flowering to pod fill-initiation (d) (50–70 DAS)							
Irrigated	106	71	84	94	102	92	4.7
Drought	74	57	57	68	61	66	
Cumulative intercepted PAR (MJ m⁻²)							
Irrigated	346	320	345	340	353	355	na†
Drought	300	273	287	314	291	297	
Maximum leaf area index							
Irrigated	5.33	3.81	4.26	4.92	5.83	4.63	na
Drought	4.05	2.92	3.11	3.52	3.66	3.43	

† na = not available.

Table 3. Apparent canopy extinction coefficient (k) determined for pigeonpea genotypes under contrasting watering regimes. Values were derived by regressing fractional light interception [$\ln(1 - f)$] against leaf area index for $0.4 \leq f \leq 0.96$ and are presented with associated standard errors.

Genotype	Canopy k	
	Irrigated	Drought
ICPL 83015	0.59 ± 0.11	0.32 ± 0.08
ICPL 84023	0.41 ± 0.10	0.52 ± 0.09
ICPL 85010	0.62 ± 0.10	0.57 ± 0.10
ICPL 88032	0.65 ± 0.09	0.52 ± 0.11
ICPL 88039	0.57 ± 0.11	0.56 ± 0.12
ICPL 89002	0.56 ± 0.15	0.54 ± 0.11

moisture regime that could be attributed to their determinate or indeterminate growth habit.

Genotypes differed in apparent canopy extinction coefficient (k) under both watering regimes (Table 3). The k generally declined under drought, from 0.61 under irrigation to 0.52 under drought, but was not significantly different. The k values among genotypes ranged from 0.41 to 0.65 under irrigated conditions and from 0.32 to 0.57 under drought. Genotypes differed in the effect of moisture deficit on k . In ICPL 84023, k increased under moisture deficit, whereas it was little affected or decreased in other genotypes (Table 3). Cumulative intercepted PAR was significantly ($P \leq 0.01$) reduced under drought to 86% of its value in the irrigated treatment (Table 2). The CIR ranged from 320 to 355 MJ m⁻² under irrigated conditions and from 273 to 315 (MJ m⁻²) under drought (Table 2).

Crop Growth Rate, Dry Matter Accumulation, and Grain Yield

Crop growth rate (g m⁻² d⁻¹), differed significantly ($P \leq 0.05$) among genotypes under both moisture regimes (Table 4). Genotypes varied in CGR from 10.4 (ICPL 84023) to 14.3 g m⁻² d⁻¹ (ICPL 83015) under irrigation and from 6.6 (ICPL 84023) to 8.9 g m⁻² d⁻¹ (ICPL 89002) under drought conditions. Crop growth rate under irrigation did not correlate with CGR under drought ($r^2 = -0.01$; $n = 6$).

Genotypes differed significantly ($P \leq 0.01$) in their dry matter production at physiological maturity (PM) and at harvest under both water regimes (Table 5). In the drought treatment, about 67% of the dry matter accumulation occurred after 36 DAS (data not shown). In the irrigated treatment, the dry matter accumulated after 36 DAS amounted to 75% of the dry matter produced at PM (data not shown). Grain yield was signifi-

Table 4. Parameters for linear regressions describing the crop growth rate, accumulation of dry matter from 38 to 90 d after sowing (DAS) in pigeonpea genotypes under contrasting moisture regimes.

Genotype	Irrigated		Drought	
	CGR†	r^2	CGR	r^2
	g m ⁻² d ⁻¹		g m ⁻² d ⁻¹	
ICPL 83015	14.34 ± 1.04	0.94**	7.44 ± 1.08	0.79**
ICPL 84023	10.40 ± 0.75	0.94**	6.60 ± 1.46	0.61*
ICPL 85010	11.87 ± 0.20	0.98**	8.40 ± 1.31	0.76**
ICPL 88032	13.66 ± 1.30	0.90**	7.35 ± 1.26	0.72**
ICPL 88039	12.59 ± 1.24	0.90**	7.83 ± 1.39	0.71**
ICPL 89002	11.12 ± 0.80	0.94**	8.90 ± 0.59	0.96**

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

† CGR = Crop growth rate between 38 and 90 DAS.

cantly ($P \leq 0.01$) affected by water deficit. Genotypes differed significantly ($P \leq 0.01$) in their grain yield under both the moisture regimes. The genotype × moisture treatment interaction for grain yield was not significant. The overall relationship of TDM with grain yield at maturity was highly significant and accounted for 90% of the total variation.

