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Correlation and combining ability analysis of physiological traits and some agronomic traits in maize

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Abstract

Combining ability information on the physiological traits in maize (*Zea mays* L) and the relationship between physiological traits and biomass, grain yield (GY) and yield components (YC) can help maize breeders design experiments for improving inbred lines and/or developing hybrids with improved GY or YC (GYYC). A six-parent diallel experiment (Griffing method 3) was conducted for combining ability and correlation analyses. The objectives of this study were to 1) study the correlation between physiological traits and biomass at seedling stage; 2) study which physiological traits at seedling stage have significant correlation with biomasses at both seedling and later growth stages and GYYCs; 3) evaluate combining ability of the physiological traits that are significantly correlated with either GY or one of the YCs. Results showed plant heights at 20 day, 40 day, and leaf area were highly correlated with both dry weights of shoots and roots. All chlorophyll-related organelles were significantly correlated with only dry weights of shoots. However, dry matter at seedling stage seemed not to be related to dry matter in later growth stages. Five physiological traits (stomatal conductance, transpiration rate, net photosynthetic rate, two quantum yield related traits) at seedling stage were identified to greatly impact dry matter at later growth stages. Results also showed that 13 out of 35 physiological traits studied were significantly correlated with GYYCs. Different germplasms for improving GYYCs could be used based on both correlation between the 13 traits and GYYCs and combining ability effects of each line for the 13 selected traits.

Keywords: combining ability analysis, maize breeding, correlation analysis, physiological traits

Introduction

Identifying early-stage physiological traits related to GYYC and knowing the combining ability effects of these physiological traits would allow maize breeders to identify and select appropriate materials for line and hybrid development at an early growth stage. Many plant physiological traits are related to biomass itself or biomass production or photosynthetic rate. Thus, they are important for maize GY improvement (Sharma-Natu and Ghildiyal, 2005; Long et al, 2006). Understanding of the interrelationship and combining ability of these physiological traits, especially those related to photosynthesis and plant growth and/or biomass accumulation, is a key to improving maize GY (Richards, 2000; Long et al, 2006).

Relationships between some physiological traits and GY have been reviewed by Sharma-Natu and Ghidiyal (2005). It was suggested that to increase GY, crop biomass should be increased. Maize biomass can theoretically be increased by improving photosynthesis as it provides raw material and energy for the formation of biomass (Long et al, 2006). Studies on both model simulation and field experiments in maize and rice have shown that hybrids with higher photosynthetic efficiency had a considerable yield advantage (Sinclair and Sheehy, 1999; Tian et al, 2011).The photosynthetic efficiency is associated with the interception and utilization of solar radiation, which is influenced by both canopy architecture and individual leaf photosynthesis (Long et al, 2006). Improvement of canopy architecture can be achieved by selecting maize genotypes with appropriate leaf area (LA), specific leaf area (SLA), and so on (Sharma-Natu and Ghildiyal, 2005). Efficient utilization of solar radiation is determined by the integration of net photosynthetic rate (Pn), stomatal conductance (Gs), chlorophyll (Chl) content, photosystem II (PSII) capability, activities of ribulose-1,5-bisphosphate carboxylase / oxygenase (RuBPCase), phosphoenolpyruvate-carboxylase (PEPCase), etc (Ghannoum, 2009; Zhao et al, 2013). Higher net photosynthetic rate was observed in some maize genotypes with high yield and germplasms with higher net photosynthetic rate were scarce in a maize breeding program aimed at increasing photosynthesis rate and GY improvement (Wang, 2011). The stomatal conductance was associated with photosynthetic efficiency and GY; increasing stomatal conductance by optimizing canopy could improve ventilation and transportation of CO_2 (Sharma-Natu and Ghildiyal, 2005). Chlorophyll is the

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key factor affecting capture of light in plant. RuBPCase catalyzes carboxylation and oxygenation of ribulose-1,5-bisphosphate for fixing carbon to initiate photosynthesis and photorespiration and sometimes, it might act as a rate-limiting enzyme in carbon assimilation (Spreitzer and Salvucci, 2002; Parry et al, 2013). PSII is one of the most important components in the photosynthetic system. It catalyzes water oxidation by using the energy absorbed by photosystem I to provide the electrons for entire photosynthetic process and hydrogen ions (protons) for creation of proton gradient that is used to generate ATP (Rochaix, 2011; Zhao et al, 2013). PEPCase plays an important role of carbon fixation in C4 plants, including maize, by catalyzing the incorporation of HCO_3^- into phosphoenolpyruvate, yielding oxaloacetic acid, related four-carbon organic acids (particularly malic acid) and Pi (O'Leary, 1982; Chollet et al, 1996). Any improvements in these traits might provide an opportunity to improve GY, particularly under stressful environmental conditions.

