Chain correlation between variables of gas exchange and yield potential in different winter wheat cultivars

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Abstract

Variables of gas exchange of flag leaves and grain yield potentials of five representative winter wheat (*Triticum aestivum* L.) cultivars varied greatly across different development stages under the same management and irrigation. The cultivars with high yield potential had higher net photosynthetic rate (P_N), PPFD (photosynthetic photon flux density) saturated photosynthetic rate (P_{sat}), stomatal conductance (g_s), and maximum apparent quantum yield of CO_2 fixation ($\Phi_{m,app}$) than those with low grain yield, but their dark respiration rate (R_D) and compensation irradiance (I_c) were remarkably lower. Compared with overall increase of yield potential of 71 % from low yield cultivars to high yield ones, P_N, P_{sat}, $\Phi_{m,app}$, and g_s were 13, 19, 57, and 32 % higher, respectively; but R_D and I_c decreased by 19 and 76 %, respectively. Such difference was evidently large during anthesis stage (*e.g.*, P_N by 33 %), which indicated that this period could be the best for assisting further selection for better cultivars. However, transpiration rate (E) and water use efficiency (WUE) differed only little. At different development stages, especially at anthesis, P_N and P_{sat} were positively correlated with $\Phi_{m,app}$, g_s, and yield potential, and negatively correlated with R_D and I_c. Thus the high-yield-potential winter wheat cultivars possess many better characters in photosynthesis and associated parameters than the low-yield cultivars.

Additional key words: apparent quantum yield of CO_2 fixation; compensation irradiance; cultivars with high and low yield potentials; dark respiration; flag leaf; net photosynthetic rate; stomatal conductance; transpiration; water use efficiency.

Introduction

In order to raise the grain yield of wheat, two main approaches are important. Firstly, the improvement of environment such as applying adequate water and fertilizers is essential for both crop development and grain yield increasing. For example, nitrogen is substantial for high yields (Hirose and Werger 1987, Evans and Terashima 1988, Lakkineni *et al.* 1995). Secondly, the increase of photosynthetic rates of particular cultivars has been intensively considered (Singh and Tsunoda 1978, Fischer *et al.* 1981, Rawson *et al.* 1993, Wada *et al.* 1994), since photosynthesis is the initial process of biomass and yield formation. At least 90 % of the dry matter of higher plants is derived from CO_2 assimilated by photosynthesis (Zelitch 1982). During the past decades, canopy photosynthesis has been greatly improved by increasing the leaf area index (LAI) and the effective PPFD-acceptation by leaf areas of wheat.

Differences among the rates of photosynthesis of certain wheat cultivars and other grain crops and relationship between P_N and grain yield have been extensively investigated during the past decade (Peng *et al.* 1991, Kongjika 1995, Frederick 1997, Xiao *et al.* 1998). Although some authors reported a positive relationship between photosynthetic rates at the canopy level and plant productivity of wheat (cf. Puckridge 1971), a definite conclusion for the interrelationship between P_N at the single leaf level and grain yield in wheat cultivars has not yet been reached. Some authors believe that P_N at the single leaf level might be treated as a breeding criterion only under resource limitation (Wada *et al.* 1994) or just within particular times of day when measuring photosynthesis (Zhang *et al.* 1997). Previous studies have considered only few variables such as photosynthetic rate (Du *et al.* 1995) or stomatal conductance (*e.g.*, Fischer *et*

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Abbreviations: E - transpiration rate; g_s - stomatal conductance; I_c - compensation irradiance; P_N - net photosynthetic rate; P_{sat} - PPFD saturated photosynthetic rate; R_D - dark respiration rate; $\Phi_{m,app}$ - maximum apparent quantum yield of CO_2 fixation.
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al. 1998). The question therefore remains whether variables such as P_N, P_{sat}, R_D, E, g_s, WUE, I_c, $\Phi_{m,app}$, and finally the grain yield are closely related. Crop cultivars with different genotypes or ecotypes may have different values in variables of gas exchange, and trying to find key variables mostly related with the grain yield is of practicable importance for selection of the suitable cultivar for breeding.

