Genotype variability in photosynthetic characteristics in finger millet

Desiraju SUBRAHMANYAM*

All India Coordinated Small Millet Improvement Project, G.B. Pant University of Agriculture & Technology, Hill Campus, Ranichauri-249 199, Tehri-Garhwal, U.P., India

Abstract

High variability in leaf gas exchange and related traits were found in 30 genotypes of field grown finger millet. The variability in carbon exchange rate per unit leaf area (P_N) can be partly attributed to the differences in the stomatal conductance (g_s) and area leaf mass (ALM). The P_N was positively correlated with total dry matter (TDM). However, no relationship between P_N and seed yield was found. The leaf area showed a positive and significant correlation with total biomass. None of the other gas-exchange traits had significant relationship either with TDM or with seed yield. The ALM showed a strong positive association with P_N. However, it was not correlated with either total biomass or seed yield. As a result, the use of ALM as surrogate for P_N for identifying high biomass producing genotypes only had a limited value. Hence selection for high P_N would result in higher biomass producing types.

Additional key words: area leaf mass; *Eleusine coracana*; grain mass; harvest index; internal CO_2 concentration; leaf area; net photosynthetic rate; stomatal conductance; transpiration.

Introduction

Manipulation of morphological and physiological processes, which control photosynthesis, is one of the reasonable approaches for improving crop productivity (Mythili and Nair 1996). Dornhoff and Shibles (1970) found that high yielding cultivars of soybean tended to have high net photosynthetic rate (P_N) while Harrison *et al.* (1981) found that the seed yield of soybean and canopy photosynthesis were significantly related. Significant correlation between flag leaf P_N at booting, anthesis, and grain filling with above-ground biomass and grain yield was observed in wheat (Reynolds *et al.* 1994). Similarly, Kumar *et al.* (1998) also reported significant positive association between leaf P_N and grain yield in wheat genotypes. However, regular correlations between leaf P_N and yield have been difficult to demonstrate and selection for higher P_N has not led to increase in crop growth. In wheat, Rawson *et al.* (1983) found no relation between peak P_N of leaves in different positions on the culm and no correlation between P_N and yield. This may be due to the fact that P_N is often negatively correlated with leaf area (Wilson 1984). An inverse relationship between P_N and leaf area was observed among wheat species and within *Triticales* (Planchon 1979).

Nevertheless, genotypic variation in P_N per unit of leaf area may be useful in increasing productivity of crop plants, but only if it can be demonstrated to be related to growth in field stands (Mahon 1990). Such variability exists in several crops such as wheat (Evans and Dunstone 1970, Austin *et al.* 1982, Morgan and LeCain 1991), maize (Heichel and Musgrave 1969), soybean (Curtis *et al.* 1969, Buttary *et al.* 1981, Bhatia *et al.* 1996), chick pea (Gupta *et al.* 1989, Mythili and Nair 1996), and barnyard millet (Subrahmanyam and Rathore 1999). However, the information about the extent of variability in finger millet genotypes grown at high altitudes is lacking and the relationships reported for other crops and environments may not hold true for finger millet grown at high altitudes. Therefore, the present study was undertaken to check genotypic variability in leaf gas-exchange traits and to examine their relationship with other leaf characters such as leaf area, area leaf mass, and seed yield in finger millet genotypes.

Received 30 December 1999, *accepted* 10 May 2000.

Abbreviations: ALM = area leaf mass; C_i = internal CO_2 concentration; DAE = day after emergence; E = transpiration rate; g_s = stomatal conductance; P_N = net photosynthetic rate per unit leaf area; TDM = total dry matter.

Acknowledgements: The author gratefully acknowledge the suggestions and help provided by Dr. Rajendra Prasad and Dr. M. Dutta in statistical analysis and by Mr. G.P. Arya in gas exchange measurements.

Materials and methods

Field experiments were conducted during the rainy seasons of 1996 and 1997 at Hill Campus farm, G.B. Pant University of Agriculture and Technology, Ranichauri located in central Himalyan region (30°15'N; 78°30'E) at an altitude of 1950 m above sea level on north aspect.

