Annals of Arid Zone 62(1): 91-96, 2023

Association of Photosynthesis of Flag Leaves with Grain Yield in Pearl Millet [*Pennisetum glaucum* (L.) R. Br.]

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Received: March 2023

Abstract: The grain yield of pearl millet has increased continuously in past decades through development of hybrids and improved production practices. Elite inbred lines are crucial for innovating new germplasm/traits to break the yield plateau. Hence, 64 inbred lines of pearl millet were evaluated to assess the extent of genetic variability and association among agronomic, physiological and grain yield contributing traits. Analysis of variance showed significant differences among the lines for all the traits indicating sufficient variability for genetic exploitation. The preferred arid adaptation traits, early flowering and high tillering were associated with each other making them amenable for simultaneous selection and these two traits were not associated with grain yield. Hence, for deriving ideotypes suitable for arid adaptation, intensive selection for grain yield in early flowering background was suggested. In productive regions, the plants having greater plant height, larger size of leaves including flag leaf, larger panicle size to accommodate the photosynthates are desirable and these traits were found to be associated among themselves and with grain yield in the current study. Though the maximal photosynthetic efficiency, Fv/Fm was significantly associated with leaf length, flag leaf length, flag leaf width and actual PSII efficiency (Y(II)), these physiological parameters did not significantly associate with grain yield directly and their effects are confounded within the leaf morphological variation.

Key words: Pearl millet, Flag leaf, Fv/Fm, PSII, Photosynthates

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Citation

Reddy, P. S., Srividhya, S., Khandelwal, V. and Satyavathi, C. T. 2023. Association of photosynthesis of flag leaves with grain yield in pearl millet (Pennisetum glaucum (L.) R. Br.). Annals of Arid Zone 62(1): 91-96.

doi: 10.59512/aaz.2023.62.1.10

https://epubs.icar.org.in/index.php/AAZ/article/view/135826

In the past several decades, productivity increases were made in several crops including pearl millet exploiting the genetic variability especially for panicle traits. This led to an increase in harvest index and consequently over a period of time yield plateau was attained in most of the crops (Yang *et al.*, 2007). For further increasing of grain yield with similar harvest index, biomass need to be improved (Richards, 2000). The photosynthetic efficiency of the crop/genotype determines the biomass and yield production potential (Horton, 2000). The relation between yield progress and higher photosynthetic trait has been observed in wheat (Fischer *et al.*, 1998), rice (Wang *et al.*, 2020) and maize (Li *et al.*, 2015). As the assimilates produced in the flag leaf directly contribute towards dry matter accumulation in grain (Makunga *et al.*, 1978), improving the photosynthetic capacity of flag leaf is subject of study in many crops (Yang *et al.*, 2007). In wheat, it has been shown that genetic gain for yield can be achieved through selection for flag-leaf photosynthetic rate in F5 progenies and a linear relationship exists between photosynthetic rate, yield and biomass (Gutierrez-Rodrı´guez *et al.*, 2000). Reynolds *et al.*, (2000) proposed that significant genetic improvement can be made by selecting parents with superior photosynthetic traits along with other yield contributing traits. Promoting large numbers of progeny in the breeding process improves the chance of identifying phenotypes with higher radiation use efficiency and higher yield potential.

Pearl millet [*Pennisetum glaucum* (L.) R. Br.] is the most widely cultivated staple food crop after rice, wheat and maize in India playing a vital role of addressing food and nutritional security in regions where other cereal crops cannot be successfully grown (Sanjana Reddy *et al.*, 2021). It is consumed mainly in the western Rajasthan and parts of Gujarat, where it contributes more than 50% of the total cereal consumption and also in parts of Telangana, Karnataka, Maharashtra, and Haryana. Given the increase in global climatic temperatures by 5°C above pre-industrial level by 2100 (Tollefson, 2020), crops like pearl millet [*Pennisetum glaucum* (L.) R. Br.] with efficient photosynthetic system (C4) and tolerance to abiotic stresses (heat and salinity) are termed as climate-smart as they meet the food and fodder requirements even under harsh environmental conditions. India is the largest producer of this crop, both in terms of area (6.93 mha) and production (8.61 mt) (Sanjana Reddy *et al.*, 2021). Pearl millet productivity has increased from 303 kg ha^{-1} during 1950-1954 to 1239 kg ha^{-1} during 2015-2019 which is more than 300% as a result of genetic improvement for yield and disease resistance and dissemination of improved production technology (Yadav *et al.*, 2021). There is a need to incorporate new traits/ genes for further increase in productivity.