Portable photosynthesis measurement systems have been greatly improved recently for studying simultaneously a range of variables within the crop. The hypothesis of this study is that the different wheat variables with different grain yield potential could be indicated by some particular variables of gas exchange, not only under resource limited habitats but also on resource non-limited environments. Some of such traits might be closely related. In this paper, we therefore chose two kinds of cultivars with known yield potentials (high and low) and grew them in the same environment, trying to discover the above mentioned relationships.

Materials and methods

Plants: Five representative cultivars of wheat (*Triticum aestivum* L.) grown in Beijing farmland areas, *e.g.*, Jing 411, Jingdong 8, Jingnong S4055 (high yield potential at 0.6 kg m^{-2}), and Shi 4155 (low yield at 0.4 kg m^{-2}) and Nongda 3338 (0.3 kg m^{-2}) were used in this study. From the low yield cultivars to high yield ones, the grain yield potential increased by as much as 71 %. All the cultivars were sown in spare lines and managed in the same soil and microclimate. The experiment was conducted on the 15 ha Experimental Farmland of Beijing Academy of Agroforestry (39°09'N, 116°04'E). Soil water was maintained within 10 % of field capacity. The crops eceived the same amount of fertilizer, *i.e.*, 27 g(N) m^{-2} and 4 g(P) m^{-2}, with other nutrient adjusted to avoid potential deficiencies. All the growing environments were similar to those in the agriculture fields of Beijing areas, North China. The development stages were very similar.

Determination of P_N: Measurements on the flag leaves in middle to upper crown were carried out on 11-12 May (anthesis), 21-22 May (milk ripe), and 1 June (hard dough) of 1999. P_N and E were measured during clear days, with recorded photosynthetic photon flux density (PPFD) of >1600 μmol m^{-2} s^{-1}. P_N, R_D, E, g_s, PPFD, leaf temperature (T_{leaf}), and leaf-to-air water vapour pressure deficit (VPD) were simultaneously measured using a *LCA-4* portable photosynthesis system (*ADC*, Hoddesdon, UK). For R_D measurement, cuvette of the machine was covered with a black-red cloth bag (measured PPFD 0 μmol m^{-2} s^{-1}). The response of P_N to step changes in PPFD was examined in the field using the method we have improved (Jiang and He 1999). P_N-PPFD curves were plotted using the mean values of P_N and PPFD measured in different time of the same growth period. Further, P_{sat}, I_c, and $\Phi_{m,app}$ were calculated by fitting an asymptotic function [P_N = a (1 - e^{-bx}) + C] between the values of P_N (the dependent variable) and PPFD (the independent variable) (Jacob *et al.* 1995). Five replications for determining gas exchange and three for the P_N-PPFD curves were done on each single individual distributing in the different location of the fields. All plants from each cultivar were harvested at maturity and the grain yield per plant was calculated.

Result analysis: The large data set was entered into an *EXCELL* spread sheet which included physiological measurements, leaf areas, sites, and cultivars. Results were subjected to analysis of variance (ANOVA) test and the least significant differences (LSD) between the means were estimated at 95 % confidence level. Such calculations including the determination of P_{sat}, I_c, and $\Phi_{m,app}$ (using the least square method) were performed in a *STASTISTICA* program.

