Indian natn. Sci. Acad. **B53** No. 5 & 6 pp 535–540 (1987)

Phtosynthetic Efficiency of Agricultural and Natural Populations of *Vigna* Savi

S IGNACIMUTHU* and C R BABU
Department of Botany, University of Delhi, Delhi 110 007

Low yields constitute the major constraint in the productivity of pulse crops. The gene pools of crops' wild relatives are known to possess productivity promoting gene assemblies. With the objective to locate and utilize such gene assemblies as well as to understand the role of natural and artificial selections in moulding yield promoting gene combinations, two agricultural populations (*Vigna mungo* and *V. radiata)* and one natural population (*V. sublobata)* have been evaluated for net leaf assimilation rate, RuBP carboxylase activity, glycolate oxidase activity, malate dehydrogenase activity, specific leaf weight, harvest index and yield.

The results suggest that: (i) the high net leaf assimilation rate and RuBPCase activity in natural populations as compared to agricultural ones, at the vegetative stage, is due to high photosynthetic rate per unit leaf area; (ii) the high net leaf assimilation rate and RuBPCase activity in agricultural populations as compared to the natural ones, at reproductive stage, can be explained in terms of larger sink size; (iii) the natural population is characterized by low activity profiles of glycolate oxidase and malate dehydrogenase; (iv) the SLW and HI in the natural population are low as compared to agricultural populations, but the yield in the former is as high as that of the latter; and (v) there is a positive correlation among net leaf assimilation rate, RuBPCase activity, SLW, HI and yield for natural and agricultural populations. These observations imply that domestication accompanied by directional selection did alter substantially the photosynthetic traits, but natural selection favoured productivity promoting gene assemblies.

Key Words: Photosynthetic efficiency, Agricultural and natural populations, Productivity promoting gene assemblies

Introduction

Plants evolve a multitude of evolutionary strategies in response to environmental stresses. These strategies are end products of gene complexes selected and spread throughout the population by natural selection coupled with evolutionary genetic mechanisms such as genetic drift, stochastic processes and molecular drive (Dover 1982). Consequently, the natural populations of crops' wild relatives possess adaptive strategies which enable them to endure unpredictable spatial and temporal environmental perturbations (Jain 1979, Mooney & Gulnon 1980, Frankel & Brown 1984). For example, the genetic system of a species, under stressed environmental conditions, enables to achieve minimum productivity with optimum level of reproductive efficiency, and at the same time permits maximum productivity with maximum reproductive efficiency under favourable conditions. The C_3–C_4 intermediate photosynthetic strategy is perhaps associated with such adaptive strategies (Peisker 1986). In fact, the limited C_4 photosynthesis in C_3 plants with concomitant reduction in photorespiration rate exemplify the existence of productivity-promoting gene assemblies in wild genetic resources.

Keeping these aspects in view, we have evaluated *Vigna mungo* (L.) Hepper and *V. radiata* (L.) Wilczek, the two major Asian pulse crops and *V. sublobata* (Roxb.) Babu & Sharma, the GP_2 wild race of the pulse crops, with the chief objective of locating the productivity-promoting gene assemblies.

Materials and Methods

Two agricultural populations, *Vigna mungo cv.* T 9 and *V. radiata cv.* PS 16 (obtained from Pulse Research Laboratory, Indian Agricultural Research

Table 1 *Net leaf photosynthetic rate, RuBP Carboxylase, Glycolate oxidase, Malate dehydrogenase, Specific leaf weight, Harvest index and yield in the three species at vegetative (V stage), flowering and early pod development (F stage) and late pod development (P Stage) stages**