The soil of Hill Campus farm was silky clay loam in texture, low in available nitrogen (17.5 g m^{-2}) and available phosphorus [0.95 g(P_2O_5) m^{-2}], rich in available potassium [37.0 g(K_2O) m^{-2}], and contained 1.02 % organic carbon. The soil pH varied from 5.3 to 5.6. The mean monthly maximum/minimum temperatures varied between 8.5–27.4/1.0–17.1 °C in 1996 and 10.5–24.2/1.4–17.2 °C in 1997. The total rainfall received during the crop season (June to November) was 1067 mm with 55 rainy days in 1996 and 701.8 mm with 53 rainy days in 1997, respectively (Table 1). During 1996 very little rain was received between October and November (6.2 mm with 3 rainy days) whereas in 1997 the crop received a total of 118.8 mm (with 9 rainy days) during the same period.

The seeds of thirty finger millet genotypes were obtained from the Project Coordinator, All India Coordinated Small Millets Improvement Project, University of Agricultural Sciences, Bangalore. The seeds were sown in 3×2-m size plots with a distance of 25 cm between rows, with four replications. The crop was sown during June and harvested in the last week of November. Recommended doses (6, 4, and 2 g m^{-2}) of N, P, and K, respectively, were applied. Two weeks after germination the seedlings were thinned so that a distance of 5 cm was left between the plants.

Photosynthesis and related traits were measured on fully expanded leaves between 10:00-13:00 on cloudless days at 60 vegetative stage (60 DAE) and seed filling stage (95 DAE). Two measurements were made per each replication and the mean value was used for analysis. P_N was measured using *CIRAS-I* (*PP Systems*, Hitchin, UK) portable photosynthesis measuring system fitted with broad leaf cuvette (exposed area 250 mm^2). P_N and related traits were measured on fully expanded leaves at vegetative stage and on subsequent stages measurements were made on the flag leaf. During P_N measurements, the cuvette temperature varied between 23.4 and 24.7 °C at vegetative stage, 23.6 and 25.7 °C at seed filling stage. Gas flow rates to the cuvette were set at 5 cm^3 s^{-1}, boundary layer conductance was 3.57 mol m^{-2} s^{-1}, and leaf temperatures were estimated using the instrument's facility to calculate leaf energy balance. A transmission coefficient of 0.15 was used.

Immediately after P_N measurement, the leaf was excised and the leaf area was measured using a portable leaf area meter model *C-201* (*CID*, Vancouver, USA) with *C-201S* scan board. The leaf was dried at 70 °C for 48 h and the dry mass was determined for ALM (Area Leaf Mass) determination.

Total leaf area per plant was recorded using *CI-252* (*CID*, Vancouver, USA) automatic leaf area meter after harvesting 0.5 m long rows of each genotype from the middle rows. Plants were dried and the dry mass of above-ground biomass was also recorded. Finger number was recorded on the main ear at dough stage. Finger length from base to the tip of longest finger on the main tiller and finger width across the centre of any finger on main tiller were measured at dough stage. At maturity, number of grains per spikelet was recorded. At harvest, total dry mass (above-ground biomass) and seed yield were recorded after harvesting 0.5 m long rows for each genotypes from the middle rows. 1000-grain mass was also recorded.

The values for both 1996 and 1997 were similar hence the mean of both the years was used for statistical analysis. Analysis of variance (ANOVA) was performed using randomised block design. Correlations and other statistical analyses were done using statistical software developed by the Computer Centre of G.B. Pant University of Agriculture and Technology, Pantnagar based on the procedures described by Snedecor and Cochran (1967).

Results

All the gas-exchange traits showed a high degree of variability as indicated by the F-ratios, which were highly significant. The ALM showed significant variability only at 60 and 90 DAE (Table 1). Significant variation was noticed among different genotypes for days to 50 % flowering, days to maturity, yield, and other yield contributing characters (Table 1).