Results

P_N and R_D: Cultivars of wheat differed greatly for P_N at the anthesis stage, ranging from 16.88 μmol(CO_2) m^{-2} s^{-1} (Nongda 3338) to 23.94 μmol(CO_2) m^{-2} s^{-1} (Jingdong 8), very close to values reported elsewhere for well watered and fertilized wheat crops (Table 1). R_D also differed from 3.31 μmol(CO_2) m^{-2} s^{-1} (Jing 411) to 5.16 μmol (CO_2) m^{-2} s^{-1} (Nongda 3338). The g_s was lower in the two low yield cultivars [250-340 mmol(H_2O) m^{-2} s^{-1}], and higher in two of the high yield cultivar [540-600 mmol(H_2O) m^{-2} s^{-1}]. However, Jing 411, which belongs to the high yield cultivars, had a low g_s [260 mmol(H_2O) m^{-2} s^{-1}]. There was a general trend that the cultivar with high grain yield possessed high P_N and g_s, but low R_D, but there were small differences in E and WUE between the two types of cultivar. During anthesis, even under the same environment with the same amount of water and fertilizer applied, the shift of wheat genotype from low grain yield to high yield potentials could increase P_N and g_s by 33 and 56 %, respectively, but decrease R_D by 30 % (Fig. 1*A*, values not shown). For the whole growth period, the differences were 13, 32, and 19 %, respectively, for P_N, g_s, and R_D.

Response of P_N to PPFD: The ecophysiology of

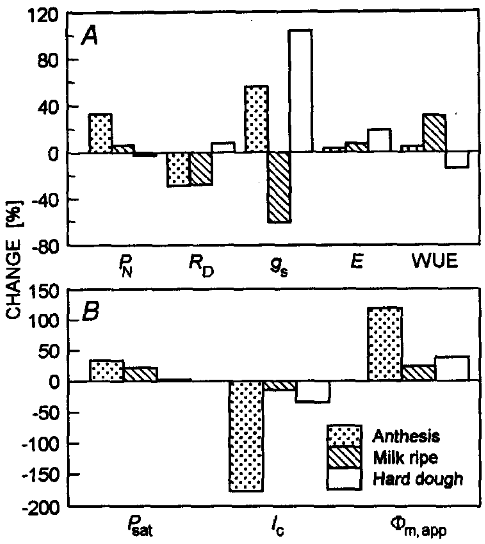

Fig. 1. Increase in percent of variables of gas exchange (*A*) and P_N-PPFD response curves (*B*) from the low yield cultivars to the high yield potential cultivars of winter wheat during the different development stages. Data of low yield cultivars are means of Shi 4185 and Nongda 3338, and high yield cultivars are means of Jing 411, Jingdong 8, and Jingnong S4055.

wheat with high and low yield potentials is also reflected by their P_N-PPFD response curves (Fig. 2). There was obvious difference between the two kinds of genotype in the P_{sat}, I_c, and $\Phi_{m,app}$ (Table 2). For example, during anthesis, P_{sat} and $I_{c\ m,app}$ of high yield cultivars were 33 and 114 %, respectively, higher than those of low yield wheat. But I_c was 176 % lower in the high yield cultivars than in the low yield ones (Fig. 1*B*, values not shown).

Such pattern remained unchanged through the whole developmental stage, only the difference in the milk ripe and hard dough stage was somewhat weak, because of the natural senescence process, with the values of P_{sat} and $\Phi_{m,app}$ of both genotypes decreasing but I_c increasing. Even though, for the whole development stage, P_{sat} and $\Phi_{m,app}$ of high yield cultivars were 19 and 57 %, respectively, higher than those of low-yield ones. However, I_c was 76 % lower.

Chain correlation between gas exchange variables and yields: The relationship between P_N, P_{sat}, R_D, I_c, $\Phi_{m,app}$, *E*, g_s, WUE, and the grain yield potentials of different cultivars are presented in Table 3. At different growth stages, various levels of correlation between variables of gas exchange were noted. For example, P_N positively correlated with $\Phi_{m,app}$ ($r^2 = 0.51$-0.78^+) and P_{sat} ($r^2 = 0.46$-0.94^{**}), while negatively correlated with R_D ($r^2 = -0.77^+$-0.92^{**}, see meaning of symbols in Table 3) and I_c ($r^2 = -0.61$-0.89^+). For the three development stages, anthesis showed mostly close correlation between the different traits. Among the different gas exchange variables, P_N, P_{sat}, and I_c were the most important since they had chain relation with many other variables, which could be treated as better indicators for the identification of wheat cultivars.

