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Natural Variation in Photosynthetic Traits Measured at Pre and Post Anthesis Stages for 36 Field Grown Wheat Genotypes

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ABSTRACT

The experiment was conducted during November–March of 2018–19 and 2019–20 at the University Farm of Uttar Banga Krishi Viswavidyalaya, Pundibari, Cooch Behar, West Bengal, India to assess the variability of 36 selected wheat genotypes for key morpho-phenetic traits as well as photosynthetic parameters and also to study their associations pattern at various growth stages. Photosynthetic parameters were recorded by Gas exchange (GE) measurement under open field condition at both pre- and post-anthesis stages The genotypes showed significant variation for photosynthetic parameters such as P_n, *E*, C_i, and g_s, for pre-anthesis measurements while in post-anthesis measurements, all the parameters found to be non-significant except P_n. All these traits showed higher value in pre-anthesis stage indicating higher physiological efficiency at this stage. Most of the traits showed high heritability coupled with higher genetic advance except g_s in both pre and post anthesis stages indicating higher role of additive gene action. This study found no significant correlation between pre and post-anthesis photosynthetic traits and grain yield or biomass when all cultivars were compared. Cultivars with the highest photosynthetic performance did not equate with the highest yields. However, path analysis revealed a positive and high direct effect of *E*, *WUE* (both pre and post anthesis stage); g_s, (Pre-anthesis stage only) on grain yield while a negative direct impact of BY and P_n (pre-anthesis stage). PCA analysis also confirmed the importance of photosynthetic parameters such as P_n, *E*, g_s, *Ci*, *LUE*, and *WUE* measured at both pre and post-anthesis stages towards the divergence of wheat genotypes.

KEYWORDS: Photosynthetic efficiency, pre and post anthesis, wheat

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1. INTRODUCTION

Wheat production in India has witnessed an extraordinary period of growth since last 50 years, after the introduction of photoperiod insensitive and semi-dwarf wheat genotypes in the mid-sixties (Eliazer Nelson et al., 2019; Pingali, 2012; John and Giridhara, 2021; Hazel, 2020). However, with a predicted 9 billion world population in 2050, the demand for wheat is expected to increase by 34% from the present yield status and to sustain the fast-growing human population, wheat production must increase by at least 50% by 2030 (Ray et al., 2013). Yield gains in wheat are currently estimated at about 0.5 to 1% per annum which is below the 2.4% required to satisfy global demand (Crespo-Herrera et al., 2018).

The maximum yield obtained (yield potential) is the yield achieved when a crop is grown under optimal conditions with no biotic or abiotic stress (Evans and Fischer, 1999; Dreisigacker et al., 2021). It is the result of three key determinants: (i) light capture; (ii) radiation use efficiency (RUE) or energy conversion efficiency (the product of which is biomass); and (iii) harvest index (HI) (Reynolds et al., 2009, Simkin et al., 2020). RUE which is mainly dependent on photosynthetic efficiency, can be improved by manipulating diverse aspects of leaf tissue, including altering key enzymes within the Calvin–Benson cycle (CBC) (Simkin et al., 2015; Driever et al., 2017; Simkin et al., 2017a), electron transport (Simkin et al., 2017b; Yadav et al., 2018; Ermakova et al., 2019), photorespiration (Lopez-Calcagno et al., 2018) and the kinetics of non-photochemical quenching (NPQ) (Kromdijk et al., 2016; Glowacka et al., 2018). This can improve yield potential in both glasshouse and field grown plants (Simkin, 2019; Simkin et al., 2019).

Advances in photosynthesis research in recent years have identified a number of key traits for improved carbon assimilation and biomass production (Driever et al., 2017, Simkin et al., 2015). A positive relationship between photosynthetic rates and biomass (Kruger and Volin, 2006) and yield (Fischer et al., 1998) has been observed in wheat. Physiological traits such as enhanced photosynthetic capacity, stomatal conductance, transpiration rate, water-use efficiency and chlorophyll content are also found positively associated with wheat grain yield (Lopes et al., 2012). Variation in flag leaf photosynthetic rate, and in GY was previously reported for 64 field-grown cultivars in UK but no significant correlation was found between maximum photosynthetic rates measured under optimal conditions before ear emergence (Zadoks 4.3–4.5) and GY (Driever et al., 2014). Gaju et al. (2016), in contrast, reported a strong positive relationship between flag leaf photosynthetic rates and GY for 15 genotypes over two field seasons. Similar study in North China Plain indicated grain yield, yield components, and ratio of grain weight: leaf area were positively correlated with contribution of ear photosynthesis under both rainfed and irrigated condition (Wang et al., 2016). Molero and Reynolds, 2020 found significant variation for spike photosynthetic rate which also contributed to grain weight positively under open field condition. Thus, the existing genotypic variation in wheat for these traits can be exploited by identifying promising cultivars as well as the key traits and their association with final grain yield across different environments (Chen et al., 2012; Liu et al., 2015; Gaju et al., 2014; Carmo-Silva et al., 2017; Rivera-Amado et al., 2020).

Therefore, the present study has been conducted to investigate the variability pattern of different photosynthetic traits (measured at both pre and post-anthesis stages) and its association with major yield component traits along with other morphological traits of importance.

2. MATERIALS AND METHODS

The experiment was conducted during November- March season of 2018-19 and 2019-20 at the University Farm of Uttar Banga Krishi Viswavidyalaya, Pundibari, Cooch Behar, West Bengal (736165), India. Thirty-six genotypes of wheat were collected from the All India Coordinated Wheat and Barley Improvement Project, Cooch Behar Centre, UBKV. A detail of all these genotypes, along with traits of importance, is given in Table 1. The experimental design was randomized block design (RBD) with two replications under timely sown irrigated condition.

Morphological traits such as Plant height (PH), Days to heading (DH), Days to maturity (DM), Tillers m^{-1} (TM), grans $spike^{-1}$(GPS), thousand grain weight (TGW), Spike length (SPL), grain yield (GY) [t ha^{-1}], biological yield (BY) [t ha^{-1}] and harvest index (HI) has been measured at the appropriate physiological stage.

In-situ CO_2 exchange rates were measured under field conditions using a portable open circuit steady-state gas-exchange system (Model: CI-340 Hand-held Photosynthesis System, CID-Bioscience, USA). Gas exchange (GE) measurements were taken at pre- and post-anthesis stages on five pre-selected plants from each replication between 8.00 am and 11.00 am as per the techniques described by Long and Bernacchi (2003). Simultaneous measurements of CO_2 to H_2O vapor flux, air and leaf temperature, incident photosynthetically active radiations (PAR), and ambient CO_2 and O_2 concentration in the air were also considered. Different formulae were used to calculate the following physiological parameters:

(I) Net photosynthesis Rate (P_n: μmol CO_2 m^{-2} s^{-1}):

