GENOTYPIC VARIABILITY IN GAS EXCHANGE CHARACTERISTICS AT FOUR CRITICAL GROWTH STAGES OF FIELD-GROWN COWPEA (*Vigna unguiculata* (L.) Walp.)

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ABSTRACT

Genotypic variability in gas exchange characteristics and their relationship to seed yield of twelve field-grown cowpea varieties were evaluated at four critical growth stages. Net photosynthesis, intercellular CO_2 concentration (Ci), stomatal resistance, transpiration efficiency, and chlorophyll meter reading were measured at early vegetative, leaf area development, flowering and seed development stages. In addition, specific leaf weight, total dry weight and seed yield were recorded. Pronounced variations in genotypic ranking of gas exchange characteristics were observed at different growth stages. Except for Ci, genotypic differences in net photosynthesis, stomatal resistance and transpiration efficiency were significant at all growth stages. The net photosynthesis, Ci and transpiration efficiency came to a peak at seed development stage. Mean net photosynthesis of 12 genotypes significantly varied by about 47% from a low of 16 μmol m^2/sec to a high of 23 μmol m^2/sec. Transpiration efficiency ranged from 0.10 to 0.344 μmol CO_2/μmol H_2O. Net photosynthesis and transpiration efficiency of recommended varieties were higher than in others. Genotypes with higher net photosynthesis were found to have high transpiration efficiency, chlorophyll meter reading and low Ci and stomatal resistance. The genotypic range between high to low values of average stomatal resistance was 48%. Net photosynthesis at flowering and at seed development stages was significantly correlated with total dry weight and seed yield. Highly significant correlations were found between net photosynthesis and Ci (r = -0.770), and net photosynthesis, and transpiration efficiency (r = 0.831**) at the seed development stage. No correlation was observed between gas exchange parameters and specific leaf weight.**

KEY WORDS: Cowpea genotypes, Intercellular CO_2 concentration, Net photosynthesis, Stomatal resistance, Transpiration efficiency.

INTRODUCTION

Cowpea is a minor component of subsistence agriculture in South east asia with predominant importance in human nutrition. Over the past century, the genetic yield potential of the majority of field crops, cowpeas being no exception, has improved by raising the harvest index that represents the physiological capacity of the plant to mobilize photosynthates and translate it to organs of economic value (Gupta, 1992). Though harvest index computes the dry matter ratio at harvest, the crop yield is an ultimate outcome of rates, duration and interactions of many processes at all stages of growth and development. Therefore, harvest index may fail to indicate the comparative yields of cultivars that differ in leaf area, photosynthesis, and light interception. Marschner (1986) reported even mineral nutrient content of source leaves as a yield-limiting factor when seeds are dominant sink sites and nutrient uptake by the roots is declining. Therefore, progress in selecting and breeding for genotypes with a high harvest index might be severely restricted because of the limited amount of mineral nutrients that are available for retranslocation from source to sink. These facts clearly indicate that there is a finite limit to the yield increase via increased harvest index and the need to explore alternative physiological traits for yield improvement. Since the amount of leaf area per plant declines in proportion to reproductive growth, genotypes with higher net photosynthetic rates per unit leaf area will be a better breeding strategy in the future.

Although photosynthesis is the key to dry matter production it has, however, been found inconsistently related to economic yield (Elmore, 1980) primarily because partitioning of photosynthates to the economic organs may not proportionately increase with increasing photosynthetic efficiency (Gupta, 1992). Gupta also indicated that improvement in photosynthetic rate can be brought about by identifying genotypes with higher photosynthetic efficiency while assimilate partitioning can be brought about by manipulating the growth functions of organs and the interactions between them. Attention has been focused on the diffusion of CO_2 and H_2O. Photosynthesis can be treated as a diffusive process which is regulated mainly through stomatal conductance or its reciprocal, stomatal resistance (Loomis and Connor, 1992; Wallace *et al.*, 1972). On the other hand, it has been shown that high stomatal resistance in plants would be advantageous in water use efficiency and drought resistance (Ojima and Kawashima, 1968; Wilson, 1972). These traits, particularly because cowpea is a crop grown in water-limited environments, may have greater applicability as selection criteria in varietal development programs.