As for the relationships between grain yield potentials and leaf traits, it was found that during anthesis, P_N ($r^2 = 0.81^*$) and P_{sat} ($r^2 = 0.66$) were positively correlated to grain yields, while R_D ($r^2 = -0.98^{***}$) and I_c ($r^2 = -0.64$) were negatively related.

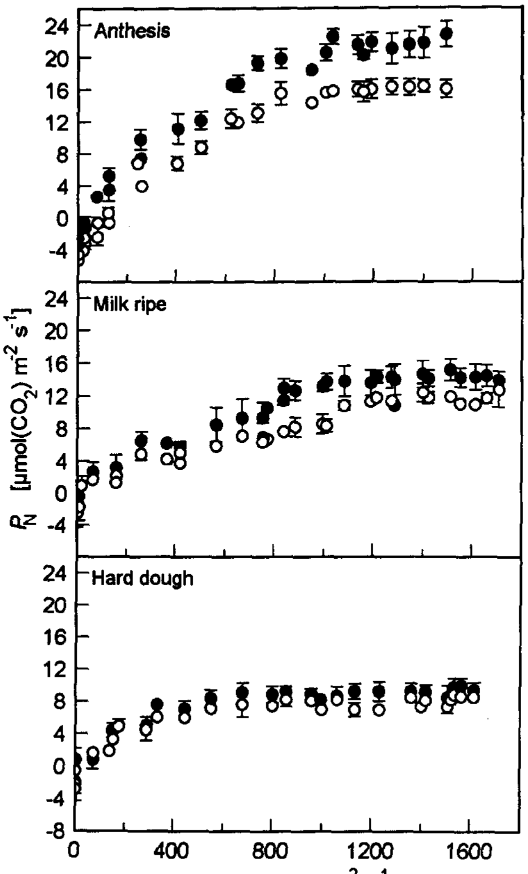

Fig. 2. Net photosynthetic rate (P_N) to photosynthetic photon flux density (PPFD) of high yield potential (●) and low yield (○) of winter wheat measured in different development stages. Each point is a mean of 6-9 observations. SEs are shown.

Discussion

Grain yield in different genotypes or ecotypes of wheat is not necessary related to the gas exchange variables, such as P_N (Crosbie *et al.* 1978, Evans 1993, Du *et al.* 1995), or the relation is found only during some special period (Wang *et al.* 1998) or some day time used for measurement (Zhang *et al.* 1997). Some authors believe that the correlation between grain yield and P_N only exists when the cultivars are grown under soil water limited habitats rather than under favourable soil water conditions (Wada *et al.* 1994). Therefore, crop physiologists have repeatedly failed to demonstrate an association between breeding process for yield and leaf gas exchange variables, in particular increased photosynthetic activity (Evans 1993, Austin 1994). Part of the reason is owing to the inaccuracy of values obtained by the old photosynthesis measurement systems. Many technical innovations in photosynthesis methods now enable us to rapidly and accurately measure leaf gas exchange within some 30 s, and the correct relationship between the yield and physiological traits in wheat might be expected.

Table 1. Net photosynthetic rate (P_N) [μmol(CO_2) m^{-2} s^{-1}], dark respiration rate (R_D) [μmol(CO_2) m^{-2} s^{-1}], gas stomatal conductance (g_s) [mmol (H_2O) m^{-2} s^{-1}], transpiration rate (E) [mmol (H_2O) m^{-2} s^{-1}], and water use efficiency (WUE) [μmol(CO_2) $mmol^{-1}$(H_2O)] of different winter wheat cultivars at the different development stages. Means (n = 5) and SDs are shown. Values followed by the same letters are not significantly different (p>0.05).