The relationship between different leaf gas-exchange traits, leaf area, ALM, and above-ground biomass, measured at different growth stages, was studied by computing the correlation coefficients. The P_N showed positive and significant ($p = 0.01$) relation with transpiration rate (E) and g_s (Table 2). However, P_N showed a negative relationship with internal CO_2 concentration (C_i). The relationship was significant only at seed filling stage. A positive relationship was observed

Table 1. Variation in transpiration rate, E [mmol m^{-2} s^{-1}], net photosynthetic rate, P_N [mmol m^{-2} s^{-1}], stomatal conductance, g_s [mmol m^{-2} s^{-1}], internal CO_2 concentration, C_i [µmol mol^{-1}], leaf area [cm^2 plant^{-1}], area leaf mass [g(DM) m^{-2}], and yield attributes in finger millet genotypes. Each mean value represent the average of 30 genotypes ± SE. TDM – total dry matter. $^*p = 0.05$, $^{**}p = 0.01$.

Parameter	DAE	Mean	Range	F-ratio
E	60	9.51±0.66	7.13-12.99	5.05**
	90	7.51±0.40	6.08-08.80	3.87**
P_N	60	42.69±5.15	31.4-57.2	3.05**
	90	47.51±3.86	29.8-60.4	3.21**
g_s	60	438.3±49.4	287.5-722.7	5.92**
	90	442.9±45.1	322.5-598.5	3.11**
C_i	60	317.8±19.0	281.3-363.3	1.26
	90	310.2±17.6	220.5-443.8	6.82**
P_N/E	60	4.5±0.41	3.33-5.55	2.10**
	90	6.4±0.42	4.27-7.60	2.54**
P_N/g_s	60	101.9±12.16	75.8-126.9	1.94**
	90	110.4±09.09	72.8-136.5	3.29**
P_N/C_i	60	0.139±0.03	0.087-0.260	1.42
	90	0.612±0.02	0.070-0.237	2.81**
ALM	60	7.47±0.70	5.37-11.30	3.75**
	90	7.23±0.59	5.82-13.82	7.13**
Leaf area	60	183.3±0.85	155.1-350.1	3.55**
	90	271.0±0.82	124.1-434.6	4.32**
Days to 50% flower.	-	80.5±1.30	76-92	1.98*
Days to maturity	-	125.5±2.2	119-151	2.01*
TDM [kg m^{-2}]	-	1.47±0.11	0.88-3.60	2.68**
Seed yield [kg m^{-2}]	-	0.31±0.12	0.15-0.45	3.72**
1000 grain mass [g]	-	3.19±0.01	2.22-3.82	1.93*
Fingers/head		8.3±0.81	7.00-11.25	2.36**
Finger length [cm]		6.4±0.42	4.87-9.65	6.77**
Grains/spikelet		6.16±0.39	5.25-7.50	1.96*
Harvest Index		0.26±0.06	0.16-0.39	3.01**

between P_N and ALM at both the growth stages studied. However, the relationship was significant ($p = 0.01$) only at seed filling stage. A non-significant negative association was observed between leaf area and P_N at seed filling stage. Similar association between leaf area and ALM was observed. P_N showed a positive and significant association ($r = 0.41$, $p = 0.05$ with above-ground biomass) only at seed filling stage (Table 2). Nevertheless, a significant positive association ($r = 0.396$, $p = 0.05$) between seasonal mean P_N and above-ground biomass recorded at harvest was observed. The seasonal mean P_N showed a positive non-significant association with seed yields (Table 3).

The E showed a significant positive association with g_s. A non-significant positive association between E and total above-ground biomass was observed at both growth stages (Table 2). The leaf area was measured by harvesting 0.5-m long rows for each genotype at all the three growth stages. The leaf area exhibited a strong ($p = 0.01$) positive relationship with total dry matter at both growth stages. The relationship between some important characters such as finger length, finger width, finger number, 1000-grain mass, and harvest index was also studied. All the above-mentioned characters showed a positive and significant relationship with seed yield. However, the relations between the 1000-grain mass and seed yield and between finger width and seed yield were not significant (Table 3). The total biomass recorded at harvest showed a positive non-significant relationship with the seed yield.