$$Pn=-W\times(C_o-C_i)=-2005.39\times\frac{V\times P}{T_a-A}\times(C_o-C_i)$$

Table 1: List of genotypes along with their pedigree

Sl. No.	Genotypes	Pedigree of genotypes	Year of release	Remarks
1.	RW 3684	PASTOR/FLORKWA.1//PASTOR	Stock	
2.	DBW 14	RAJ 3765/PBW343	2002	
3.	KRL 1-4	KHARCHIA65/ WL 711	1990	Salt tolerant
4.	HW 2044	HD226*5/SUNSTAR*6/C-80-1	1999	
5.	PDW 314(d)	AJAIA12/F3 LOCAL (SEL. ETHIO.135.85)//PLATA 13/3/ SOMAT 3/4/SOOTY9/RASCON 37	2010	*T. durum* L.
6.	KRL 213	CNDO/RI43/ENTE/MEXL-2/3/AE.SQUARROSA 9TAUS) /4/WEAVER/5/28KAUZ	2010	Salt tolerant
7.	HI 8498(d)	CR "S'-GS'S' /A-9-30-1//RAJ 911	1999	*T. durum* L.
8.	GW 322	GW 173/GW196	2002	
9.	DBW 71	PRINIA/UP2425	2013	
10.	WH 1105	MILAN/S87230//BABAX	2013	
11.	RAJ 4229	HW2048/RAJ4000	2012	
12.	BH 1146	PONTA GROSSA1//FRONTEIRA/MENTANA	Stock (1987)	
13.	HD 2009	LR 64A /NAI 60	1975	
14.	DBW 17	CMH79A.95/3*CNO 79//RAJ3777	2006	
15.	WH1021	NYOT95/SONAK	2007	
16.	UP 262	S 308 /BJ 66	1978	
17.	HD 2967	ALD/COC//URES/HD2160M/HD2278	2011	
18.	DBW 16	RAJ 3765/WR 484//HUW 468	2006	
19.	NW 1067	TR380-16-30614/CHAT'S'	2004	
20.	HI 1563	MACS 2496*2/MC 10	2011	
21.	KRL 3-4	HD1982/ KHARCHIA 65	Stock (2009)	Salt tolerant
22.	DBW 46	PBW343/INQ21	Stock (2011)	
23.	NW 4092	SITE/MO//MILAN/3/PBW343	Stock	
24.	HD 2733	ATTILA /3/ TUI /CARC // CHEN / CHTO /4/ ATTILA	2001	
25.	KRL 210	PBW65/2*PASTOR	2010	Salt tolerant
26.	NW 4018	VEE/PJN//KAUZ/3/PASTOR	2013	
27.	RAJ 4238	HW2021/RAJ3765	2012	
28.	Kharchia-65	KHARCHIA LOCAL/ EG 953	1970	Land race
29.	CBW 38	CNDO/R 143/ENTE/MEXI_2/3/AE.SQUARROSA (TAUS)/4/ WEAVER/5/2*PASTOR	2008	
30.	KRL 19	PBW255/KRL 1-4	2000	Salt tolerant
31.	DBW 51	SITE/MILAN	2010	
32.	K 0307	K 8321/UP 2003	2007	
33.	DPW 621-50	HUW 202/K 7537/MUTANT OF HD 2160	2011	Lodging resistant
34.	HD 2932	KAUZ/STAR//HD 2643	2008	
35.	MACS 6222	HD 2189*2//MACS 2496	2010	
36.	DBW 39	ATTILA/HUI	2010	

(II) Transpiration rate (E; millimol H_2O m^{-2} s^{-1}):

$$E=\frac{e_o-e_i}{P-e_o}\times W\times 10^3$$

$e_o=hr_o\times e_s/100$

$e_i= hr_i\times e_s/100$

$$e_s=6.13753\times 10\text{-}3\times e\ T_a\times\frac{18.564-\frac{T_a}{254.4}}{T_a+255.57}$$

(von Caemmerer and Farquhar, 1981)

(III) Intercellular CO2 concentration (Ci; μmol mol^{-1}):

$CO_{2inL}=C_i-1.6\times P_n\ (Rh+R_{leaf})$

(IV) Stomatal conductance to water (g_s; millimol H_2O m^{-2} s^{-1}):

$$C_{leaf}=\frac{W}{\frac{e_{leaf}-e_o}{e_o-e_i}\times\frac{P-e_o}{P}-R_bW}\times 1000$$

$$e_{leaf}=6.13753\times 10\text{-}3\times e\,T_{leaf}\times\frac{18.564-\frac{T_{leaf}}{254.4}}{T_{leaf}+255.57}$$

(V) Light use efficiency (LUE, %):

$LUE=PN$ (μmol m^{-2} s^{-1})/PAR (μmol m^{-2} s^{-1})×100 (Evrendilek et al., 2008)

(VI) Water use efficiency (WUE, %):

$WUE=(PN$ (μmol m^{-2} s^{-1})/E (μmol m^{-2} s^{-1}))×100 (Evrendilek et al., 2008)

During the study average air pressure was measured as 101.0 kPa. Statistical software used was R studio.

3. RESULTS AND DISCUSSION

3.1. Morphological traits

The thirty-six wheat genotypes differed significantly for all the morphological traits except GY (Table 2). The years also differed significantly for all the traits except GPS. Genotype×Year interaction component was found significant for only traits such as PH, DM, TM, BY and HI where differential response of the wheat genotypes to the varying environments was envisaged for these characters.

Plant height was found to be lowest (Table 2) in DBW 17 (33.28 cm) among the genotypes, while among the year, Year 2 showed better performance (45.03 cm). The

Table 2: Mean performance and ANOVA for morphological traits in wheat over two years

Genotypes	PH	DH	DM	TM	GPS
RW 3684	39.283^{jklm}	80^{abc}	116^{bc}	120^{cdefgh}	50.7^{efghi}
DBW 14	59.700^{abc}	57^{k}	100^{n}	141^{abc}	51.8^{efghi}
KRL 1-4	53.417^{cdef}	69^{gh}	106^{jklm}	118^{cdefgh}	52.0^{efghi}
HW 2044	59.208^{abc}	60^{ijk}	104^{klmn}	156^{ab}	45.8^{ghijk}
PDW 314 (d)	36.692^{klm}	78^{abcdef}	116^{bcde}	94^{hi}	44.7^{ghijk}
KRL 213	39.800^{jklm}	78^{abcde}	116^{bcd}	127^{cdef}	68.7^{ab}
HI 8498(d)	43.817^{hij}	72^{defgh}	110^{fghij}	84^{i}	58.2^{cde}
GW 322	42.550^{ijk}	73^{cdefgh}	111^{efghi}	124^{cdefg}	59.5^{bcde}
DBW 71	46.733^{ghi}	68^{hi}	107^{hijkl}	119^{cdefgh}	47.9^{fghij}
WH 1105	46.717^{ghi}	72^{defgh}	108^{hijk}	106^{efghi}	72.0^{a}
RAJ 4229	59.633^{abc}	68^{hi}	104^{klmn}	154^{ab}	40.1^{jkl}
BH 1146	61.783^{ab}	69^{gh}	109^{ghij}	124^{cdefg}	32.7^{l}
HD 2009	63.483^{a}	66^{hij}	110^{fghij}	120^{cdefgh}	52.8^{defghi}
DBW 17	33.283^{m}	79^{abcd}	116^{bcde}	112^{defgh}	50.6^{efghi}
WH1021	51.683^{defg}	68^{hi}	107^{ijklm}	158^{a}	44.8^{ghijk}
UP 262	51.533^{defg}	70^{fgh}	110^{fghij}	127^{cdef}	52.2^{efghi}
HD 2967	39.783^{jklm}	78^{abcdef}	122^{a}	127^{cdef}	54.0^{defg}
DBW 16	35.200^{lm}	84^{a}	119^{ab}	141^{abc}	51.5^{efghi}
NW 1067	46.467^{ghi}	71^{efgh}	110^{fghij}	117^{cdefgh}	48.2^{fghij}
HI 1563	59.033^{abc}	60^{jk}	106^{jklm}	102^{fghi}	45.8^{ghijk}
KRL 3-4	51.450^{defg}	73^{bcdefgh}	117^{bc}	125^{cdefg}	37.6^{kl}
DBW 46	46.683^{ghi}	77^{abcdef}	115^{bcde}	137^{abcd}	44.3^{hijk}

Table 2: Continue...

Genotypes	PH	DH	DM	TM	GPS
NW 4092	41.800^{ijk}	78^{abcdef}	113^{cdefg}	112^{defgh}	65.3^{abc}
HD 2733	41.233^{ijkl}	76^{bcdefg}	115^{bcde}	125^{cdefg}	41.1^{jkl}
KRL 210	44.267^{hij}	72^{cdefgh}	110^{fghij}	117^{cdefgh}	53.3^{defgh}
NW 4018	42.700^{ijk}	81^{ab}	115^{bcde}	112^{defgh}	58.0^{cde}
RAJ 4238	56.417^{bcde}	66^{hij}	102^{mn}	140^{abc}	36.9^{kl}
Kharchia-65	56.867^{bcd}	70^{fgh}	114^{cdefg}	131^{bcde}	44.8^{ghijk}
CBW 38	44.467^{hij}	77^{abcdef}	114^{cdefg}	134^{abcd}	36.9^{kl}
KRL 19	58.667^{abc}	67^{hij}	103^{lmn}	120^{cdefgh}	51.8^{efghi}
DBW 51	43.067^{ijk}	77^{abcdef}	114^{cdef}	127^{cdef}	62.1^{bcd}
K 0307	41.633^{ijkl}	72^{defgh}	112^{defgh}	120^{cdefgh}	44.8^{ghijk}
DPW 621- 50	36.950^{klm}	77^{abcdef}	115^{bcde}	98^{ghi}	53.7^{defgh}
HD 2932	50.033^{efgh}	67^{hij}	107^{hijkl}	133^{abcde}	43.8^{ijk}
MACS 6222	47.367^{fghi}	73^{cdefgh}	112^{defgh}	99^{ghi}	53.3^{defghi}
DBW 39	41.367^{ijkl}	76^{bcdefg}	110^{fghij}	96^{hi}	56.5^{cdef}
Year					
Year-1	50.23^{a}	70.68^{b}	111.19 ^{a}	100.95 ^{b}	49.15
Year-2	45.03^{b}	73.56^{a}	110.64 ^{b}	143.35 ^{a}	51.30
ANOVA (Probability)					
Genotype (Factor-A)	0.000	0.000	0.000	0.000	0.000
Year (Factor-B)	0.000	0.002	0.000	0.000	0.054
Genotype×Year	0.029	0.607	0.000	0.000	0.595

Table 2: Continue...