Combining ability analyses for individual traits are usually the first step for a breeder to make decision on which inbred lines to be selected as parents and what mating design to use (Fan et al, 2008a; Yao et al, 2013). Diallel design is a widely used technique for combining ability analyses (Fan et al, 2002, 2008a; Zhang et al, 2005; Melani and Carena, 2005; Barata and Carena, 2006). However, because of laboratory-intensive work and destructive sampling of plants for evaluating certain physiological traits, reports on combining ability analysis of maize physiological traits are limited. Zhou and Zhang (2008), by employing Griffing method 2 and Hayman method, found that maize varieties Luyuan 92 and A150 had high GCA for photosynthetic rate, chlorophyll content, and stomata width. Wang et al (2011), by conducting a Griffing method 2 diallel experiment, discovered that JN2 had high GCA for photosynthetic rate and leaf area, and JN73 was developed with increased GCA for photosynthetic rate, leaf area, and chlorophyll content. Wang et al (2011) suggested that these inbred lines could be used as ideal parents for improving photosynthetic efficiency of a hybrid in traditional cross-breeding projects. The combining ability studies related to photosynthetic traits revealed that chlorophyll content (Zhou and Zhang, 2008), light saturation point (LSP), light compensation point (LCP), maximum photosynthesis (Pmax), total protein content (CPRO), PEPCase activities and RuBPCase activity (Cai et al, 2012), photosynthetic rate (Zhou and Zhang, 2008; Wang et al, 2011) and stomatal width (Zhou and Zhang, 2008), were influenced more by additive gene effects than non-additive gene effects.

Long et al (2006) point out that plant breeding brings harvest index, and efficiency of light capture close to their theoretical maxima. The only area left to enhance GY is to improve the efficiency of conversion of the intercepted light into biomass. Lack of information on the correlation between many physiological traits and GYYC and combining ability of many biomass-production-related physiological traits restricts maize breeders from further improving maize GY. A six-parent diallel experiment was conducted in 2010; and a total of 35 biomass and photosynthesis-related physiological traits, GY, and 6YCs were recorded for the correlation and combining ability study. Results on seven of the traits have previously been reported (Cai et al, 2012). With GY and YCs data available, we furthered the study with the objectives to 1) identify all physiological traits that are correlated with biomass and GYYCs; 2) evaluate combining ability of the physiological traits correlated with either GY or one of the YCs.

Materials and Methods

Plant Materials

The six maize lines were used in this diallel study where Griffing's method 3 (Griffing, 1956) was employed. A total of 30 crosses were made in 2009 at Kaiyuan (summer season) and Jinghong (winter season) in Yunnan province, China. The 30 crosses and six parental lines were used for measuring physiological traits (see Supplementary Table 1) that related to plant growth, photosynthesis and chlorophyll fluorescence. Some of the traits were measured at two different stages (20 days and 40 days after planting) and some were measured only at one stage. If a trait was measured at two different stages, the trait measurements were regarded as two different traits and they were all used for correlation analysis. Thus, in total, observations on 35 traits were made in this study. All traits significantly correlated with GY or with one of the YCs were subjected to combining ability analysis.

Seed treatment and growth conditions

Uniform seeds for the 30 crosses and 6 parental lines were treated with NaClO (0.1%) for 10 min, washed with distilled water before the seeds were soaked for 24 h and placed in Petri dishes lined with filter paper for germination in dark. After germination, 15-18 seeds from each cross and parental lines were transplanted to 21 cm × 18 cm (height × diameter) plastic pots with three plants in each pot. For better plant growth, dried soil was sifted through sieves of1 cm aperture first and then potting soil was mixed with 1 g of KH_2PO_4 and 1.5 g of NH_4NO_3 per kg of the dried soil. Three kg of the soil was then put into each pot for planting. The pots were kept in a greenhouse under natural lighting at a temperature of 25.2 ± 7.2°C and relative humidity of 56.4 ± 12.9%. Some physiological traits were measured at 20thand 40th days (at the 6th leaf full extension) after germination.