The objective of this study was to investigate the physiological basis of the high yield in the inbred lines of pearl millet as this physiological basis could be a significant selection indicator in breeding programs. Thus, we examined the variability for Fv/Fm, photosystem II (PSII) photochemistry (YII) in the flag leaves along with other yield contributing traits and studied their association under field conditions.

Materials and Methods

The material for the study included 64 inbred lines of pearl millet. These stabilized inbred lines represented 15 restorer lines and 49 maintainer lines. The material was evaluated in a randomized block design with two replications. Each entry in every replication was sown in a plot size of 0.9 m^2 having 15 plants. Standard agronomic practices were followed to raise a healthy crop. In addition, water was supplied sufficiently throughout, to avoid potential nutrients and drought stress.

Data were recorded on agronomic, physiological and yield traits. The flowering time (DF) was measured as the number of days taken for 50% of plants to show full stigma emergence from the date of sowing. The length of fully matured plant from the base of the plant to the top of the ear head in centimeters was recorded as plant height (PHT). The number of productive tillers (NPT) is counted as the total number of tillers bearing earhead with grains. The panicle length (PL) was measured from base of the panicle to its tip and recorded in centimeters. The panicle diameter (PD) was measured at the maximum thickness of the panicle in centimeters. Grain yield (GY) was estimated by weighing the grains obtained after drying and threshing of panicles at approximately 12% moisture content obtained by drying for seven days and expressed in grams. Then the weight per plot is extrapolated into t ha^{-1}. For measuring 1000-grain weight (1000 GWT), a sample of 200 grains were counted randomly from the threshed seed, extrapolated and the weight is recorded in grams.

Handy photosynthetic efficiency analyzer (Hansatech PEA+) was used to measure the chlorophyll fluorescence, which is an indicator of photosynthetic efficiency. The maximum photochemical efficiency of Photosystem II (Fv/ Fm) was measured after the leaves were dark adapted using leaf clips for 15 minutes. During dark adaptation, all reaction centers within the sample are fully oxidised making them available for photochemistry and any latent chlorophyll fluorescence yield is quenched. With all available reaction centers closed, or chemically reduced, maximum fluorescence is measured. The difference between maximum fluorescence and minimum fluorescence is Fv, or variable fluorescence. Fv/Fm is a normalized ratio created by dividing variable fluorescence by maximum fluorescence. It is a measurement ratio that represents the maximum potential quantum efficiency of Photosystem II if all capable reaction centers were open (Kitajima and Butler, 1975). Like Fv/Fm, Y(II) represents a measurement ratio of plant efficiency, but in this case, it is an indication of the amount of energy used in photochemistry by photosystem II under steady-state photosynthetic lighting conditions. In the field, plants in full sunlight, and not under canopy, or partly cloudy conditions, are considered to be at steady state. Both Fv/Fm and Fv'/Fm' are closely related to the actual activity of plant photosynthetic tissue, and have been applied to monitor the physiological status of plants and their reactions to the environment (Kitajima and Butler, 1975). These parameters were measured between 10:00 and 12:00 h.

The phenotypic data was subjected to RBD analysis using Genstat 12edn. and correlations were estimated using Microsoft Excel.