	V. sublobata			*V. radiata*			*V. mungo*		
Stage	V	F	P	V	F	P	V	F	P
Net leaf assmilation rate (mg CO_2 dm^{-2} hr^{-1})	5.16 ± 0.35	11.00 ± 0.41	6.95 ± 0.23	3.61 ± 0.23	11.69 ± 0.26	7.06 ± 0.24	2.80 ± 0.42	11.66 ± 0.18	8.40 ± 0.26
RuBP Carboxylase (mg CO_2 dm^{-2} hr^{-1})	1.09 ± 0.05	2.08 ± 0.04	1.76 ± 0.06	1.05 ± 0.04	2.15 ± 0.07	1.52 ± 0.05	0.86 ± 0.03	2.16 ± 0.06	1.63 ± 0.04
Glycolate oxidase (m moles of DCPIP reduced dm^{-2} hr^{-1})	5.31 ± 0.19	8.15 ± 0.26	5.76 ± 0.21	7.15 ± 0.24	8.65 ± 0.22	7.65 ± 0.21	6.99 ± 0.19	9.69 ± 0.26	7.57 ± 0.26
Malate dehydrogenase (moles of NADH formed dm^{-2} hr^{-1})	146.00 ± 6.00	198.00 ± 8.00	124.00 ± 5.00	194.00 ± 9.00	240.00 ± 9.00	128.00 ± 6.00	166.00 ± 8.00	204.00 ± 9.00	92.00 ± 4.00
Specific leaf weight	0.67 ± 0.06	0.72 ± 0.03	0.66 ± 0.03	1.53 ± 0.08	0.97 ± 0.06	0.76 ± 0.05	1.04 ± 0.08	1.02 ± 0.05	0.41 ± 0.06
Harvest index (%)			21.00 ± 2.00			38.00 ± 2.50			39.00 ± 1.50
Yield			21.00 ± 0.88			21.00 ± 1.16			20.00 ± 1.16

*The values are mean of three replicates ± SE
V, Vegetative stage; *F*, Flowering stage; *P*, Pod stage

Institute, New Delhi), and one natural population of *V. sublobata* (sampled from the Palney Hills of the Western Ghats of Tamil Nadu) were evaluated for genetic variability in: (i) Net leaf assimilation rate (NLAR), (ii) RuBP Carboxylase activity (RuBPCase), (iii) Glycolate oxidase activity (GOA) as a measure of photorespiration, (iv) Malate dehydrogenase activity (MDH) as a measure of dark respiration, (v) Specific leaf weight (SLW), (vi) Harvest index (HI), and (vii) Yield. The leaf disc method outlined by Bassham and Calvin (1957) and Joshi and Karadge (1979) was followed with slight modification for the estimation of NLAR (expressed as mg CO_2 fixed $dm^{-2}hr^{-1}$). The method outlined by Wareing et al. (1968) was followed for the estimation of RuBPCase activity (expressed as mg CO_2 fixed $dm^{-2}hr^{-1}$). GOA was determined by Zelitch and Ochoa's (1953) method (expressed as m moles of DCPIP reduced $dm^{-2}hr^{-1}$). MDH was estimated as described by Ochoa (1955) (expressed as moles of NADH formed $dm^{-2}hr^{-1}$). SLW was calculated as the ratio of dry weight of leaf (g) to the leaf area (dm^2) and HI as the ratio of weight of seeds/plant (g) to dry weight of the plant (g). The mean number of pods/plant was taken as a measure of the yield. Except HI and yield, all other traits were evaluated at three stages of growth and development—(i) vegetative, (ii) flowering

Table 2 *'r' values for different character associations involving Net leaf assimilation rate (NLAR), RuBPCase activity, Glycolate oxidase (GOA), Malate dehydrogenase (MDH), Specific leaf weight (SLW), Harvest index (HI) and yield in V. sublobata*

VEGETATIVE STAGE

	NLAR	RuBPCase	GOA	MDH	SLW	HI	Yield
NLAR	—	0.70	−0.98*	−0.95	0.75	0.63	0.78
RuBPCase		—	0.57	−0.46	0.99*	0.99*	0.96*
GOA			—	0.99*	−0.62	−0.51	−0.66
MDH				—	−0.51	−0.39	−0.56
SLW					—	0.97*	0.98*
HI						—	0.98*
Yield							—