Measurements of plant growth traits and biomass

Plant height was measured at 20 (PH_{20}) and 40 days (PH_{40}) after germination. The leaf area (LA_{40}), specific leaf area (SLA_{40}), and two biomass traits of dry weights of shoots ($DW_{Shoot40}$) and of roots (DW_{Root40})

Table 1 - Correlation between two biomass traits and 33 physiological traits at earlier growth stage.

Trait†	DW_{Shoot}	DW_{Root}	Trait	DW_{Shoot}	DW_{Root}
PH_{20}	0.573**	0.563**	Fs_{40}	-0.195	-0.198
Pn_{20}	-0.051	-0.150	$F'm_{40}$	-0.153	-0.027
Gs_{20}	-0.046	-0.190	$\phi PSII_{40}$	0.143	0.231
Ci_{20}	-0.153	-0.136	$F0_{40}$	-0.198	-0.246
Tr_{20}	-0.091	-0.229	Fm_{40}	-0.232	-0.106
Chl_{20}	0.376*	0.289	Fv/Fm_{40}	0.056	0.204
Fs_{20}	-0.059	-0.009	LA_{40}	0.899**	0.618**
$F'm_{20}$	0.083	0.267	SLA_{40}	-0.232	-0.258
$\phi PSII_{20}$	0.135	0.287	$C_{Water40}$	-0.245	-0.182
$F0_{20}$	-0.014	-0.071	LS_{40}	0.312	0.289
Fm_{20}	0.100	0.021	LCP_{40}	-0.048	0.170
Fv/Fm_{20}	0.245	0.174	AQE_{40}	0.140	0.150
PH_{40}	0.699**	0.552**	$Pmax_{40}$	0.120	0.250
$Chla_{40}$	-0.472**	-0.295	$Cpro_{40}$	0.081	-0.054
$Chlb_{40}$	-0.384*	-0.215	$PEPC_{40}$	0.066	0.101
$Chla/b_{40}$	-0.097	-0.171	$RuBPC_{40}$	0.058	-0.132
Chl_{40}	-0.453**	-0.277			

*, ** statistically significant at 0.05 and 0.01 probability levels, respectively. †See abbreviations of all physiological traits in Supplementary Table 1.

of individual seedlings were measured at 40 days after germination. The SLA_{40} was determined by dividing LA_{40} by its dry weight of 2 g fresh leaf and LA_{40} was measured with a portable leaf area meter. Moreover, water content ($C_{Water40}$) was calculated.

Measurements of plant photosynthetic traits

Several photosynthetic parameters, including intercellular CO_2 concentration (C_i), stomatal conductance and transpiration rate (Tr), and net photosynthetic rate were measured for individual lines and hybrids. Li-6400 (LI-COR Inc, Lincoln, NE, USA) equipped with a light-emitting diodes source leaf chamber (6400-02b) was used for the measurement by keeping photosynthetic photon flux density at 1,200 μmol m^{-2} s^{-1} and temperature at 25°C (Cai et al, 2012).

Determination of chlorophyll fluorescence parameters

The chlorophyll fluorescence parameters were measured by using a portable fluorometer Mini-PAM (Walz, Germany). The parameters measured included minimum fluorescence intensity (F0) and maximum fluorescence intensity (Fm) in the dark-adapted state for 2 h, maximum fluorescence intensity (F'm) in the light-adapted state and chlorophyll fluorescence intensity at the steady-state (Fs), and then, effective quantum yield of photochemical energy conversion in PSII (ϕPSII) and maximal efficiency of PSII photochemistry (Fv/Fm) were calculated.

Chlorophyll content assay

Chlorophyll from the 6th youngest fully extended leaf was extracted with 80% acetone and assayed by spectrophotometer at 663 nm and 646 nm. The contents of chlorophyll a and b (Chla, Chlb), ratio of Chla to Chlb (Chla/b), and total chlorophyll (Chl) were calculated via the following formulas:

Chla (mg g^{-1}) = (12.21A663-2.81A646 ×V)/(FW×1000)

Chlb (mg g^{-1}) = (20.13A646-5.03A663×V)/(FW×1000)

where V (ml) is extraction volume and FW (g) is the fresh weight of the leaf sample;

Chla/b = Chla / Chlb;

Chl = Chla + Chlb.

