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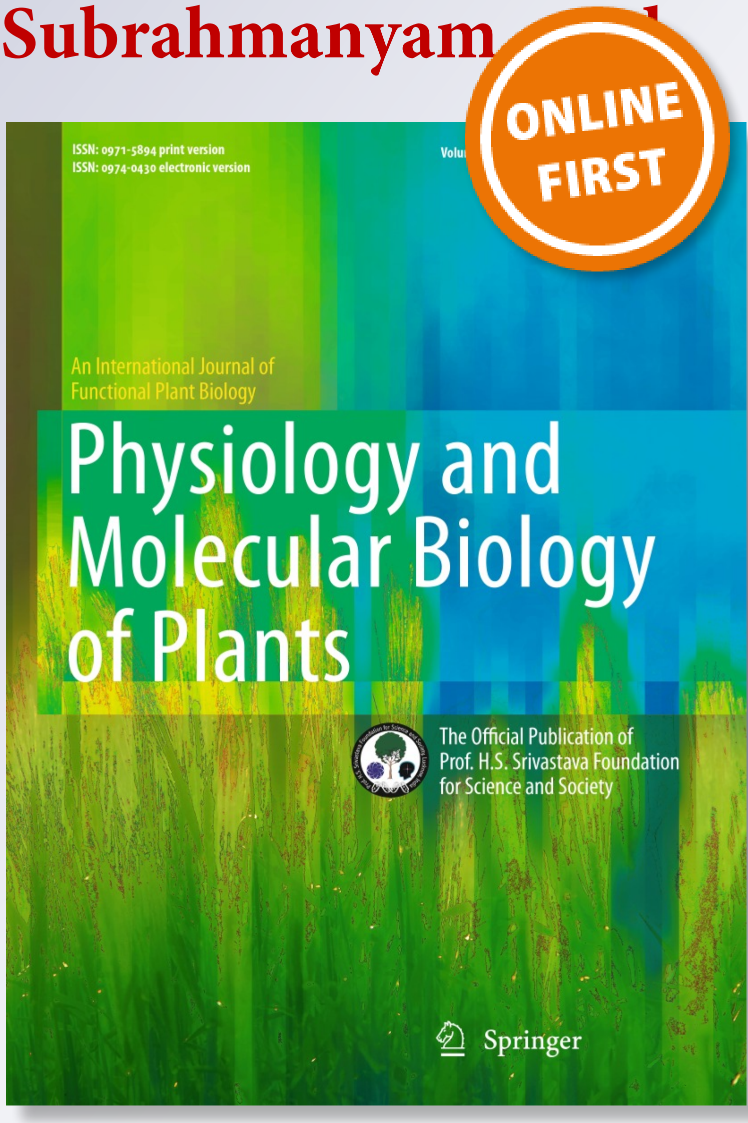

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RESEARCH ARTICLE

Characterization of backcross introgression lines derived from *Oryza nivara* accessions for photosynthesis and yield

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Abstract Improvement of photosynthetic traits is a promising strategy to break the yield potential barrier of major food crops. Leaf photosynthetic traits were evaluated in a set of high yielding *Oryza sativa*, cv. Swarna × *Oryza nivara* backcross introgression lines (BILs) along with recurrent parent Swarna, both in wet (Kharif) and dry (Rabi) seasons in normal irrigated field conditions. Net photosynthesis (P_N) ranged from 15.37 to 23.25 μmol (CO_2) m^{-2} s^{-1} in the BILs. Significant difference in P_N was observed across the seasons and genotypes. Six BILs showed high photosynthesis compared with recurrent parent in both seasons. Chlorophyll content showed minimum variation across the seasons for any specific BIL but significant variation was observed among BILs. Significant positive association between photosynthetic traits and yield traits was observed, but this association was not consistent across seasons mainly due to contrasting weather parameters in both seasons. BILs 166s and 248s with high and consistent photosynthetic rate exhibited stable high yield levels in both the seasons compared to the recurrent parent Swarna. There is scope to exploit photosynthetic efficiency of wild and weedy rice to identify genes for improvement of photosynthetic rate in cultivars.

Keywords BILs · *Oryza nivara* · Photosynthesis · Seasonal variation · Yield

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Abbreviations

Chl a	Chlorophyll a content (mg g^{-1} fresh mass)
Chl b	Chlorophyll b content (mg g^{-1} fresh mass)
Chl a + b	Total chlorophyll content (mg g^{-1} fresh mass)
P_N	Net photosynthetic rate per unit leaf surface area (μmol CO_2 m^{-2} s^{-1})
C_i	Internal CO_2 concentration (μmol CO_2 mol^{-1})
E	Transpiration rate per unit leaf surface area (mmol H_2O m^{-2} s^{-1})
g_s	Stomatal conductance (mol H_2O m^{-2} s^{-1})
P_N/C_i (CE)	Carboxylation efficiency (μmol CO_2 mol^{-1} air)
P_N/E (WUE)	Water use efficiency (μmol CO_2 $mmol^{-1}$ H_2O)
P_N/g_s ($_i$WUE)	Intrinsic water use efficiency (μmol CO_2 mol^{-1} H_2O)

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SLA	Specific leaf area (cm_2 mg^{-1})
SLM	Specific leaf mass (mg cm^{-2})
TDM	Total dry matter (g $plant^{-1}$)
HI	Harvest index (%)

Introduction

The need to increase productivity is a major challenge faced by agriculture. In case of rice, the maximum yield per unit area has remained constant while the rate of grain production is decreasing every decade (Mann 1999). Yields per hectare across the major rice producing countries showed an average 36% improvement from 1970 to 1980; however, the rate of increase was only 7% from 2000 to 2010 (Long 2014). Over the past 50 years, harvest index of crop genotypes has improved but the conversion efficiency of solar energy is far less. Therefore, more focus has to be given on enhancing the photosynthetic and respiratory rates in order to break the yield potential barrier (Long et al. 2015).

The improved nitrogen use efficiency and management practices in the past decades enhanced grain yield but improving photosynthetic efficiency will play a major role in any further increase in the yield potential. Photosynthesis is one of the most important factors that influence biomass and yield and studies on genetics of photosynthesis is very important for physiological breeding of rice (Teng et al. 2004). Xu and Shen (1994) found that leaf photosynthetic rate was correlated with crop yield (Teng et al. 2004). The contribution to biomass from leaf photosynthesis was estimated as 30% (Ohno 1976). It was proposed that augmentation of photosynthetic rate is one of the feasible ways to enhance yield potential in food crops through either conventional breeding or transgenic approaches (Gibson et al. 2011; Ambavaram et al. 2014). Recent progress in breeding for cereal yields were mostly associated with increased photosynthetic parameters (Fischer and Edmeades 2010). Enhancing photosynthesis has a vital role in increasing the genetic yield potential of crops which has high prospective to improve biological production limits (Long et al. 2015). The flag leaves, the second and third leaves from the top of the plant are considered to be functional leaves during grain filling. Studies on the photosynthetic features of flag leaves at grain-filling stage have contributed to understanding their physiological status and the grain production potential of the plant (He et al. 2014). Giuliani et al. (2013) showed that there is diversity of leaf structure related to photosynthesis and transpiration among representative cultivated species and wild relatives in the genus *Oryza*. Thus, wild species or derived lines need to be evaluated for photosynthetic parameters to identify elite lines (Kiran et al. 2013; Haritha et al. 2017).

Identification and utilization of potential donors from wild genotypes for yield traits, input use efficiency, tolerance to biotic and abiotic stresses and utilizing them for gene discovery and crop improvement is a promising strategy (Swamy and Sarla 2008; Gaikwad et al. 2014). Genetic variation for photosynthetic traits is essential for any further yield augmentation and higher photosynthetic rates were also reported from wild species of *Oryza* compared to *O. sativa cultivars* (Zhao et al. 2010; Kiran et al. 2013; Haritha et al. 2017). Masumoto et al. (2004) reported that *O. nivara* and *O. rufipogon* accessions with high P_N are the possible source to increase the photosynthetic ability of *O. sativa*. Among many factors associated with yield, photosynthesis is one of the important processes having significant influence on yield. Several studies identified that wild accessions possess genes or alleles to increase the yield and component traits, although their yield levels are comparatively lower than cultivated species, explaining the scope to explore wild rice species to increase photosynthetic efficiency and thus the yield of cultivars (Yeo et al. 1994; Masumoto et al. 2004; Malathi et al. 2017). Swamy and Sarla (2008) reported stable and consistent major effect yield-enhancing QTLs derived from wild species in several crops. Identification of genes or QTL for photosynthesis parameters is a significant step in enhancing yield due to the key role of photosynthesis in determining crop growth.

Therefore this study was aimed to assess the extent of variation for leaf photosynthesis (P_N) and associated traits in selected *O. sativa* Cv. Swarna × *O. nivara* backcross introgression lines (BILs) at BC_2F_8 generation compared with popular variety and recurrent parent Swarna under irrigated conditions. BILs were grown in two growing seasons viz, Kharif (wet season) and Rabi (dry season) to assess the seasonal variation and to identify the genotypes with high photosynthesis for further use in breeding programme for QTL mapping and yield improvement.

Materials and methods

Plant materials

Backcross introgression lines derived from a cross between an elite cultivar Swarna (*O. sativa)* as a recurrent parent and a wild accession *O. nivara* (IRGC81848) as a donor parent (Swamy et al. 2011) were advanced from BC_2 generation by consecutive self-pollination to obtain BC_2F_8 progenies by single panicle selection. The 14 BILs (14S, 14-3S, 148S, 166S, 166-1, 166-2, 248S, 65S, 70S, 75S, 24K, 250K, 3-1K and 7K) selected based on desirable yield contributing traits along with recurrent parent Swarna were used in this study.

Plant growth conditions

Field experiments were conducted at Indian Institute of Rice Research (IIRR) India, located at 17°19′N and 78°29′E at an altitude of 549 m above mean sea level during two seasons, Wet Season/Kharif-2013 and Dry Season/Rabi-2014 in RCBD (Randomised Complete Block Design) with 3 replications. Crop was grown in alkaline vertisol with a pH of 7.94 at irrigated field conditions. Seeds were sown in nursery beds and 25 days old seedlings were transplanted as single seedling per hill in the field. Each block was represented by 100 plants transplanted in 5 rows of 20 plants adopting a uniform spacing of 20 cm between rows and 15 cm between plants. Standard agronomic practices and need based plant protection measures were implemented during crop growth.

Flag leaf photosynthesis measurement

Leaf photosynthesis was measured in five plants per genotype at the complete heading stage using LI6400XT portable photosynthesis measuring system (LI-COR Environmental, USA). Measurements were done between 11 and 13 h, leaf temperature was kept at 30 °C and PAR was maintained at 1000 μmol m^{-2} s^{-1}. Measurements were made at ambient CO_2 levels (387 ppm). Leaf photosynthetic parameters were recorded once the expanded flag leaf was enclosed in the chamber and the photosynthesis rate reached steady state. The measured photosynthesis parameters were rate of photosynthesis (P_N) [μmol (CO_2) m^{-2} s^{-1}], stomatal conductance (g_s) [mol (H_2O) m^{-2} s^{-1}], transpiration rate (E) [mmol (H_2O) m^{-2} s^{-1}], internal CO_2 concentration (C_i) [μmol mol^{-1}]. From these data, three parameters were derived viz., water use efficiency (P_N/E), intrinsic water use efficiency (P_N/g_s) and carboxylation efficiency (P_N/C_i) used for analysis.

