Photosynthetic characteristics in wild, cultivated species and interspecific inbred lines of safflower

KAMMILI ANJANI, PASALA RATNAKUMAR* AND S N SUDHAKARA BABU

ICAR-Indian Institute of Oilseeds Research, Rajendranagar, Hyderabad-500 030, Telangana

(Received: July 15, 2021; Revised: November 24, 2021; Accepted: January 4, 2022)

ABSTRACT

Safflower (*Carthamus tinctorius* L.), a multipurpose oilseed crop is the only cultivated species in the Carthamus genus. *Carthamus* spp. have been explored for resistance to biotic and abiotic stresses but not for physiological efficiency. Photosynthetic traits of ten wild and ten cultivated species and six interspecific inbred lines were studied to understand the expression of the photosynthetic traits among them, and for trait introgression from wild species in interspecific derivatives. Relations among some physiological traits in interspecific inbred lines differed from those observed in wild and cultivated species. The high photosynthesis (Pn), low transpiration (E) and high intrinsic water use efficiency (iWUE) could be introgressed from the wild species, *C. lanatus* and *C. turkesthanicus* into safflower cultivars. Inheritance of photosynthetic traits from wild to cultivated species indicated that wild species are exploitable for safflower improvement. This study suggests the utilization of wild species for their high Pn, low E and iWUE characteristics for developing abiotic stress-tolerant safflower cultivars.

Keywords: Photosynthesis, Safflower, Wild species, intrinsic Water Use Efficiency

Safflower (*Carthamus tinctorius* L.) is the only cultivated species in the genus Carthamus. Kazakhstan, Russian Federation, the USA, Mexico, Turkey, India and China are the other major safflower producing countries (http://faostat3.fao.org as of 15 March 2019). Safflower is used for many purposes such as edible oil, biofuel, bird feed, pharmaceutical applications, dye-making, food colouring and flavouring, etc (Neelima *et al.*, 2021). Crop improvement in safflower has been targeted for incorporating quantitative agronomic traits and has met with incremental success. This approach is reaching saturation in terms of exploitable genetic variability. Assessing the basic physiological process of photosynthetic parameters is a grey area with huge opportunities for carbon fixation ultimately resulting in crop's productivity improvement. Further increase in crop yield will depend largely on increasing photosynthesis. Elevated CO_2 research has shown a remarkably close relation between yield and photosynthesis (Long *et al.*, 2006). Literature suggests that the plant with lower canopy temperature (CT) gives higher yield as reported in other studies (Beebe *et al.*, 2013; Pandey *et al.*, 2021; Sravanthi *et al.,* 2021) and leaf temperature is considered as an important trait for selection of high yielding lines (Ainsworth and Rogers, 2007). Cooler canopy temperatures are the consequence of transpiration (Ratnakumar *et al.*, 2009) and varies depending on soil water availability. The importance of evaporative cooling is a major component of the leaf energy balance, and leaf temperature can be used as an indicator for the rates of water loss or stomatal opening. Also, a lowered CT and increased stomatal conductance ensure higher CO_2 inside the leaf and in turn higher carbon fixation efficiency (Pandey *et al.*, 2021; Sravanthi *et al.*, 2021). Similar to this, water use efficiency (WUE) is defined as the amount of carbon assimilated as biomass or grain produced per unit of water used by the crop and at the leaf level it is directly related to the physiological processes controlling the gradients of CO_2 and H_2O. The effect of increasing CO_2 on photosynthetic rate (Pn) and WUE is normally positive as the difference between the ambient air and the intercellular spaces is increased and under light, CO_2 within the leaf is rapidly converted to carbohydrates.

Wild species of crops are the sources of novel genes and are widely used for improving crop species. Approximately 25 species have been reported in the Carthamus genus. The wild species grow naturally from northwestern India westwards to and around the Mediterranean Sea (Knowles, 1980). Natural and artificial hybridization of safflower with wild species has been reported (Ashri and Knowles, 1960; Schank and Knowles, 1964; Ashri and Rudich, 1965; Heaton and Klisiewicz, 1981; Mayerhofer *et al.,* 2011). Living materials of only 13-15 Carthamus species are available in various gene banks. Six wild Carthamus spp. *viz., C. oxyacantha, C. palaestinus, C. glaucus, C. creticus, C. lanatus* and *C. turkesthanicus* are maintained at ICAR-Indian Institute of Oilseeds Research (ICAR-IIOR), Hyderabad, India. The wild species, *C. oxyacantha* was collected through explorations in India (Anjani *et al.,* 1999) and the remaining species were introduced from the USDA, USA through ICAR-National Bureau of Plant Genetic Resources, New Delhi, India. The wild species were self-pollinated for

---

*Corresponding author's E-mail: ratna.pasala@icar.gov.in several years to bring genetic uniformity within each species. Some of the Carthamus wild species were identified as the source of resistance to biotic and abiotic stresses of safflower (Bassiri and Sionit, 1975; Pallavi *et al.,* 2007; Prasad and Anjani, 2008; Sabzalian *et al.,* 2010; Majidi *et al.,* 2011) and were used for improving safflower for disease resistance (Anjani *et al.,* 2007; Pallavi *et al.,* 2007, Prasad and Anjani, 2008). One of the wild species, *C. oxyacantha* was the donor of sterile cytoplasm for developing cytoplasmic-genic male sterility system in safflower (Anjani, 2008). Wild species have been also widely utilized in several crop species for improving resistance to biotic and abiotic stresses as well as quality and yield traits. They have also been identified as potential sources of physiological traits for crop improvement (Masumoto *et al.,* 2004; Rajesh *et al.,* 2016). With no information on physiological characteristics of safflower wild species, the present study was undertaken to assess the photosynthetic traits in wild and cultivated species and interspecific inbred lines; and their inheritance into cultivated species were also assessed.