GY and YC determination

In 2010, the 30 crosses and 6 parental lines were planted at Kunming and Qujing in Yunnan province, China. A randomized complete-block design with three replications was used. Each experimental unit was a single-row plot with a row-to-row spacing of 0.7 m and row length of 5 m. The distance between two adjacent plants was 0.25 m and the population density was approximately 57,140 plants ha^{-1}. Dry matter at 6-leaf stage ($DM6^{th}$), 14-leaf stage ($DM14^{th}$), silking (DM_{Silk}) and at harvest (DM_{end}) were measured. At maturity, a 10-ear sample was harvested from 10 consecutive plants from the middle of each row. After harvest, kernels were air-dried until constant moisture of 130 g kg^{-1} was achieved, and then data on ear length (EL), ear diameter (ED), number of kernel-rows per ear (KR), kernel ratio of kernel dry weight to total plant dry weight (KRATE),100-kernel weight (KW), GY per plot and several other traits were collected.

Statistical analyses

Analyses of variance and correlation analysis were carried out via SAS (SAS version 9.2; SAS Institute, 2005). The GCA, SCA, REC, MAT, and NMAT were determined via DIALLEL-SAS05 (Zhang et al, 2005). The following model for Griffing diallel method 3 (Griffing, 1956) was used:

$$Y_{ijl} = \mu + p_l + v_{ij} + e_{ijl}$$

$$v_{ij} = g_i + g_j + s_{ij} + r_{ij}$$

$$r_{ij} = m_i + m_j + n_{ij}$$

Table 2 - Correlation coefficients between the 35 physiological traits and GY and its components.

Traits†	GY§	EL	ED	RE	KR	KW	KRATE	DM^{6th}	DM^{14th}	DM^{Silk}	DM^{end}
PH_{20}	0.243	-0.089	-0.203	-0.255	0.153	0.343	0.663**	0.001	-0.069	-0.378	-0.132
PH_{40}	0.212	0.197	-0.238	-0.081	0.157	0.194	0.527**	0.168	0.0468	-0.235	-0.190
LA_{40}	0.267	0.143	-0.097	0.158	0.267	0.116	0.395*	0.184	-0.222	-0.341	-0.000
SLA_{40}	0.351	0.292	0.014	0.023	0.301	0.238	0.237	0.033	0.139	-0.311	0.203
$DW_{Shoot40}$	0.117	0.088	-0.242	0.093	0.231	-0.032	0.393*	0.286	-0.309	-0.185	-0.181
DW_{Root40}	-0.034	0.103	-0.348	-0.176	0.267	-0.187	0.228	0.190	-0.295	0.182	-0.086
$C_{Water40}$	0.313	0.389**	-0.062	-0.263	0.453*	0.172	0.134	0.175	0.242	-0.252	0.051
Ci_{20}	-0.113	-0.199	0.027	-0.163	0.008	-0.124	-0.138	-0.145	0.040	-0.080	0.140
Gs_{20}	0.173	0.04	0.046	-0.349	0.138	0.188	0.079	-0.162	0.387*	-0.333	0.046
Tr_{20}	0.195	0.112	0.036	-0.398*	0.168	0.206	0.076	-0.119	0.435*	-0.318	-0.000
Pn_{20}	0.18	0.117	0.039	-0.344	0.103	0.226	0.076	-0.064	0.408*	-0.223	-0.071
Chl_{20}	0.24	0.157	0.335	0.097	0.138	0.156	-0.047	-0.059	0.216	0.070	0.026
$Chla_{40}$	0.095	-0.105	0.097	-0.051	0.076	0.065	0.016	0.134	0.310	0.043	-0.011
$Chlb_{40}$	0.096	-0.112	0.084	-0.052	0.077	0.062	0.05	0.137	0.252	0.071	-0.032
$Chla/b_{40}$	-0.051	0.099	-0.022	0.031	-0.065	-0.003	-0.107	-0.064	0.045	-0.153	0.059
Chl_{40}	0.095	-0.107	0.094	-0.051	0.076	0.065	0.024	0.136	0.297	0.050	-0.016
Fv/Fm_{20}	0.062	-0.385*	0.498**	0.281	-0.380*	0.246	-0.185	-0.189	-0.112	0.088	0.270
$\phi PSII_{20}$	-0.267	-0.179	-0.052	-0.288	0.012	-0.261	-0.255	-0.166	-0.243	-0.221	-0.303
Fv/Fm_{40}	-0.039	-0.159	0.295	0.223	-0.104	-0.15	-0.306	-0.190	-0.334	0.622**	0.108
$\phi PSII_{40}$	-0.192	-0.306	0.222	0.307	-0.32	-0.162	-0.274	-0.384*	-0.244	0.405*	0.241
LSP_{40}	0.351	0.281	0.012	-0.478**	0.509**	0.232	0.274	-0.021	0.172	-0.269	-0.001
LCP_{40}	0.258	0.317	-0.12	-0.189	0.329	0.099	0.156	-0.070	0.176	0.180	-0.193
AQE_{40}	-0.007	0.17	-0.139	-0.004	0.274	-0.192	0.014	0.320	0.126	-0.053	0.099
$Pmax_{40}$	0.295	0.418*	-0.188	-0.4483*	0.519**	0.13	0.321	-0.039	0.083	-0.140	-0.082
$CPro_{40}$	0.246	0.198	-0.021	0	0.082	0.264	0.276	0.257	0.262	-0.303	-0.133
$RUBP_{40}$	-0.187	0.153	-0.176	-0.004	0.008	-0.224	-0.142	-0.127	-0.112	-0.108	0.093
$PEPC_{40}$	-0.123	-0.295	0.246	0.158	-0.036	-0.244	-0.34	-0.163	-0.413*	0.336	0.175
Fm_{20}	-0.266	-0.282	-0.112	0.05	-0.425*	0.023	0.052	-0.166	-0.243	-0.221	-0.303
$F0_{20}$	-0.268	-0.128	-0.29	-0.052	-0.274	-0.052	0.134	-0.091	-0.176	-0.264	-0.398*
$F'm_{20}$	-0.446*	-0.176	-0.211	-0.142	-0.069	-0.460*	-0.370*	0.154	0.0126	0.322	-0.202
Fs_{20}	-0.308	-0.043	-0.239	0.117	-0.11	-0.322	-0.201	0.444*	0.274	0.301	-0.320
Fm_{40}	-0.069	0.036	0.000	-0.104	-0.042	-0.039	-0.169	0.037	0.308	0.144	0.073
$F0_{40}$	0.030	0.154	-0.217	-0.244	0.069	0.137	0.163	0.172	0.468**	-0.437*	-0.039
$F'm_{40}$	0.018	0.478**	-0.212	-0.207	0.4135*	-0.236	-0.229	0.199	0.270	0.294	0.154
Fs_{40}	0.166	0.486**	-0.272	-0.336	0.466**	0.005	0.091	0.403*	0.318	-0.147	-0.072