Chlorophyll content determination

The same flag leaves on which leaf photosynthesis was measured in the field were used to estimate chlorophyll content. Leaf photosynthetic pigments were extracted with a mortar and pestle in cold 80% acetone. The extract was centrifuged at 4 °C for 5 min and chlorophyll and carotenoid content were determined spectro-photometrically (Spectra scan UV 2600, Toshniwal Instruments Pvt. Ltd., India) by determining the absorbance at 663.2 nm (Chl a), 646.8 (Chl b), and 470 nm(Car). The pigment concentration was estimated according to Lichtenthaler and Wellburn (1983).

Specific leaf area and specific leaf mass

Specific leaf mass was calculated as the leaf mass to leaf area ratio, and specific leaf area as the inverse of specific leaf mass. LI-3100C electronic leaf area meter (LI-COR Environmental, USA) was used to measure leaf area. Specific leaf area (SLA) and specific leaf mass (SLM) were calculated.

Grain yield

Yield and dry parameters were taken from the same five tagged plants on which photosynthesis was measured. The five plants were collected and oven-dried for 48 h at 80 °C to measure their dry weight.

Weather data

Weather data for the both growing seasons were obtained from Meteorology Department, ANGRAU, Hyderabad on the parameters viz., temperature, relative humidity, rainfall, rainy days, sunshine hours, Wind speed (km h^{-1}), evaporation.

Statistical analysis

The field trial was conducted in a randomized completely block design with three replications. Statistical significance of the trait means were estimated by performing the LSD test and standard deviations (SD) and were carried out using R statistical software (R Core Team 2012). Multiple correlations between leaf photosynthetic traits and related parameters were performed using INDOSTAT software.

Genotyping

Leaf tissues of the BILs and checks were collected from young leaves (20 days after transplantation) for genomic DNA was isolation using CTAB method (Doyle and Doyle 1987). Purity and concentration of DNA was monitored using Nano Drop ND-1000 Spectrophotometer (Wilmington, USA). Genotypes were screened using previously identified microsatellite markers on the QTL regions linked to photosynthesis by Zhao et al. 2008 and Gu et al. 2012, these five markers linked to the Photosynthesis parameters (Supplementary Table 1). PCR reactions were carried out in Thermal cycler (Veriti PCR, Applied Biosystems, USA) with the total reaction volume of 10 μl containing 15 ng of genomic DNA, 1X assay buffer, 200 μM of dNTPs, 1.5 mM $MgCl_2$, 10 pmol of forward and reverse primer and 1 unit of Taq DNA polymerase (Therma Scientific). PCR cycles were programmed as follows: initial denaturation at 94 °C for 5 min followed by 35 cycles of 94 °C for 45 s, 55 °C for 30 s, 72 °C for 45 s and a final extension of 10 min at 72 °C. Amplified products were resolved on 4% metaphor agarose gels prepared in 0.5× TAE buffer and electrophoresis was conducted at 120 V for 2 h. Gels were stained with ethidium bromide and documented using gel documentation system (Alfa imager, USA). Genotyping was conducted on BILs using previously reported markers linked to photosynthetic traits. Amplified fragments were scored for the presence or absence of alleles for each primer genotype combination.

Results

Growing conditions in experiments

Maximum temperature during the crop period in dry season was higher than in wet season, and minimum temperature in wet season was higher than in dry season. In dry season, maximum temperature, sunshine hours, and evaporation were higher than in wet season. In wet season, minimum temperature, relative humidity, rainfall and wind speed were higher. From sowing to harvesting, the mean temperature ranged from 21.40 to 28.25 °C in the wet season. In dry season, mean temperature ranged from 19.05 to 30.81 °C. In dry season, average sunshine hours (8.15 h) were much higher compared with wet season (4.78 h). The net photosynthesis was comparatively higher in the wet season than dry season, with an average of 20.74 and 18.00 [μmol (CO_2) m^{-2} s^{-1}] respectively. Effects of weather parameters on net photosynthesis were noticed from the weather data across the whole crop period (Table 1). The observations on physiological parameters were taken on onset of anthesis between October to November in wet season that are generally cooler months and in April to May in dry season which are the hottest months in the region. Compared to total crop growing seasons, these specific months showed significant difference in weather parameters. The mean temperature during flowering was 24.86 °C in wet season but 30.81 °C during dry season. During anthesis period in wet and dry seasons, mean relative humidity was 86.89 and 77.10, mean rainfall was 168.03 and 33.90 mm, sunshine hours were 4.78 and 8.13 h, wind speed was 5.71 and 2.72 km/h and evaporation was 4.32 and 5.09 mm respectively. The cumulative rainfall was 703 and 223 mm and rainy days were 29 and 13 in wet and dry seasons respectively. These contrasting weather parameters might also influence the variation in photosynthetic traits along with genotypic differences.

Photosynthesis and related characters

Among BILs, mean P_N ranged from 15.37(70S) to 23.25(148S) with an overall mean value of 19.37 [μmol

Table 1 Weather parameters during crop seasons

	Temperature (°C)			R.H. (%)		Rainfall (mm)	Rainy days	Sunshine (Hrs.)	Wind speed (km/Hr)	Evaporation (mm)	Crop stage
	Max.	Min.	Mean Temp.	I	II						
Wet season-2013											
Jul-13	32.64	23.92	28.25	81.83	56.83	150.2	9	4.56	10.55	4.69	Sowing
Aug-13	28.49	21.94	25.21	89.90	75.93	158.1	1	3.39	6.36	4.02	Transplanting
Sep-13	31.05	20.59	25.82	87.07	64.33	110.6	8	5.71	3.05	4.69	Vegetative stage
Oct-13	29.99	19.73	24.86	88.77	63.33	253.2	9	5.45	2.87	3.86	Heading/observations on P_N
Nov-13	28.42	14.38	21.40	86.27	50.43	31	2	6.66	1.72	2.69	Harvesting
Mean	30.54	21.54	26.04	86.89	65.11	168.03	6.75	4.78	5.71	4.32	
Dry season-2014											
Dec-13	28.02	10.09	19.05	83.10	36.58	0	0	8.87	1.75	2.70	Sowing
Jan-14	28.69	13.25	20.97	84.74	40.29	0	0	8.17	2.49	3.07	Transplanting
Feb-14	31.20	16.55	23.88	78.36	32.75	0	0	8.99	2.93	4.62	Vegetative stage
Mar-14	33.23	20.36	26.80	79.58	36.39	56.8	5	7.35	2.69	4.61	Vegetative stage
Apr-14	37.60	22.04	29.82	76.73	36.07	72.6	2	7.72	2.02	6.02	Heading/observations on P_N
May-14	37.74	23.87	30.81	66.10	33.84	40.1	3	8.39	3.47	7.11	Heading/observations on P_N
Jun-14	37.02	24.60	30.81	68.57	45.07	53.6	3	7.90	10.17	8.14	Harvesting
Mean	33.69	19.22	26.45	77.10	35.87	33.90	2.00	8.13	2.72	5.09	

(CO_2) m^{-2} s^{-1}]. Significant variation was observed in mean P_N between Swarna 18.56 [μmol (CO_2) m^{-2} s^{-1}] and BILs (19.37) for both seasons (Table 2). Variation observed for the trait in wet and dry seasons among the BILs was also significant. Many BILs (166S, 65S, 248S, 148S, 75S, 24K, 7K, and 3-1K) showed higher photosynthetic rate than recurrent parent Swarna in wet season. In dry season, eleven BILs showed high photosynthesis compared with Swarna. Stomatal conductance (g_s) ranged from 0.293 (3-1K) to 0.403 (75S) with a mean value of 0.347 [mol (H_2O) m^{-2} s^{-1}] among BILs. Significant difference was observed in both seasons and genotypes. g_s was higher in wet season compared with dry season. In wet season, 166S showed high g_s. In dry season, 148S, 75S, 248S, 14S, 166-2, 7K, 24K and 65S also showed higher g_s than mean of Swarna.

Variation was observed in C_i in both seasons, internal CO_2 concentration was higher in wet season. In BILs, mean C_i ranged from 239 (166-2) to 267 (14-3) with overall mean value of 255 [μmol mol^{-1}]. In wet season, 166-1, 7K, 70S, 14-3, 75S, and 250K showed higher C_i than parent. In dry season, ten lines showed better C_i than Swarna. In both seasons, five BILs showed higher C_i than Swarna. A wide variation in E was also observed in wet and dry seasons. In BILs, mean E ranged from 9.01(70S) to 12.46(65S) with overall mean value of 11.27 [mmol (H_2O) m^{-2} s^{-1}]. In wet season, comparing with parent Swarna, it was found that five lines showed higher E. In dry season, ten lines showed higher E than Swarna. Seven BILs showed higher E compared with recurrent parent mean for both seasons. Significant differences were observed for intrinsic water-use efficiency (P_N/g_s), carboxylation efficiency (P_N/C_i) and water use efficiency (P_N/E) in both seasons (Table 3). Among BILs, the mean WUE_i at both seasons ranged from 51.5 (14-3) to 67.8 (166-2) with a mean value of 58.9. WUE_i was found to be higher in dry season in BILs compared to wet season. The mean *CE* at two seasons ranged from 0.058(70S) to 0.094(148S) with overall mean of 0.077. In BILs, mean WUE ranged from 1.54 (14-3) to 1.95 (148S) with overall mean value 1.74. P_N/E decreased during dry season compared to wet season. Significant differences among genotypes were noticed in both seasons.

Chlorophyll content

The significant variation was observed in the chlorophyll content in both seasons (Table 4). Among BILs, mean total Chlorophyll ranged from 1.40 (3-1K) to 2.24 (148S) with overall mean value 1.78. Chlorophyll b content was low in wet season compared with dry season. The total chlorophyll content also varied appreciably among the tested lines in both seasons. Chl a/b ratio was high in dry season (3.95) compared with wet season (3.65) (Fig. 1).

Leaf traits

Significant difference was noticed in SLA in both the seasons. In BILs, mean SLA ranged from 7K (171.5) to 14S (202.1) with a mean value 183.3. SLA was high in wet season compared with dry season (Fig. 2). SLM is higher in dry season compared with wet season, In BILs, mean SLM ranged from 70S (4.97) to 148S (5.87) with a mean value 5.50.

Grain yield

Grain yield was relatively higher in dry season compared to wet season, significant difference was noticed amongst the BILs (Table 5). The mean grain yield ranged from 9.56 (14-3) to 166S (30.22) with a mean of 20.41. In wet season, nine BILs showed higher grain yield than recurrent parent. In dry season, 166S and 248S showed higher grain yield than Swarna. 166S and 248S performed better in both seasons.

Significant seasonal variation was observed in total dry matter production which was very high in dry season compared to wet season. Total dry matter ranged from 28.96 (14-3) to 60.42 (166S) with overall mean value 47.18. Harvest index is higher in dry season; significant difference was observed in seasons and genotypes. In BILs, mean HI ranged from 33.79 (14-3) to 50.19 (14S) with overall mean value 43.24. The higher grain yield during the dry season might be due to increased dry matter accumulation and harvest index.