Genotypes	TGW	SPL	GY	BY	HI
RW 3684	41.84^{cdefghijk}	10.28^{fghi}	5.54	22.45^{efghijk}	0.26^{cdefghi}
DBW 14	39.22^{lmno}	9.05^{jkl}	4.92	14.13^{lm}	0.35^{ab}
KRL 1-4	41.45^{defghijkl}	10.58^{efgh}	5.75	20.80^{fghijkl}	0.28^{bcdefg}
HW 2044	42.97^{abcdefg}	9.90^{hijk}	5.79	16.05^{klm}	0.34^{abc}
PDW 314(d)	43.99^{abc}	6.83^{m}	4.68	21.02^{efghijkl}	0.24^{efghij}
KRL 213	35.60^{p}	10.63^{efgh}	6.50	24.20^{cdefghi}	0.27^{bcdefg}
HI 8498(d)	42.03^{cdefghijk}	7.48^{m}	4.72	11.80^{m}	0.39^{a}
GW 322	43.38^{abcdef}	10.90^{defg}	6.08	23.95^{cdefghi}	0.25^{efghij}
DBW 71	41.41^{defghijkl}	10.85^{defgh}	5.89	23.73^{defghij}	0.26^{cdefghi}
WH 1105	37.65^{op}	11.15^{cdef}	4.41	20.70^{fghijkl}	0.24^{efghij}
RAJ 4229	38.50^{no}	8.54^{l}	5.66	16.57^{jklm}	0.34^{abcd}
BH 1146	41.25^{fghijkl}	9.88^{hijk}	5.18	25.73^{bcdefg}	0.20^{ghijk}
HD 2009	43.74^{abcde}	10.25^{fghi}	5.17	27.46^{abcdef}	0.20^{ghijk}
DBW 17	41.05^{fghijklm}	10.70^{efgh}	5.12	25.72^{bcdefg}	0.21^{ghijk}
WH1021	42.61^{bcdefgh}	10.85^{defgh}	5.47	20.32^{fghijkl}	0.26^{cdefgh}
UP 262	43.93^{abc}	11.30^{bcde}	5.66	21.57^{efghijk}	0.27^{bcdefg}
HD 2967	42.39^{cdefgh}	10.89^{defg}	5.62	25.55^{bcdefgh}	0.22^{fghijk}

Table 2: Continue...

Genotypes	TGW	SPL	GY	BY	HI
DBW 16	38.76^{mno}	10.02^{ghij}	5.60	31.67^{ab}	0.18^{hijk}
NW 1067	35.77^{p}	10.23^{fghi}	4.82	$18.49^{ghijklm}$	$0.26^{cdefghi}$
HI 1563	43.37^{abcdef}	10.48^{efgh}	4.77	18.34^{hijklm}	0.26^{defghi}
KRL 3-4	39.73^{jklmno}	11.00^{def}	4.57	33.15^{a}	0.14^{k}
DBW 46	45.27^{a}	12.25^{b}	5.21	31.70^{ab}	0.17^{jk}
NW 4092	$43.15^{abcdefg}$	13.35^{a}	5.85	$22.35^{efghijk}$	$0.26^{bcdefgh}$
HD 2733	$40.97^{fghijklm}$	9.00^{kl}	5.64	27.32^{abcdef}	0.20^{ghijk}
KRL 210	39.61^{klmno}	9.99^{ghij}	6.33	30.22^{abcd}	0.21^{ghijk}
NW 4018	$39.97^{ijklmno}$	11.03^{def}	5.34	$22.29^{efghijk}$	0.24^{efghij}
RAJ 4238	$42.21^{cdefghi}$	8.80^{l}	5.95	$18.64^{ghijklm}$	0.31^{abcde}
Kharchia-65	43.79^{abcd}	9.93^{ghijk}	4.46	$21.05^{efghijkl}$	0.22^{ghijk}
CBW 38	37.86^{op}	9.10^{jkl}	5.26	31.15^{abc}	0.17^{ijk}
KRL 19	$40.73^{ghijklmn}$	11.18^{cdef}	5.67	17.93^{ijklm}	0.30^{bcdef}
DBW 51	$41.33^{efghijkl}$	12.08^{bc}	5.31	19.47^{ghijkl}	0.27^{bcdefg}
K 0307	$41.70^{cdefghijk}$	11.83^{bcd}	5.63	$23.83^{cdefghij}$	0.24^{efghij}
DPW 621- 50	$41.50^{defghijkl}$	11.79^{bcd}	4.75	$21.54^{efghijk}$	0.22^{fghijk}
HD 2932	44.97^{ab}	9.30^{ijkl}	5.69	$21.37^{efghijkl}$	$0.26^{bcdefgh}$
MACS 6222	$40.35^{hijklmn}$	11.33^{bcde}	5.00	$21.04^{efghijkl}$	0.23^{efghij}
DBW 39	$42.04^{cdefghij}$	10.35^{efgh}	5.48	28.18^{abcde}	0.20^{ghijk}
Year					
Year-1	41.65^{a}	9.98^{b}	4.10^{b}	19.36^{b}	0.22^{b}
Year-2	40.91^{b}	10.75^{a}	6.65^{a}	26.28^{a}	0.27^{a}
ANOVA (Probability)					
Genotype	0.000	0.000	0.138	0.000	0.000
Year	0.01	0.000	0.000	0.000	0.000
Genotype×Year	0.478	0.619	0.124	0.000	0.000

genotype DBW 14 exhibited the lowest DH (57) and DM (99.75), while Year 1 was lowest for DH (70.68) and Year 2 was lowest for DM (110.64). Among the major yield components, TM was found to be highest in WH 1021 (158), GPS in WH 1105 (72), TGW in DBW 46 (45.27), and SPL in NW 4092 (13.35 cm). The year-wise performance showed better Year 2 for TM (143.35) and SPL (10.75 cm) while better Year 1 for TGW (41.65). GY did not differ significantly among the genotypes. However, it differed significantly year-wise, and Year 2 performed better (6.65 t ha^{-1}). BY was found to be highest in KRL-3-4 (33.15 t ha^{-1}), which is a salt-tolerant genotype, while Year 2 (26.28 t $ha^{-1)}$ was highest among the years. The Harvest index was highest in HI 8498(d) [0.394] which is a durum genotype. Among the years, year 2 (0.27) showed better performance for HI.

Among the genetic parameters studied, high GCV and PCV (Table 4) were exhibited by the Traits BY and HI among the ten morphological traits. However, the difference between the GCV and PCV was found to be low for most of the traits except GY. Thus, the seasonal difference over the two years played a key role and contributed more to the expression of GY which was further confirmed by the low heritability of GY (0.352) compared to other traits. Most of the traits showed higher genetic advance (GAM) except DH (14.05), DM (8.685), TGW (9.585), and GY (8.483). High heritability, along with high GAM, is desirable for any trait as it indicates control by additive genes, resulting in a more significant response to selection. The traits such as PH, TM, GPS, SPL, BY, and HI had high heritability and GAM and thus would be more responsive to selection. Earlier workers such as Dhananjay et al., 2012 reported moderate GCV and high PCV for spike length; Singh et al., 2013 for GPS, Nath et al., 2021 for GY which were in conformity with the present findings.

3.2. Photosynthetic parameters

Photosynthetic parameters such as Net photosynthesis Rate (*Pn*), Transpiration rate (*E*), Intercellular CO_2 concentration (*Ci*), and Stomatal conductance (g_s), which were estimated by gas exchange measurements in both the pre and post-anthesis stage, exhibited significant variation among genotypes in case of pre-anthesis measurements while in post-anthesis measurements, all the parameters found to be non-significant for genotypic variation except *Pn* (Table 3). Seasonal variation was significant for almost all the traits except *Pn* in the pre-anthesis stage and *E* in the post-anthesis stage. A similar result of higher seasonal variation of photosynthetic traits was reported by earlier workers like Gebbing et al., 1999 in wheat and Bernacchi et al., 2006 in Soybean for gas exchange measurements.