MATERIALS AND METHODS

Plant material and experimental set up: Ten accessions of six wild species *viz., C. oxyacantha* (2n=24), *C. palaestinus* (2n=24), *C. glaucus* (2n=20), *C. creticus* (2n=64), *C. lanatus* (2n=44) and *C. turkesthanicus* (2n=64), three cultivated varieties *viz.,* A1, 'Nira', and 'Manjira' and seven genotypes namely, 96-506-1-21, SFS-9990, JSI-116, PI 537598, EC 543318, 1831-P8 and GMU-2484 belonging to cultivated species, *C. tinctorius* (2n=24) and six inbred lines derived from crosses between *C. tinctorius* (A1, 'Manjira' and 'Nira') and four wild species *viz., C. oxyacantha, C. palaestinus, C. glaucus* and *C. turkesthanicus* were planted at research farm of ICAR-Indian Institute of Oilseeds Research (ICAR-IIOR), at ICRISAT, Patancheru, Hyderabad, India (17.366°N and 78.478°E) during the post rainy winter season (October) in the year 2010. The experimental materials were grouped into cultivated species, wild species and interspecific inbred lines for convenience of comparison of results between the groups. Each experimental material was grown in two rows of 5 m length in six replications following the complete randomized block design (CRBD). The spacing between rows was 45 cm and between plants was 20 cm. The soil of experimental plot was Vertisols; fertilizers were applied as per the recommendation and need based plant protection measures were adopted. The crop was raised under receding soil moisture as normal practice and no irrigation was provided. The maximum temperature during crop period (October 2010- February 2011) has ranged from 28-35.6°C and the minimum was between 11.2-22.6°C. The relative humidity was between 91 and 97%, and the total rainfall received during the crop period was 204 mm.

The hybrid nature of the six interspecific inbred lines used in the present study was primarily confirmed through examining the morphological traits in F_1 generation. These traits were intermediate to both wild and cultivated species confirming introgression of genome from both parents in F_1 background. The hybrid nature of F_1 of each cross was further confirmed through genotyping of wild and cultivated species parents and F_1 using SSR markers (Anjani *et al.*, 2011; Anjani *et al.*, 2018).

Gas exchange parameters: Physiological parameters such as net photosynthesis (Pn, µ mol/m^2/s), stomatal conductance (gs, mol/m^2 /s), leaf intercellular CO$_2$ concentration (Ci, µ mol CO^2 /mol), transpiration (E, m mol/m^2/s) were recorded at full flowering stage using portable IRGA i.e., photosynthesis system (LICOR-6400-40 Fluorometer) and intrinsic water use efficiency (iWUE, µ mol/m^2/s/m mol/m^2/s^1) was calculated as ratio of Pn to E and carboxylation efficiency was calculated as ratio of Pn to Ci. Gas exchange measurements were made between 11:00 and 13:00h of IST on cloud free sunny days using six replicates for each test material at 45 days after planting. For measuring Pn, gs, Ci and E, photosynthetic leaf chamber (2 inch) was clipped onto fully expanded leaf, which had been exposed to sunlight. The chamber was held in such an angle that the enclosed leaf surface faced the sun, to avoid the shading inside the curette. Photosynthetic active radiation (PARi) at the upper surface of the leaf chamber was measured by calibrated sensor mounted on the same surface of the leaf chamber. It varied between 1150 and 1350 µ mol/m^2/s during the most Pn measurements. Atmospheric CO$_2$ was 400ppm, ambient temperature was 34 to 36°C and RH was 55 to 60% recorded during gas exchange measurements.

Statistical analysis: The aggregate mean values were subjected to statistical analysis. The essential statistics like variance and coefficient of variation were calculated using the method described by Panse and Sukhatme (1964). The analysis of variance was analysed using complete randomized block design (CRBD) to understand the significance levels. The Pearson correlation coefficients in Carthamus wild species, cultivated species (*C. tinctorius*), and interspecific inbred lines was also estimated. The diagonal histogram and scatter plots of bivariate correlation were developed using R statistical programming language (R-3.5.2 win) in an integrated development environment (RStudio-1.0.143). The simple graphical representation of mean values was developed using MS Office Excel 2007 programme (www.microsoft.com) where Carthamus wild species (W), cultivated species, *C. tinctorius* (C) was taken on X-axis and photosynthetic traits such as Pn: net photosynthesis; gs: stomatal conductance; Ci: leaf intracellular CO$_2$ concentration; E: transpiration; iWUE:

intrinsic water use efficiency; Pn/Ci: carboxylation efficiency were taken on Y-axis.