Results and Discussion

The results revealed that the pearl millet inbred lines differed significantly for all the traits evaluated ($P < 0.001$ to 0.05). The mean performance of the genotypes showed a wide range of variability for all the traits (Table 1). The trait associations are given in Table 2.

Depending on the climatic conditions/levels of aridity, two specific ideotypes of pearl millet are grown. In arid regions, cultivars with early flowering, high tillering, medium sized panicles in high yielding background are preferred. In the current study, the days to flowering in the inbred lines ranged from 43 to 63 days. The B-line 788B (43 days) was the earliest to flower followed by 790B (47 days). Seven genotypes flowered in less than 50 days. Days to flowering was significantly and negatively associated with number of productive tillers depicting that the early flowering lines had more tillering. The late flowering lines had longer leaves, greater flag leaf width, bigger panicle length and width. Though there was good variability in the number of productive tillers, it did not associate significantly with any of the traits apart from early flowering and smaller flag leaf width. Hence, while breeding for inbred lines suitable for arid tracts, large number of progenies should be screened for higher yields in the crosses made involving early flowering lines.

While breeding for productive regions/ semi-arid tracts, the ideotypes adapted usually have less number of productive tillers, greater plant height with resistance to lodging, greater panicle parameters in high grain yield background. In the current study, the plant height ranged from 75 to 160 cm. It was positively associated with greater leaf and flag leaf lengths as well as grain yield attributes such as panicle length and width apart from grain yield. The yield of the grains depends on the source, the sink and their relationship. Apart from the leaves, the top leaves, especially the flag leaf, are often the most important primary source for the assimilating of the grain yield. Flag leaf is an immediate source providing photosynthates required for plant growth and panicle development (Tian *et al.,* 2015). In Rice, the size of the fag leaf is related to the weight of a thousand grains, the weight of the grains per panicle, and other characteristics related to yield (Wang *et al.,* 2020). Improving the traits of flag leaves brings about a high increase in the grain yield (Rahman *et al.,* 2014). Wide variability has been seen in the leaf length (27 cm to 54 cm), leaf width (1.4 to 3.6 cm), flag leaf length (15.3 to 37 cm) and flag leaf width (1.7 to 3.6 cm). These four parameters are significantly associated among themselves as well as positively and highly significantly associated with panicle length ($r = 0.44$ to 0.50), panicle width ($r = 0.45$ to 0.57) and grain yield ($r = 0.27$ to 0.62). The 1000 grain weight was associated with only greater leaf width and reflected in more panicle width. Thus, for improving the grain yield in the productive regions, the plants should have more plant height, larger size of leaves including flag leaf, larger panicle size to accommodate the photosynthates.

On further investigation of the possible causes of higher photosynthetic capacity of the inbred lines by examining both light reaction and the dark reaction by analyzing Chl fluorescence parameters revealed that the changes in the

Table 1. Mean performance of pearl millet inbred lines for agronomic, yield and physiological traits, 2022 summer season, IIMR, Hyderabad