Correlation

Pearson's multiple correlation was performed with mean of two seasons and individually performed for both seasons (Table 6). The characters possessed positive significant correlations with Net photosynthesis (P_N), g_s, E, P_N/Ci, P_N/E, SLM and PDP. The relationship between P_N and C_i was negative non significant correlation. g_s showed significant positive association with E, P_N/C_i, SLM, Chl a, Chl b and total chlorophyll content. Yield and related traits like PDP, TDM and HI also showed positive correlation with net photosynthesis. Season wise trait correlations were also studied.

Wet season 2013

The phenotypic correlation performed among the different gas-exchange characteristics and yield traits is shown in Table 7. The net photosynthesis showed positive significant correlation with related traits, E, P_N/C_i, chl b and Chl (a/b). g_s showed positive correlation with photosynthesis. Only two traits, C_i and E were significantly correlated with

Table 2 Variation in leaf photosynthetic characteristics in back cross introgression lines

Entry	Net photosynthetic rate (P_N) [μmol(CO_2) m^{-2} s^{-1}]			Stomatal conductance (g_s) [mmol (H_2O) m^{-2} s^{-1}]		
	Kha-2013	Rabi-2014	Mean	Kha-2013	Rabi-2014	Mean
14-3	17.68 ± 2.9^{klm}	14.31 ± 1.3^{n}	16.00 ± 2.8^{gh}	0.404 ± 0.02^{cdef}	0.241 ± 0.01^{lm}	0.323 ± 0.09^{defg}
148S	22.30 ± 1.5^{abcd}	24.21 ± 1.0^{a}	23.25 ± 1.5^{a}	0.412 ± 0.05^{cdef}	0.357 ± 0.05^{fgh}	0.384 ± 0.06^{ab}
14S	18.95 ± 2.1^{ghijkl}	21.89 ± 1.0^{bcde}	20.42 ± 2.2^{bc}	0.413 ± 0.05^{cdef}	0.312 ± 0.04^{hijk}	0.362 ± 0.07^{abcd}
166-1	17.32 ± 1.4^{lm}	18.77 ± 2.2^{ghijkl}	18.05 ± 1.9^{ef}	0.427 ± 0.06^{bcde}	0.250 ± 0.05^{klm}	0.338 ± 0.05^{bcdefg}
166-2	20.16 ± 0.9^{efghi}	19.42 ± 1.8^{fghijk}	19.79 ± 1.4^{bcd}	0.310 ± 0.04^{hijk}	0.299 ± 0.04^{hijkl}	0.305 ± 0.07^{efg}
166S	23.58 ± 1.4^{ab}	18.65 ± 1.4^{hijkl}	21.12 ± 2.9^{b}	0.501 ± 0.05^{a}	0.241 ± 0.04^{lm}	0.371 ± 0.04^{abc}
248S	22.85 ± 0.7^{abc}	18.60 ± 0.6^{hijkl}	20.73 ± 2.3^{bc}	0.410 ± 0.05^{cdef}	0.317 ± 0.02^{hij}	0.363 ± 0.06^{abcd}
24K	21.06 ± 2.5^{cdef}	18.85 ± 1.1^{ghijkl}	19.96 ± 2.2^{bcd}	0.362 ± 0.08^{efgh}	0.297 ± 0.03^{hijkl}	0.329 ± 0.07^{cdefg}
250K	20.52 ± 1.6^{defgh}	18.83 ± 2.2^{ghijkl}	19.67 ± 2.0^{cd}	0.433 ± 0.05^{bcd}	0.251 ± 0.05^{jklm}	0.342 ± 0.05^{bcdef}
3-1K	20.57 ± 1.6^{defgh}	13.64 ± 2.1^{n}	17.11 ± 4.1^{fg}	0.388 ± 0.06^{defg}	0.198 ± 0.06^{mn}	0.293 ± 0.06^{g}
65S	22.88 ± 1.4^{abc}	17.88 ± 1.5^{jklm}	20.38 ± 3.0^{bc}	0.466 ± 0.06^{abc}	0.281 ± 0.02^{ijkl}	0.374 ± 0.04^{abc}
70S	19.71 ± 1.5^{fghij}	11.02 ± 1.3^{o}	15.37 ± 4.8^{h}	0.427 ± 0.06^{bcde}	0.174 ± 0.04^{n}	0.301 ± 0.05^{fg}
75S	22.14 ± 2.1^{bcde}	18.88 ± 1.4^{ghijkl}	20.51 ± 2.4^{bc}	0.482 ± 0.04^{ab}	0.325 ± 0.02^{ghi}	0.403 ± 0.03^{a}
7K	20.77 ± 2.1^{defg}	18.43 ± 1.1^{ijklm}	19.60 ± 2.0^{cd}	0.450 ± 0.05^{abcd}	0.299 ± 0.03^{hijkl}	0.374 ± 0.04^{abc}
Swarna	20.55 ± 0.7^{defgh}	16.56 ± 0.5^{m}	18.56 ± 2.2^{de}	0.437 ± 0.02^{abcd}	0.259 ± 0.02^{ijklm}	0.449 ± 0.02^{bcde}
Mean	20.74 ± 1.6^{a}	18.00 ± 1.4^{b}	19.37 ± 2.5	0.435 ± 0.09^{a}	0.273 ± 0.04^{b}	0.354 ± 0.11
HSD (entry)	1.43			0.088		
HSD (season)	0.52			0.032		
HSD (entry × season)	2.02			0.125		
CV	8.32			28.12		

Entry	Trasnpiration rate (E) [mmol(H_2O) m^{-2} s^{-1}]			Intercellular CO_2 concentration (C_i) [μmol mol^{-1}]		
	Kha-2013	Rabi-2014	Mean	Kha-2013	Rabi-2014	Mean
14-3	10.1 ± 0.5^{hijk}	10.73 ± 0.9^{fghijk}	10.43 ± 0.7^{e}	283 ± 11.6^{abc}	252 ± 10.4^{fghij}	267 ± 19.6^{a}
148S	11.3 ± 1.1^{defgh}	12.65 ± 0.7^{abcde}	11.99 ± 1.1^{ab}	258 ± 5.0^{efgh}	238 ± 14.3^{ijkl}	248 ± 14.7^{de}
14S	11.2 ± 1.0^{efgh}	13.44 ± 2.0^{ab}	12.34 ± 1.9^{a}	273 ± 6.8^{abcde}	237 ± 14.0^{ijkl}	255 ± 21.9^{bcd}
166-1	10.6 ± 1.0^{ghijk}	11.32 ± 1.9^{defgh}	10.94 ± 1.5^{bcde}	287 ± 3.5^{a}	218 ± 15.8^{m}	252 ± 38.2^{bcd}
166-2	9.5 ± 1.6^{ijkl}	12.14 ± 1.4^{bcdef}	10.81 ± 2.0^{de}	236 ± 31.7^{jkl}	242 ± 16.6^{hijk}	239 ± 24.0^{e}
166S	13.2 ± 1.2^{abc}	10.40 ± 1.5^{ghijk}	11.80 ± 2.0^{abcd}	275 ± 20.5^{abcd}	222 ± 22.6^{lm}	249 ± 34.7^{cde}
248S	11.0 ± 1.2^{fghi}	12.90 ± 0.6^{abcd}	11.93 ± 1.4^{abc}	267 ± 11.4^{cdef}	253 ± 6.8^{fghi}	260 ± 11.5^{abc}
24K	9.4 ± 1.9^{jkl}	12.16 ± 1.3^{bcdef}	10.76 ± 2.1^{de}	264 ± 13.8^{defg}	243 ± 6.4^{hijk}	254 ± 14.8^{bcd}
250K	10.6 ± 1.1^{fghijk}	11.01 ± 2.0^{fghi}	10.83 ± 1.5^{cde}	280 ± 4.8^{abcd}	229 ± 9.8^{klm}	254 ± 27.4^{bcd}
3-1K	10.8 ± 0.7^{fghijk}	9.20 ± 2.2^{kl}	9.98 ± 1.7^{ef}	268 ± 12.9^{bcdef}	228 ± 20.5^{klm}	248 ± 26.4^{cde}
65S	13.0 ± 0.5^{abc}	11.89 ± 0.5^{bcdefg}	12.46 ± 0.8^{a}	264 ± 11.8^{defg}	246 ± 7.7^{hij}	255 ± 13.2^{bcd}
70S	10.1 ± 1.1^{hijk}	7.98 ± 1.8^{l}	9.01 ± 1.8^{f}	284 ± 7.5^{ab}	242 ± 17.5^{hijk}	263 ± 25.4^{ab}
75S	11.7 ± 0.5^{cdefg}	13.02 ± 0.7^{abc}	12.37 ± 0.9^{a}	280 ± 3.8^{abcd}	247 ± 13.7^{ghij}	264 ± 19.5^{ab}
7K	10.9 ± 0.7^{fghij}	13.85 ± 1.4^{a}	12.37 ± 1.9^{a}	285 ± 8.3^{ab}	239 ± 5.0^{ijk}	262 ± 24.9^{ab}
Swarna	11.1 ± 0.5^{fgh}	10.95 ± 0.8^{fghi}	11.01 ± 0.7^{bcde}	276 ± 11.4^{abcd}	236 ± 14.4^{ijkl}	256 ± 24.0^{abcd}
Mean	11.0 ± 1.0^{b}	11.58 ± 1.3^{a}	11.27 ± 1.5	272 ± 11.0^{a}	238 ± 13.0^{b}	255 ± 22.7
HSD (entry)	1.108			11.98		
HSD (season)	0.405			4.37		
HSD (entry × season)	1.57			16.94		
CV	11.11			5.3		

P_N net photosynthetic rate (μmol m^{-2} s^{-1}), g_s stomatal conductance (mol m^{-2} s^{-1}), C_i internal CO_2 concentration (μmol mol^{-1}), E transpiration (mmol m^{-2} s^{-1})]. Each value represents mean of five replications ± SD

Table 3 Variation in leaf photosynthetic characteristics in back cross introgression lines