FLOWERING AND EARLY POD DEVELOPMENT STAGE

	NLAR	RuBP Case	GOA	MDH	SLW	HI	Yield
NLAR	—	0.63	−0.93	−0.63	0.79	0.97*	0.96*
RuBPCase		—	−0.67	−0.97*	0.98*	0.50	0.65
GOA			—	0.32	−0.53	−0.97*	−0.92
MDH				—	−0.97*	−0.50	−0.65
SLW					—	0.69	0.82
HI						—	0.99*
Yield							—

LATE POD DEVELOPMENT STAGE

	NLAR	RuBP Case	GOA	MDH	SLW	HI	Yield
NLAR	—	0.50	−0.67	−0.78	0.80	0.96*	0.98*
RuBPCase		—	−0.94	−0.92	0.91	0.50	0.65
GOA			—	0.98*	−0.98*	−0.67	−0.79
MDH				—	−0.96*	−0.78	−0.88
SLW					—	0.60	0.80
HI						—	0.97*
Yield							—

*Significant at $P \leq 0.05$

and early pod development, and (iii) late pod development—from the plants grown under uniform environmental conditions of the experimental garden located at St. Joseph's College, Tiruchirapalli.

Results and Discussion

At vegetative stage, the wild relative showed higher NLAR and RuBPCase activity as compared to the cultigens (table 1) which may be attributed to higher rate of photosynthesis per unit leaf area in the wild relative as compared to the cultigens. Similar observations have been reported by Evans (1983). In fact, genotypic differences in photosynthetic rates and RuBPCase activity have been reported in other crop plants (Curtis et al. 1969, Hanson & Yeh 1979, Frey & Moss 1976, Kuo et al. 1980).

The higher photosynthetic rate in the cultigens as compared to the wild relative at reproductive stages (table 1) can be explained in terms of larger sink size in the cultigens (Egli et al. 1976, Peet et al. 1977, Lorimer 1981, Evans 1983, Mc Cree 1983). The GOA and MDH were low in the wild relative as compared to the cultigens (table 1) suggesting that indirect selection for higher photosynthetic rates is accompanied by higher glycolate oxidase activity during domestication and improvement of cultigens. SLW and HI were low

Table 3 *'r' values for different character associations involving Net leaf assimilation rate (NLAR), RuBP Case activity, Glycolate Oxidase (GOA), Malate Dehydrogenase (MDH), Specific leaf weight (SLW), Harvest index (HI) and Yield in V. radiata*

VEGETATIVE STAGE

	NLAR	RuBPCase	GOA	MDH	SLW	HI	Yield
NLAR	—	0.81	−0.82	−0.64	0.84	0.60	0.50
RuBPCase		—	−0.99*	−0.96*	0.97*	0.95*	0.91
GOA			—	0.96*	−0.98*	−0.94	−0.90
MDH				—	−0.95*	−0.97*	−0.98*
SLW					—	0.93	0.88
HI						—	0.98*
Yield							—

FLOWERING AND EARLY POD DEVELOPMENT STAGE

	NLAR	RuBP Case	GOA	MDH	SLW	HI	Yield
NLAR	—	0.85	−0.82	−0.98*	0.83	0.70	0.61
RuBPCase		—	−0.97*	−0.92	0.97*	0.96*	0.93
GOA			—	0.90	−0.99*	−0.98*	−0.95*
MDH				—	−0.92	−0.81	−0.74
SLW					—	0.97*	0.94
HI						—	0.99
Yield							—