Radiation Use Efficiency

Dry matter accumulation was linearly related to CIR under both water regimes (Fig. 1). Radiation use efficiency, the slope of relationship between TDM vs. CIR, was significantly ($P \leq 0.05$) decreased by water deficit (Fig. 1). Genotypes differed significantly ($P \leq 0.01$), ranging from 1.70 to 2.19 g MJ⁻¹ under irrigation and from 1.30 to 1.66 g MJ⁻¹ under drought in RUE under both water regimes (Table 6). Radiation use efficiency of cultivars under irrigation was poorly correlated to RUE under drought ($r^2 = 0.22$; $n = 6$), indicating possible interaction of genotype × environment.

Relationship between Canopy Attributes and Dry Matter Production

Total dry matter at PM was significantly correlated with total LAD (i.e., 0–90 DAS) ($r^2 = 0.90$ ** $;$ $n = 12$). In the irrigated treatment, TDM was strongly correlated with LAD for total LAD ($r^2 = 0.83$ ** $;$ $n = 6$), LAD from flowering to maturity ($r^2 = 0.94$ ** $;$ $n = 6$), and LAD between flowering and pod initiation ($r^2 = 0.83$ ** $;$ $n = 6$). Similarly, LAD was significantly correlated with CGR under irrigated conditions ($r^2 = 0.83$ ** $;$ $n = 6$). However, under drought, there was no significant correlation between LAD and CGR ($r^2 = 0.008$; $n = 6$), or

Table 5. Total dry matter (g m⁻²) at physiological maturity (90 d after sowing, DAS), at final harvest (110 DAS), and grain yield (g m⁻²) in pigeonpea genotypes under contrasting watering regimes.

Genotype	TDM at 90 DAS		TDM at 110 DAS		Grain yield	
	Irrigated	Drought	Irrigated	Drought	Irrigated	Drought
	g m ⁻²					
ICPL 83015	783	491	673	375	225	125
ICPL 84023	601	451	545	334	172	112
ICPL 85010	675	523	581	343	204	137
ICPL 88032	743	507	639	406	211	135
ICPL 88039	720	515	687	380	238	167
ICPL 89002	664	543	557	380	191	130
SE (for interaction) ±		21		20		51