*, ** statistically significant at 0.05 and 0.01 probability levels, respectively. §ED, ear diameter; EL, ear length; RE, number of kernel rows per ear; GY, grain yield; KR, number of kernel-rows per ear; KRATE, kernel ratio of kernel dry weight to all plant dry weight; KW, 100-kernel weight, DM^{6th}, DM^{14th}, DM_{silk} and DM_{end} are the dry matter at growth stages of 6^{th} leaves, 14^{th} leaves, silking, and at harvest, respectively. †See abbreviations of all physiological traits in Supplementary Table 1.

where Y_{ijl} = observed value from each experimental unit; μ = population mean; p_l = plant effect; v_{ij} = F_1 hybrid effect; g_i = general combining ability (GCA) for i^{th} parent; g_j = GCA effect for j^{th} parent; s_{ij} = specific combining ability (SCA) for ij^{th} F_1 hybrid; r_{ij} = reciprocal (REC) effect of a cross between i^{th} and j^{th} parents; m_i = maternal effect (MAT) of i^{th} parent; m_j = maternal effect of j^{th} parent; n_{ij} = non-maternal (NMAT) effect between i^{th} parent and j^{th} parent); e_{ijl} = random residual effect.

Results and Discussion

Analyses of variance (ANOVA) for all 28 physiological traits

The analyses of variance wereconductedfor 28physiological traits; the other 7 traits used in this study have been reported in our previous paper (Cai et al, 2012). The results (Supplementary Table 2) revealed that entry (genotype) mean squares for 21 out of 28 traits were statistically significant. Even if entry mean square for a trait was not significant, itsgenetic parameters were computed. Interestingly, we found that even when entry mean square was not statistically significant, at least one genetic parameter out of GCA, SCA, REC, MAT, and NMAT was statistically significant. Examples can be seen on SCA for Chl_{40}, $Chla_{40}$, $Chlb_{40}$, and F_{040}, GCA for F_{040} and Fs40, and REC/MAT for Fs_{40}. These results seem to conflict with our general statistical knowledge that no further partition should be donewhen entry mean square is not significant. The possible explanation for the conflicting results might be that entry means were affected by GCA, SCA, and REC effects and they mightcancel each other out. Thus, even when an entry meansquare is not statistically significant, any combining ability effects (GCA, SCA, etc) can be statistically significant (though it may be at a lower confidence level). Therefore, for diallel analysis, even when the entry mean square is not significant, partition of the genetic components from the entry might still be needed.