Cultivar	P_N	R_D	g_s	E	WUE
Anthesis					
Jing 411	23.62^{a}	3.31^{a}	260^{a}	3.07^{a}	6.81^{a}
	(0.44)	(0.32)	(59)	(0.24)	(1.12)
Jingdong 8	23.94^{a}	3.55^{a}	590^{c}	4.48^{b}	4.01^{b}
	(0.40)	(0.07)	(63)	(0.31)	(0.56)
Jingnong S4055	20.38^{b}	3.55^{a}	540^{c}	4.34^{b}	4.24^{b}
	(0.64)	(0.17)	(72)	(0.79)	(0.34)
Shi 4185	17.21^{c}	4.80^{b}	340^{b}	4.21^{ab}	4.29^{b}
	(0.74)	(0.33)	(110)	(1.21)	(0.62)
Nongda 3338	16.88^{c}	5.16^{c}	250^{a}	3.20^{a}	5.42^{ab}
	(0.39)	(0.17)	(65)	(0.25)	(0.92)
Milk ripe					
Jing 411	15.50^{a}	2.28^{a}	110^{a}	1.55^{a}	9.90^{a}
	(0.54)	(0.06)	(43)	(0.56)	(1.25)
Jingdong 8	13.09^{b}	3.21^{b}	110^{a}	1.76^{a}	7.44^{b}
	(1.25)	(0.95)	(59)	(0.24)	(2.11)
Jingnong S4055	13.72^{b}	2.75^{a}	160^{a}	2.50^{b}	5.51^{c}
	(0.38)	(0.18)	(62)	(0.44)	(0.76)
Shi 4185	13.82^{b}	2.93^{ab}	330^{b}	3.36^{c}	4.10^{c}
	(0.55)	(0.08)	(82)	(0.82)	(0.37)
Nongda 3338	12.70^{b}	4.13^{c}	80^{a}	1.70^{a}	7.49^{b}
	(1.32)	(0.11)	(21)	(0.60)	(1.66)
Hard dough					
Jing 411	11.87^{a}	3.11^{a}	430^{b}	3.74^{a}	3.21^{a}
	(1.27)	(0.03)	(84)	(0.65)	(0.34)
Jinggong 8	9.20^{b}	3.68^{b}	320^{b}	3.25^{a}	3.23^{a}
	(0.71)	(0.03)	(96)	(0.77)	(0.45)
Jingnong S4055	9.78^{b}	4.34^{c}	570^{a}	4.32^{b}	2.43^{b}
	(0.58)	(0.21)	(129)	(0.34)	(0.26)
Shi 4185	11.27^{ab}	3.71^{b}	210^{c}	3.45^{a}	3.11^{a}
	(1.03)	(0.04)	(54)	(0.38)	(0.55)
Nongda 3338	9.53^{b}	4.33^{c}	220^{c}	2.90^{c}	3.65^{a}
	(1.30)	(0.05)	(86)	(0.73)	(0.73)

Table 2. Photosynthetic photon flux density (PPFD) saturated net photosynthetic rate (P_{sat}) [μmol(CO_2) m^{-2} s^{-1}], maximum apparent quantum yield of CO_2 fixation ($\Phi_{m,app}$) [mmol(CO_2) mol^{-1}(PPFD)], and compensation irradiance (I_c) [μmol m^{-2} s^{-1}] of different winter wheat cultivars at the different development stages. Means (n = 3) and SDs are shown. Values followed by the same letters are not significantly different (p>0.05).