Entry	WUE_i (P_N/g_s) Intrinsic water-use efficiency			CE (P_N/Ci) Carboxylation efficiency			WUE (P_N/E) Water use efficiency		
	Kha-2013	Rabi-2014	Mean	Kha-2013	Rabi-2014	Mean	Kha-2013	Rabi-2014	Mean
14-3	43.6 ± 5.4^{abcd}	59.5 ± 6.4^{a}	51.5 ± 10.1^{d}	0.063 ± 0.01^{hijk}	0.057 ± 0.01^{k}	0.060 ± 0.01^{g}	1.74 ± 0.2^{efghij}	1.34 ± 0.2^{n}	1.54 ± 0.3^{f}
148S	55.0 ± 4.0^{defgh}	69.3 ± 9.4^{ab}	62.1 ± 10.2^{abc}	0.086 ± 0.01^{bcd}	0.102 ± 0.01^{a}	0.094 ± 0.01^{a}	1.98 ± 0.1^{bcd}	1.92 ± 0.2^{cde}	1.95 ± 0.1^{a}
14S	46.1 ± 3.7^{efghij}	71.0 ± 9.4^{ab}	58.6 ± 14.8^{bcd}	0.069 ± 0.01^{ghij}	0.093 ± 0.01^{ab}	0.081 ± 0.01^{bcd}	1.69 ± 0.1^{fghijk}	1.66 ± 0.3^{hijkl}	1.67 ± 0.2^{cdef}
166-1	40.9 ± 2.7^{fghijk}	76.3 ± 10.0^{abc}	58.6 ± 19.9^{bcd}	0.060 ± 0.00^{ijk}	0.087 ± 0.01^{bcd}	0.073 ± 0.02^{ef}	1.64 ± 0.1^{hijklm}	1.67 ± 0.2^{ghijkl}	1.66 ± 0.1^{def}
166-2	69.6 ± 19.1^{ghijkl}	66.1 ± 12.2^{abc}	67.8 ± 15.2^{a}	0.087 ± 0.01^{bcd}	0.081 ± 0.01^{cde}	0.084 ± 0.01^{bc}	2.16 ± 0.3^{ab}	1.62 ± 0.3^{hijklm}	1.89 ± 0.4^{ab}
166S	49.5 ± 11.6^{hijklm}	79.0 ± 13.6^{abcd}	64.2 ± 19.6^{ab}	0.087 ± 0.01^{bc}	0.085 ± 0.01^{bcd}	0.086 ± 0.01^{b}	1.80 ± 0.2^{defgh}	1.82 ± 0.3^{defgh}	1.81 ± 0.2^{abcd}
248S	56.7 ± 8.0^{hijklm}	58.9 ± 4.3^{bcde}	57.8 ± 6.2^{bcd}	0.087 ± 0.01^{bcd}	0.074 ± 0.00^{efg}	0.080 ± 0.01^{bcde}	2.11 ± 0.3^{abc}	1.44 ± 0.1^{lmn}	1.78 ± 0.4^{bcde}
24K	59.7 ± 9.4^{ijklm}	63.8 ± 3.4^{cdef}	61.7 ± 7.0^{abc}	0.080 ± 0.01^{cdef}	0.077 ± 0.00^{cdefg}	0.079 ± 0.01^{cde}	2.30 ± 0.3^{a}	1.56 ± 0.1^{ijklmn}	1.93 ± 0.4^{ab}
250K	47.6 ± 2.5^{jklm}	75.9 ± 7.3^{cdef}	61.7 ± 15.8^{abc}	0.074 ± 0.01^{efg}	0.082 ± 0.01^{cde}	0.078 ± 0.01^{cde}	1.93 ± 0.1^{cde}	1.73 ± 0.2^{efghijk}	1.83 ± 0.2^{abc}
3-1K	53.9 ± 7.6^{jklm}	71.8 ± 14.2^{cdefg}	62.8 ± 14.3^{abc}	0.077 ± 0.01^{cdefg}	0.060 ± 0.01^{jk}	0.068 ± 0.01^{f}	1.92 ± 0.2^{cde}	1.52 ± 0.2^{jklmn}	1.72 ± 0.3^{cde}
65S	49.7 ± 6.4^{jklm}	63.7 ± 4.6^{cdefg}	56.7 ± 9.1^{cd}	0.087 ± 0.01^{bcd}	0.073 ± 0.01^{efgh}	0.080 ± 0.01^{bcde}	1.76 ± 0.1^{defghi}	1.50 ± 0.1^{klmn}	1.63 ± 0.2^{ef}
70S	46.6 ± 4.8^{klm}	65.2 ± 11.2^{cdefg}	55.9 ± 12.7^{cd}	0.070 ± 0.01^{fghij}	0.046 ± 0.01^{l}	0.058 ± 0.01^{g}	1.97 ± 0.1^{bcd}	1.42 ± 0.2^{mn}	1.69 ± 0.3^{cdef}
75S	45.9 ± 1.8^{klm}	58.5 ± 8.0^{defghi}	52.2 ± 8.6^{d}	0.079 ± 0.01^{cdefg}	0.077 ± 0.01^{defg}	0.078 ± 0.01^{cde}	1.89 ± 0.2^{cdefg}	1.46 ± 0.2^{lmn}	1.67 ± 0.3^{cdef}
7K	46.4 ± 4.6^{lm}	61.9 ± 3.6^{efghi}	54.2 ± 9.1^{d}	0.073 ± 0.01^{efgh}	0.077 ± 0.01^{cdefg}	0.075 ± 0.01^{def}	1.91 ± 0.2^{cdef}	1.34 ± 0.1^{n}	1.62 ± 0.3^{ef}
Swarna	49.2 ± 6.5^{m}	64.8 ± 7.8^{efghi}	57.0 ± 10.6^{bcd}	0.077 ± 0.01^{cdefg}	0.070 ± 0.01^{fghi}	0.074 ± 0.01^{ef}	1.89 ± 0.1^{cdefg}	1.53 ± 0.2^{jklmn}	1.71 ± 0.2^{cde}
Mean	50.7 ± 6.5^{b}	67.0 ± 8.4^{a}	58.9 ± 12.2	0.077 ± 0.01^{a}	0.076 ± 0.01^{a}	0.077 ± 0.01	1.91 ± 0.2^{a}	1.57 ± 0.2^{b}	1.74 ± 0.3
LSD (entry)	7.461			0.007			0.163		
LSD (season)	2.724			0.003			0.059		
LSD (entry × season)	10.551			0.01			0.23		
CV	14.313			10.77			10.555		

WUE_i (P_N/g_s)—intrinsic water-use efficiency; WUE (P_N/E)—water use efficiency; CE (P_N/C_i)—carboxylation efficiency. Each value represents mean of five replications ± SD

Table 4 Variation in leaf pigment content [mg g^{-1} (FM)] and other traits in back cross introgression lines

Entry	Chlorophyll—a [mg g^{-1} (FM)]			Chlorophyll—b [mg g^{-1} (FM)]		
	Kha-2013	Rabi-2014	Mean	Kha-2013	Rabi-2014	Mean
14-3	1.34 ± 0.2^{hijkl}	1.92 ± 0.1^{b}	1.63 ± 0.4^{b}	0.34 ± 0.07^{fghi}	0.48 ± 0.03^{bc}	0.41 ± 0.09^{abc}
148S	1.18 ± 0.0^{klmno}	2.36 ± 0.1^{a}	1.77 ± 0.6^{a}	0.33 ± 0.04^{fghi}	0.60 ± 0.05^{a}	0.47 ± 0.15^{a}
14S	1.23 ± 0.2^{ijklmno}	1.59 ± 0.2^{cdef}	1.41 ± 0.3^{cd}	0.36 ± 0.03^{defghi}	0.38 ± 0.06^{cdefghi}	0.37 ± 0.05
166-1	1.12 ± 0.1^{mno}	1.42 ± 0.1^{fghi}	1.27 ± 0.2^{efg}	0.27 ± 0.04^{hi}	0.37 ± 0.02^{defghi}	0.32 ± 0.06^{de}
166-2	1.24 ± 0.1^{ijklmno}	1.21 ± 0.0^{jklmno}	1.23 ± 0.1^{fgh}	0.32 ± 0.04^{fghi}	0.32 ± 0.01^{fghi}	0.32 ± 0.03^{de}
166S	1.76 ± 0.3^{bc}	1.56 ± 0.2^{cdefg}	1.66 ± 0.2^{ab}	0.49 ± 0.08^{b}	0.39 ± 0.04^{bcdefg}	0.44 ± 0.08^{ab}
248S	1.43 ± 0.1^{efghi}	1.36 ± 0.1^{hijkl}	1.39 ± 0.1^{cde}	0.40 ± 0.03^{bcdefg}	0.33 ± 0.04^{fghi}	0.37 ± 0.05^{cd}
24K	1.30 ± 0.2^{hijklmn}	1.43 ± 0.2^{efghi}	1.36 ± 0.2^{def}	0.37 ± 0.04^{defghi}	0.35 ± 0.05^{efghi}	0.36 ± 0.05^{cde}
250K	1.25 ± 0.2^{ijklmno}	1.32 ± 0.1^{hijklm}	1.29 ± 0.1^{def}	0.33 ± 0.04^{fghi}	0.33 ± 0.05^{fghi}	0.33 ± 0.04^{de}
3-1K	1.12 ± 0.1^{mno}	1.09 ± 0.2^{o}	1.10 ± 0.2^{h}	0.32 ± 0.04^{fghi}	0.27 ± 0.06^{i}	0.30 ± 0.06^{e}
65S	1.10 ± 0.2^{no}	1.16 ± 0.2^{lmno}	1.13 ± 0.2^{gh}	0.31 ± 0.04^{ghi}	0.28 ± 0.05^{hi}	0.29 ± 0.05^{e}
70S	1.63 ± 0.1^{cde}	1.42 ± 0.3^{fghi}	1.52 ± 0.2^{bc}	0.46 ± 0.03^{bcde}	0.38 ± 0.09^{cdefghi}	0.42 ± 0.08^{abc}
75S	1.64 ± 0.2^{cd}	1.59 ± 0.1^{cdef}	1.62 ± 0.2^{b}	0.47 ± 0.06^{bcd}	0.42 ± 0.02^{bcdef}	0.45 ± 0.05^{ab}
7K	1.39 ± 0.2^{fghij}	1.38 ± 0.1^{ghijk}	1.39 ± 0.2^{cde}	0.38 ± 0.05^{cdefghi}	0.36 ± 0.02^{defghi}	0.37 ± 0.04^{cd}
Swarna	1.35 ± 0.1^{hijkl}	1.46 ± 0.1^{defgh}	1.41 ± 0.1^{cde}	0.39 ± 0.02^{bcdefg}	0.38 ± 0.02^{cdefgh}	0.38 ± 0.02^{bcd}
Mean	1.34 ± 0.2^{b}	1.48 ± 0.1^{a}	1.41 ± 0.2	0.37 ± 0.04^{a}	0.38 ± 0.04^{a}	0.37 ± 0.06
LSD (entry)	0.147			0.041		
LSD (season)	0.054			0.015		
LSD (entry × season)	0.207			0.058		
CV	11.74			12.45		