Genotype	Days to 50% flowering	Plant height (cm)	No. of productive tillers	Leaf length (cm)	Leaf width (cm)	Flag leaf length (cm)	Flag leaf width (cm)	Fv/ Fm	Y(II)	Panicle length (cm)	Panicle width (cm)	Grain yield (t ha^{-1})	1000 - grain weight (g)
1003R	51	110	1.2	43.0	2.1	29.3	2.3	0.77	0.62	18.0	2.1	3.41	8.9
1004R	57	85	1.3	30.5	2.1	17.3	2.3	0.74	0.55	15.3	1.7	0.93	7.6
1009R	55	90	0.6	35.5	2.3	22.3	2.9	0.79	0.67	15.7	2.1	1.60	7.4
1015R	57	110	1.6	44.5	2.2	22.3	2.8	0.78	0.59	17.7	2.4	3.99	10.4
1017R	57	130	1.1	43.0	3.0	28.0	3.2	0.78	0.66	20.3	3.1	2.74	10.3
1018R	53	150	2.3	53.5	2.6	31.7	2.6	0.79	0.61	24.0	2.6	4.98	8.9
1024R	53	140	1.7	48.5	2.9	25.3	2.4	0.78	0.64	21.0	2.1	3.63	7.7
1025R	55	140	1.0	48.5	2.7	29.3	2.3	0.78	0.66	19.0	2.2	4.61	7.7
1026R	54	120	2.2	39.0	1.4	21.3	2.0	0.78	0.61	17.3	1.5	1.78	7.3
1027R	50	110	1.3	48.5	3.1	20.7	2.0	0.75	0.37	21.7	2.4	5.30	9.9
1037R	60	80	0.4	43.0	3.3	23.3	2.7	0.80	0.63	16.3	2.2	2.42	8.4
1040R	58	110	0.7	40.0	2.1	22.7	2.6	0.76	0.39	14.0	1.7	1.33	7.1
1054R	55	130	1.3	51.5	3.2	23.7	2.4	0.77	0.60	17.7	2.8	4.11	10.8
1057R	48	110	0.8	31.5	2.7	22.7	2.5	0.79	0.63	14.7	2.2	1.76	7.9
1063R	50	90	1.4	49.5	2.9	29.0	3.6	0.79	0.59	16.3	2.4	2.92	6.7
702B	53	100	0.4	39.0	3.1	26.7	3.2	0.78	0.67	23.0	2.1	2.58	8.2
704B	55	130	0.5	51.5	2.6	30.0	3.3	0.77	0.65	20.7	2.5	2.40	8.6
706B	61	120	0.5	49.5	2.7	30.3	3.0	0.78	0.68	22.7	2.8	3.39	10.4
708B	55	110	1.4	37.0	2.4	28.0	2.8	0.79	0.69	15.7	2.0	2.03	11.1
710B	52	100	1.7	29.0	1.9	23.7	2.5	0.78	0.68	16.0	1.6	0.48	12.5
712B	55	150	0.5	51.0	2.5	31.3	2.9	0.78	0.68	22.7	2.4	2.66	8.1
714B	55	135	1.0	49.5	3.1	26.0	2.5	0.77	0.68	14.0	3.0	4.69	8.0
716B	51	110	2.6	41.5	2.9	26.0	2.3	0.77	0.68	17.7	1.9	3.17	7.8
718B	47	110	1.0	38.5	2.3	31.7	2.9	0.78	0.66	18.3	2.2	3.49	10.8
720B	50	110	3.2	43.0	2.1	27.8	2.2	0.79	0.73	16.0	2.0	1.68	8.6
722B	56	160	0.8	50.5	3.3	26.3	3.3	0.78	0.66	20.7	2.3	1.82	8.6
724B	54	125	0.1	51.5	3.3	27.7	3.4	0.77	0.67	21.3	3.0	2.59	10.1
726B	52	75	0.0	32.0	2.4	18.3	2.3	0.74	0.61	14.0	2.1	1.11	9.0
728B	54	110	1.4	36.0	1.6	21.7	1.7	0.78	0.67	13.3	1.9	1.68	3.2
730B	56	110	1.0	44.0	3.5	23.8	3.1	0.77	0.68	19.7	3.2	2.74	14.8
732B	54	100	1.6	38.5	3.4	22.3	2.9	0.74	0.63	20.3	2.2	3.38	9.8
734B	55	130	1.1	44.0	2.8	24.7	2.4	0.78	0.68	17.0	2.6	3.19	11.2
736B	53	135	4.3	45.0	2.5	28.3	2.4	0.76	0.66	16.0	2.0	2.92	9.9
738B	55	140	1.8	37.0	2.3	26.8	2.3	0.77	0.66	16.0	2.0	3.49	9.5
740B	52	130	2.0	40.0	3.2	30.3	2.7	0.77	0.67	16.0	2.0	4.38	10.1
744B	48	130	5.0	33.0	2.0	21.0	1.8	0.77	0.67	15.7	2.0	1.69	8.5
746B	53	105	0.6	41.0	3.1	24.7	3.3	0.78	0.67	22.7	2.6	3.74	9.4
748B	54	100	1.3	32.0	2.7	18.7	2.3	0.76	0.65	19.7	2.1	1.76	7.6
752B	58	110	2.7	44.5	3.2	23.3	3.4	0.77	0.67	20.3	2.6	3.94	10.3
754B	53	110	2.7	36.0	2.7	31.0	3.4	0.77	0.70	22.0	2.0	4.27	10.3
756B	54	90	1.7	38.0	2.1	20.8	2.3	0.76	0.65	13.3	1.8	2.27	12.1
760B	53	90	0.2	33.5	3.1	19.0	2.0	0.76	0.48	16.0	2.0	1.62	10.4
762B	54	75	1.4	34.0	2.8	22.0	2.4	0.77	0.66	16.3	2.1	1.54	8.3
764B	54	100	0.5	35.5	3.0	25.3	2.6	0.76	0.66	18.3	2.2	1.91	9.7
766B	57	125	0.4	49.5	2.4	37.0	3.0	0.79	0.69	16.7	3.3	3.50	6.7
768B	50	120	1.4	43.0	2.8	23.8	2.5	0.75	0.68	20.3	2.5	2.73	8.7
770B	54	130	0.9	34.5	2.5	22.7	2.5	0.76	0.66	19.0	2.5	2.96	10.3