RESULTS AND DISCUSSION

Gas exchange traits: The Carthamus wild species, cultivated species (*C. tinctorius*), and interspecific inbred lines were evaluated for photosynthetic traits and analysis of variance indicated significant variation for gs, Pn, and Pn/Ci (Table 1). The mean data on various photosynthetic parameters observed in wild and cultivated species and interspecific inbred lines are illustrated in Table 2 and in Figure 1. The Pn ranged from 55.68±0.75 to 65.48±1.55 μ mol/m^2/s^1 among wild species with a mean of 62.17 μ mol/m^2/s^1 and 39±0.63 to 51.17±0.13 μ mol/m^2/s^1 among cultivated species genotypes with a mean of 46.08 μ mol/m^2/s^1. Among interspecific inbred lines, Pn was between 47.50±0.49 and 60.44±0.62 μ mol/m^2/s^1 with a mean of 54.09 μ mol/m^2/s1. The per se performance of Pn was higher in wild species followed by interspecific lines, indicating that the trait might have been inherited from wild in these interspecific lines. Furthermore, stomatal conductance (gs) was between 0.12±0.02 and 0.38±0.09 mol/m^2/s^1 among wild species with a mean of 0.25 mol/m^2/s^1 and between 0.08±0.01 and 0.18±0.03 mol/m^2/s^1 among cultivated species with a mean of 0.13 mol/m^2/s^1. In case of interspecific inbred lines, gs ranged from 0.04±0.01 to 0.18±0.04 mol/m^2/s^1 with a mean 0.12 mol/m^2/s^1. The Transpiration rate (E) ranged from 5.68±0.56 to 12.81±1.42 μ mol/m^2/s^1 among wild species and 4.89±0.58 to 12.03±1.03 μ mol/m^2/s^1 among cultivated species genotypes while it was between 2.71±0.56 and 8.46±1.53 μ mol/m^2/s^1 among interspecific inbred lines. The mean E in interspecific inbred lines group was 6.61 m mol/m^2/s^1 while it was 9.43 m mol/m^2/s^1 and 7.07 m mol/m^2/s^1 in wild and cultivated species groups, respectively. Similar to Pn, a higher gs and E were observed among the wild species; however in cultivated and interspecific lines it was almost similar suggesting that gs and E were not inherited characters from wild in the interspecific lines. Another important photosynthesis related trait, leaf intracellular CO_2 was found higher in wild (321.56 μ mol/m^2/s^1) and cultivated (339.71μ mol/m^2/s^1) groups as compared to that in interspecific inbred lines (168.9 μ mol/m^2/s^1), indicating that wild species maintained a higher intracellular CO_2 which was due to higher gs and E. Together by maintaining a higher gs, E and intracellular CO_2, wild species ensured higher Pn rates compared to interspecific lines and cultivated species. On the other hand, lower gs among the cultivated species might be due to stomatal limitation. The mean carboxylation efficiency of interspecific inbred lines (0.38) was higher than that of wild (0.20) and cultivated species (0.14). The iWUE ranged from 4.90±0.62 to 10.26±1.2 μ mol/m^2/s^1/m mol/m^2/s^1 among wild species with a mean of 6.87 μ mol/m^2/s^1/ m mol/m^2/s^1; whereas from 4.19±0.40 and 9.62±1.07 μ mol/m^2/s^1 /m mol/m^2/s^1 among cultivated species genotypes with a mean of 7.05 μ mol/m^2/s^1 /m mol/m^2/s^1. The mean iWUE of interspecific inbred lines group was 8.46 μ mol/m^2/s1 /m mol/m^2/s^1 with a range of 6.45±1.19 to 25.95±5.0 μ mol/m^2/s^1 /m mol/m^2/s^1. The interspecific lines showed a higher iWUE which attributed to lower E rates indicating their adaptation to warm and dry conditions.

Among wild species, the lowest gs (0.12±0.02 m mol/m^2/s^1) and E (5.68±0.56 m mol/m^2/s^1) and the highest iWUE (10.26±1.2 μ mol/m^2/s^1 /m mol/m^2/s^1) were observed in *C. lanatus* accession, CART 57/83. The interspecific inbred line, A1-57/83, derived from (A1 x CART 57/83) cross showed high iWUE (11.04±0.79 μ mol/m^2/s^1 /m mol/m^2/s^1). The highest gs (0.42±0.08 mol/m^2/s^1) and E (12.81±1.42 m mol/m^2/s^1) and the lowest iWUE (4.9±0.62 μ mol/m^2/s^1 /m mol/m^2/s^1) were observed in *C. creticus* accession, CART 10/79.

Among the interspecific inbred lines, the highest Pn (62.13±0.39 μmolm^{-2}s^{-1}) and iWUE (25.95±5.0 μ mol/m^2/s^1 /m mol/m^2/s^1) and the lowest gs (0.04±0.01 mol/ m^2/s) and E (2.71±0.56 m mol/m^2/s^1) were observed in the interspecific inbred line, A1-63/79 derived from (A1 x CART 63/79) cross. The interspecific inbred line, Man-63/79 derived from (Manjira x CART 63/79) cross also recorded higher Pn (53±0.67 μ mol/m^2/s^1) and iWUE (10.38 ±1.6 μ mol/m^2/s^1 /m mol/m^2/s^1) as compared to its cultivated species parent. The wild species parent (*C. turkesthanicus* accession, CART 63/79) of A-63/79 and Man-63/79 had very high Pn and iWUE compared to cultivated species parents, A1 and 'Manjira'.

Correlations among traits: Correlations among physiological traits were studied separately for wild species, cultivated species and interspecific inbred lines (Fig.2). Pn had negative association with Ci and iWUE and positive relation with gs and E in wild and cultivated species while it had significantly strong positive association with Ci and iWUE and negative relation with gs and E in interspecific inbred lines. The stomatal conductance (gs) showed significantly strong positive relation with E and negative relation with Ci and iWUE in all three categories of experimental material i.e. wild and cultivated species and interspecific inbred lines. Ci had negative association with E and positive association with iWUE while E had significantly strong negative association with iWUE in all three groups.