To our knowledge very little work has been done on the variation in gas exchange characteristics during growth and development of *Vigna* species under field conditions. To evaluate the gas exchange parameters as yield determinants, it is essential to measure these processes at critical growth stages of growth and development. Therefore, the present study was planned with the following objectives. (a) to quantify the rates and magnitudes of photosynthesis and related gas exchange parameters during critical stages of growth under field-grown conditions, (b) to examine whether cowpea genotypes of varying yield levels varied in gas exchange traits, (c) to examine any relationship between gas exchange characteristics, dry matter production and seed yield.

MATERIALS AND METHODS

Twelve cowpea genotypes selected for varying yielding ability were grown under rain fed conditions at the experimental field of Faculty of Agriculture, Kagawa University, Japan. Among the genotypes MI 35, Arlington and Waruni are currently recommended cowpea cultivars in Sri Lanka. Lanka Kadala is a very popular land race and the other genotypes were newly developed varieties of the Field Crops Research and Development Institute (FCRDI), Department of Agriculture, Mahailluppallama, Sri Lanka. Seeds were planted in June 1996, in plots of 1.8 x 1.8 m at the spacing of 30 x 15 cm in a randomized complete block design with four replicates. Plots were fertilized with 16 kg N, 63 kg P_2O_5 and 56 kg K_2O/ha. Net photosynthesis, transpiration, stomatal resistance and intercellular CO_2 concentration of the most distal leaflet of the third or the fourth leaf (most active leaves) on the main stem below the terminal bud were measured in sixteen plants per genotype. Measurements were taken at four critical growth stages namely, early vegetative (20 days after emergence (DAE), leaf area development (30-40 DAE), flowering and seed development stage using a portable photosynthesis system (LI-6200 Primer, LI-COR Inc., USA). Before each measurement CO_2 concentration and relative humidity of the leaf chamber were kept at ≥340 ppm and 65-70%, respectively. The photosynthetic photon flux densities (PPFD) reaching the adaxial leaf surfaces were maintained at ≥1500 μmol /m²/sec for all measurements. During the above measurement, chlorophyll meter reading of the same leaflet (6 points per leaflet) was measured, using portable chlorophyll meter (SPAD 502, Minolta Camera Co. Ltd., Japan). After these measurements were taken at each growth stage, two representative plants from each replicate were sampled and leaf area and dry weights of leaves, stems, pods etc., were recorded. Seed yields were also measured at maturity. Transpiration efficiency and the ratio of carbon gain by photosynthesis to water loss by transpiration was calculated using transpiration and net photosynthesis data generated by LI-COR. Climatic data was obtained from the automated meteorological station of the Kagawa University.

RESULTS

The growing season was characterized by higher precipitation during the initial growth stage and comparatively less precipitation during subsequent growth stages (Fig. 1). Highest mean temperature (28.2°C) was observed during August where maximum and minimum temperatures were 32.3°C and 24.5°C, respectively. Day length was 14.26, 14.02, 13.21 and 12.37 h during June, July, August and September, respectively.