LATE POD DEVELOPMENT STAGE

	NLAR	RuBP Case	GOA	MDH	SLW	HI	Yield
NLAR	—	0.79	−0.83	−0.81	0.77	0.98*	0.98*
RuBPCase		—	−0.98*	−0.97*	0.99*	0.74	0.65
GOA			—	0.98*	−0.99*	−0.83	−0.77
MDH				—	−0.99*	−0.82	−0.75
SLW					—	0.77	0.70
HI						—	0.98*
Yield							—

* Significant at $P \leq 0.05$

in natural populations as compared to agricultural populations but the yield was slightly higher in natural populations (table 1). It is well established that leaf characteristics such as leaf area and dry weight are associated with photosynthetic rates, harvest index and yield (Evans & Dunstone 1970, Peet et al. 1977, Evans 1983). In fact, selection for high photosynthetic rates based on SLW has been practiced (Dornhoff & Shibles 1970, Ojima 1974).

There was a positive correlation among net leaf assimilation rate, RuBPCase activity, SLW, HI, and yield; but glycolate oxidase and malate dehydrogenase activities were negatively correlated with the above traits both in natural and agricultural populations. (tables 2–4). Similar observations have been made in many crop plants (Peet et al. 1977, Kuo et al. 1980, Buttery et al. 1981, Wells et al. 1982, Mahon et al. 1983). These observations suggest that: (i) domestication accompanied by directional selection did alter substantially the photosynthetic traits; (ii) natural selection favoured productivity-promoting gene assemblies; and (iii) the yield-promoting gene assemblies of the wild relative can be successfully utilized in the improvement of cultigens.

Table 4 *'r' values for different character associations involving Net leaf assimilation rate (NLAR), RuBC Case activity, Glycolate oxidase (GOA), Malate dehydrogenase (MDH), Specific Leaf weight (SLW), Harvest index (HI) and Yield in V. mungo*

VEGETATIVE STAGE

	NLAR	RuBP Case	GOA	MDH	SLW	HI	Yield
NLAR	—	0.97*	−0.97*	−0.99*	0.92	0.75	0.94
RuBPCase		—	−0.89	−0.97*	0.98*	0.88	0.84
GOA			—	0.97*	−0.82	−0.59	−0.99*
MDH				—	−0.93	−0.76	−0.94
SLW					—	0.94	0.76
HI						—	0.50
Yield							—

FLOWERING AND EARLY POD DEVELOPMENT STAGE

	NLAR	RuBP Case	GOA	MDH	SLW	HI	Yield
NLAR	—	0.90	−0.86	−0.63	0.91	0.79	0.92
RuBPCase		—	−0.57	−0.25	0.66	0.46	0.99*
GOA			—	0.93	−0.98*	−0.98*	−0.60
MDH				—	−0.89	−0.97	−0.29
SLW					—	0.97*	0.69
HI						—	0.50
Yield							—

LATE POD DEVELOPMENT STAGE

	NLAR	RuBP Case	GOA	MDH	SLW	HI	Yield
NLAR	—	0.98*	−0.71	−0.99*	0.75	0.57	0.99*
RuBPCase		—	−0.81	−0.98*	0.80*	0.64	0.98*
GOA			—	0.69	−0.99*	−0.96*	−0.69
MDH				—	−0.69	−0.50	−0.98*
SLW					—	0.97*	0.69
HI						—	0.50
Yield							—

* *Significant at* $P \leq 0.05$

References

Bassham J A and Calvin M 1957 *The Path of Carbon in Photosynthesis* pp 43–44 (New Jersey: Prentice Hall Inc.)