High *Pn*, which is the most desirable trait for photosynthetically efficient genotypes, was found in genotypes like RAJ 4238 (24.135 µmol CO_2 m^{-2} s^{-1}) and HD 2009 (15.452 µmol CO_2 m^{-2} s^{-1}) in pre and post-anthesis measurements respectively. Year 2 showed better performance for *Pn* in both pre and post-anthesis stages. Overall, pre-anthesis *Pn* was much higher in both years,

Table 3: Mean performance and ANOVA for photosynthetic traits in wheat over two years

Genotypes	P_n		E		C_i	
	Pre	Post	Pre	Post	Pre	Post
RW 3684	9.82^{hij}	$12.47^{abcdefg}$	1.47^{hij}	3.08	206.50^{cdefgh}	184.62
DBW 14	12.13^{efghij}	$9.68^{efghijk}$	1.89^{fghij}	2.77	222.00^{ab}	177.25
KRL 1-4	14.32^{defghi}	$11.09^{bcdefghij}$	3.50^{abc}	3.01	184.25^{j}	178.50
HW 2044	17.54^{abcdef}	$12.34^{abcdefgh}$	3.76^{a}	3.61	190.25^{ij}	175.20
PDW 314(d)	14.30^{defghi}	$9.72^{efghijk}$	1.95^{fghij}	2.47	$208.50^{bcdefgh}$	173.61
KRL 213	$15.30^{bcdefghi}$	9.15^{fghijk}	1.96^{fghij}	3.87	213.50^{abcdef}	169.94
HI 8498(d)	$16.48^{bcdefgh}$	7.76^{jk}	2.03^{efghij}	2.977	214.75^{abcdef}	174.72
GW 322	11.87^{fghij}	14.18^{abc}	3.16^{abcd}	3.82	202.50^{efghi}	175.90
DBW 71	$13.98^{defghij}$	12.665^{abcdef}	2.78^{abcdef}	3.92	190.75^{ij}	176.46
WH 1105	21.79^{ab}	$12.29^{abcdefgh}$	2.78^{abcdef}	3.87	219.00^{abcd}	175.51
RAJ 4229	16.76^{bcdefg}	8.98^{ghijk}	$2.29^{defghij}$	3.11	$211.00^{abcdefg}$	167.11
BH 1146	18.00^{abcdef}	8.93^{ghijk}	$2.54^{bcdefgh}$	2.96	203.00^{efghi}	159.23
HD 2009	19.37^{abcd}	15.45^{a}	$2.48^{cdefghi}$	3.71	214.50^{abcdef}	179.71
DBW 17	9.50^{ij}	12.82^{abcde}	1.33^{j}	3.92	215.25^{abcde}	172.38
WH1021	9.54^{ij}	$11.10^{bcdefghij}$	1.39^{ij}	2.91	225.75^{a}	177.33
UP 262	10.73^{ghij}	$9.987^{efghijk}$	1.69^{ghij}	3.08	221.50^{abc}	178.011
HD 2967	$16.35^{bcdefgh}$	14.38^{ab}	$2.727^{abcdefg}$	4.14	203.25^{efghi}	172.83
DBW 16	$16.06^{bcdefghi}$	8.74^{hijk}	2.92^{abcdef}	2.70	205.25^{defghi}	183.35
NW 1067	17.33^{bcdefg}	$9.49^{efghijk}$	2.84^{abcdef}	2.84	214.00^{abcdef}	172.92
HI 1563	7.45^{j}	7.73^{jk}	1.85^{fghij}	3.71	154.25^{k}	164.62
KRL 3-4	17.42^{bcdef}	14.23^{abc}	$2.74^{abcdefg}$	4.27	204.50^{defghi}	177.8
DBW 46	18.38^{abcdef}	$12.09^{abcdefghi}$	$2.57^{bcdefgh}$	3.89	$212.25^{abcdefg}$	173.96
NW 4092	$14.98^{cdefghi}$	9.090^{fghijk}	$2.75^{abcdefg}$	3.39	199.75^{fghi}	157.98
HD 2733	19.16^{abcd}	$10.61^{cdefghijk}$	3.49^{abc}	3.47	200.75^{efghi}	173.39
KRL 210	$14.91^{cdefghi}$	14.54^{ab}	$2.67^{abcdefg}$	3.95	$207.00^{bcdefgh}$	178.78
NW 4018	18.47^{abcdef}	8.00^{jk}	2.89^{abcdef}	2.557	202.50^{efghi}	164.90
RAJ 4238	24.14^{a}	8.53^{ijk}	3.22^{abcd}	3.50	215.50^{abcde}	168.71
Kharchia-65	$16.23^{bcdefgh}$	$9.43^{efghijk}$	2.91^{abcdef}	3.32	197.00^{ghij}	165.26
CBW 38	$15.98^{bcdefghi}$	$10.54^{defghijk}$	$2.75^{abcdefg}$	3.70	203.25^{efghi}	170.18

Table 3: Continue...

Genotypes	P_n		E		C_i	
	Pre	Post	Pre	Post	Pre	Post
KRL 19	18.27[abcdef]	13.71abcd	3.17[abcd]	4.53	209.00[bcdefgh]	170.868
DBW 51	17.34[bcdefg]	7.32k	2.87[abcdef]	2.67	204.00[defghi]	157.31
K 0307	21.16[abc]	10.65cd[efghijk]	3.1[abcde]	3.76	203.00[efghi]	175.06
DPW 621- 50	17.42[bcdef]	12.33[abcdefgh]	3.21[abcd]	3.43	204.00[defghi]	178.19
HD 2932	13.29[defghij]	12.01[abcdefghi]	3.11[abcde]	4.33	181.75[j]	175.43
MACS 6222	18.58[abcde]	9.60[efghijk]	3.59[ab]	3.64	194.50[hij]	167.89
DBW 39	10.73[ghij]	10.31[defghijk]	3.25[abcd]	3.85	199.75[fghi]	169.56
Year						
Year-1	15.30	9.51[b]	3.04[a]	3.52	191.71[b]	151.31[b]
Year-2	16.09	12.27[a]	2.27[b]	3.41	217.08[a]	193.94[a]
ANOVA (Probability)						
Genotype	0.000	0.000	0.000	0.233	0.000	0.140
Year	0.256	0.000	0.000	0.522	0.000	0.000
Genotype× Year	0.013	0.972	0.000	1.00	0.000	1.000

Table 3: Continued

Genotypes	g_s		*LUE*		*WUE*	
	Pre	Post	Pre	Post	Pre	Post
RW 3684	350.74[efgh]	422.93	2.16[defghi]	1.84	0.66[abcdef]	0.43
DBW 14	729.87[a]	277.06	3.02[abcdefg]	1.84	0.64[abcdef]	0.36
KRL 1-4	401.29[cdefgh]	290.17	1.86[hij]	1.96	0.46[defg]	0.41
HW 2044	351.04[efgh]	338.02	2.40[bcdefghi]	1.45	0.50[cdefg]	0.37
PDW 314(d)	499.25[bcdefgh]	244.26	2.45 [bcdefghi]	1.76	0.75[abcd]	0.39
KRL 213	548.04[abcdef]	353.64	2.41[bcdefghi]	1.72	0.81[ab]	0.28
HI 8498(d)	579.06[abcd]	378.58	3.02[abcdefg]	1.61	0.82[ab]	0.26
GW 322	498.34[bcdefgh]	380.12	2.07[efghi]	1.77	0.44[efg]	0.39
DBW 71	433.20[cdefgh]	386.82	1.55[ij]	1.71	0.54[bcdefg]	0.34
WH 1105	530.02[abcdefg]	488.28	3.43[ab]	1.85	0.78[abc]	0.32
RAJ 4229	589.08[abc]	305.23	2.83[abcdefgh]	1.37	0.85[a]	0.29
BH 1146	511.04[abcdefg]	189.45	2.62[abcdefghi]	1.02	0.7[abcde]	0.32
HD 2009	570.55[abcde]	366.26	3.4[abc]	1.76	0.79[abc]	0.46
DBW 17	571.15[abcde]	388.20	1.95[ghi]	1.35	0.61[abcdefg]	0.32
WH1021	663.01[ab]	300.52	3.13[abcdef]	1.81	0.61[abcdef]	0.42
UP 262	554.24[abcdef]	404.11	3.18[abcd]	1.43	0.58[abcdefg]	0.36
HD 2967	585.95[abc]	342.27	2.22[defghi]	1.87	0.62[abcdef]	0.38
DBW 16	386.79[cdefgh]	439.33	2.07[efghi]	1.55	0.6[abcdefg]	0.38
NW 1067	306.69[gh]	252.12	3.13[abcdef]	1.37	0.66[abcdef]	0.33
HI 1563	342.91[fgh]	280.22	0.77[j]	1.28	0.40[fg]	0.23
KRL 3-4	374.89[cdefgh]	471.60	2.77[abcdefgh]	1.75	0.67[abcdef]	0.35