Entry	Total chlorophyll [mg g^{-1} (FM)]			Carotenoids [mg g^{-1} (FM)]		
	Kha-2013	Rabi-2014	Mean	Kha-2013	Rabi-2014	Mean
14-3	1.67 ± 0.30^{defgh}	2.40 ± 0.16^{b}	2.04 ± 0.45^{abc}	0.88 ± 0.13^{bcdefg}	1.09 ± 0.09^{b}	0.99 ± 0.15^{ab}
148S	1.51 ± 0.08^{gh}	2.96 ± 0.20^{a}	2.24 ± 0.78^{a}	0.81 ± 0.02^{defgh}	1.38 ± 0.06^{a}	1.10 ± 0.30^{a}
14S	1.60 ± 0.22^{efgh}	1.97 ± 0.25^{bcdefg}	1.79 ± 0.30^{cde}	0.82 ± 0.10^{defgh}	0.95 ± 0.09^{bcde}	0.89 ± 0.11^{bcde}
166-1	1.39 ± 0.13^{h}	1.79 ± 0.10^{cdefgh}	1.59 ± 0.23^{efg}	0.73 ± 0.05^{fgh}	0.82 ± 0.05^{defgh}	0.78 ± 0.07^{ef}
166-2	1.56 ± 0.16^{fgh}	1.54 ± 0.06^{fgh}	1.55 ± 0.12^{efg}	0.81 ± 0.06^{defgh}	0.76 ± 0.02^{efgh}	0.78 ± 0.05^{def}
166S	2.25 ± 0.38^{bc}	1.96 ± 0.21^{bcdefg}	2.10 ± 0.32^{ab}	1.07 ± 0.16^{bc}	0.92 ± 0.06^{bcdef}	0.99 ± 0.14^{ab}
248S	1.83 ± 0.13^{cdefgh}	1.69 ± 0.16^{defgh}	1.76 ± 0.16^{cde}	0.89 ± 0.06^{bcdefg}	0.78 ± 0.05^{defgh}	0.84 ± 0.08^{cdef}
24K	1.67 ± 0.21^{defgh}	1.78 ± 0.26^{cdefgh}	1.72 ± 0.23^{def}	0.78 ± 0.09^{defgh}	0.83 ± 0.12^{defgh}	0.80 ± 0.11^{cdef}
250K	1.58 ± 0.20^{fgh}	1.64 ± 0.16^{defgh}	1.61 ± 0.17^{efg}	0.74 ± 0.07^{efgh}	0.77 ± 0.07^{efgh}	0.75 ± 0.07^{efg}
3-1K	1.44 ± 0.17^{h}	1.36 ± 0.28^{h}	1.40 ± 0.23^{g}	0.65 ± 0.07^{h}	0.62 ± 0.10^{h}	0.63 ± 0.08^{g}
65S	1.41 ± 0.22^{h}	1.44 ± 0.25^{h}	1.43 ± 0.22^{fg}	0.77 ± 0.09^{efgh}	0.70 ± 0.11^{gh}	0.73 ± 0.10^{fg}
70S	2.09 ± 0.14^{bcde}	1.79 ± 0.39^{cdefgh}	1.94 ± 0.32^{abcd}	0.98 ± 0.05^{bcd}	0.88 ± 0.21^{cdefg}	0.93 ± 0.15^{bc}
75S	2.11 ± 0.26^{bcd}	2.01 ± 0.11^{bcdef}	2.06 ± 0.20^{abc}	0.95 ± 0.12^{bcde}	0.88 ± 0.05^{bcdefg}	0.92 ± 0.09^{bcd}
7K	1.77 ± 0.27^{cdefgh}	1.74 ± 0.12^{defgh}	1.76 ± 0.20^{cde}	0.83 ± 0.15^{defgh}	0.73 ± 0.05^{fgh}	0.78 ± 0.11^{ef}
Swarna	1.74 ± 0.09^{defgh}	1.84 ± 0.08^{cdefgh}	1.79 ± 0.10^{bcde}	0.81 ± 0.04^{defgh}	0.82 ± 0.03^{defgh}	0.81 ± 0.03^{cdef}
Mean	1.71 ± 0.20^{b}	1.86 ± 0.19^{a}	1.78 ± 0.27	0.83 ± 0.08^{a}	0.86 ± 0.08^{a}	0.85 ± 0.11
LSD (entry)	0.185			0.08		
LSD (season)	0.068			0.029		
LSD (entry × season)	0.262			0.114		
CV	11.723			10.7		

Each value represents mean of five replications ± SD

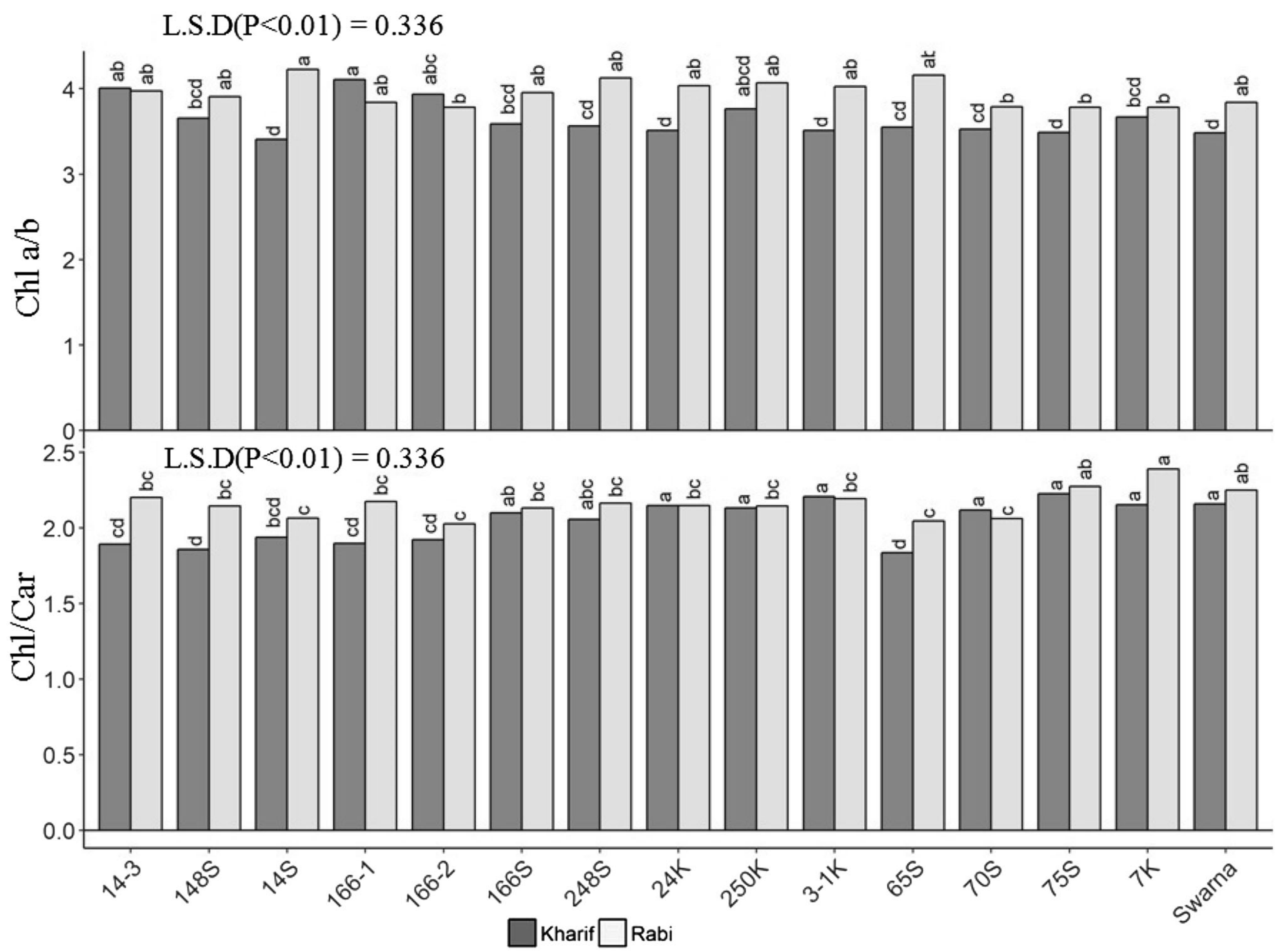

Fig. 1 Variation in leaf photosynthetic pigment content (Chlorophyll a/b, Chlorophyll/Carotenoid) in rice

stomatal conductance. The P_N/g_s, P_N/C_i, and P_N/E showed negative non significant correlation with C_i. Grain yield, PDP and HI showed positive significant correlation with photosynthesis during wet season.

Dry season 2014

The characteristics that possessed positive significant correlation with photosynthesis were g_s, E, P_N/C_i, P_N/E, Chl a, total chlorophyll and carotenoid content (Table 8). The other traits C_i and SLA showed negative non significant correlation with photosynthesis. The characters like E, P_N/C_i and Chl a showed positive significant correlation with stomatal conductance. PDP was positively correlated with carboxylation efficiency. In dry season, grain yield related traits like PDP, TDM and HI showed significant correlation with grain yield.

Genotyping

The genotypes were screened for reported markers and the scoring data was subjected to graphical genotyping (supplementary Fig. 1). 148s showed different marker alleles than rest of the BILs at chromosome 8 in a region between RM223and RM264. Similarly 3_1K with higher PN/gs across the seasons showed distinct allelic pattern at chromosome 11 at RM209—RM229. 70s, 166s, 166-1,148s showed different allelic pattern at chromosome 9 with one marker allele from Swarna and other from *O. nivara*.

Discussion

Photosynthesis is affected by genotypic variation due to difference in physiological, morphological and anatomical features and by environmental factors. It is a complex trait controlled by many genes, and has a low heritability rates in progenies (Horton 2000). Sasaki and Ishii (1992) and Ishii (1995) studied photosynthetic variation among