Table 2. Relationship between the gas exchange traits and total dry mass of above ground biomass (TDM) of finger millet genotypes. A – leaf area, TDM – total dry matter. $^*p = 0.05$, $^{**}p = 0.01$.

	DAE	E	g_s	C_i	ALM	A	TDM
P_N	60	0.74**	0.72**	-0.16	0.27	0.05	0.33
	90	0.73**	0.63**	-0.46**	0.49**	-0.06	0.41*
E	60		0.90**	0.39*	0.17	0.13	0.23
	90		0.96**	0.41*	0.21	0.08	0.31
g_s	60			0.47**	0.05	0.09	0.23
	90			0.54**	0.03	0.11	0.34
C_i	60				-0.05	0.01	-0.13
	90				-0.14	0.11	0.23
ALM	60					0.01	0.17
	90					-0.11	0-18
A	60						0.69**
	90						0.48**

Table 3. Correlation coefficients between the leaf photosynthesis, ALM, and yield contributing characters and seed yield in finger millet genotypes.

Parameter	r
Seed yield and:	
Net photosynthetic rate [mmol m^{-2} s^{-1}]	0.216
Area leaf mass (ALM)	0.116
Time to maturity [d]	-0.421*
Number of fingers	0.390*
Finger length [cm]	0.604**
Finger width [cm]	0.278
Number of grains/spikelet	0.479**
1000 seed mass [g]	0.279
Harvest Index	0.652**
Total dry matter at harvest	0.208

Discussion

Highest P_N was observed at seed filling stage. Seasonal pattern in photosynthetic characters over different growth stages was reported for different crops (Subrahmanyam and Rathore 1992, Bhatia *et al.* 1996). The higher P_N at seed filling stage can be attributed to increased demand for photosynthates by the developing seeds (Clough *et al.* 1981, Subrahmanyam and Rathore 1999). Our results are in agreement with the above mentioned reports.

Variability in photosynthetic characters has been reported for different crop plants (Bhatia *et al.* 1996, Kumar *et al.* 1998, Subrahmanyam and Rathore 1999). Variation in P_N is often associated with g_s (Hobbs and Mahon 1982), chlorophyll content (Buttery and Buzzell 1977), leaf size (Bhagsari and Brown 1986), and specific leaf mass (Hesketh *et al.* 1981). However, the exact reason for this variability is not known. The strong positive relationship between seasonal mean g_s and P_N ($r = 0.75$, $p = 0.01$) observed in this study suggests that the variability in P_N in finger millet is associated with the g_s. However, internal leaf factors such as mesophyll and carboxylation resistances are also related to genotypic variation in P_N (Dornhoff and Shibles 1970).

Significant positive correlation between P_N and ALM was observed only at seed filling stage ($r = 0.49$, $p = 0.01$). A strong association between ALM and P_N was reported for different crops; this simple parameter can be used as a surrogate for P_N (Bhatia *et al.* 1996, Suresh *et al.* 1997). Genotypic variation in P_N is often attributed to differences in ALM. But the relationship largely depends on species and may not hold true for all species and environments (Bhagsari and Brown 1986).

The leaf area at seed filling (90 DAE) exhibited a tendency of negative, though non-significant, association with P_N and ALM. Negative association between P_N and leaf area was reported for different crop species (Planchon 1979). Suresh *et al.* (1997) suggested that the negative relationship between leaf area and P_N was due to the negative correlation between P_N and ALM.