Genotypes	g_s		*LUE*		*WUE*	
	Pre	Post	Pre	Post	Pre	Post
DBW 46	406.048[cdefgh]	357.52	2.87[abcdefgh]	1.58	0.81[ab]	0.33
NW 4092	357.561[defgh]	196.33	2.32[cdefghi]	1.15	0.56[abcdefg]	0.29
HD 2733	447.03[bcdefgh]	301.36	2.28[defghi]	2.23	0.56[abcdefg]	0.31
KRL 210	309.71[gh]	403.32	2.58[abcdefghi]	1.91	0.7[abcdef]	0.37
NW 4018	367.64[cdefgh]	349.28	2.22[defghi]	1.03	0.67[abcdef]	0.34
RAJ 4238	280.98[h]	301.50	3.62[a]	1.21	0.75[abcd]	0.25
Kharchia-65	333.62[fgh]	231.32	2.45[bcdefghi]	1.29	0.57[abcdefg]	0.29
CBW 38	408.44[cdefgh]	287.84	2.37[bcdefghi]	1.55	0.64[abcdef]	0.29
KRL 19	545.84[abcdef]	335.34	3.17[abcde]	1.16	0.58[abcdefg]	0.30
DBW 51	415.3[cdefgh]	184.09	2.61[abcdefghi]	0.9	0.66[abcdef]	0.27
K 0307	412.20[cdefgh]	393.92	2.49[bcdefghi]	1.81	0.77[abc]	0.28
DPW 621- 50	458.67[bcdefgh]	379.92	2.51[bcdefghi]	1.57	0.66[abcdef]	0.35
HD 2932	317.98[gh]	456.25	2.96[abcdefgh]	1.75	0.43[efg]	0.28
MACS 6222	439.21[bcdefgh]	307.66	2.26[defghi]	1.50	0.56[abcdefg]	0.27
DBW 39	390.70[cdefgh]	336.83	2.04[fghi]	1.45	0.31[g]	0.27
Year						
Year-1	364.66[b]	309.55[b]	2.37[b]	1.17 [b]	0.51 [b]	0.28 [b]
Year-2	539.13[a]	363.88 [a]	2.70 [a]	1.95 [a]	0.75 [a]	0.38 [a]
ANOVA (Probability)						
Genotype	0.002	0.513	0.017	0.244	0.022	0.767
Year	0.000	0.039	0.020	0.000	0.000	0.000
Genotype × Year	0.047	0.998	0.844	0.997	0.120	0.983

Table 4: Genetic parameters for the different morphological traits in wheat

Traits	Mean	Range		SEm±	GCV	PCV	Heritability (Broad sense)	GA as percentage of mean
		Maximum	Minimum					
PH	47.63	64.80	32.30	2.399	16.725	18.179	0.846	31.697
DH	72.11	85.00	56.50	2.361	7.905	9.161	0.744	14.05
DM	110.91	122.5000	99.5000	1.1048	4.425	4.644	0.908	8.685
TM	122.15	159.4290	82.6250	2.77	13.832	14.199	0.949	27.756
GPS	50.22	77.6314	32.4784	3.003	16.612	18.64	0.794	30.497
TGW	41.28	46.4688	34.6277	0.833	5.287	6.008	0.774	9.585
SPL	10.36	13.4000	6.4500	0.376	11.955	13.012	0.844	22.627
GY	5.37	6.91	3.96	0.358	6.942	11.703	0.352	8.483
BY	22.8192	35.2000	10.8000	1.30	21.37	22.838	0.875	41.190
HI	0.2475	0.4239	0.1361	0.017	20.998	23.214	0.818	39.117

which is desirable regarding physiological efficiency. Similar result was reported by Lefebvre et al., 2005 where mature plants showed increased SBPase activity but the young leaves showed the highest rates of carbon fixation.

Transpiration rate (E), an indicator of water loss by stomata and thus a negative predictor for photosynthetically efficient genotypes, was higher in the post-anthesis stage in both years. Among the genotypes, it was found lowest in DBW 17 (1.33 millimole H_2O $m^{-2}s^{-1}$) in the case of the pre-anthesis stage, while in the post-anthesis stage, genotypes did not differ significantly. Among the years, Year 2 exhibited higher value in both pre (217.08 millimole H_2O $m^{-2}s^{-1}$) and post anthesis stage (193.94 millimol H_2O $m^{-2}s^{-1}$) respectively.

Intercellular CO_2 concentration (*Ci*), measured by gas exchange mechanism, is a critical component of photosynthetic efficiency, and a higher value indicates a higher efficiency. The pre-anthesis stage showed a higher value of *Ci* and, thus, higher efficiency than the post-anthesis stage in both years. Genotypes such as WH 1021 showed a higher value (225.75 μmol mol^{-1}) in the pre-anthesis stage, while in the case of post-anthesis, the genotypic variation was found to be non-significant. Year 2 exhibited higher *Ci* values in pre- (217.08 μmol mol^{-1}) and post (193.95 μmol mol^{-1}) anthesis stages.

Stomatal conductance (g_s) is a crucial component in regulating transpiration loss of water by plants. By decreasing their stomatal conductance, plants can partially limit transpiration rate and decreased leaf water status. A lower value of g_s was found in the post-anthesis stage during both years. Among the genotypes, lower g_s was exhibited by RAJ 4238 (280.98 millimole H_2O $m^{-2}s^{-1}$) in the pre-anthesis stage, while in the post-anthesis stage, the genotypic variation was found to be non-significant. Year 1 exhibited lower g_s values in both pre (364.66 H2O $m^{-2}s^{-1}$) and post anthesis (309.55 H_2O $m^{-2}s^{-1}$) stages indicating less water loss by transpiration.

Light use efficiency (LUE), calculated by gas exchange measurement, indicated better efficiency in the pre-anthesis stages in both years. Among the genotypes, RAJ 4238 exhibited higher LUE (3.62) in the pre-anthesis stage, while the variation was non-significant in the post-anthesis stage. Among the years, Year 2 showed better LUE in both pre (2.70) and post (1.95) anthesis stages.

Water use efficiency (WUE), also calculated from gas exchange parameters, indicated better efficiency at the pre-anthesis stage in both years. At the genotypic level, higher WUE was exhibited by RAJ 4229 (0.84) in the pre-anthesis stage, while the variation was non-significant at the post-anthesis stage. Among the years, Year 2 exhibited higher efficiency in both pre (0.75) and post (0.38) anthesis stages.

Among the genetic parameters low GCV and PCV was shown (Table 5) by all the photosynthetic traits and the difference between these two parameters was high in almost all the traits barring C_i indicating higher influence of environment over the expression of these traits. Most of the traits showed high heritability coupled with higher genetic advance (GAM) except g_s in both pre and post anthesis stages (0.36 and 0.29) indicating higher role of additive gene action for governing these traits and thus selection could be effective. Poddar et al., 2022 reported similar pattern of findings for physiological traits such as CTD where high GAM was observed.