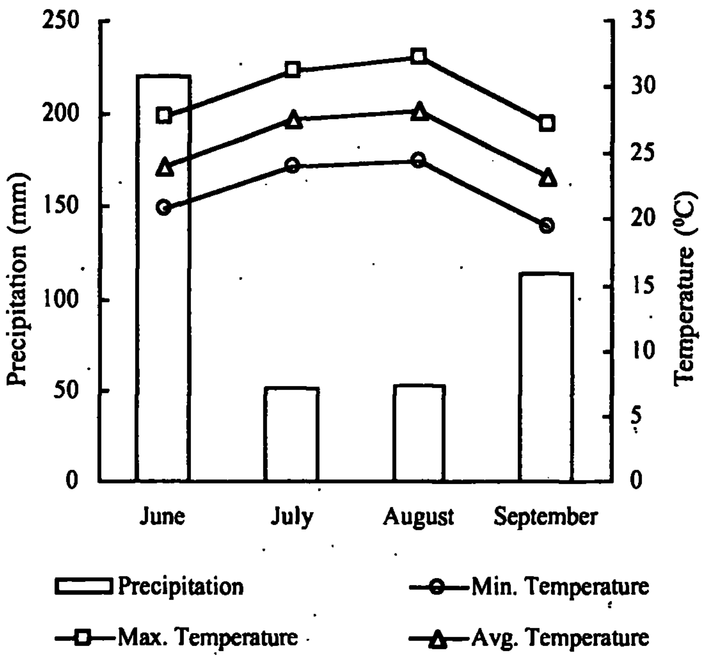

Fig. 1. Some climatic factors observed during the growing season (1996).

Table 1. Some phenological data of twelve cowpea genotypes.

Genotype	Days to Flowering	Maturity
ICP 413	58 (34)*	77 (50)
ICP 432	51 (36)	68 (50)
ICP 434	48 (36)	65 (50)
ICP 454	56 (45)	72 (55)
ICP 461	62 (38)	81 (52)
ICP 464	49 (35)	67 (50)
ICP 481	64 (37)	85 (55)
ICP 482	44 (33)	60 (49)
MI 35	52 (36)	67 (52)
Arlington	55 (34)	70 (55)
Waruni	53 (34)	68 (48)
Lanka Kadala	63 (50)	84 (78)

* Figures in the paranthesis show the observations made at FCRDI, Mahailluppallama (Half yearly Report; 1995/1996 Maha).

Table 1 compares some phenological data of 12 cowpea genotypes observed during the present experimentation with the data observed at FCRDI, Mahailluppallama, Sri Lanka. Regardless of the genotype number of days to flowering and the number of days to maturity seemed to be extended under climatic conditions in Japan. Genotype, ICP 482 took the shortest duration to mature (60 days) whereas ICP 481 took the longest duration (85 days) to mature. Luxurious vegetative growth was observed for all genotypes.

Early vegetative stage

Analysis of variance revealed that the genotypic differences were significant for net photosynthesis, stomatal resistance, transpiration efficiency and SPAD but not for Ci. As shown in Table 2 Lanka Kadala recorded the highest net photosynthesis while ICP 461 recorded the lowest with about a 54% range in rates between the low and the high values. Net photosynthesis of recommended varieties and ICP 434 and ICP 482 was not significantly different from Lanka Kadala. The Ci was in the range of about 2 % between the low to high genotypes. Among the genotypes Arlington recorded the highest Ci (222 ppm). Almost all genotypes had higher stomatal resistance at this growth stage. The lowest stomatal resistance (0.855 cm/sec) were observed for MI 35. The transpiration efficiency was significantly higher for MI 35 and Arlington than the other genotypes tested (Table 3). Lanka Kadala had higher specific leaf weight. ICP 432 recorded the highest SPAD.

Leaf area development stage

In comparison to the early vegetative stage, at this stage genotypes exhibited an increasing trend in all measurements except

Table 2. Net photosynthesis (Np; μmol/m²/sec), Intercellular CO_2 concentration (Ci; ppm) and stomatal resistance (Rs; sec/cm) of twelve cowpea genotypes at four critical stages of growth.