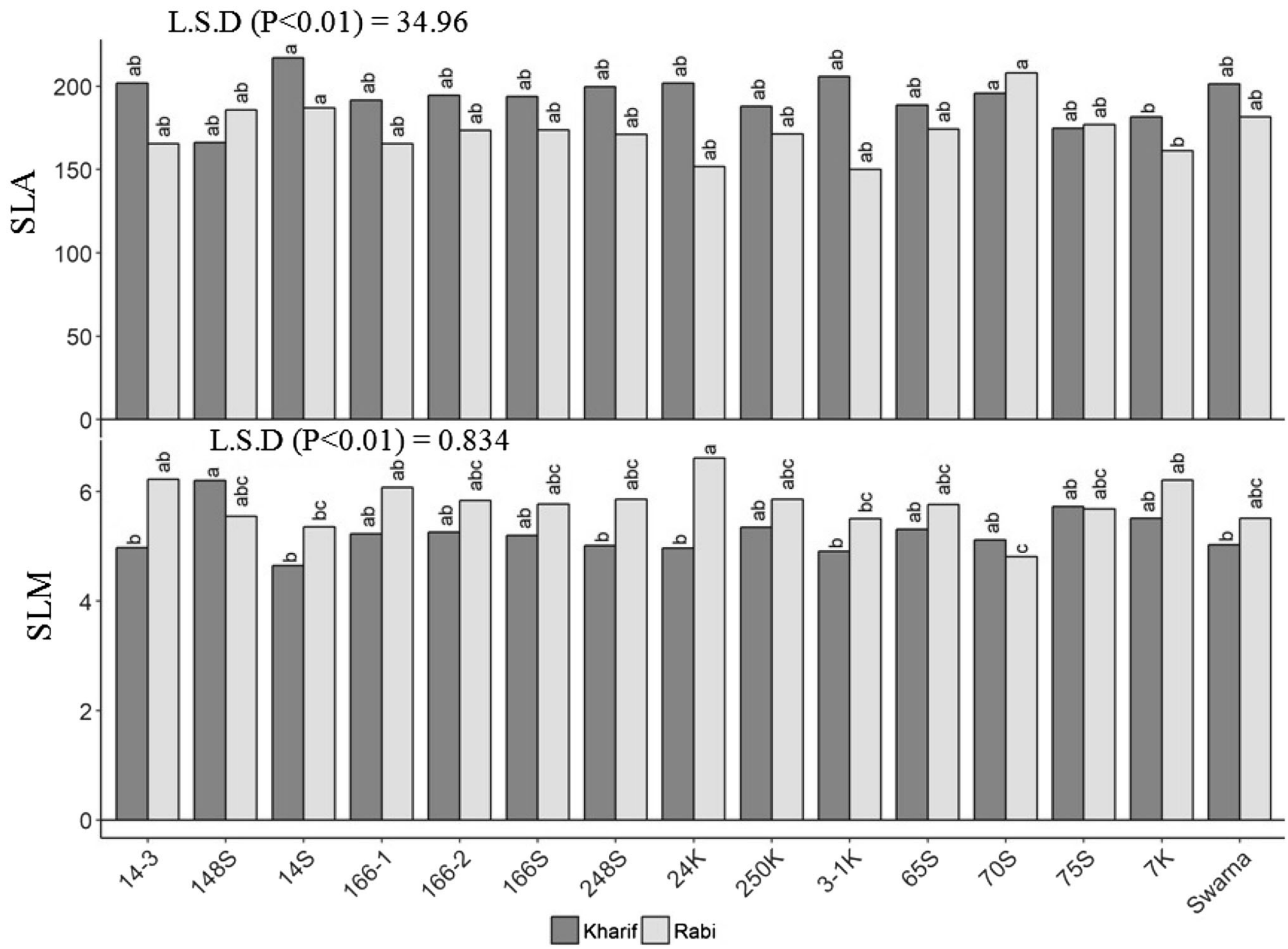

Fig. 2 Variation in specific leaf mass (SLM), specific leaf area (SLA) in rice. Each value represents the mean of five replications ± SD

varieties of *japonica* rice. Yeo et al. (1994) studied 22 wild species and found significant variation for carbon assimilation rate. Masumoto et al. (2004) evaluated BC_2 populations derived from *O. rufipogon* and *O. sativa* and reported higher photosynthetic rates than parents; Teng et al. (2004) studied doubled haploids derived from *indica*/*japonica* cross and found significant variation in photosynthesis related traits. These studies focussed on genotypic variation for photosynthesis along with interaction to environmental factors. In our study, the mean photosynthetic rate of the genotypes was relatively lower during dry season compared to wet season except in 14S, 148S and 166-1. These three genotypes can be recommended for dry season due to their better photosynthetic efficiency during the particular crop season. The reduction in P_N during the dry season in most of the genotypes might be due to reduction in mesophyll conductance and closure of stomata under moderate stress situation (Flexas et al. 2004; Chaves et al. 2009; Ashraf and Harris 2013), as photosynthesis is known to be a function of stomatal behaviour and water loss from leaf coupled with synthesis of carbohydrates. During dry season, the crop experienced moderate cold stress at sowing and heat stress at grain filling stage and this could have led to the lower photosynthetic rate.

Photosynthesis is influenced by higher temperatures as it declines the carboxylation and photorespiration rates (Kimball et al. 2002; Nowak et al. 2004; Dwivedi et al. 2015), however temperature effect is also depended on other seasonal climate factors (Borjigidai et al. 2006). In this study, P_N showed a significant variation among genotypes. It was observed that mean photosynthetic rate of all the BILs was higher than that of recurrent parent in both seasons. BILs viz, 166-2, 148S and 166-1 showed comparatively stable photosynthetic rates in both the seasons and these BILs can be improved to develop stable high yielding genotypes. However major differences in P_N were observed in 70S and 3-1K across seasons. Similar variations were reported in previous studies; Kawamitsu and Agata (1987) studied 50 rice varieties with a range of P_N 14.0–32.2 µmol m^{-2} s^{-1}. Ohsumi et al. 2007 observed P_N variation of 10–30 µmol m^{-2} s^{-1} in ten rice varieties. Kanemura et al. (2007) studied 64 high yielding

Table 5 Variation in grain yield per plant (g Plant^{-1}) and yield related traits in back cross introgression lines

Entry	Grain yield (g Plant^{-1})			PDP		
	Kha-2013	Rabi-2014	Mean	Kha-2013	Rabi-2014	Mean
14-3 Mar	11.17 ± 1.1^{ij}	7.95 ± 1.3^{j}	9.56 ± 2.0^{f}	0.108 ± 0.01^{jkl}	0.056 ± 0.01^{l}	0.082 ± 0.03^{h}
148S	21.00 ± 4.1^{bcdefg}	12.05 ± 1.8^{hij}	16.52 ± 5.6^{e}	0.273 ± 0.06^{a}	0.097 ± 0.01^{kl}	0.185 ± 0.10^{bc}
14S	25.03 ± 3.8^{bcd}	26.28 ± 2.0^{bc}	25.66 ± 3.0^{b}	0.244 ± 0.04^{abc}	0.196 ± 0.01^{cde}	0.220 ± 0.04^{ab}
166-1	15.71 ± 1.3^{fghi}	18.09 ± 0.4^{efgh}	16.90 ± 1.6^{e}	0.153 ± 0.01^{efghijk}	0.118 ± 0.00^{ijk}	0.135 ± 0.02^{fg}
166-2	17.08 ± 1.5^{efghi}	21.68 ± 1.8^{bcdefg}	19.38 ± 2.9^{de}	0.170 ± 0.02D^{efghi}	0.146 ± 0.01^{efghijk}	0.158 ± 0.02^{cdefg}
166S	26.96 ± 2.9^{ab}	33.47 ± 3.1^{a}	30.22 ± 4.4^{a}	0.260 ± 0.03^{ab}	0.212 ± 0.03^{bcd}	0.236 ± 0.04^{a}
248S	21.10 ± 3.7^{bcdefg}	27.18 ± 3.1^{ab}	24.14 ± 4.5^{bc}	0.189 ± 0.04^{cdef}	0.177 ± 0.02^{defgh}	0.183 ± 0.03^{bcd}
24K	19.77 ± 4.9^{cdefg}	19.09 ± 2.6^{defg}	19.43 ± 3.7^{de}	0.171 ± 0.05^{defghi}	0.124 ± 0.02^{hijk}	0.147 ± 0.04^{defg}
250K	21.67 ± 3.9^{bcdefg}	23.54 ± 3.1^{bcde}	22.60 ± 3.5^{bcd}	0.203 ± 0.04^{bcde}	0.152 ± 0.02^{efghijk}	0.177 ± 0.04^{cde}
3-1K	21.33 ± 3.0^{bcdefg}	22.39 ± 3.5^{bcdef}	21.86 ± 3.1^{bcd}	0.202 ± 0.03^{bcde}	0.144 ± 0.02^{efghijk}	0.173 ± 0.04^{cde}
65S	15.61 ± 1.6^{ghi}	16.49 ± 1.2^{fghi}	16.05 ± 1.5^{e}	0.137 ± 0.02^{fghijk}	0.107 ± 0.01^{jkl}	0.122 ± 0.02^{g}
70S	19.74 ± 2.7^{cdefg}	20.05 ± 3.5^{cdefg}	19.90 ± 3.0^{cde}	0.189 ± 0.03^{cdef}	0.128 ± 0.02^{ghijk}	0.159 ± 0.04^{cdefg}
75S	19.79 ± 1.1^{cdefg}	23.25 ± 3.4^{bcde}	21.52 ± 3.0^{bcd}	0.185 ± 0.01^{defg}	0.157 ± 0.02^{defghij}	0.171 ± 0.02^{cdef}
7K	15.94 ± 0.9^{fghi}	23.47 ± 3.1^{bcde}	19.71 ± 4.5^{de}	0.134 ± 0.00^{fghijk}	0.149 ± 0.02^{efghijk}	0.142 ± 0.02^{efg}
Swarna	18.63 ± 2.3^{defgh}	26.86 ± 1.9^{ab}	22.74 ± 4.8^{bcd}	0.155 ± 0.02^{defghijk}	0.171 ± 0.01^{defghi}	0.163 ± 0.02^{cdef}
Mean	19.37 ± 2.6^{b}	21.46 ± 2.4^{a}	20.41 ± 3.4	0.185 ± 0.03^{a}	0.142 ± 0.02^{b}	0.164 ± 0.03
LSD (entry)	2.414			0.021		
LSD (season)	0.882			0.008		
LSD (entry × season)	3.414			0.03		
CV	13.357			14.591		

Entry	TDM (g Plant^{-1})			HI		
	Kha-2013	Rabi-2014	Mean	Kha-2013	Rabi-2014	Mean
14-3 Mar	34.73 ± 5.9^{gh}	23.18 ± 4.2^{h}	28.96 ± 7.7^{e}	32.65 ± 4.1^{fg}	34.93 ± 7.2^{efg}	33.79 ± 5.7^{f}
148S	47.99 ± 8.7^{bcdefg}	40.02 ± 6.0^{efgh}	44.01 ± 8.2^{bcd}	43.69 ± 1.2^{bcde}	30.65 ± 5.6^{g}	37.17 ± 7.9^{ef}
14S	56.60 ± 5.5^{abcde}	46.78 ± 2.7^{cdefg}	51.69 ± 6.6^{abc}	44.21 ± 4.9^{bcde}	56.17 ± 2.8^{a}	50.19 ± 7.3^{a}
166-1	35.79 ± 2.6^{gh}	42.07 ± 1.7^{defg}	38.93 ± 3.9^{de}	43.91 ± 2.3^{bcde}	43.03 ± 1.2^{bcdef}	43.47 ± 1.8^{abcde}
166-2	36.99 ± 5.0^{fgh}	46.56 ± 5.4^{cdefg}	41.78 ± 7.0^{cd}	46.54 ± 4.2^{abcd}	46.86 ± 4.5^{abcd}	46.70 ± 4.1^{abcd}
166S	51.43 ± 6.1^{bcdefg}	69.42 ± 10.1^{a}	60.42 ± 12.3^{a}	52.54 ± 2.9^{ab}	47.18 ± 3.6^{abcd}	49.86 ± 4.2^{ab}
248S	47.88 ± 6.8^{bcdefg}	58.58 ± 8.1^{abcd}	53.23 ± 9.0^{ab}	44.34 ± 6.9^{bcde}	46.82 ± 5.6^{abcd}	45.58 ± 6.0^{abcd}
24K	50.72 ± 8.7^{bcdefg}	44.89 ± 6.3^{defg}	47.81 ± 7.8^{bcd}	38.61 ± 3.1^{defg}	42.58 ± 2.2^{bcdef}	40.60 ± 3.3^{def}
250K	49.90 ± 12^{bcdefg}	57.98 ± 6.7^{abcd}	53.94 ± 10.1^{ab}	44.14 ± 4.8^{bcde}	40.68 ± 4.0^{cdefg}	42.41 ± 4.5^{cde}
3-1K	48.43 ± 10.0^{bcdefg}	54.03 ± 9.2^{abcdef}	51.23 ± 9.5^{abc}	44.61 ± 3.6^{bcde}	41.59 ± 3.2^{cdef}	43.10 ± 3.6^{bcde}
65S	34.40 ± 3.6^{gh}	48.61 ± 8.5^{bcdefg}	41.51 ± 9.7^{cd}	45.41 ± 2.1^{abcde}	34.64 ± 5.7^{efg}	40.03 ± 7.0^{def}
70S	42.96 ± 6.6^{defg}	45.69 ± 10.6^{defg}	44.33 ± 8.4^{bcd}	46.09 ± 2.6^{abcd}	44.37 ± 2.9^{bcde}	45.23 ± 2.7^{abcd}
75S	45.50 ± 6.4^{defg}	45.33 ± 5.5^{defg}	45.42 ± 5.6^{bcd}	43.96 ± 4.8^{bcde}	51.24 ± 3.9^{abc}	47.60 ± 5.6^{abc}
7K	37.28 ± 3.3^{fgh}	64.65 ± 9.3^{ab}	50.96 ± 15.8^{abc}	42.92 ± 2.9^{bcdef}	37.31 ± 9.4^{defg}	40.12 ± 7.2^{def}
Swarna	43.59 ± 5.4^{defg}	63.43 ± 3.2^{abc}	53.51 ± 11.3^{ab}	42.98 ± 4.9^{bcdef}	42.49 ± 3.7^{bcdef}	42.73 ± 4.1^{cde}
Mean	44.28 ± 6.4^{b}	50.08 ± 6.5^{a}	47.18 ± 8.9	43.77 ± 3.7^{a}	42.70 ± 4.4^{a}	43.24 ± 5.0
LSD (entry)	6.162			3.895		
LSD (season)	2.25			1.422		
LSD (entry × season)	8.715			5.509		
CV	14.75			10.174		