Previous studies suggested that the wild species could act as potential donors of physiological traits in rice and other crops (Zhao *et al.,* 2008; Dutra *et al.,* 2011). Investigating physiological parameters in wild species and information on inheritance of physiological traits from wild to cultivated species would help in improving resource-use efficiency in modern cultivars. Clear differences in physiological traits have been reported earlier among many crop species and their wild relatives as well as among the progenies derived from crosses between cultivated and wild species (Dornhoff and Shibles, 1970; Criswell and Shibles, 1971; Zhao *et al.,* 2008; Zhao *et al.,* 2010; Haritha *et al.,* 2019).

Table 1 Analysis of variance of among wild, cultivated species and interspecific inbred lines for photosynthetic traits

Traits	DF	SS	MSS	F value	Pr(>F)
Pn	5	338.4	338.4	7.225	0.0129*
gs	5	361.6	361.6	6.041	0.0216*
Ci	5	5.6	5.59	0.075	0.787
E	5	225.4	225.4	3.44	0.076
iWUE	5	66.6	66.55	0.923	0.346
Pn/Ci	5	627.8	627.8	12.88	0.00148**

*0.05 and **0.01 significance level. Pn: Net photosynthesis, gs: stomatal conductance, Ci: leaf intracellular CO2, E: transpiration, iWUE: intrinsic water use efficiency and Pn/Ci: carboxylation efficiency

Table 2 Net photosynthesis (Pn), stomatal conductance (gs), leaf intracellular CO_2 (Ci), transpiration (E), intrinsic water use efficiency (iWUE) and carboxylation efficiency (Pn/Ci) in wild and cultivated species and interspecific inbred lines

Genotype	Identity code/name	Pn (μmolm^{-2}s^{-1})	gs (molm^{-2}s^{-1})	Ci (μmolCO$_2$mol^{-1})	E (mmolm^{-2}s^{-1})	iWUE (μmolm^{-2}s^{-1}/mmolm^{-2}s^{-1})	Pn/ Ci
Wild species							
C. lanatus	CART 7/77	62.13±0.70	0.25±0.02	321.58±0.84	9.57±0.36	6.49±0.23	0.19
	CART 65/76	64.92±0.65	0.38±0.09	317.55±0.93	11.05±0.87	5.88±0.48	0.20
	CART 57/83	55.68±0.75	0.12±0.02	331.67±1.02	5.68±0.56	10.26±1.2	0.17
C. creticus	CART 10/79	62.72±1.66	0.42±0.08	319.30±2.26	12.81±1.42	4.90±0.62	0.20
C. glaucus	CART 43/76	63.10±1.47	0.19±0.03	320.31±2.00	8.95±0.85	7.05±0.55	0.20
C. oxyacantha	2563-p9-p2	65.30±1.18	0.23±0.03	317.30±1.50	9.76±0.89	6.69±0.84	0.21
	IP-16	62.30±0.35	0.14±0.01	320.66±0.96	7.10±0.24	8.81±0.31	0.19
C. turkesthanicus	CART 63/79	63.50±1.10	0.18±0.04	320.30±1.77	7.80±1.25	8.14±2.36	0.20
	CART 66/76	60.28±1.66	0.26±0.07	324.47±2.49	9.90±1.69	6.09±0.97	0.19
C. palaestinus	PI 235663		0.19±0.04	318.12±2.40	7.83±1.50	8.36±3.59	0.21
Cultivated species							
C. tinctorius	A1	40.27±1.92	0.18±0.03	350.34±1.93	7.06±1.33	5.70±0.87	0.11
	'Manjira'	42.63±0.90	0.09±0.01	340.36±1.19	5.43±0.60	7.94±0.83	0.14
	'Nira'	49.37±1.70	0.17±0.04	334.98±3.36	8.86±1.00	5.80±0.85	0.16
	96-506-1-21	39.00±0.63	0.17±0.03	350.61±0.80	7.02±1.04	5.78±0.76	0.11
	SFS-9990	42.77±0.62	0.10±0.01	347.05±0.80	5.22±0.34	8.26±0.56	0.12
	JSI-116	48.77±0.66	0.08±0.01	338.63±0.86	5.39±0.43	9.16±0.67	0.14
	PI 537598	45.80±0.46	0.08±0.01	342.83±0.76	4.89±0.58	9.62±1.07	0.13
	EC 543318	51.17±0.13	0.16±0.01	334.23±0.14	8.82±0.13	5.80±0.10	0.15
	1831-P8	50.50±0.74	0.18±0.02	323.08±1.22	12.03±1.03	4.19±0.40	0.16
	GMU-2484	50.53±0.43	0.09±0.02	336.15±0.89	6.06±0.89	8.64±1.03	0.15
Interspecific inbred lines							
A1 x CART 63/79	A1-63/79	62.13±0.39	0.04±0.01	308.10±4.94	2.71±0.56	25.95±5.0	0.20
A1 x CART 57/83	A1-57/83	60.44±0.62	0.10±0.01	251.46±6.30	5.60±0.44	11.04±0.7	0.24
Manjira x CART 63/79	Man-63/79	53.42±0.67	0.11±0.03	163.65±4.30	6.09±1.23	10.38±1.6	0.20
Nira x IP16	Nira-IP16	51.80±0.26	0.14±0.03	122.00±3.01	6.96±0.91	7.82±0.74	0.42
A1 x CART 43/76	A1-43/76	49.26±0.19	0.13±0.02	100.13±2.02	6.81±0.70	7.54±0.76	0.49
Manjira x CART 43/76	Man-43/76	47.50±0.49	0.18±0.04	68.07±1.65	8.46±1.53	6.45±1.19	0.70