The seasonal mean P_N showed a significant positive association with total biomass at harvest. Similar association between TDM and P_N has been reported for different crop species (Saitoh *et al.* 1991, Reynolds *et al.* 1994, Subrahmanyam and Rathore 1999). The seasonal mean P_N showed a positive but non-significant relationship with seed yield. A positive association between P_N and seed yield has been reported for different crops (Peet *et al.* 1977, Babu *et al.* 1985, Reynolds *et al.* 1994, Kumar *et al.* 1998). However, significant correlation between P_N and seed yield has been very difficult to demonstrate in the field and selection for high photosynthesis has not always led to higher yield and crop growth. This may be due to the negative association between P_N and leaf area (Wilson 1984). A positive and highly significant correlation was observed between seed yield and other important yield contributing characters. In rice, yield attributes such as number of productive tillers, grain number per panicle, and 1000-seed mass always had positive relation to grain yield (Reuben and Katuli 1989, Suarez *et al.* 1989). Such associations were reported for finger millet (Ramakrishna *et al.* 1996) and wheat (Perry and D'Antuono 1989). The poor correlation between total biomass and seed yield observed in this study shows poor partitioning of dry matter into reproductive parts, as indicated by poor harvest index. Furthermore, the significant negative association between days to maturity and seed yield observed in this study indicates that the seed filling in long duration genotypes was very poor. This may be due to the low temperatures prevailing at this altitude (1950 m a.s.l.) or might be partly a result of mild water deficit (the rain fall during October and November was small).

References

Austin, R.B., Morgan, C.L., Ford, M.A., Bhawat, S.G.: Flag leaf photosynthesis of *Triticum aestivum* and related diploid and traploid species. - Ann. Bot. **49**: 177-189, 1982.

Babu, R.C., Srinivasan, P.S., Natarajaratnam, N., Rangasamy, S.R.S.: Relationship between leaf photosynthetic rate and yield in black gram [*Vigna mungo* (L.) Hepper] genotypes. - Photosynthetica **19**: 159-163, 1985.

Bhagsari, A.S., Brown, R.H.: Leaf photosynthesis and its correlation with leaf area. - Crop Sci. **26**: 127-132, 1986.

Bhatia, V.S., Tiwari, S.P, Joshi, O.P.: Inter-relationship of leaf photosynthesis, specific leaf mass and leaf anatomical charracters in soybean. - Indian J. Plant Physiol. (New Ser.) **1**: 6-9, 1996.

Buttery, B.R., Buzzell, R.I.: The relationship between chlorophyll content and rate of photosynthesis in soybeans. - Can. J. Plant Sci. **57**: 1-5, 1977.

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

Clough, J.M., Peet, M.M., Kramer, P.J.: Effects of high atmospheric CO_2 and sink size on rates of photosynthesis of a soybean cultivar. - Plant Physiol. **67**: 1007-1010, 1981.

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

Dornhoff, G.M., Shibles, R.M.: Varietal differences in net photosynthesis of soybean leaves. - Crop Sci. **10**: 42-45, 1970.

Evans, L.T., Dunstone, R.L.: Some physiological aspects of evolution in wheat. – Aust. J. biol. Sci. **23**: 725-741, 1970.

Gupta, S.K., Bhatia, V.S., Singh, D.N., Ganguly, S.B.: Genotypic variation and relationship of specific leaf mass with photosynthesis in chickpea (*Cicer arietinum* L). - Indian J. Plant Physiol. **32**: 224-227, 1989.

Harrison, S.A., Boerma, H.R., Ashley, D.A.: Heritability of canopy-apparent photosynthesis and its relationship to seed yield in soybeans. - Crop Sci. **21**: 222-226,. 1981.

Heichel, G.H., Musgrave, R.B.: Varietal differences in net photosynthesis of *Zea mays* L. - Crop Sci. **9**: 483-486, 1969.

Hesketh, J.D., Ogren, W.L., Hageman, M.E., Peters, D.B.: Correlations among leaf CO_2 exchange rates, areas and enzyme activities among soybean cultivars. - Photosynth. Res. **2**: 21-30, 1981.

Hobbs, S.L.A., Mahon, J.D.: Variation, heritability and relationship to yield of physiological characters in peas. - Crop Sci. **22**: 773-779, 1982.