Genotype	Early vegetative			Leaf area development			50% flowering			Seed development		
	Np	Ci	Rs	Np	Ci	Rs	Np	Ci	Rs	Np	Ci	Rs
ICP 413	13.8 bc	218	1.08 cd	15.8 cde	227	0.75 d	18.5 cd	229	0.80 a	28.3 b	240	0.65 bcd
ICP 432	14.4 bc	221	1.20 bc	19.2 ab	225	0.79 cd	21.6 ab	233	0.54 d	28.1 bc	237	0.75 b
ICP 434	15.7 ab	219	1.35 ab	19.6 ab	223	1.72 a	21.4 ab	236	0.78 a	24.3 de	239	1.08 a
ICP 454	13.9 bc	218	1.59 a	17.0 bcd	227	0.76 d	18.5 cd	237	0.69 b	20.4 f	244	0.72 bc
ICP 461	11.6 c	218	1.39 ab	14.0 e	222	1.32 ab	15.4 e	240	0.65 bc	21.1 f	236	0.72 bc
ICP 464	14.1 bc	221	0.93 d	20.6 a	226	0.67 d	22.9 ab	235	0.42 e	25.4 cd	236	0.59 cd
ICP 481	13.0 bc	219	1.35 ab	14.9 de	223	1.24 ab	16.4 de	237	0.58 cd	22.3 ef	240	1.09 a
ICP 482	16.3 ab	219	1.02 cd	20.5 a	223	0.81 cd	21.0 b	234	0.85 a	27.2 bc	239	0.73 bc
MI 35	16.0 ab	221	0.86 d	19.1 ab	223	0.64 d	23.8 a	232	0.53 d	28.9 b	239	0.58 d
Arlington	16.3 ab	222	0.93 d	18.9 ab	224	0.59 d	20.4 bc	231	0.51 d	27.6 bc	234	0.54 d
Waruni	15.8 ab	221	1.18 bc	17.5 bc	225	0.74 d	25.1 b	229	0.61 c	32.6 a	233	0.69 bc
Lanka Kadala	17.8 a	219	1.14 bc	18.0 abc	225	0.73 d	22.2 ab	236	0.62 bc	30.0 b	233	0.68 bc
Grand mean	14.9	220	1.17	17.9	225	0.96	20.3	234	0.63	26.3	238	0.73
F- value (11, 44)	2.84*	ns	8.09**	6.49**	ns	5.51**	9.28**	ns	30.21**	16.63**	ns	16.96**
CV (%)	15.35	7.01	14.86	10.55	5.08	35.49	9.27	5.21	8.30	7.76	6.29	13.49

Figures with the same letters are not significantly different at 0.05 level according to DMRT.

*,**: Significant at 0.05 and 0.01 level, respectively.

ns; Not significant.

Table 3. **Specific leaf weight (SLW; g/m^2), transpiration efficiency (TE; µmol CO_2/µmol H_2O) and chlorophyll meter reading (SPAD; SPAD units) of twelve cowpea genotypes at four critical stages of growth.**