Table 1. Contd...

Genotype	Days to 50% flowering	Plant height (cm)	No. of productive tillers	Leaf length (cm)	Leaf width (cm)	Flag leaf length (cm)	Flag leaf width (cm)	Fv/ Fm	Y(II)	Panicle length (cm)	Panicle width (cm)	Grain yield (t ha^{-1})	1000 - grain weight (g)
772B	55	95	0.0	40.5	3.3	24.3	2.9	0.77	0.63	16.7	2.6	2.25	9.6
774B	49	120	0.2	34.5	2.3	29.3	2.6	0.78	0.67	19.0	2.1	1.67	8.2
776B	54	130	1.3	36.5	2.3	21.3	2.2	0.76	0.65	17.0	1.8	2.46	9.9
778B	54	90	1.3	34.5	2.7	17.0	2.7	0.77	0.67	15.3	1.8	1.28	8.3
780B	51	140	1.5	44.5	3.1	21.8	2.9	0.77	0.67	18.3	2.1	3.83	6.4
782B	53	120	1.9	44.0	3.4	21.8	2.7	0.76	0.64	17.3	2.3	3.86	12.8
784B	56	140	1.8	43.5	3.1	30.3	2.5	0.77	0.68	23.0	2.4	4.09	8.7
786B	49	140	1.0	41.0	2.2	28.8	1.9	0.78	0.70	19.3	2.1	1.86	8.9
788B	43	100	1.6	33.0	2.1	20.2	2.0	0.77	0.68	13.7	1.7	1.27	6.1
790B	45	110	0.7	41.0	2.8	28.0	2.6	0.78	0.68	15.3	2.2	1.63	8.6
792B	63	110	0.3	41.0	2.3	29.7	3.0	0.78	0.65	15.7	2.5	1.97	10.5
796B	53	110	1.0	26.5	1.9	15.3	2.2	0.76	0.68	16.0	1.8	1.33	7.9
800B	53	140	1.3	44.0	3.6	23.8	3.2	0.77	0.67	20.0	2.7	4.47	11.7
802B	52	100	1.4	43.0	3.5	15.8	2.0	0.78	0.66	17.3	2.0	3.31	9.9
804B	63	95	1.3	48.0	3.0	25.0	3.1	0.78	0.67	23.0	1.8	3.47	8.6
806B	59	120	1.8	41.5	3.1	33.3	3.0	0.79	0.68	24.7	2.8	4.92	10.0
808B	58	150	1.0	51.5	3.0	30.7	2.6	0.76	0.70	23.0	2.2	2.72	11.6
Mean	54	115	1.3	41.3	2.7	25.1	2.6	0.77	0.65	18.2	2.2	2.78	9.2
CV	5.65	18.61	19	10.25	15.03	22.2	15.1	2.4	8.4	11.1	13.3	24.0	21.0
LSD (≤0.05)	3.7	19.65	0.9	6.5	0.5	6.0	0.6	0.03	0.06	3.0	0.4	1.1	2.8
P value	0.000	0.012	<0.001	0.003	0.004	0.001	0.001	0.050	0.001	0.000	0.003	0.002	0.029