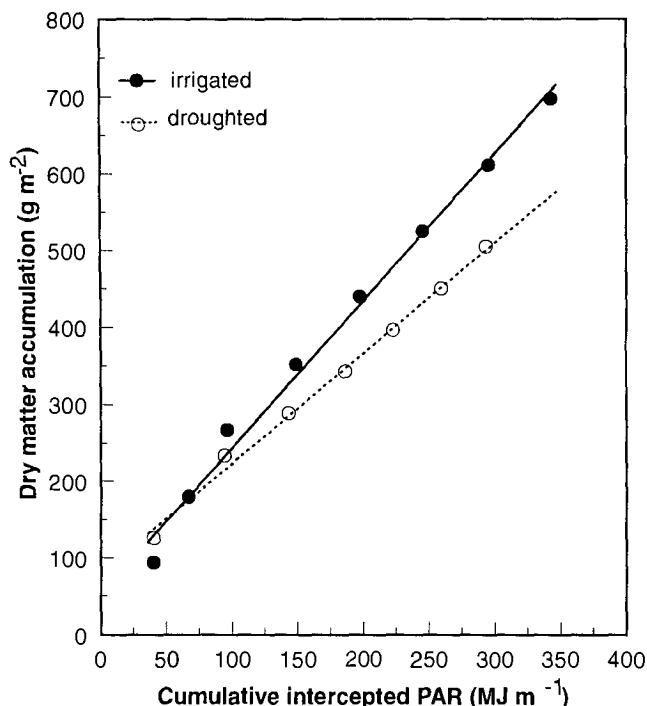


Fig. 1. Relationship between dry matter accumulation and cumulative intercepted photosynthetically active radiation in pigeonpea under contrasting moisture regimes (each point is the mean of six genotypes). The regression equations are (for irrigated) $y = 51.4 + 0.86x$; $r^2 = 0.98$, and (for droughted) $y = 79.1 + 0.65x$; $r^2 = 0.98$.

LAD and TDM ($r^2 = 0.06$; $n = 6$). Total dry matter produced did not correlate with CIR under irrigated ($r^2 = 0.26$; $n = 6$) or drought conditions ($r^2 = 0.23$; $n = 6$).

Only 27% of the variation in RUE can be accounted for by the variation in k ($r^2 = 0.27$; $n = 12$). Radiation use efficiency and k were not significantly correlated under irrigated ($r^2 = 0.30$; $n = 6$) or drought conditions ($r^2 = 0.09$; $n = 6$). Significant correlations were observed between RUE and CGR under irrigated ($r^2 = 0.96^{**}$; $n = 6$) and under drought ($r^2 = 0.92^{**}$; $n = 6$) conditions. Similarly the relationship between TDM and RUE was significant under irrigated ($r^2 = 0.86^{**}$; $n = 6$) and drought ($r^2 = 0.66^*$; $n = 6$) conditions (Fig. 2). Variation in grain yield (either due to genotypic or moisture regime) was associated with variation in RUE ($r^2 = 0.76^*$; $n = 12$). Under well watered conditions, grain yield correlated with TDM at PM ($r^2 = 0.71^*$; $n = 6$), but

Table 6. Radiation use efficiency (RUE, $g MJ^{-1}$ of intercepted photosynthetically active radiation, PAR) of pigeonpea genotypes grown under contrasting watering regimes. Values were derived by regressing shoot dry matter accumulation ($g m^{-2}$) against cumulative intercepted PAR ($MJ m^{-2}$) and are presented with associated standard errors.

Genotype	RUE ($g MJ^{-1}$)	
	Irrigated	Drought
ICPL 83015	2.19 ± 0.08	1.38 ± 0.04
ICPL 84023	1.73 ± 0.07	1.30 ± 0.04
ICPL 85010	1.83 ± 0.07	1.57 ± 0.05
ICPL 88032	2.07 ± 0.09	1.30 ± 0.03
ICPL 88039	1.94 ± 0.07	1.43 ± 0.04
ICPL 89002	1.70 ± 0.06	1.65 ± 0.04

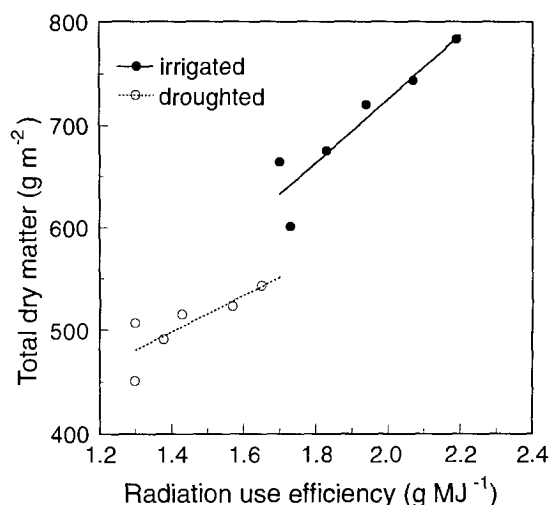


Fig. 2. Relationship between radiation-use-efficiency and total dry matter accumulation at physiological maturity of six pigeonpea genotypes under contrasting moisture regimes. The regression equations are (for irrigated) $y = 106.8 + 309.4x$, $r^2 = 0.86$, and (for droughted) $y = 257.1 + 176.5x$, $r^2 = 0.66$.

not with CGR ($r^2 = 0.61$; $n = 6$) and RUE ($r^2 = 0.50$; $n = 6$). Grain yield under drought did not correlate with TDM (at PM) ($r^2 = 0.29$; $n = 6$), CGR ($r^2 = 0.13$; $n = 6$), or RUE ($r^2 = 0.04$; $n = 6$).