±: standard error of mean

The present investigation showed within and between species variation for photosynthetic traits. Safflower wild species recorded higher Pn than the cultivated species. Higher photosynthesis in wild species than the modern cultivars was reported in other crop species also (Evans and Dunstone, 1970; Pradhan and Panda, 2018; Masumoto *et al.,* 2004; Zhao *et al.,* 2010). The high net photosynthesis ability of wild species is encouraging to exploit wild species for improving cultivated safflower for photosynthetic efficiency. Enhancing photosynthesis has a vital role in enhancing yield potential of crops (Long *et al.,* 2015). Recent progress in breeding for seed yields in cereal crops was mostly associated with photosynthetic parameters (Fischer and Edmeades, 2010). There were reports of introgression of high photosynthesis efficiency of wild species into cultivated rice (Zhao *et al.,* 2003; Haritha *et al.,* 2017).

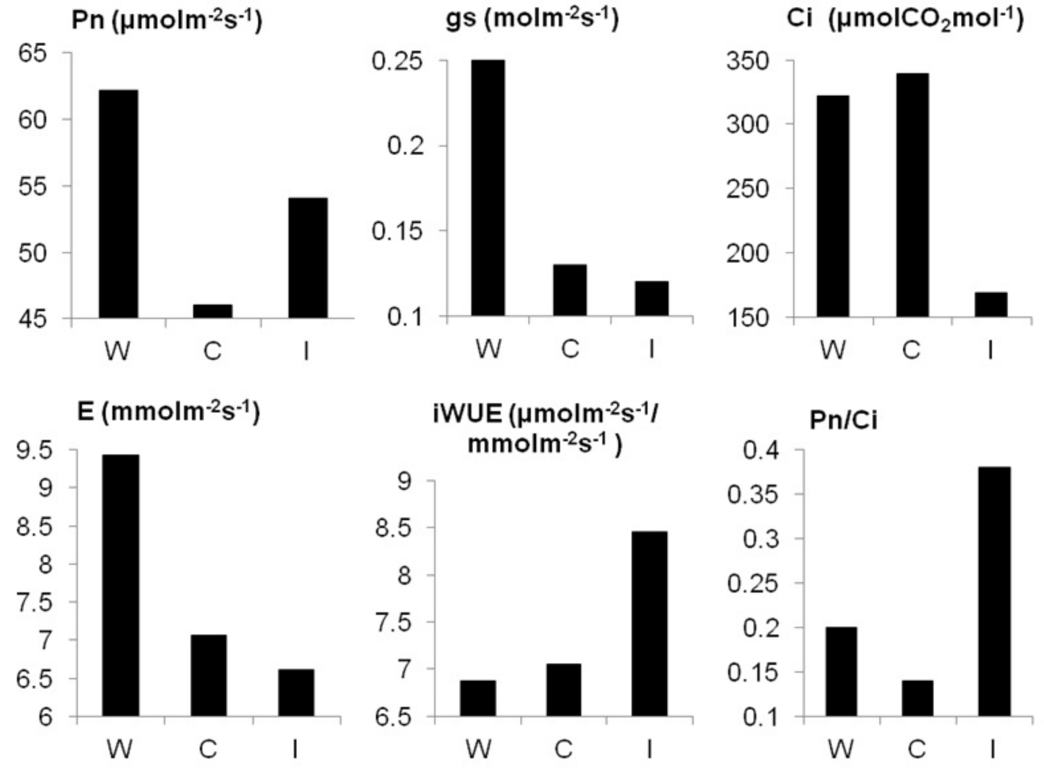

Fig. 1. Mean values of physiological traits in Carthamus wild species (W), cultivated species, C. Tinctorius (C) and interspecific inbred lines (I). Pn: net photosynthesis; gs: stomatal conductance; Ci: leaf intracellular CO_2 concentration; E: transpiration; iWUE: intrinsic water use efficiency; Pn/Ci: carboxylation efficiency

Many studies reported positive linear correlations among Pn, gs and E (Evans and Loreto, 2000; Sergiu *et al.,* 2014; Pushp, 2015). Similar positive correlations were observed in wild and cultivated species but in interspecific inbred lines Pn was negatively related to gs and E whereas gs and E were positively related. The negative relation between Pn and E was because of positive relation between gs and E.

The strong positive association of Pn with iWUE and Ci in interspecific inbred lines differed from those observed in wild and cultivated species where the relations were negative. iWUE showed strong negative relationship with gs and E, which indicated regulatory role of stomatal conductance in maintaining the water use efficiency. The association of Pn in interspecific inbred lines was strongly negative with E and gs and positive with iWUE. The negative relation of Pn with gs and E and its positive relation with iWUE and Ci in interspecific inbred lines hint at the possibility of developing high yielding drought tolerant varieties through wide hybridization in safflower.