Each value represents mean of five replications ± SD

Table 6 Relationship between leaf photosynthetic efficiency and related traits using combined seasons mean

	PN	*gs*	*E*	*Ci*	*Pngs*	*Pnci*	*PnE*	*SLA*	*SLM*	*Chl a*
PN	1.00									
gs	0.74**	1.00								
E	0.80**	0.90**	1.00							
Ci	− 0.40	0.22	0.01	1.00						
Pngs	0.35	− 0.32	− 0.14	− 0.94**	1.00					
Pnci	0.97**	0.59**	0.70**	− 0.60**	0.54**	1.00				
PnE	0.56**	− 0.04	− 0.04	− 0.68**	0.79**	0.65**	1.00			
SLA	− 0.34	− 0.28	− 0.30	0.14	− 0.06	− 0.31	− 0.18	1.00		
SLM	0.47*	0.43*	0.41*	− 0.05	− 0.01	0.43*	0.26	− 0.88**	1.00	
Chl a	0.23	0.44*	0.15	0.32	− 0.27	0.14	0.10	0.08	0.19	1.00
Chl b	0.23	0.45*	0.14	0.33	− 0.28	0.12	0.11	0.11	0.13	0.98**
Total	0.23	0.44*	0.15	0.32	− 0.27	0.14	0.10	0.08	0.18	1.00**
Car	0.26	0.38	0.15	0.20	− 0.17	0.20	0.14	0.19	0.13	0.96**
Chl ab	− 0.08	− 0.22	− 0.04	− 0.14	0.14	0.00	− 0.10	− 0.15	0.22	− 0.25
ab xc	0.15	0.15	0.09	0.06	− 0.03	0.16	0.04	0.05	0.25	0.58**
Yield	0.34	0.21	0.22	− 0.26	0.39	0.36	0.30	0.27	− 0.37	0.00
DFF	− 0.39	− 0.18	− 0.14	0.28	− 0.21	− 0.42*	− 0.32	− 0.04	− 0.12	− 0.53**
PDP	0.52**	0.28	0.27	− 0.39	0.49*	0.55**	0.46*	0.27	− 0.31	0.21
TDM	0.39	0.24	0.24	− 0.23	0.37	0.38	0.35	0.08	− 0.22	− 0.05
HI	0.18	0.10	0.15	− 0.26	0.31	0.23	0.13	0.43*	− 0.49*	− 0.07

	Chl b	*Total*	*Car*	*Chl ab*	*ab xc*	*Yield*	*DFF*	*PDP*	*TDM*	*HI*
PN										
gs										
E										
Ci										
Pngs										
Pnci										
PnE										
SLA										
SLM										
Chl a										
Chl b	1.00									
Total	0.99**	1.00								
Car	0.91**	0.95**	1.00							
Chl ab	− 0.43*	− 0.29	− 0.12	1.00						
ab xc	0.41*	0.54*	0.71**	0.62**	1.00					
Yield	0.10	0.03	− 0.07	− 0.42*	− 0.35	1.00				
DFF	− 0.45*	− 0.51*	− 0.66**	− 0.18	− 0.65**	0.21	1.00			
PDP	0.28	0.23	0.20	− 0.36	− 0.10	0.90**	− 0.23	1.00		
TDM	0.05	− 0.03	− 0.16	− 0.45*	− 0.45*	0.93**	0.28	0.82**	1.00	
HI	0.02	− 0.05	− 0.07	− 0.33	− 0.29	0.83**	0.12	0.75**	0.59**	1.00

P_N = Rate of photosynthesis [μmol m^{-2} s^{-1}], g_s = Stomatal Conductance [mol m-2s-1], E = Transpiration [mmol m-2s-1], C_i = internal CO_2 concentration [μmol mol-1], P_N/E = Transpiration efficiency, P_N/g_s = Intrinsic Water Use Efficiency (WUEi), P_N/C_i = Carboxylation efficiency (CE), Chl = Chlorophyll, Car = Carotenoids, DFF = Days to 50% flowering, PDP = Per day productivity, TDM = Total dry matter, HI = Harvest index, SLA = Specific leaf area, SLM = Specific leaf mass, The significance of each correlation is indicated: *$P < 0.05$; **$P < 0.01$

Table 7 Relationship between leaf photosynthetic efficiency and related traits during wet season

	PN	*gs*	*Ci*	*E*	*PN/gs*	*PN/ci*	*PN/E*	*SLA*	*SLM (mg)*	*Chl. A*
PN	1.00									
gs	0.38	1.00								
Ci	−0.33	0.65**	1.00							
E	0.61**	0.81**	0.15	1.00						
PN/gs	0.36	−0.71**	−0.93**	−0.33	1.00					
PN/ci	0.89**	−0.02	−0.72**	0.39	0.70**	1.00				
PN/E	0.35	−0.57**	−0.57**	−0.52**	0.81**	0.52**	1.00			
SLA	−0.40	−0.33	0.03	−0.25	0.03	−0.31	−0.07	1.00		
SLM (mg)	0.39	0.26	−0.12	0.24	0.03	0.35	0.08	−0.98**	1.00	
Chl. A	0.35	0.49*	0.32	0.23	−0.16	0.12	0.09	−0.11	0.06	1.00
Chl.B	0.46*	0.51*	0.29	0.30	−0.13	0.21	0.13	−0.07	0.02	0.96**
Total	0.38	0.50*	0.32	0.25	−0.15	0.14	0.10	−0.10	0.05	1.00**
Caro	0.32	0.46*	0.21	0.32	−0.15	0.16	−0.03	−0.13	0.10	0.92**
Chl (a/b)	−0.57**	−0.29	0.02	−0.35	−0.06	−0.40	−0.19	−0.15	0.12	−0.29
(a + b)/(x + c)	0.23	0.21	0.32	−0.09	−0.04	0.02	0.33	0.06	−0.12	0.51*
Plant yield	0.47*	0.23	−0.09	0.36	0.13	0.37	0.10	0.14	−0.08	0.34
DFF	0.04	0.17	0.28	−0.01	−0.11	−0.09	0.09	0.39	−0.51*	0.14
PDP	0.41*	0.13	−0.21	0.32	0.16	0.38	0.05	−0.12	0.22	0.19
TDM	0.31	0.06	−0.03	0.11	0.11	0.22	0.20	0.25	−0.18	0.22
HI	0.53**	0.33	−0.19	0.54**	0.16	0.49*	−0.05	−0.15	0.15	0.31

	Chl.B	*Total*	*Caro*	*Chl (a/b)*	*(a + b)/(x + c)*	*Plant yield*	*DFF*	*PDP*	*TDM*	*HI*
PN										
gs										
Ci										
E										
PN/gs										
PN/ci										
PN/E										
SLA										
SLM (mg)										
Chl. A										
Chl.B	1.00									
Total	0.98**	1.00								
Caro	0.86**	0.91**	1.00							
Chl (a/b)	−0.54**	−0.35	−0.18	1.00						
(a + b)/(x + c)	0.59**	0.53**	0.14	−0.49*	1.00					
Plant yield	0.48*	0.38	0.28	−0.60**	0.35	1.00				
DFF	0.18	0.15	−0.06	−0.25	0.49*	−0.19	1.00			
PDP	0.29	0.22	0.24	−0.40	0.05	0.89**	−0.61**	1.00		
TDM	0.38	0.26	0.12	−0.63**	0.39	0.90**	−0.16	0.80**	1.00	
HI	0.36	0.33	0.30	−0.29	0.14	0.66**	−0.11	0.58**	0.28	1.00

P_N = Rate of photosynthesis [μmol m^{-2} s^{-1}], g_s = Stomatal Conductance [mol m-2s-1], E = Transpiration [mmol m-2s-1], C_i = internal CO_2 concentration [μmol mol-1], P_N/E = Transpiration efficiency, P_N/g_s = Intrinsic Water Use Efficiency (WUEi), P_N/C_i = Carboxylation efficiency (CE), Chl = Chlorophyll, Car = Carotenoids, DFF = Days to 50% flowering, PDP = Per day productivity, TDM = Total dry matter, HI = Harvest index, SLA = Specific leaf area, SLM = Specific leaf mass, The significance of each correlation is indicated: $*P < 0.05$; $**P < 0.01$

Table 8 Relationship between leaf photosynthetic efficiency and related traits during dry season

	PN	*gs*	*Ci*	*E*	*PN/gs*	*PN/ci*	*PN/E*	*SLA*	*SLM (mg)*	*Chl. A*
PN	1.00									
Gs	0.87**	1.00								
Ci	– 0.10	0.35	1.00							
E	0.79**	0.92**	0.29	1.00						
PN/gs	0.19	– 0.31	– 0.92**	– 0.32	1.00					
PN/ci	0.97**	0.74**	– 0.34	0.67**	0.40	1.00				
PN/E	0.64**	0.24	– 0.60**	0.04	0.76**	0.76**	1.00			
SLA	– 0.03	– 0.05	0.13	– 0.20	– 0.01	– 0.05	0.14	1.00		
SLM (mg)	0.25	0.32	0.08	0.45*	– 0.15	0.22	– 0.11	– 0.79**	1.00	
Chl. A	0.42*	0.41*	0.12	0.20	– 0.05	0.38	0.37	0.31	– 0.02	1.00
Chl.B	0.37	0.38	0.10	0.17	– 0.07	0.34	0.33	0.33	– 0.04	0.99**
Total	0.41*	0.40	0.12	0.20	– 0.06	0.38	0.36	0.31	– – 0.02	1.00**
Caro	0.42*	0.38	0.11	0.14	0.00	0.39	0.44*	0.40	– 0.10	0.98**
Chl (a/b)	0.21	0.12	0.11	0.15	0.13	0.16	0.14	– 0.17	0.06	– 0.12
(a + b)/(x + c)	– 0.05	0.12	0.00	0.28	– 0.30	– 0.06	– 0.39	– 0.40	0.36	0.11
Plant yield	0.07	– 0.05	– 0.33	0.05	0.31	0.14	0.14	0.06	– 0.21	– 0.44*
DFF	– 0.62**	– 0.57**	– 0.14	– 0.38	– 0.02	– 0.56**	– 0.47*	– 0.29	0.14	– 0.80**
PDP	0.20	0.07	– 0.31	0.15	0.31	0.26	0.22	0.12	– 0.27	– 0.34
TDM	0.06	– 0.06	– 0.36	0.04	0.29	0.13	0.13	– 0.06	– 0.11	– 0.45**
HI	0.05	0.02	– 0.08	0.11	0.10	0.07	– 0.01	0.20	– 0.26	– 0.31