Combination of Canopy Attributes and Total Dry Matter Production

Forward stepwise multiple regression of CGR and TDM on the canopy attributes (CIR, RUE, and LAD) indicated that nearly 99% of the variation in CGR under irrigated conditions was best explained by RUE, CIR, and LAD. All three canopy attributes had a significant effect on CGR under irrigation (Table 7). However, RUE alone accounted for 87% of the variation. Under drought, RUE contributed 95% of the variation in

Table 7. Forward stepwise multiple regressions of cumulative intercepted photosynthetically active radiation, radiation use efficiency, and leaf area duration to crop growth rate and dry matter production under contrasting watering regimes in pigeonpea genotypes ($n = 6$).

Variable added	Model R^2
CGR under irrigation	
CIR	0.117
CIR + RUE	0.987**†
CIR + RUE + LAD	0.997**
CGR under drought	
CIR	0.049
CIR + RUE	0.994**
Pooled CGR (irrigated + drought)	
CIR	0.741**
CIR + RUE	0.993**
TDM under irrigation	
CIR	0.258
CIR + RUE	0.997**
TDM under drought	
CIR	0.228
CIR + RUE	0.943**
Pooled TDM (irrigated + drought)	
CIR	0.803**
CIR + RUE	0.990**

† Contribution of added variable (partial R^2) significant at $P < 0.01$. CIR = cumulative intercepted PAR. RUE = radiation use efficiency. LAD = leaf area duration (0–90 DAS).

CGR, and by including CIR, the predictability improved to 99% of variation in CGR (Table 7). Radiation use efficiency accounted for 73% of the variation in TDM (at PM) under irrigation, and predictability increased to 99% of variation among genotypes by including CIR (Table 7). Under drought, RUE accounted for 71% of the variation in TDM, and predictability increased to 94% by including CIR. Inclusion of LAD did not improve the predictability of TDM production under either moisture regime.

DISCUSSION

Leaf area index, LI, LAD, and RUE are important attributes of the crop canopy. Pigeonpea genotypes varied in their LAI, LAD, CIR, k , and RUE under both moisture regimes. Radiation use efficiency is dependent on canopy attributes such as k , biochemical conversion efficiency, and CO_2 exchange coefficient (Monteith, 1977). Distribution of solar radiation within the canopy is significant because individual leaves do not respond to all levels of solar radiation proportionately (Shibles and Weber, 1966). Thus, arrangement of leaves (concentration and orientation) within the crop canopy, quantified in terms of k has been suggested as an important factor in influencing the distribution of solar radiation over the leaf surfaces within a crop community (Kasana and Monsi, 1964; Saeki, 1960; Donald, 1962). Variation in RUE can be attributed to canopy characteristics like k . However, in pigeonpea, variation in k , due to genotypic or soil-water status, accounted for only 27% of the variation in RUE under well watered conditions, and only 9% under water deficits. Physiological mechanisms such as osmotic adjustment have been reported to play a critical role in the maintenance of better plant water status and in maintaining photosynthetic rate under low leaf water potentials. These mechanisms may contribute to improved RUE under water deficits (Flower and Ludlow, 1987).

Dry matter accumulation is a function of LI and RUE. It is generally believed that most of the variation in CGR, and thus dry matter accumulation, is attained through variation in LI. This suggests that RUE is a constant feature in many crops (Gallagher and Biscoe, 1978; Gifford et al., 1984; Green, 1987; Jones and Kiniry, 1986). The variation in CIR in this study could not explain the genotypic differences in dry matter production ($r^2 = 0.26$; $r^2 = 0.23$; $n = 6$; ns) under either moisture regime, thereby indicating the importance of RUE in dry matter accumulation. Thus, selecting for RUE is likely to have a greater impact on biomass production than selecting for higher LAD, particularly under water-deficit environments. This is further indicated by the lack of significant correlation between LAD and biomass production under water deficit ($r^2 = 0.06$; $n = 6$).