	Early vegetative			Leaf area development			50% flowering			Seed development		
Genotype	SLW	TE	SPAD	SLW	TE	SPAD	SLW	TE	SPAD	SLW	TE	SPAD
CP 413	29.3	0.086 cd	38.9 e	34.3	0.091 cd	47.6 bc	35.2	0.121 ab	51.4 b	35.3	0.132 bcde	53.8 bc
ICP 432	31.8	0.091 bcd	51.1 a	33.9	0.098 bcd	50.4 ab	40.0	0.113 abc	53.3 ab	41.5	0.130 bcdef	56.1 ab
ICP 434	31.3	0.095 bcd	48.8 ab	31.8	0.095 bcd	49.9 ab	39.0	0.107 bc	52.9 b	39.1	0.127 bcdef	54.4 bc
ICP 454	30.6	0.098 bc	43.9 cd	30.6	0.105 bc	43.7 cd	32.4	0.108 bc	46.8 c	41.4	0.117 f	50.8 de
ICP 461	31.1	0.083 d	41.1 de	34.9	0.095 bcd	42.5 d	35.9	0.105 c	51.8 b	38.5	0.118 ef	47.8 e
ICP 464	26.6	0.099 bc	46.1 bc	31.8	0.094 bcd	47.5 bc	39.4	0.107 bc	51.5 b	40.2	0.125 cdef	54.5 bc
ICP 481	29.6	0.086 cd	42.5 de	30.8	0.091 d	49.9 ab	38.3	0.103 c	52.3 b	42.4	0.121 def	52.7 cd
ICP 482	30.1	0.099 bc	50.3 a	31.0	0.109 b	50.5 ab	34.8	0.112 abc	57.0 a	35.1	0.134 bcd	57.4 a
MI 35	31.8	0.121 a	43.0 cd	32.6	0.127 a	47.3 bc	36.2	0.104 c	49.5 bc	39.8	0.123 def	54.7 bc
Arlington	32.6	0.127 a	45.5 bc	33.2	0.133 a	49.6 ab	34.5	0.114 abc	51.8 b	37.8	0.140 b	50.6 d
Waruni	27.4	0.090 cd	43.2 cd	33.7	0.126 a	49.8 ab	40.6	0.106 c	53.6 ab	42.6	0.162 a	54.5 bc
Lanka Kadala	32.9	0.123 b	48.4 ab	34.9	0.099 bcd	52.8 a	34.6	0.123 a	51.0 bc	45.2	0.139 bc	57.3
Grand mean	30.4	0.098	45.2	33.0	0.102	48.5	33.0	0.110	51.9	36.2	0.131	53.7
F-value (11,44)	-	3.14**	8.28**	-	8.24**	4.58**	-	2.57*	2.92**	-	3.93**	3.59**
CV (%)	-	17.47	6.53	-	11.88	6.37	-	17.31	6.39	-	10.72	3.59

Figures with the same letter are not significantly different at 0.05 level according to DMRT.

*,**: Significant at 0.05 and 0.01 level, respectively.

stomatal resistance. Genotypic differences were highly significant for all measurements. As Table 2 shows most of the recommended varieties recorded a higher net photosynthesis than the others at this growth stage. Net photosynthesis of ICP 482 and ICP 464 were not significantly different from those of the recommended varieties. The range between the low and the high net photosynthesis was about 48%. The net photosynthesis at this stage was 20% higher than that at the early vegetative growth stage. Increased level of Ci was observed for all genotypes while stomatal resistance showed a decreasing trend. Intercellular CO_2 concentration ranged from 222 to 227 ppm (an overall increase of 2% when compared with initial growth stage). However, genotypic difference for Ci was not significant. Range of stomatal resistance was from 0.64 to 1.717 cm/sec and was 22% lower than in the early vegetative growth stage. Arlington recorded the highest transpiration efficiency followed by MI 35 (Table 3). Mean transpiration efficiency of MI 35, Arlington and Waruni were not significantly different. Transpiration efficiency increased by 4% as compared to early vegetative growth stage. Both specific leaf weight and SPAD were higher in Lanka Kadala than in other genotypes.

Flowering stage

This stage was characterized by further increase in the levels of net photosynthesis (13%), Ci (4%), transpiration efficiency (8%) and SPAD (7%) compared to those at the leaf the area development stage (Tables 2 and 3). Percentage increase of these parameters over the early vegetative growth stage revealed an increase of 36%, and 6% and 12% for net photosynthesis, Ci and transpiration efficiency, respectively. The Ci of all the genotypes failed to produce significant differences. The rates and magnitudes of the increase in Ci differed among genotypes. In comparison to early vegetative growth stage, the increase in net photosynthesis was recorded with the range of 3.88 to 6.02 $\mu mol/m^2/sec$. Net photosynthesis at this stage varied by 62% between the lowest and the highest genotypes. Stomatal resistance at flowering stage decreased by 86% and 52% when compared to that at the early vegetative growth and leaf area development stages, respectively.