actual PSII efficiency (Y(II)) and the maximal efficiency of PSII photochemistry (Fv/Fm) of the flag leaves varied significantly among the lines. The Fv/Fm was significantly associated with leaf length, flag leaf length, flag leaf width and Y(II), while Y(II) was in addition was associated with flag leaf length. However, these parameters did not significantly associate with grain yield in this data set. Their effects might have been confounded in the leaf size traits. Several studies indicate flag leaf assimilates as the most important contributor to the dry weight accumulation in grains (Evans *et al.*, 1969; Austin *et al.*, 1977; Makunga *et al.*, 1978)

Table 2. Association among agronomic, yield and physiological traits in pearl millet inbred lines, 2022 summer season, IIMR, Hyderabad

Trait	Days to 50% flowering	Plant height (cm)	No. of productive tillers	Leaf length (cm)	Leaf width (cm)	Flag leaf length (cm)	Flag leaf width (cm)	Fv/ Fm	Y(II)	Panicle length (cm)	Panicle width (cm)	Grain yield (t ha^{-1})
Plant height (cm)	0.01	1.00										
No. of productive tillers	-0.23*	0.19	1.00									
Leaf length (cm)	0.30*	0.54**	-0.05	1.00								
Leaf width (cm)	0.19	0.09	-0.19	0.45**	1.00							
Flag leaf length (cm)	0.13	0.48**	-0.03	0.54**	0.08	1.00						
Flag leaf width (cm)	0.37**	0.06	-0.27*	0.40**	0.49**	0.45**	1.00					
Fv/Fm	0.07	0.14	-0.02	0.30*	-0.06	0.46**	0.30*	1.00				
PSII	-0.04	0.23	0.16	0.00	0.01	0.32**	0.18	0.32**	1.00			
Panicle length (cm)	0.27*	0.41**	-0.06	0.50**	0.44**	0.44**	0.46**	0.08	0.13	1.00		
Panicle width (cm)	0.28*	0.32**	-0.26	0.57**	0.52**	0.45**	0.52**	0.16	0.14	0.41**	1.00	
Grain yield (t ha^{-1})	0.17	0.44**	0.17	0.62**	0.50**	0.40**	0.27*	0.09	-0.02	0.53**	0.49**	1.00
1000-grain weight (g)	0.17	0.07	0.03	0.10	0.36**	0.07	0.24	-0.14	0.06	0.22	0.31*	0.23

and the factors that decrease the photosynthetic activity of the flag leaf during the grain-filling period could potentially limit grain yield.

Conclusion

Significant differences among the inbred lines and wide range observed for all the recorded traits showed extensive variability in the pearl millet inbred lines for further exploitation in cultivar development. Careful choice of traits needs to be made for obtaining desirable ideotypes. As early flowering and high tillering are tightly linked and not associated with grain yield, intensive selection for grain yield in early maturity back ground is desirable for obtaining genotypes suitable for arid ecology. However, for yield improvement in productive regions, greater biomass traits (plant height, leaf length, leaf width, flag leaf length and flag leaf width) along with panicle traits (panicle length and panicle width) need to be considered and due to their significant association with grain yield, simultaneous selection is possible. The Chlorophyll fluorescence parameters influenced grain yield via leaf parameters.

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Printed in March 2023