The highest iWUE (25.95±5.01 μ mol/m^2/s^1 /m mol/m^2/s^1) observed in the interspecific inbred line, A1-63/79 derived from (A1 x CART 63/79) cross was due to high Pn (62.13±0.39 μ mol/m^2/s^1), low gs (0.04±0.01) and low E (2.71±0.56 m mol/m^2/s^1). Similar results were also reported in tomato species and interspecific lines (Zeist *et al.,* 2018). The interspecific inbred lines *viz.,* Man-63/79 and A1-57/83 also had high iWUE and low E. The low E in these inbred lines might be due to low stomatal conductance because the relation of E with gs was strongly positive. High Pn associated with low gs was observed in water stress tolerant plants which had higher iWUE (Pazzagli *et al.,* 2016). Borba *et al.* (2017) reported high Pn and low gs and E, and better water use efficiency in F_2BC1 population of *Solanum pennellii* x *S. lycopersicum* cross. Both A1-63/79 and Man-63/79 were better than their respective parents with respect to iWUE. They were better than their cultivated species parents and close to their wild species parent (*C. turkesthanicus*, accession CART 63/79) with respect to net photosynthesis. The low E, high iWUE and high net photosynthesis capability of *C. lanatus* accession, CART 57/83 have been introgressed into the interspecific inbred line, A1-57/83 derived from (A1 x CART 57/83) cross. The high Pn, low E and high iWUE make the inbred lines capable of tolerating water stress. High Pn, low gs and low E were found to be promising in selecting water stress tolerant tomato genotypes (Borba *et al.,* 2017, Zeist *et al.,* 2018). Selection for increased photosynthetic efficiency *per se* was mostly successful in maize (Crosbie *et al.,* 1977).

The results of our experiment indicate the opportunity that exists for safflower improvement for gas exchange traits and iWUE through exploiting the gene pools of wild relatives. Inclusion of wild species in breeding may enhance genetic variation and help in selecting progenies with better recombinants for desirable physiological traits. The results have demonstrated introgression of high Pn, low E and high iWUE characteristics of the wild species, *C. lanatus* and *C. turkesthanicus* into cultivated species, and occurrence of better recombinants for these traits in interspecific inbred lines derived from crosses between these species and cultivated one. High Pn and low E will have apparent positive effects on iWUE improvement. E and iWUE directly influence yield, any increase in E would have a negative effect in crop growth rate, and this negative impact can be reduced by selecting for high Pn. So it is necessary to select genotypes where interdependence between iWUE and E is lower. Among the several adoptive strategies, improving the efficiency of water use for biomass production along with photosynthetic rate is perhaps the most relevant mechanism for achieving optimum productivity under drought. This study suggests utilization of *C. lanatus* and *C. turkesthanicus* for developing drought tolerant safflower cultivars.

ACKNOWLEDGEMENTS

The authors acknowledge the data analysis support received from Dr B B Pandey and technical support received from Mr. K. Sayendra, Technical Officer during conduction of the experiments at research farm of ICAR-Indian Institute of Oilseeds Research (IIOR), Hyderabad, India.

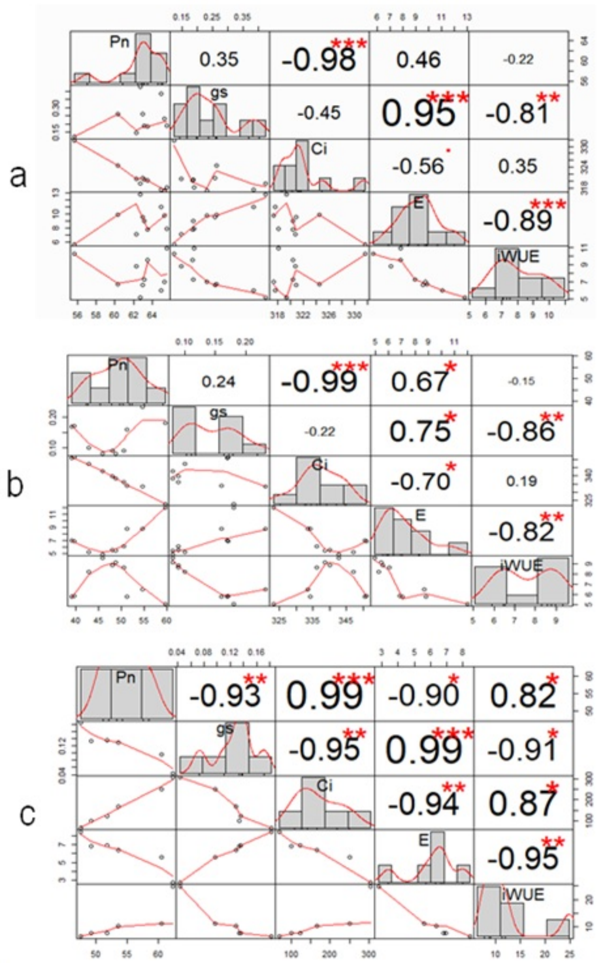

Fig. 2. Pearson correlation coefficients in a) Carthamus wild species, b) cultivated species (*C. tinctorius*), and c) interspecific inbred lines. Significance of correlations among pairs of physiological traits are indicated above the diagonal. The size of asterisk is proportional to significance level. Histograms of each trait are shown on the diagonal, and scatter plots of bivariate correlation among pairs of traits are shown below the diagonal histograms

REFERENCES

Anjani K 2018. Development of cytoplasmic?genic male sterility in safflower. *Plant Breeding* **124**(3): 310-312. https://doi.org/10.1111/j.1439-0523.2005.01089.x.