Seed development stage

As shown in Tables 2 and 3 most of the measurements reached peak levels at this growth stage. Stomatal resistance increased by about 13% compared to that at the flowering stage. Net photosynthesis of cultivars ranged from 20.4 to 33 $\mu mol/m^2/sec$. This is 77% increase compared that in the early vegetative phase, 47% increase over leaf area development stage and 30% increase over flowering stage. Waruni recorded the highest rates of net photosynthesis, transpiration efficiency, and lowest Ci compared to other genotypes. Mean net photosynthesis of Waruni was significantly different from the other genotypes. Differences in Ci were not significant among genotypes. At this growth stage Ci recorded 20% and 8% increase over vegetative and leaf area development phases respectively. The highest mean stomatal resistance was recorded by ICP 481. It was observed that the specific leaf weight of genotypes increased with time. Both Arlington and Lanka Kadala recorded higher total dry weight than other genotypes (Table 4).

Growth stage means

Means of the gas exchange measurements given in Table 4 shows the superiority of the recommended varieties over the other genotypes. However, physiological

Table 4. Seasonal means of the rate of net photosynthesis (Np; µmol/m²/sec), intercellular CO_2 concentration (Ci; ppm), stomatal resistance (Rs; cm/sec), specific leaf weight (SLW; g/m²), transpiration efficiency (TE; µmol CO_2/µmol H_2O), chlorophyll meter reading (SPAD; SPAD units), total dry weight (TDW; g/m²) and seed yield (Yd; g/m²) of twelve cowpea genotypes.

Genotype	Np	Ci	Rs	TE	SLW	SPAD	TDW	Yd
ICP 413	19.1 bc	229	0.82 bc	0.108	33.5	47.9 def	1033	90.1 b
ICP 432	20.9 ab	229	0.82 bc	0.108	36.8	52.7 ab	965	72.1 c
ICP 434	20.2 ab	229	1.23 a	0.106	35.8	51.5 abc	1140	58.2 d
ICP 454	17.4 cd	232	0.94 b	0.107	33.8	46.3 ef	996	32.5 g
ICP 461	15.5 cd	229	1.02 ab	0.100	35.1	45.8 f	1009	38.6 fg
ICP 464	20.8 ab	229	0.65 c	0.106	34.5	49.9 bcd	980	74.5 c
ICP 481	16.6 cd	229	1.06 ab	0.100	35.3	49.4 bcde	1050	40.6 f
ICP 482	21.2 ab	229	0.85 bc	0.114	32.8	53.8 a	935	68.1 c
MI 35	21.9 ab	229	0.65 c	0.119	35.1	48.6 cdef	1022	100.3 a
Arlington	20.8 ab	228	0.64 c	0.129	34.5	49.4 bcde	1218	88.8 b
Waruni	22.7 a	227	0.81 bc	0.121	36.1	50.3 bcd	1098	86.6 b
Lanka Kadala	22.0 ab	228	0.79 bc	0.121	36.9	52.4 ab	1362	48.8 e
Mean	19.9	229	0.88	0.112	35.4	49.8	1067	66.6
F-value (11, 33)	3.024**	ns	4.60**	ns	ns	5.90**	-	88.62**

Values with the same letters are not significantly different at 0.05 level according to DMRT.
**; Significant at 0.01 level.
ns; Not significant.

characteristics of the genotypes such as ICP 432, ICP 464, ICP 434 and ICP 482 were comparable to those of recommended varieties.. When averaged over the growth stage it was observed that varieties with lower stomatal resistance had higher net photosynthesis and transpiration efficiency. Genotypes, ICP 434 had higher mean stomatal resistance than other genotypes followed by ICP 461 and ICP 481. The lowest stomatal resistance was recorded for MI 35. Arlington had higher transpiration efficiency than others. Genotypic differences in seed yield were highly significant. MI 35 outyielded the others by producing significantly higher yield followed by ICP 413. Genotype, ICP 454 gave the lowest yield.