Cultivars	P_{sat}	$\Phi_{m,app}$	I_c
Anthesis			
Jing 411	24.94^{a}	18.16^{a}	33.16^{a}
	(1.05)	(2.12)	(4.33)
Jingdong 8	23.75^{a}	20.32^{a}	35.31^{a}
	(0.86)	(3.97)	(5.27)
Jingnong S4055	20.70^{ab}	19.96^{a}	35.68^{a}
	(2.14)	(2.47)	(2.39)
Shi 4185	16.61^{c}	7.89^{b}	101.10^{b}
	(1.47)	(1.54)	(10.61)
Nongda 3338	18.24^{c}	8.58^{c}	92.24^{b}
	(0.69)	(3.70)	(12.38)
Milk ripe			
Jing 411	16.98^{a}	13.74^{a}	21.79^{b}
	(2.13)	(1.01)	(5.12)
Jingdong 8	15.34^{b}	14.66^{a}	21.13^{b}
	(1.16)	(2.49)	(2.85)
Jingnong S4055	15.61^{b}	12.08^{b}	38.21^{a}
	(0.97)	(1.18)	(11.58)
Shi 4185	12.85^{c}	10.61^{c}	15.11^{b}
	(1.25)	(1.18)	(7.64)
Nongda 3338	13.02^{c}	11.35^{c}	27.00^{b}
	(1.36)	(2.11)	(3.66)
Hard dough			
Jing 411	12.43^{a}	14.45^{a}	69.12^{a}
	(1.38)	(1.75)	(14.27)
Jinggong 8	10.26^{b}	5.66^{b}	54.71^{b}
	(1.23)	(2.83)	(13.19)
Jingnong S4055	9.57^{c}	5.95^{b}	68.25^{b}
	(0.58)	(0.67)	(12.29)
Shi 4185	11.23^{ab}	5.56^{b}	76.45^{a}
	(0.46)	(1.10)	(54)
Nongda 3338	9.78^{c}	13.35^{a}	96.44^{c}
	(0.89)	(1.46)	(8.60)

Our measurements on wheat cultivars differing in yield potential (71 % difference) showed that the gas exchange variables of different cultivars were different (Fig. 1). The high yield cultivars had higher P_N, P_{sat}, $\Phi_{m,app}$, and g_s, but lower I_c and R_D (Tables 1 and 2). Such large difference was not found in E and WUE. Thus the cultivars with high yield potential could assimilate CO_2 at a higher rate under lower PPFD (a longer time for P_N during the growth days was expected for the high yield cultivars since they had lower I_c) and the consumption of the fixed CO_2 through dark respiration (Fig. 2). This provided a better physiological basis for the formation of biomass and yield for the high yield cultivars. At anthesis, P_N, P_{sat}, $\Phi_{m,app}$, and g_s were positively correlated with each other, but negatively with I_c and R_D (Table 3).

Because the cultivars were grown with the same amount of water and fertilizer during the whole growth period, the differences in gas exchange originated independently from the different cultivars themselves. The mechanism in heritability for such phenomenon, however, remained unclear to us. Even though, from such a result, we believe that the breeders had incorporated many useful characteristics in gas exchange (P_N and R_D) in the cultivars they tried to acquire. Such results had never been reported elsewhere. Even through, some phenomena need further investigation. For example, our results showed that P_N had a remarkably negative correlation with R_D and yield (Table 3), but some authors did not find such relations (Bhagwat *et al.* 1997). Despite of the above fact, our results imply that during the process of selecting cultivars, the incorporation of plant physiology and breeding is necessary.

During the other two growth periods, although there were some correlations between gas exchange variables and the yield of a particular cultivar, their relation was weak (Table 3). This could be due to the prolonged growth period, when different cultivars entered the senescence stage and thus gradually fell into a decline in eco-physiological process which led to a dwindle in difference of gas exchange variables between cultivars. Such progress, however, is natural in wheat development. Similar trend was found between the treatments on wheat with and without CO_2 elevation (Garcia *et al.* 1998).

Fischer *et al.* (1998) carefully studied the yield of wheat associated with g_s, P_N, and canopy temperature depression (CTD), and concluded that g_s and CTD may be potential indirect selection criteria for yield. However, in our study, although there was a good correlation between P_N and g_s at anthesis ($r^2 = 0.82^*$), g_s was not correlated with grain yield potentials and not correlated at the other two development stages.