Anjani K, Bhavna P, Mishra D and Prasad R D 2018. Identification of simple sequence repeat markers linked to Fusarium wilt (*Fusarium oxysporum* f.sp. *carthami*) resistance and marker assisted selection for wilt resistance in safflower *(Carthamus tinctorius* L.) interspecific off springs. *Plant Breeding* **137**(6):895-902. https://doi.org/ 10.1111/pbr.12636.

Anjani K, Ramayya P J and Kumar M V 2011. Molecular differentiation of Fusarium wilt resistant wild and cultivated species of safflower. *International Symposium Genomics of Crops, Medicinal Plants and Microbes*, 29-31 May 2011, KAU, Thiruvananthapuram.

Anjani K and Pallavi M 2006. Cryptic genomic exchange between cultivated safflower (*Carthamus tinctorius* L.) and wild species *C. glaucus, M.Bieb* subsp. *anatolicus* (Bioss). -*Proc. of Second National Plant Breeding Congress.* Indian Society of Plant Breeders; TNAU, Coimbatore, India. pp. 187-193.

Anjani K, Pallavi M and Prasad R D 2007. Transmission and expression of resistance to Alternaria leaf spot in a cross between *Carthamus palaestinus* x *C. tinctorius*. In *'Extended Summary: National Seminar on Changing Global Vegetable Oils Scenario: Issues and Challenges Before India*; Hyderabad, India, pp. 56-57.

Anjani K, Yadav W S and Duhoon S S 1999. Safflower germplasm collecting in northwestern India. IPGRI Newsletter for Asia. *The Pacific and Oceania,* **28**: 8-9.

Ashri A and Knowles P F 1960. Cytogenetics of safflower (*Carthamus* L.) species and their hybrids. *Agronomy Journal*, **52**(1): 11-17.

Ashri A and Rudich J 1965. Unequal reciprocal natural hybridization rates between two *Carthamus* L. species. *Crop Science* **5**(2): 190-191.

Bassiri A and Sionit N 1975. Emergence and seedling growth of a cultivated and a wild strain of safflower under various amounts of simulated rainfall. *Physiolgia Plantarum*, **34**: 226-229.

Borba M E A, Maciel G M and Fraga Junior E F 2017.Gas exchanges and water use efficiency in the selection of tomato genotypes tolerant to water stress. *Genetics and Molecular Research*, **16**(2): 1-9.

Criswell J G and Shibles R M 1971. Physiological basis for genotypic variation in net photosynthesis of oat leaves. *Crop Science,* **11**(4): 550-553. https://doi.org/10.2135.

Crosbie T M, Mock J J and Pearce R B 1977. Variability and selection advance for photosynthesis in Iowa Stiff Stalk Synthetic maize population. *Crop Science*, **17**(4): 511-514. Doi: https://doi.org/10.2135/cropsci1977.0011183X001700040007x.

Dornhoff G M and Shibles R M 1970.Varietal differences in net photosynthesis of soybean leaves. *Crop Science,* **10**: 42-45. https://doi.org/10.2135/cropsci1970.0011183X 001000010016x.

Dutra W F, Guerra Y L, Ramos J P C, Fernandes P D, Silva C R C, Bertioli D J and Santos R C 2018. Introgression of wild alleles into the tetraploid peanut crop to improve water use efficiency, earliness and yield. Plos One. https://doi.org/10.1371/journal.pone.0198776.

Evans L T and Dunstone R L 1970. Some physiological aspects of evolution in wheat. *Australian Journal of Biological Sciences,* **23**(4): 725-741. https://doi.org/10.1071/BI9700725.

Fischer R A and Edmeades G O 2010. Breeding and cereal yield progress. *Crop Science,* **50**: 585-598. https://doi.org/10.2135/cropsci2009.10.0564.

Haritha G, Vishnukiran T and Yugandhar P 2017. Introgressions from Oryzarufipogon increase photosynthetic efficiency of KMR3 rice lines. *Rice Science,* **24**: 85-96. https://doi.org 10.1016/j.rsci.2016.07.006.

Haritha G, Vishnukiran T and Rao Y V 2019.Characterization of *Oryza nivara* introgression lines: A potential prebreeding resource to improve net photosynthetic rate in elite cultivars of rice. *Photosynthetica,* **57**(1): 47-60.doi: 10.32615/ps.2019.003.

Heaton T C and Klisiewicz J M 1981. A disease-resistant safflower alloploid from *Carthamus tinctorius* L. *Canadian Journal of Plant Sciences*, **61**: 219-224.

Knowles P F 1980. *Safflower-Hybridization of crop plants.* Fehr W Rand Hadley H H (Eds.), ASA-CSA, Madison, WI, pp. 535-547.

Long SP, Marshall-Colon A, Zhu XG 2015. Meeting the global food demand of the future by engineering crop photosynthesis and yield potential. *Cell,* **161**(1):56-66. https://doi.org/10.1016/j.cell.2015.03.019

Long S P, Xin-Guang Z and Naidu S L 2006. Can improvement in photosynthesis increase crop yields?. *Plant Cell and Environment,* **29**(3): 315-330. https://doi.org/10.1111/j.1365-3040.2005.01493.x.