Correlations of net photosynthesis, total dry weight and seed yield with Ci, stomatal resistance, transpiration efficiency, specific leaf weight and SPAD of twelve cowpea cultivars for individual growth stages and pooled over four growth stages are shown in Table 5. Correlation between net photosynthesis, total dry weight and seed yield were positive. Significant correlation between net photosynthesis, total dry weight and seed yield were found during flowering stage and seed development stage. Pooled correlation for total dry weight (r = 0.697*) and seed yield (r = 0.686*) were found to be significant. Intercellular CO_2 concentration was positively correlated with the net photosynthesis at early vegetative stage and was negatively correlated at flowering (r = -0.580*) and seed development stage (r = -0.770**). When data were pooled over growth stages, Ci produced a significant negative correlation with net photosynthesis (r = -0.599*). Stomatal resistance seemed negatively correlated with all the measured parameters including total dry weight and seed yield. Correlation between net photosynthesis, total dry weight and seed yield with gas exchange parameters was not clear for the leaf area development stage. Net photosynthesis was significantly correlated with SPAD at seed development stage (r = 0.640*) and the overall correlation was also significant (r = 0.679*).

DISCUSSION

The luxurious vegetative growth and the prolonged crop duration observed for the genotypes could be attributed to the climatic conditions that prevailed during the growing season. Both day length and temperature were found (Dow el-medina and Hall, 1986; Huxley and Summerfield, 1974; Lush *et al.*, 1980; Vietor and Musgrave, 1979) to play an important role in determining the reproductive development in cowpea as well as in other grain legumes. Long days and low temperature in Japan may have increased the number of days to flowering. In addition, high moisture availability during initial growth may have caused a longer growing season through a mechanism called developmental plasticity, a facultative response in cowpea (Ludlow and Muchow, 1990).

The reasons for difference in the rate of net photosynthesis are due to interaction among plant factors, such as the leaf age, canopy development, stomatal behaviour, amount and activity of Rubisco and environmental factors i.e., light intensity, temperature, water deficit etc. (Serrano *et al.*, 1990). The low net photosynthesis during early vegetative phase may be attributed to relatively low chlorophyll contents of the leaves (low SPAD) and high stomatal resistance and low Ci (may be due to low stomatal density and activity). Stomatal resistance seemed to be the limiting factor for low net photosynthesis observed in genotypes such as ICP 461 and ICP 481 at the leaf area development stage. However, net photosynthesis, total dry weight or seed yield

Table 5. **Correlation of net photosynthesis (Np), total dry weight (TDW) and seed yield (Yd) with intercellular CO_2 concentration (Ci), stomatal resistance (Rs), transpiration efficiency (TE), specific leaf weight (SLW) and chlorophyll meter reading (SPAD) of twelve cowpea cultivars at four growth stages (n = 12).**

Growth stage		Np	Ci	Rs	TE	SLW	SPAD
I [+]	Np	-	0.355	-0.482	0.753**	0.329	0.477
	TDW	0.492	0.485	-0.534	0.328	-0.306	0.285
	Yd	0.395	0.647*	-0.832**	0.382	-0.144	0.066
II	Np	-	0.097	-0.299	0.035	-0.306	0.471
	TDW	0.476	-0.457	-0.253	0.078	-0.405	0.227
	Yd	0.435	0.074	-0.513	0.573	0.363	0.254
III	Np	-	-0.580*	-0.271	0.114	0.389	0.160
	TDW	0.613 *	-0.188	-0.419	0.300	-0.073	-0.249
	Yd	0.622 *	-0.888**	-0.206	0.153	0.242	0.208
IV	Np	-	-0.770**	-0.102	0.831**	0.107	0.640*
	TDW	0.599 *	-0.674*	-0.336	0.576*	0.206	0.308
	Yd	0.739**	-0.454	-0.542	0.486	-0.365	0.302
ALL	Np	-	-0.599*	-0.560	0.379	0.288	0.679*
	TDW	0.697 *	-0.511	-0.468	0.788**	0.580*	0.574
	Yd	0.686 *	-0.641*	-0.670 *	0.587*	0.200	0.218

[+]: I; Early vegetative stage, II; Leaf area development, III; Flowering stage, IV; Seed development stage.