Radiation use efficiency values obtained from this study were similar to the values reported for pigeonpea and for other legumes such as mungbean [*Vigna radiata* (L.) Wilczek var. *radiata*], cowpea [*Vigna unguiculata* (L.) Walp. subsp. *unguiculata*], groundnut (*Arachis hypogaea* L.), and soybean [*Glycine max* (L.) Merr.] (Pallas

and Stansell, 1978; Littleton et al., 1979; Nageswara Rao, 1992). Radiation use efficiency was significantly decreased by water deficit, indicating that water deficits affect dry matter accumulation through reducing the RUE, which is in addition to its effect on limiting LAD. Earlier reports indicate that water deficits reduced RUE in pigeonpea and several legumes such as soybean, and groundnut (Shibles and Weber, 1966; Monteith, 1977; Hughes and Keatinge, 1983; Muchow, 1985).

Genotypic variation in RUE has been reported under optimum nutrient and water availability (Kiniry et al., 1989; Squire, 1990; Nageswara Rao, 1992; Goynes et al., 1993). Variation in RUE ranged from 0.75 to 1.20 in groundnut (Nageswara Rao, 1992). Intraspecific variation in RUE (based on multiple location evaluation trials) for sorghum [*Sorghum bicolor* (L.) Moench], ranging from 2.1 to 3.9, and maize (*Zea mays* L.), ranging from 2.4 to 3.2, have been reported (Kiniry et al., 1989). This raises the question of the conservativeness of RUE and the general belief that RUE cannot be improved through genetic means within a crop species. Our results provide evidence that pigeonpea genotypes differ in RUE both under well watered and water-limiting conditions. Under water deficit, it is evident that RUE was the determining factor for the differences in CGR, as it accounted for nearly 71% of the genotypic variation in TDM. Most of the dry matter accumulated (nearly 67% of the total dry matter) after the drought stress was imposed (i.e., 36 DAS) in the water-deficit treatment.

The lack of correlation between RUE under irrigated conditions and RUE under water deficit raises the possibility that the relative sensitivity of a genotype's RUE to moisture deficit can vary. This could possibly be the physiological reason for the large genotype \times environment interactions encountered when genotypes are tested in different moisture and climatic environments (Y.S. Chauhan, D.H. Wallace, C. Johansen, and Laxman Singh, 1996, ICRISAT personal communication). The variation in RUE under nonlimiting water as well as water-limiting environments indicates that RUE can vary among genotypes and is strongly influenced by the soil moisture status. This suggests that RUE could be genetically modified through selection and breeding and may not be as conservative as was initially thought. This opens the way for genetic improvement of RUE, and thus for higher dry matter accumulating ability and, ultimately, higher yields in crops. While the variation in RUE (either due to genotypic or soil moisture regimes) accounted for 76% of the variation in grain yield, RUE does not explain the genotypic variation in grain yield within a moisture regime (i.e., either well watered or water deficit) ($r^2 = 0.50$; 0.040 ; $n = 6$; ns), perhaps because of differences in partitioning factors between genotypes that are independent of RUE. Nevertheless, it is likely that improving RUE will have a positive impact on grain yield under both moisture regimes through its effect on dry matter accumulation.

From our study, it is evident that genotypic variation in RUE could be substantial, of the order of 30% under both watering regimes, in contrast with the general be-

lief of its conservativeness. Further, its possible role in dry matter accumulation was indicated. However, more genotypes with a wide range of canopy attributes should be tested to quantify the magnitude of genetic variation in RUE in pigeonpea. Also, direct selection for RUE may be difficult given the necessity for sequential dry matter sampling and radiation interception measurements on a large number of genotypes. Nevertheless, identification of specific canopy attributes and physiological mechanisms determining RUE would facilitate improving RUE indirectly through selection for these attributes.

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