Table 5: Genetic parameters for the different photosynthetic traits in wheat at pre and post anthesis stage

Traits	Physiological stage	Mean	Range		SEm±	GCV	PCV	Heritability (Broad sense)	GA as percentage of mean
			Maximum	Minimum					
P_n	Pre-anthesis	29.18	6.13	15.69	2.32	18.55	27.97	0.44	25.34
	Post-anthesis	17.39	5.43	10.89	1.03	17.84	22.30	0.64	29.40
E	Pre-anthesis	4.19	1.31	2.66	0.26	21.89	25.91	0.71	38.12
	Post-anthesis	4.59	1.95	3.47	0.26	13.62	17.21	0.63	22.21
C_i	Pre-anthesis	230.50	147.00	204.40	3.42	6.24	6.67	0.87	12.01
	Post-anthesis	193.20	147.46	172.63	3.21	3.27	4.20	0.61	5.24
g_s	Pre-anthesis	817.62	197.69	451.89	83.39	15.73	30.47	0.27	16.74
	Post-anthesis	656.53	167.25	336.72	52.77	16.58	27.68	0.36	20.46
LUE	Pre-anthesis	4.23	0.68	2.53	0.42	15.04	28.02	0.29	16.63
	Post-anthesis	2.60	0.51	1.56	0.18	15.36	22.71	0.46	21.40
WUE	Pre-anthesis	1.03	0.25	0.63	0.10	13.24	25.21	0.28	14.32
	Post-anthesis	0.50	0.16	0.33	0.05	9.07	21.80	0.17	7.77

Association analysis

Association study between yield components and photosynthethetic parameters was done at both pre and post anthesis stages and presented in Table 6 and 7 respectively. Positive correlation at genotypic level was found between

Table 6: Genotypic correlation between yield attributes and photosynthetic traits at pre-anthesis stage in wheat

Traits	PH	DH	DM	TM	GPS	TGW	SPL	BY
PH	1.00**	-0.960**	-0.773**	0.406*	-0.416*	0.155	-0.146	-0.399*
DH		1.00**	0.966**	-0.313	0.304	-0.209	0.228	0.587**
DM			1.00	-0.238	0.157	-0.020	0.221	0.644**
TM				1.00**	-0.416*	-0.033	-0.002	0.051
GPS					1.00**	-0.234	0.445**	-0.175
TGW						1.00**	0.088	-0.064
SPL							1.00**	0.283
BY								1.00**
HI								
P_n								
E								
G_s								
C_i								
LUE								
WUE								
GY								

Table 6: Continue...

Traits	HI	P_n	*E*	g_s	C_i	*LUE*	*WUE*	GY
PH	0.391*	0.125	0.050	0.280	-0.112	0.504**	-0.02	-0.105
DH	-0.58**	-0.055	-0.071	-0.45**	0.203	-0.339*	0.22	0.055
DM	-0.71**	0.021	-0.081	-0.255	0.029	-0.419*	0.21	-0.131
TM	0.125	0.037	-0.024	0.122	0.203	0.449**	0.11	0.584**
GPS	0.218	-0.117	-0.038	0.273	0.175	-0.048	-0.08	0.257
TGW	-0.006	-0.344*	0.003	-0.187	-0.316	-0.156	-0.53**	-0.120
SPL	-0.353*	0.016	0.208	-0.268	-0.097	-0.266	-0.35*	0.187
BY	-0.94**	0.013	0.129	-0.339*	0.003	-0.289	-0.10	0.182
HI	1.00**	-0.025	-0.096	0.405*	0.077	0.297	0.14	0.035
P_n		1.00**	0.711**	-0.51**	0.274	0.586**	0.51**	-0.141
E			1.00**	-0.99**	-0.369*	0.047	-0.26	0.281
g_s				1.00**	0.853**	0.675**	0.87**	-0.355*
C_i					1.00**	1.041**	0.86**	-0.041
LUE						1.00**	0.58**	-0.363*
WUE							1.00**	-0.312
GY								1.00**

*: (p=0.05) probability level; **: (p=0.01) probability level

P_n and *E* (0.711), P_n and *LUE* (0.586), P_n and *WUE* (0.51), g_s and HI (0.405), g_s and C_i (0.853), g_s and *LUE* (0.675), g_s and *WUE* (0.87), C_i and *LUE* (0.99), C_i and *WUE* (0.86), LU*E* and PH (0.504), LU*E* and TM (0.449), *LUE* and *WUE* (0.58) while negative association was found between P_n and TGW (-0.344), P_n and g_s (-0.51), g_s and DH (-0.45), g_s and BY (-0.339), *E* and g_s (-0.99), *E* and C_i (-0.369), LU*E* and DH (-0.339), *LUE* and DM (-0.419), WU*E* and TGW (-0.53),WU*E* and SPL (-0.35) at pre anthesis stage. GY was found negatively correlated with g_s (-0.355)

Table 7: Genotypic correlation (rg) between yield attributes and photosynthetic traits at post-anthesis stage in wheat

Traits	PH	DH	DM	TM	GPS	TGW	SPL	BY
PH	1.00**	-0.96**	-0.773**	0.406**	-0.416*	0.155	-0.146	-0.391*
DH		1.00**	0.966**	-0.313	0.304	-0.209	0.228	0.587**
DM			1.00**	-0.238	0.157	-0.020	0.221	0.644**
TM				1.00**	-0.416*	-0.033	-0.002	0.051
GPS					1.00**	-0.234	0.445**	-0.175
TGW						1.00**	0.088	-0.064
SPL							1.00**	0.283
BY								1.00**
HI								
P_n								
E								
g_s								
C_i								
LUE								
WUE								
GY								

Table 7: Continue...

Traits	HI	P_n	E	g_s	C_i	*LUE*	*WUE*	GY
PH	0.391*	-0.016	0.109	-0.346*	-0.244	-0.326	-0.176	-0.105
DH	-0.58**	-0.017	-0.124	0.176	-0.023	0.041	0.185	0.055
DM	-0.71**	0.118	-0.009	0.148	0.018	0.117	0.278	-0.131
TM	0.125	0.074	-0.014	-0.045	0.117	0.028	0.341**	0.584**
GPS	0.218	0.036	0.031	0.128	-0.063	-0.034	0.074	0.257
TGW	-0.006	0.249	0.152	-0.035	-0.012	-0.009	0.300	-0.120
SPL	-0.353*	0.219	0.353*	0.135	-0.215	-0.299	-0.035	0.187
BY	-0.94**	0.484**	0.380*	0.456**	0.238	0.321	0.446**	0.182
HI	1.00**	-0.405*	-0.312	-0.271	-0.089	-0.181	-0.332*	0.035
P_n		1.00**	0.786**	0.853**	0.664**	0.467**	0.631**	0.219
E			1.00**	0.584**	0.317	0.365*	0.026	0.307
g_s				1.00**	0.980**	0.647**	0.862**	0.271
C_i					1.00**	0.753**	0.765**	0.108
LUE						1.00**	0.221	0.230
WUE							1.00**	0.289
GY								1.00**

*: (p=0.05) probability level; **: (p=0.01) probability level

and *LUE* (-0.363) at pre-anthesis stage while it showed positive correlation with TM (0.584).

During post anthesis stage almost similar trend was observed with some deviations. Positive correlation was found between P_n and *BY* (0.484), P_n and E (0.786), P_n and g_s (0.853), P_n and C_i (0.664), P_n and *LUE* (0.467), P_n and *WUE* (0.631), E and SPL (0.353), E and BY (0.38), E and g_s (0.584), E and *LUE* (0.365), g_s and BY (0.456), g_s and C_i (0.98), g_s and *LUE* (0.647), g_s and *WUE* (0.862), C_i and *LUE* (0.753), C_i and *WUE* (0.765) while negative association was found between P_n and HI (-0.405), g_s and PH (-0.346), WU*E* and HI (-0.332) at post-anthesis stage. GY was found not to be associated with any photosynthetic traits.

Path analysis revealed positive and high direct effect of *E* (4.663) and g_s (1.202) and *WUE* (1.281) on yield while negative direct effect of BY (-1.524) and P_n (-4.179) at pre anthesis stage (Table 8). Indirect effect of P_n was positive through g_s (2.140) while negative by *E* (-2.97) and C_i (-1.145). *E* showed positive indirect effect by P_n (3.314) but negative effect by g_s (-4.598) and C_i (-1.722). g_s exhibited high negative indirect effect by E (-1.186) while positive effect by C_i (1.026). *WUE* had high positive indirect effect by g_s (1.117) and C_i (1.106).