*, ** : Significant at 0.05 and 0.01 level, respectively.

were not significantly correlated with other gas exchange parameters at this stage. Herridge and Pate (1977) showed that net carbon gain per plant per day in cowpea reached a peak during flowering and seed development stage of the plant. Lush and Rawson (1979) also found that the cowpea lines which had the lowest photosynthetic rates had no flowers or pods. These findings are in agreement with the results of the present study where at seed development, net photosynthesis and other gas exchange parameters came to a peak regardless of the genotype. Compared to early vegetative growth, most of the gas exchange characteristics at the seed development stage showed a remarkable increase. These observations were further confirmed by the significant correlations of net photosynthesis with total dry weight, seed yield, Ci, transpiration efficiency, and at this growth stage. These data suggest that the photosynthetic activity in cowpea is controlled by the sink demand (developing seeds) as observed by many authors for other species like barley (Bicose *et al.*, 1975), corn (Vietor and Musgrave, 1979), soybean (Buttery *et al.*, 1981; Kokubun *et al.*, 1988; Secor *et al.*, 1982; Wells *et al.*, 1982), sunflower and tobbaco (Rawson *et al.*, 1976) and wheat (Ojima and Kawashima, 1968).

The pronounced variation of genotypic ranking in gas exchange parameters observed in this study agree with the findings reported for soybean (Buttery *et al.*, 1981; Kokubun *et al.*, 1988). It is worthy to note that the growth stage can impose a greater effect on the variation of the genotypic ranking or to weaken the differences in gas exchange parameters. Ambiguous correlation between net photosynthesis and leaf traits such as specific leaf weight and chlorophyll content ranging from very low (Secor *et al.*, 1982), inconsistent (Bhagsari *et al.*, 1977; Buttery *et al.*, 1981; Ojima and Kawashima, 1968) and non existence (Watanabe and Tabuchi, 1973) have been reported. Specific leaf weight of our results corresponded to the first case, whereas the results of SPAD corresponded to the second case. However, Ci, transpiration efficiency and SPAD showed significant correlation with net photosynthesis at seed development stage as well as when data was pooled over the growth stages. This indicated that the varietal differences in net photosynthesis might be related more to Ci, transpiration efficiency and SPAD than to the other factors during the reproductive stage. But this observation may not be true for all genotypes. For instance, although net photosynthesis of ICP 434 and Waruni (highest mean net photosynthesis) was not significantly different, stomatal resistance of ICP 434 was significantly higher than that of Waruni. This suggests that the observed higher net photosynthesis of these two genotypes may have been achieved through some other mechanism such as higher photochemical efficiency of the photosynthetic apparatus.

CONCLUSIONS

From the results of this study it can be concluded that the varieties with high rate of net photosynthesis may have high transpiration efficiency, SPAD, lower Ci, stomatal resistance and high seed yield. High net photosynthesis coupled with low stomatal resistance helped produce low Ci at each growth stage. These varieties may have inadvertently been selected for increased net photosynthesis especially during the seed development period while breeding was targeted for increased yield. Although Lanka Kadala showed better performance in gas exchange characteristic, the expression of yield was low due to excessive vegetative growth (higher total dry weight) caused by the environmental factors. The consistently high stomatal resistance recorded by ICP 454, ICP 461, ICP 481 and ICP 434 would be an important trait in water economy and drought resistance as indicated by many other researchers. Among the above genotypes ICP 434 is likely to possess both physiological (high stomatal resistance, yet comparable rates of net photosynthesis) and phenological features (short duration; an essential trait for drought escape) which may complement each other and maintain the balance required for high yield under water-limited environments.

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