Kumar, P., Dube, S.D., Chauhan, V.S.: Relationship among yield and some physiological traits in wheat. - Indian J. Plant Physiol. **3**: 229-230, 1998.

Mahon, J.D.: Photosynthetic carbon dioxide exchange, leaf area and growth of field pea genotypes. - Crop Sci. **30**: 1093-1098, 1990.

Morgan, J.A., LeCain, D.R.: Leaf gas exchange and related leaf traits among 15 winter wheat genotypes. - Crop Sci. **31**: 443-448, 1991.

Mythili, J.B., Nair, T.V.R.: Relationship between photosynthetic carbon exchange rate, specific leaf mass and other leaf characteristics in chickpea genotypes. - Aust. J. Plant Physiol. **23**: 617-622, 1996.

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

Perry, M.W., D'Antuono, M.F.: Yield improvement and associated characteristc of some Australian spring wheat cultivars introduced between 1860 and 1882. Commonwealth Scientific and Industrial Research Organization. 1950-1989. - Aust. J. agr. Sci. **50**: 457-472, 1989.

Planchon, C.: Photosynthesis, transpiration, resistance to CO_2 transfer, and water efficiency in flag leaf of bread wheat, durum wheat and triticale. - Crop Sci. **32**: 423-426, 1969.

Ramakrishna, M., Shankarae Gowda, B.T., Katti, S.M., Seetharam, A., Mantoor, S.G., Vishwanath, S., Lucy Channamma, K.A., Krishnappa, M., Vasanth, K.R., Krishnamurty, B., Jadeeshwara, K.: Evaluation of finger millet germplasm. Germplasm catalogue-1, All India Small Millet Improvement Project (ICAR), University of Agricultural Sciences, Bangalore 1996.

Rawson, H.M., Hindmarsh, J.H., Fischer, R.A., Stockman, Y.M.: Changes in leaf photosynthesis with plant ontogeny and relationships with yield per ear in wheat cultivars and 120 progeny. – Aust. J. Plant Physiol. **10**: 503-514, 1983.

Reuben, S., Katuli, S.D.: Path analysis of yield components and selected agronomic traits of upland rice breeding lines. - Int. Rice Res. Newslett. **14**: 11-12, 1989.

Reynolds, M.P., Balota, M., Delgado, M.I.B., Amani, I., Fischer, R.A.: Physiological and morphological traits associated with spring wheat yield under hot, irrigated conditions. - Aust. J. Plant Physiol. **21**: 717-730, 1994.

Saitoh, K., Kasiwagi, S., Ishihara, K.: Characteristics of dry matter production in high yielding rice cultivars. IV. Dry matter accumulation in the panicles. - Jap. J. Crop Sci. **60**: 255-263, 1991.

Snedecor, G.W., Cochran, W.G.: Statistical Methods. - Oxford and IBH Publishing Co., New Delhi 1967.

Suarez, E., Alfanso, R., Perez, R., Iglesias, J.: Correlation between yield and its components in upland rice in Cuba. - Int. Rice Res. Newslett. **14**: 11, 1989.

Subrahmanyam, D., Rathore, V.S.: $^{14}CO_2$ assimilation and translocation of ^{14}C-photosynthates by different plant parts of Indian mustard (*Brassica juncea*). - J. Agron. Crop Sci. **169**: 169-175, 1992.

Subrahmanyam, D., Rathore, V.S.: Variability in leaf photosynthetic traits in barnyard millet genotypes. - J. Agron. Crop Sci. **183**: 199-203, 1999.

Suresh, K., Rao, K.L.N, Nair, T.V.R.: Genetic variability in photosynthetic rate and leaf characters in *Brassicaceae* coenospecies. - Photosynthetica **33**: 173-178, 1997.

Wilson, D.: Identifying and exploiting genetic variation in the physiological components of production. - Ann. appl. Biol. **104**: 527-536, 1984.