Majidi M M, Tavakoli V and Mirlohi A 2011. Wild safflower species (*Carthamus oxyacanthus* Bieb.): A possible source of drought tolerance for arid environments. *Australian Journal of Crop Science*, **5**(8): 1055-1063.

Masumoto C, Ishii T and Kataoka S 2004. Enhancement of rice leaf photosynthesis by crossing between cultivated rice, *Oryza sativa,* and wild rice species, *Oryza rufipogon. Plant Production Sciences,* **7**(3): 252-259. https://doi.org/10.1626/pps.7.252.

Mayerhofer M, Mayerhofer R and Topinka D 2011. Introgression potential between safflower (*Carthamus tinctorius*) and wild relatives of the genus Carthamus. *BMC Plant Biology,* **11**: 47-53. https://doi.org/10.1186/1471-2229-11-47.

Neelima S, Prabhakar K and Ramanamma K V 2021. Genetic variability, heritability, association and divergence studies in safflower (*Carthamus tinctorius* L.) genotypes. *Journal of Oilseeds Research*, **38**(3): 265-269.

Pallavi M, Prasad R D and Anjani K 2007. Novel sources of resistance to Fusarium wilt in Carthamus species. In: *Extended summaries, National seminar on changing global vegetable oil scenario: issues and challenges before India.* 29-31 January 2007, Indian Society of Oilseeds Research, Hyderabad, India.

Pandey B B, Ratnakumar P, Usha K B, Dudhe M Y, Lakshmi G S, Ramesh K and Guhey A 2021. Identifying traits associated with terminal drought tolerance in sesame (*Sesamum indicum* L.) genotypes. *Frontiers in Plant Science.* https://doi.org/10.3389/fpls.2021.739896.

Pazzagli P T, Weinerb J and Liua F 2016. Effects of CO2 elevation and irrigation regimes on leaf gas exchange, plant water relations, and water use efficiency of two tomato cultivars. *Agricultural Water Management,* **169**:26-33. https://doi.org/10.1016/j.agwat.2016.02.015

Panse V G and Sukhatme P V 1964. *Statistical Methods for Agricultural Workers.* 2nd Eds. ICAR, New Delhi.

Pradhna B and Panda D 2018. Variation of photosynthetic characteristics and yield in wild and cultivated species of yams (*Dioscorea* spp.) from Koraput, India. *Photosynthetica*, **56**: 1010-1018. https://doi.org/10.1007/s11099-018-0823-7.

Prasad R D and Anjani K 2008. Sources of resistance to Alternaria leaf spot among Carthamus wild species. In: Safflower: Unexploited potential and world adaptability, Knights S E and Potter T D (Eds). *Proceedings of the 7th International Safflower Conference*, Wagga New South Wales, Australia.

Pushp S 2015. Relationship of photosynthesis and related traits to seed yield in oilseed *Brassicas. Journal of Applied and Natural*

Sciences, **7**(2): 851-856. https://doi.org/10.31018/jans.v7i2.695

Rajesh K, Swamy K N and Rao Y V 2016. Gas exchange, carbon balance and stomatal traits in wild and cultivated rice (*Oryza sativa* L.) genotypes. *Acta Physiolgia Plantarum*, **38**: 160. https://doi.org/10.1007/s11738-016-2173-z.

Sabzalian M R, Saeidi G and Mirlohi A 2010. Wild safflower species (*Carthamus oxyacanthus*): A possible source of resistance to the safflower flies (*Acanthiophilus helianthi*). *Crop Protection,* **29**(6): 550-555. Doi:10.1016/j.cropro.2009.12.013.

Schank S C and Knowles P F 1964. Cytogenetics of pairs of hybrids of Carthamus species (Compositae). *American Journal of Botany*, **51**(10):1093-1102. https://doi.org/ 10.1002 / j. 1537-2197.1964.tb06739.x.

Sergiu A, Emil C, Marin F C and Irina A 2014. Correlation of stomatal conductance with photosynthetic capacity of six walnut cultivars from the national assortment. *South Western Journal of Horticulture Biology Environment*, **5**(1): 1-10.

Sravanthi A L, Ratnakumar P, Reddy S N, Eswari K B, Pandey B B, Manikanta Ch L N, Ramya K T, Sonia E, Mohapatra S, Gopika K, Anusha PL and Yadav P 2021. Morpho-physiological, quality traits and their association with seed yield in sesame (*Sesamum indicum* L.) indigenous collection under deficit moisture stress. *Plant Physiology Reports,* **27**: 132-142. https://doi.org/10.1007/s40502-021-00621-0.

Zeist A R, Resende J T V and Faria M V 2018. Photosynthetic characteristics in species and interspecific hybrids of tomato. *Horticulture Brasileira*, **36**(3): 362-370.

Zhao M, Ding Z and Lafitte R 2010. Photosynthetic characteristics in Oryza species. *Photosynthetica*, **48**(2): 234-240. https://doi.org/10.1007/s11099-010-0029-0.

Zhao M, Lafitte H R and Sacks E 2008. Perennial O. sativa × O. rufipogon interspecific hybrids: I. Photosynthetic characteristics and their inheritance. *Field Crops Research,* **106**(3): 203-213. Doi: 10.1016/j.fcr.2007.12.005.

Zhao X Q, Zhao M and Xiao J T 2003. Stomatal characteristics of leaves of high-photosynthetic efficiency progenies from a cross between *Oryza sativa* and *Oryza rufipogon* and their parents. *Acta Agronomica Sinica*, **29**: 216-222.