At post anthesis stage high direct positive effect was

Table 8: Direct (diagonal) and indirect (off-diagonal) effects of different yield components and photosynthetic traits on yield at pre-anthesis stage

Traits	PH	DH	DM	TM	GPS	TGW	SPL	BY
PH	-0.286	-0.545	-0.288	0.221	0.297	-0.123	-0.066	0.596
DH	0.275	0.568	0.360	-0.170	-0.217	0.166	0.102	-0.895
DM	0.221	0.549	0.372	-0.130	-0.112	0.016	0.099	-0.981
TM	-0.116	-0.178	-0.089	0.544	0.297	0.026	-0.001	-0.078
GPS	0.119	0.173	0.058	-0.226	-0.714	0.186	0.200	0.266
TGW	-0.044	-0.119	-0.007	-0.018	0.167	-0.795	0.039	0.098
SPL	0.042	0.130	0.082	-0.001	-0.318	-0.070	0.449	-0.431
BY	0.112	0.334	0.240	0.028	0.125	0.051	0.127	-1.524
HI	-0.112	-0.332	-0.263	0.068	-0.156	0.005	-0.159	1.430
P_n	-0.036	-0.031	0.008	0.020	0.079	0.273	0.007	-0.019
E	-0.014	-0.040	-0.030	-0.013	0.027	-0.002	0.093	-0.197
G_s	-0.080	-0.250	-0.095	0.066	-0.195	0.149	-0.121	0.516
C_i	0.032	0.116	0.011	0.111	-0.125	0.252	-0.043	-0.004
LUE	-0.144	-0.192	-0.156	0.244	0.034	0.124	-0.120	0.440
WUE	0.006	0.127	0.078	0.061	0.054	0.421	-0.156	0.158

Table 8: Continue...

Traits	HI	P_n	*E*	g_s	C_i	*LUE*	*WUE*	GY (r_g)
PH	-0.382	-0.524	0.234	0.336	0.047	0.407	-0.028	-0.105
DH	0.570	0.228	-0.329	-0.530	-0.085	-0.273	0.286	0.055
DM	0.689	-0.087	-0.378	-0.307	-0.012	-0.338	0.269	-0.131
TM	-0.122	-0.154	-0.112	0.146	-0.085	0.362	0.143	0.58**
GPS	-0.212	0.463	-0.175	0.328	-0.073	-0.038	-0.097	0.257
TGW	0.006	1.436	0.012	-0.225	0.132	-0.126	-0.678	-0.120
SPL	0.344	-0.067	0.970	-0.323	0.040	-0.215	-0.446	0.187
BY	0.915	-0.052	0.602	-0.407	-0.001	-0.233	-0.133	0.182
HI	-0.975	0.104	-0.449	0.487	-0.032	0.240	0.180	0.035
P_n	0.024	-4.179	3.314	-0.615	-0.115	0.473	0.656	-0.141
E	0.094	-2.970	4.663	-1.186	0.155	0.038	-0.336	0.281
g_s	-0.395	2.140	-4.598	1.202	-0.357	0.545	1.117	-0.35*
C_i	-0.075	-1.145	-1.722	1.026	-0.419	0.841	1.106	-0.041
LUE	-0.290	-2.450	0.218	0.812	-0.436	0.808	0.743	-0.36*
WUE	-0.137	-2.139	-1.223	1.048	-0.361	0.469	1.281	-0.312

r_g=Genotypic correlation coefficient; *: (p=0.05) probability level, **: (p=0.01) probability level; Residual Effect=-0.192

exhibited by E (18.024) and WUE (8.64), GPS (8.815) and TM (8.296) on the dependent trait GY while negative direct effect was shown by PH (-13.201), DM (-10.99), SPL (-10.59), BY (-17.26), HI (-27.29) and P_n (-15.34) (Table 9). Indirect effect of P_n was also negative for other photosynthetic traits such as E (-12.05), g_s (-13.09), C_i (-10.19), LUE (-7.155) and WUE (-9.683).

3.3. *Principal component analysis*

Principal component analysis was done to reduce the volume of data and identify a few key or minimum descriptors that effectively account for most of the observed diversity (Jolliffe and Cadima, 2016). Two separate PCAs were made with pre and post-anthesis photosynthetic parameters and other morphological traits, which resulted in six principal

Table 9: Direct (diagonal) and indirect (off-diagonal) effects of different yield components and photosynthetic traits on yield at post-anthesis stage

Traits	PH	DH	DM	TM	GPS	TGW	SPL	BY
PH	-13.201	3.802	8.500	3.366	-3.670	0.186	1.549	6.746
DH	12.673	-3.960	-10.62	-2.599	2.682	-0.251	-2.414	-10.13
DM	10.205	-3.824	-10.99	-1.977	1.381	-0.024	-2.340	-11.12
TM	-5.357	1.241	2.62	8.296	-3.665	-0.039	0.025	-0.887
GPS	5.496	-1.205	-1.723	-3.449	8.815	-0.282	-4.709	3.015
TGW	-2.048	0.827	0.220	-0.270	-2.066	1.202	-0.928	1.109
SPL	1.932	-0.903	-2.431	-0.020	3.921	0.105	-10.59	-4.882
BY	5.160	-2.325	-7.082	0.426	-1.540	-0.077	-2.995	-17.26
HI	-5.170	2.316	7.765	1.034	1.921	-0.008	3.741	16.200
P_n	0.211	0.065	-1.298	0.617	0.317	0.300	-2.313	-8.360
E	-1.434	0.490	0.103	-0.115	0.275	0.182	-3.734	-6.552
g_s	4.571	-0.695	-1.631	-0.375	1.129	-0.042	-1.432	-7.861
C_i	3.214	0.091	-0.201	0.968	-0.552	-0.014	2.272	-4.105
LUE	4.300	-0.161	-1.286	0.231	-0.297	-0.011	3.163	-5.534
WUE	2.319	-0.733	-3.054	2.829	0.649	0.360	0.365	-7.706

Table 9: Continue...

Traits	HI	P_n	E	g_s	C_i	*LUE*	*WUE*	GY (r_g)
PH	-10.688	0.245	1.959	1.309	-0.347	1.656	-1.518	-0.105
DH	15.959	0.253	-2.232	-0.663	-0.033	-0.207	1.599	0.055
DM	19.270	-1.810	-0.169	-0.561	0.026	-0.595	2.399	-0.131
TM	-3.402	-1.142	-0.249	0.171	0.166	-0.142	2.947	0.58**
GPS	-5.946	-0.552	0.563	-0.484	-0.089	0.171	0.636	0.257
TGW	0.171	-3.825	2.737	0.133	-0.017	0.046	2.590	-0.12
SPL	9.642	-3.351	6.357	-0.511	-0.306	1.519	-0.298	0.187
BY	25.616	-7.430	6.842	-1.722	0.339	-1.631	3.858	0.182
HI	-27.29	6.210	-5.615	1.026	-0.126	0.920	-2.887	0.035
P_n	11.049	-15.34	14.166	-3.226	0.947	-2.372	5.454	0.219
E	8.501	-12.05	18.024	-2.206	0.451	-1.856	0.232	0.307
G_s	7.404	-13.09	10.519	-3.780	1.396	-3.290	7.449	0.271
C_i	2.418	-10.19	5.706	-3.703	1.425	-3.828	6.609	0.108
LUE	4.935	-7.155	6.581	-2.446	1.073	-5.085	1.921	0.230
WUE	9.120	-9.683	0.483	-3.259	1.090	-1.131	8.640	0.289

r_g=Genotypic correlation coefficient; *: (p=0.05) probability level, **: (p=0.01) probability level; Residual Effect=-5.318

components based on Eigen value (>1.00), which accounted for 82.73% and 83.57% cumulative proportion of variance at the pre and post-anthesis stages, respectively (Table 10).

Regarding the loading values of different characters on different PCs, it was found that characters such as PH, DH, DM, BY, and HI showed higher loadings among the morphological traits in both the PCA. However, among the photosynthetic traits, only *LUE* had a high loading value in PCA made with pre-anthesis photosynthetic data. Other traits such as *Pn*, *E*, g_s, C_i, and *WUE* exhibited higher loadings in PC II for their pre-anthesis values. In PC I, the highest loading was shown by DM, followed by DH, while in PC II, C_i exhibited the highest loading followed by WUE. Among the post-anthesis photosynthetic traits, higher loadings were found by P_n, g_s, C_i, and *LUE* in PC I. Similarly, in case of PC II, higher loadings were exhibited by P_n, C_i, and *LUE* for their post anthesis values. In PC I, the highest loading was shown by BY, followed by HI, while in PC II, *Ci* exhibited the highest loading, followed by DH (Table 11).

In terms of PCA analysis, the most divergent genotypes were identified as DBW 14, RAJ 4229, DBW 16, and RAJ 4238 with pre-anthesis photosynthetic traits. A similar result was found with post-anthesis photosynthetic traits where divergent genotypes such as DBW 14, RAJ 4229, RAJ 4238, and HI 1563 were identified (Figure 1a and b).