Different patterns of loading and unloading of photosynthates from source to sink in different types of

Table 3. Correlation analysis of physiological variables and grain yield potentials at different development stages. Each variable of gas exchange and P_N-PPFD curve of one cultivar in making the correlation is a mean of five and three measurements, respectively. Five cultivars were used (n = 5). $^+p<0.1$, $^*p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$.

	P_N	P_{sat}	R_D	E	g_s	WUE	I_c	$\Phi_{m,app}$	Yield
Anthesis									
P_N	1.0000	0.9406**	-0.8494*	0.0076	0.8249*	0.0569	-0.7913$^+$	0.7836$^+$	0.8122*
P_{sat}		1.0000	-0.7742$^+$	0.0179	0.6675	0.1565	-0.8193*	0.7625$^+$	0.6649
R_D			1.0000	0.0296	0.1063	0.0342	0.3239	-0.5842	-0.9766***
E				1.0000	0.7666$^+$	-0.8705*	0.0003	0.0004	0.0926
g_s					1.0000	0.6914	0.0983	0.0741	0.3672
WUE						1.0000	0.0356	0.0803	0.0002
I_c							1.0000	-0.7779$^+$	-0.6408
$\Phi_{m,app}$								1.0000	0.7627$^+$
Yield									1.0000
Milk ripe									
P_N	1.0000	0.4584	-0.7696$^+$	0.0058	0.1650	0.4035	-0.8958*	0.5115	0.2464
P_{sat}		1.0000	-0.5185	0.2672	02672.	0.4167	0.0782	0.6006	0.8067*
R_D			1.0000	0.0004	0.0032	0.0392	0.0452	0.0035	-0.5759
E				1.0000	0.9175**	-0.8476*	0.2309	0.0828	0.0791
g_s					1.0000	0.6273	0.1315	0.1786	0.0680
WUE						1.0000	0.3194	-0.0444	0.1202
I_c							1.0000	-0.0732	-0.7965$^+$
$\Phi_{m,app}$								1.0000	0.0029
Yield									1.0000
Hard dough									
P_N	1.0000	0.8240*	-0.9172**	0.5155	0.0568	0.0006	-0.6180	0.7851$^+$	0.0017
P_{sat}		1.0000	-0.8701*	-0.0018	0.8682*	0.0361	0.0326	0.1607	0.0484
R_D			1.0000	0.5114	0.0778	0.0000	0.3313	-0.1296	0.0279
E				1.0000	0.7977$^+$	-0.9876***	0.7284$^+$	0.0279	0.4403
g_s					1.0000	0.7742$^+$	-0.8041*	0.0461	0.3424
WUE						1.0000	0.0573	0.0296	-0.3551
I_c							1.0000	-0.1801	-0.6615
$\Phi_{m,app}$								1.0000	0.2674
Yield									1.0000

wheat cultivars in this study should be considered, in order to understand their different photosynthetic abilities. Bell and Incoll (1990) reported that after the milk filling stage, 80 % of the CO_2 fixed in flag leaves was transported to the spikes. From this point of view, the high yield cultivars must develop a larger sink than the lower yield ones, because they both have higher P_N in flag leaves (the larger source) and grain yields (the larger sink). Although stems can act partly as the source which contributes 20 % to the formation of grain (McWha 1975), this kind of source is smaller than the flag leaves. However, the relationships between sink and source and flag leaf photosynthetic abilities need further detailed studies.

As a conclusion, we found that some of the key variables of gas exchange were well chain-correlated. Among the variable, P_N and P_{sat} were the most important variables as they could be well correlated with many other variables of gas exchange or P_N-PPFD curves, and finally the yield. I_c, $\Phi_{m,app}$, and R_D were also related with grain yields and thus may be used as reference indicators of cultivars. And the anthesis stage was the best period for identification of the high-yield wheat cultivars.

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