Buttery B R, Buzzell R I and Findlay W I 1981 Relationship among photosynthetic rate, bean yield and other characters in field-grown cultivars of soybean; *Can. J. Pl. Sci.* **61** 191–198

Curtis P E, Ogren W L and Hageman R H 1969 Varietal effects in soybean photosynthesis and photorespiration; *Crop Sci.* **9** 323–327

Dornhoff G M and Shibles R M 1970 Varietal differences in net photosynthesis of soybean leaves; *Crop Sci.* **10** 42–45

Dover G 1982 Molecular drive: a cohesive mode of species evolution; *Nature* **299** 111–116

Egli D B, Gossett R D and Leggett J E 1976 Effect of leaf and pod removal on the distribution of ^{14}C labelled assimilate in soybeans; *Crop Sci.* **16** 791–794

Evans L T 1983 Photosynthetic activity and partitioning; in Chemistry and World Food Supplies: the New Frontiers Chemrawn II pp 621–631 ed. L W Shemilt (New York: Pergamon Press)

—— and Dunstone R L 1970 Some physiological aspects of evolution in wheat; *J. Biol. Sci.* **23** 725–741

Frankel O H and Brown A H D 1984 Plant genetic resources today—a critical appraisal; in *Crop Genetic Resources Conservation and Evalution* pp 249–257 eds J H W Holden and J T Williams (London: George Allen and Unwin)

Frey N M and Moss D N 1976 Variation in RuBPCase activity in barley; *Crop Sci.* **16** 209–213

Hanson W D and Yeh R Y 1979 Genotypic differences in reduction of carbon dioxide rates as associated with assimilate accumulation in soybean leaves; *Crop Sci.* **19** 54–58

Jain S 1979 Polymorphism, plasticity and homeostasis; in *Topics in Plant Population Biology* pp 160–187 eds O T Solbrig, S Jain, G B Johnson and P H Raven (Columbia University Press)

Joshi G V and Karadge B A 1979 Effect of Sodium chloride on photosynthetic $^{14}CO_2$ assimilation in *Portulaca oleracea* L.; *Indian J. exptl. Biol.* **17** 167–170

Kuo C G, Hsu F H, Tsay J S and Park H G 1980 Variation in specific leaf weight and RuBPCase activity in mung bean; *Can. J. Pl. Sci.* **60** 1059–1062

Lorimer G H 1981 The carboxylation and oxygenation of ribulose-1, 5-bisphosphate—the primary events in photosynthesis and photorespiration; *Ann. Rev. Pl. Physiol.* **32** 349–383

Mahon J D, Hobbs S L A and Salminen S O 1983 Characteristics of pea leaves and their relationships to photosynthetic CO_2 exchange in the field; *Can. J. Bot.* **61** 3283–3292

Mc Cree K J 1983 Carbon balance as a function of plant size in sorghum plants; *Crop Sci.* **23** 1173–1177

Mooney H A and Gulnon S L 1980 Environmental and evolutionary constraints on the photosynthetic characteristics of higher plants; in *Topics in Plant Population Biology* pp 316–337 eds O T Solbrig, S Jain, G B Johnson and P H Raven (Columbia University Press)

Ochoa S 1955 Malic dehydrogenase from pig heart; *Methods. Enzymol.* **1** 735–739

Ojima M 1974 Improvement of photosynthetic capacity in soybean variety; *Jap. agric Res.* **8** 6–12

Peet M M, Bravo A, Wallace D H and Ozbun J L 1977 Photosynthesis, stomatal resistance and enzyme activities in relation to yield of field grown dry bean varieties; *Crop Sci.* **17** 287–293

Peisker M 1986 Models of carbon metabolism in C_3-C_4 intermediate plants as applied to the evolution of photosynthesis; *Pl. Cell Environ.* **9** 627–636

Wareing P F, Khalifa M M and Treharne K J 1968 Rate limiting processes in photosynthesis at saturating light intensities; *Nature* **220** 453–457

Wells R, Schulze L L, Ashley D A, Boerma H R and Brown R H 1982 Cultivar differences in canopy apparent photosynthesis and their relationship to seed yield in soybeans; *Crop Sci.* **22** 886–890

Zelitch I and Ochoa S 1953 Oxidation and reduction of glycolic and glyoxylic acids in plants. I. Glycolic acid oxidase; *J. Biol. Chem.* **201** 707–718