	Chl.B	*Total*	*Car*	*Chl (a/b)*	*(a + b)/(x + c)*	*Plant yield*	*DFF*	*PDP*	*TDM*	*HI*
PN										
Gs										
Ci										
E										
PN/gs										
PN/ci										
PN/E										
SLA										
SLM (mg)										
Chl. A										
Chl.B	1.00									
Total	0.99**	1.00								
Caro	0.97**	0.98**	1.00							
Chl (a/b)	– 0.27	– 0.15	– 0.08	1.00						
(a + b)/(x + c)	0.17	0.12	– 0.07	– 0.39	1.00					
Plant yield	– 0.44*	– 0.44*	– 0.45	0.07	0.07	1.00				
DFF	– 0.75**	– 0.79**	– 0.84**	– 0.17	0.21	0.40	1.00			
PDP	– 0.35	– 0.34	– 0.34	0.13	0.02	0.98**	0.22	1.00		
TDM	– 0.44**	– 0.45*	– 0.49*	0.00	0.25	0.86**	0.51*	0.80**	1.00	
HI	– 0.32	– 0.31	– 0.27	0.09	– 0.18	0.68**	0.08	0.74**	0.23	1.00

P_N rate of photosynthesis (μmol m^{-2} s^{-1}), g_s stomatal conductance [mol m-2s-1], *E* transpiration [mmol m-2s-1], C_i internal CO_2 concentration (μmol mol-1), P_N/E transpiration efficiency, P_N/g_s intrinsic water use efficiency (WUEi), P_N/C_i carboxylation efficiency (CE), *Chl* chlorophyll, *Car* carotenoids, *DFF* days to 50% flowering, *PDP* per day productivity, *TDM* total dry matter, *HI* harvest index, *SLA* specific leaf area, *SLM* specific leaf mass, The significance of each correlation is indicated: $*P < 0.05$; $**P < 0.01$

genotypes including *indica*, *japonica* and *aus* type and reported a P_N variation ranging from 11.9 to 32.1 [μmol (CO_2) m^{-2} S^{-1}]. Higher range of P_N can be identified from the existing germplasm resources, landraces, wild and distant related species within *Oryza* genus and can be employed in improvement of photosynthetic efficiency through conventional breeding.

In case of stomatal conductance, 166-2S and 148S showed stable performance across the genotypes. All the genotypes showed better stomatal conductance during wet season compared to dry season. 148S showed high g_s even in dry season. Similarly, internal CO_2 concentration was also high in wet season compared to dry season except in case of BIL 166-2. Significant genotypic variation was observed for transpiration rate. BILs 65S, 3-1K, 70S and 166S showed high transpiration rate only in wet season, 250K, showed stable performance in both the seasons. The high transpiration rate during the dry season might be an adaptive strategy of some lines to maintain relatively cooler leaf canopies under increased temperatures of the dry season. Intrinsic water use efficiency was higher in dry season than wet season in all genotypes except 166-2 which showed highest WUE_i in wet season. BILs showed similar carboxylation efficiency across the seasons. Water use efficiency of 166-1 was high in dry season but all other genotypes showed higher WUE in wet season and 14S, 166S and 148S showed stable performance in both seasons.

Chlorophyll components showed minimum variation across the seasons in any specific genotype but significant variation was observed among genotypes. BILs with higher chlorophyll content viz., 166S and 75S could be used for their ability to produce higher biomass and leaf photosynthesis as reported by Hassan et al. (2009). No significant relationship was observed between leaf traits and photosynthesis, indicating that photosynthesis at single leaf level might be affected by traits other than specific leaf area and mass. Specific leaf area and mass showed no significant variation in genotypes across the seasons and they may be genotype specific and not much influenced by environment. Reciprocal performance was observed in specific leaf area and specific leaf mass in all the genotypes. The variation in SLA observed across the seasons can be due to the differences in genotypes and environment (Steinbauer 2001)

In India, rice is majorly grown in two seasons viz., wet season (July–November) and in dry season (December–April) with minor regional variation. These two seasons experiences contrasting weather parameters and rainfall pattern which depend on different monsoons. The varying weather conditions directly influencing photosynthesis and transpiration processes, affect crop growth and ultimately results in varying yield levels of same genotype. This also indicates the need to develop season specific genotypes. Stable high yielding genotypes across the seasons are of high demand as the climatic conditions are unpredictable. Genotypic differences in yield in both seasons were obvious, 148S and 14-3 showed significantly higher yield in the wet season but all other lines performed better in dry season. BIL 148S showed stable higher yield across the season which is the earliest flowering genotype among the genotypes studied. All these genotypes showed higher biomass production in dry season compared to wet season. Even though mean grain yield and total dry matter were high in dry season but per day productivity and harvest index was higher in wet season. There is a higher level of solar radiation and sunshine hours experienced in dry season than in wet season. Low sunshine hours affect time of flowering and duration to maturity and results in lower yields and this depend again on duration of variety and affects both early and late varieties. So, to compare varieties of different duration, per day productivity was used as the yield parameter.

Significant association between photosynthesis related traits and yield related traits in both seasons was observed. The strong positive correlation of stomatal conductance, transpiration and carboxylation efficiency with the rate of photosynthesis was noticed. Hetherington and Woodward (2003); Kiran et al. (2013); Ding et al. (2014); Sailaja et al. (2015); Haritha et al. (2017) reported significant correlation of physiological traits between g_s and P_N across genotypes and diverse environments. Radin et al. (1988) explained the correlation between photosynthetic traits as P_N is dependent on C_i, which in turn is a function of g_s. As g_s is linked with CO_2 requirement of the mesophyll, P_N and g_s association maintains the C_i/C_a ratio as constant (Wong et al. 1985; Sharkey and Raschke 1981). Ohsumi et al. (2007); Hirasawa et al. (1988); Kusumi et al. (2012) reported that stomatal conductance is strongly correlated with leaf photosynthesis in rice and there are substantial genotypic differences. Similarly positive and significant association of chlorophyll content with P_N was reported by Subrahmanyam (2002), Avenson et al. (2005) and Pawar et al. (2015).

A consistent positive association of net photosynthesis with yield related traits like grain yield, total dry matter, per day productivity and harvest index was observed in both seasons. Mitchell and Sheehy (2006), Reynolds et al. (2005), Shearman et al. (2005) and Zhu et al. (2010) suggested that improving leaf photosynthetic rate will enhance biomass production and yield. Fischer and Edmeades (2010) showed association of P_N with harvest index and grain number. Sailaja et al. (2015) reported that transpiration rate at reproductive stage showed a positive association with grain yield under heat stress. Although photosynthesis is the major contributor in crop growth and production, significant association between photosynthesis and yield related traits was not observed. The variation in association of these traits could be attributed by contrasting weather parameters that existed during both the seasons. Evans et al. (1993), Teng et al. (2004) and Driever et al. (2014) observed that leaf photosynthetic rate was not often associated with enhanced yield or biomass production. Yield and biomass is the outcome of total photosynthesis from sowing to crop maturity which is varying and this variation depends on crop growth stage and environmental conditions. Due to practical difficulties we measure photosynthesis of a unit leaf area in a unit time at specific crop stage and this may cause inconsistency in photosynthesis and crop yield correlation. The photosynthetic and physiological traits were highly influenced by environmental factors like water availability (Niinemets et al. 2009), temperature (Scafaro et al. 2011) and nutrient supply (Warren 2004). Varying crop durations also affect the sink-source relationship and finally cause limited association (Zhao et al. 2008). At the reproductive stage plants may be limited by sink capacity, and then leaf CER and is not associated with productivity (Richards 2000).

Marker based genotyping was carried out to understand marker trait association in the BILs using already known QTLs. The mean genetic distance between individuals was high and it was observed that those lines came under same genotypic constitution for photosynthesis related traits were exhibiting similar yield traits. It was found that genotypes with *O. nivara* alleles had higher rate photosynthesis related traits and biomass. There was no marker trait association established as there is a need of more number of markers for the precise genotyping. However, we found novel alleles and allelic combination in the set of 14 BILs which are different than parents for the reported QTLs viz., qPn11, qGs11, qTr11 (Zhao et al. 2008), qPn10, qSlw10, qGy10 (Zhao et al. 2008) and qA_FW_MQM_3-qA_GW_MQM_2 (Gu et al. 2012).

Conclusion

Improvement of photosynthesis and related physiological traits is the need of the hour for any further enhancement in yield potential of rice cultivars. The variations and association of photosynthetic traits observed in BILs can be exploited for further improvement of yield levels in commercial cultivars through breeding and molecular tools. BILs such as 166S, 65S, 248S, 148S, 75S and 24K showed better photosynthetic rates than the recurrent parent Swarna. Two lines 166S and 248S performed better in both seasons for yield traits and they were identified as most stable lines from multi environment testing data (Divya et al. 2016). BIL, 248S was tested under multi location trials through All India coordinated Rice Improvement Project (AICRIP) and released as a variety DRRDhan 40, and recommended for cultivation in irrigated areas of Maharashtra, Tamilnadu and West Bengal. Therefore, detailed studies involving more number of genotypes and different environments are required. Genotypes which has season specific expression of high photosynthetic rates especially 14-3 and 70S showing comparatively higher photosynthetic rates in wet season and those genotypes like 166-1 with stable photosynthesis across the seasons needs much attention and can be studied elaborately for understanding their mechanisms. Even though net photosynthetic rate and other photosynthesis related traits showed higher mean values in wet season, the average genotypic grain yield and total dry matter production was high in dry season. It was interesting to observe that per day productivity and harvest index were higher in wet season and showed similar trends in association with photosynthetic traits. This indicates while studying the effect of photosynthesis with yield parameters, comparisons can be made between traits like per day productivity or harvest index than directly using grain yield. Other parameters like duration of the crop, biomass production, and stage of the crop and weather parameters during the observations are to be considered along with grain yield to identify precise effect of photosynthesis on yield. The association of photosynthetic related traits with yield traits observed in BILs can be exploited for further improvement of yield potential through breeding and molecular approaches.

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Author contributions DB and SN conceived and planned the work. YVR, AKR, SM and TVK performed phenotypic and genotypic screening. DB and DS analyzed the data. YVR, DB and DS drafted the manuscript. SRV and SN made revisions and approved the final version of the paper.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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