Table 10: Eigen values and variability explained by each principal component (PCs) at pre and post anthesis stage

Principal component	PC1		PC2		PC3		PC4		PC5		PC6	
	Pre-a	Post-a	Pre-a	Post-a	Pre-a	Post-a	Pre-a	Post-a	Pre-a	Post-a	Pre-a	Post-a
Eigen Value	1.413	1.439	1.311	1.324	1.209	1.168	1.132	1.135	1.098	1.077	1.016	1.033
% Var. Exp.	24.91	26.81	18.47	19.23	13.36	11.63	10.26	10.39	9.08	8.40	6.65	7.11
Cum. Var. Exp.	24.91	26.81	43.38	46.04	56.74	57.67	67.00	68.06	76.08	76.46	82.73	83.57

Pre-a: Pre-anthesis; Post-a: Post-anthesis

Table 11: Individual character loadings indifferent PCs at pre and post anthesis stage

Principal component	PC1		PC2		PC3		PC4		PC5		PC6	
	Pre-a	Post-a	Pre-a	Post-a	Pre-a	Post-a	Pre-a	Post-a	Pre-a	Post-a	Pre-a	Post-a
PH	0.389	0.311	-0.151	-0.294	0.205	0.276	-0.134	0.048	0.024	0.081	-0.246	-0.078
DH	-0.428	-0.319	0.222	0.373	-0.037	-0.103	0.047	0.083	-0.020	-0.155	0.144	0.022
DM	-0.436	-0.350	0.156	0.307	-0.027	-0.014	-0.098	0.168	0.070	-0.020	0.021	-0.071
TM	0.180	0.074	0.023	-0.250	0.268	0.247	-0.307	0.191	-0.505	-0.562	0.074	0.045
GPS	-0.109	-0.088	0.130	0.165	-0.331	-0.338	0.531	-0.530	-0.177	-0.086	-0.210	-0.234
TGW	0.020	0.018	-0.250	-0.101	-0.045	0.200	-0.202	0.055	0.069	0.257	-0.449	-0.581
SPL	-0.196	-0.141	-0.050	0.139	0.037	0.292	0.227	-0.408	-0.336	-0.138	-0.639	-0.395
BY	-0.366	-0.378	0.044	0.060	0.260	0.334	-0.312	0.183	-0.139	-0.069	-0.069	0.136
HI	0.382	0.347	-0.017	-0.142	-0.228	-0.344	0.303	-0.238	-0.077	-0.134	0.233	-0.016
P_n	0.042	-0.298	0.224	-0.345	0.515	0.144	0.320	-0.143	0.173	0.111	-0.015	-0.147
E	-0.057	-0.176	-0.202	-0.186	0.457	0.369	0.412	-0.421	0.024	0.226	0.019	0.273
g_s	0.179	-0.295	0.281	-0.240	-0.327	-0.142	-0.154	-0.216	-0.111	0.139	-0.185	0.218
C_i	0.088	-0.257	0.519	-0.375	-0.023	-0.306	-0.071	0.094	-0.158	0.019	-0.098	0.009
LUE	0.247	-0.251	0.374	-0.314	0.227	-0.262	0.039	0.077	-0.007	0.045	-0.232	0.131
WUE	0.081	-0.208	0.483	-0.269	0.118	-0.186	-0.025	0.244	0.131	-0.190	0.079	-0.499
GY	-0.021	-0.060	-0.081	-0.117	0.068	0.093	0.101	-0.259	-0.693	-0.645	0.309	0.095

Pre-a: Pre-anthesis; Post-a: Post-anthesis

A similar result was obtained in wheat by Driever et al., 2014 where flag leaf photosynthesis of 64 wheat cultivars revealed significant variation in photosynthetic parameters, yield, biomass, and related traits.

This study found no significant correlation between pre and post-anthesis photosynthetic traits and grain yield or

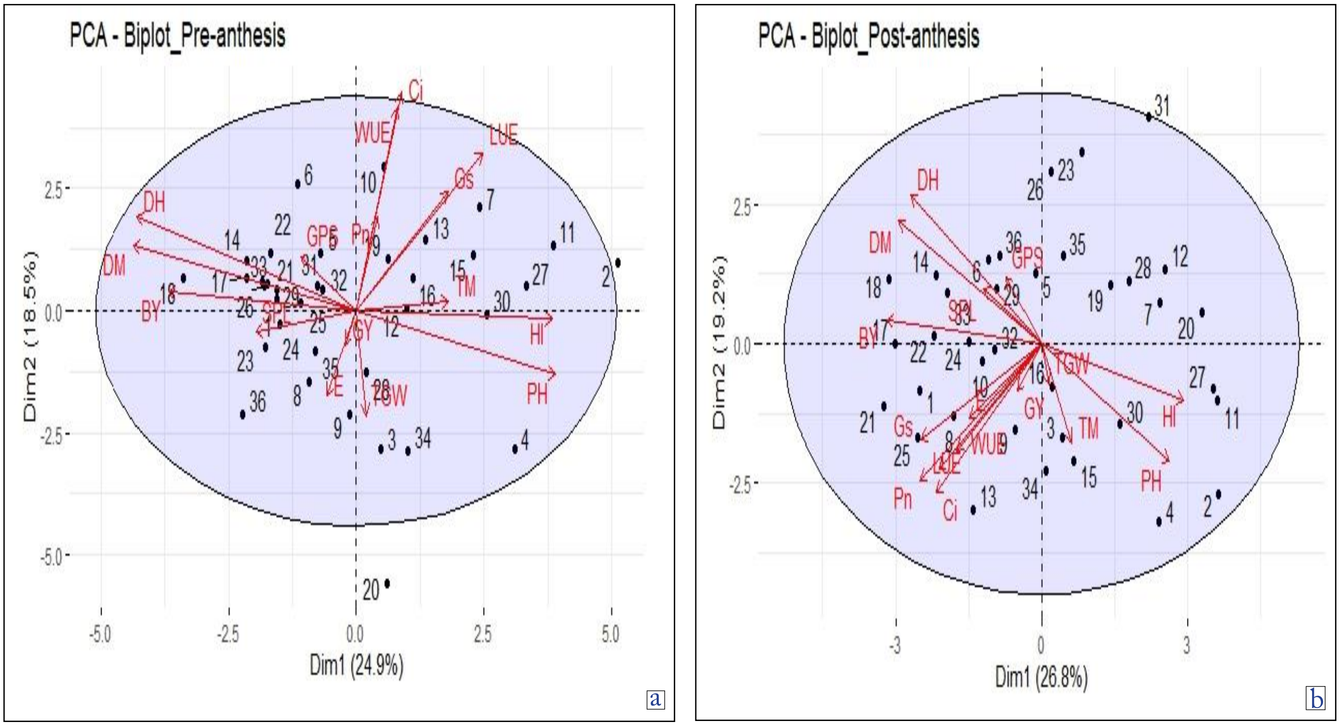

Figure 1a and b: PCA biplot (Preanthesis and Post anthesis)

biomass when all cultivars were compared. Cultivars with the highest photosynthetic performance did not equate with the highest yields. However, path analysis revealed a positive and high direct effect of *E*, g_s, and *WUE* on yield while a negative direct impact of BY and P_n at the pre-anthesis stage. At the post-anthesis stage, a high direct positive effect was exhibited by *E* and *WUE* on grain yield. PCA analysis also confirmed the importance of photosynthetic parameters such as P_n, *E*, g_s, C_i, *LUE, and WUE* measured at both pre and post-anthesis stages towards the divergence of wheat genotypes. Previous studies using a range of different cultivars had observed significant relationships between photosynthesis and yield (Fischer et al., 1981; Blum, 1990; Fischer et al., 1998; Reynolds et al., 2000), while others have not (Chytyk et al., 2011; Sadras et al., 2012) or have refrained from drawing a definitive conclusion (Watanabe et al., 1994). Most of the earlier workers have demonstrated a positive relationship between photosynthesis and crop yield when photosynthesis rates were performed on flag leaves at grain filling stage under open field conditions (Blum, 1990; Fischer et al., 1998; Reynolds et al., 2000; Furbank et al., 2013).

4. CONCLUSION

Photosynthetic efficiency was observed high at pre anthesis stage as the desirable photosynthetic traits such as higher *Pn*, *Ci*, *LUE* and *WUE* value along with lower *E*, value confirmed the experimental evidence towards such conclusion. Genotypes like RAJ 4238, WH 1105, K 0307, HD 2733, HD 2009 showed higher *Pn* values while WH 1021 and DBW 14 showed higher *Ci* values whereas DBW 17 showed lower *E* value, thus could be treated as photosynthetically efficient one among the lot.

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