Baker's (1978) ratio [$2\sigma GCA^2 / (2\sigma GCA^2 + \sigma SCA^2)$] (GSR) is frequently used (Zhang and Kang, 1997; Cho and Scott, 2000; Fan et al, 2008a; Cai et al, 2012) to determine the relative importance of GCA and SCA. The closer the GSR is to 1, the greater the importance of GCA in determining a trait. The following 11 traits had GSR>0.80: Fv/Fm_{20}, PH_{20}, Chl_{20}, Fv/Fm_{40}, $\Phi PSII_{40}$, PH_{40}, $F'm_{20}$, Fs_{40}, $F'm_{40}$, F_{040}, and $C_{Water40}$; and four traits, viz, $Chla_{40}$, $Chlb_{40}$, $Chla/b_{40}$, and Chl_{40}, had GSR <0.50. The GSR for the other 13 traits was between 0.50 and 0.80. These results indicated that GCA effects for the 11 traits with GSR>0.80 were rel-

Table 3 - General combining ability effects for 13 traits related to GY and its components.

Traits†	Line						
	KI 50	YML46	MON 2	87-1	YML1218	Xin 9101-1/o2	Correlated with
PH_{20}	-0.689**	-2.453**	1.773**	-0.756**	1.547**	0.578**	KRATE(+)
PH_{40}	-3.824**	-0.967	1.781	-2.088*	2.114*	2.985**	KRATE(+)
LA_{40}	-0.008*	-0.003	0.013**	-0.016**	0.022**	-0.007	KRATE(+)
$DW_{Shoot40}$	-0.123	-0.068	0.190*	-0.383**	0.402**	-0.018	KRATE(+)
$C_{Water40}$	0.045	-0.54	1.254**	-0.438*	-0.481*	0.16	EL(+), KR(+)
Tr_{20}	0.084**	-0.183**	0.088**	0.091**	-0.152**	0.071**	RE(-)
Fv/Fm_{20}	-0.002*	0.001	-0.002	0.003**	0.001	-0.001	EL(-), KR(-)
LSP_{40}	1.292	-155.608**	160.825**	32.067	-45.933	7.358	RE(-), KR(+)
$Pmax_{40}$	0.523	-1.662**	1.010*	-0.196	-0.846	1.172 *	EL(-),RE(-), KR(+)
Fm_{20}	-5.778	0.951	-36.049*	1.535	37.660*	1.681	KR(-)
$F'm_{20}$	-1.236	8.389	24.806**	-8.153	-16.028*	-7.778	GY(-), KW(-), KRATE(-)
$F'm_{40}$	6.326	10.951	12.701	-8.611	-30.028**	8.66	EL(+), KR(+)
Fs_{40}	0.139	-4.361	12.118 **	-7.715*	-12.028**	11.847**	EL(+), KR(+)

*, ** statistically significant at 0.05 and 0.01 probability levels, respectively; "+"and " – "display positive and negative correlation, respectively. †See abbreviations of all these physiological traits in Supplementary Table 1.

and between the all 35 traits at the seedling stage and GYYCs are given in Tables 1 and 2, respectively. The results (Table 1) showed that there were 7 and 3 physiological traits at seedling stage that were significantly correlated with $DW_{Shoot40}$ and DW_{Root40}, respectively. Three physiological traits, PH_{40}, PH_{20} and LA_{40},were found to be significantly positively correlated to both above- ($DW_{Shoot40}$) and under-ground dry matter (DW_{Root40}). These results suggested that greater plant height (PH_{40}, PH_{20}) and larger leaf area (LA_{40}) might be useful indicators of higher dry matter content (both $DW_{Shoot40}$ and DW_{Root40}). Interestingly, three chlorophyll-related traits ($Chla_{40}$,$Chlb_{40}$, and Chl_{40}) are only significantly correlated with $DW_{Shoot40}$. This may be because the dry weight of organelles themselves in photosynthesis systems is accounted for larger portion of $DW_{Shoot40}$.

The correlation between the physiological traits (measured at seedling stage) and GYYCs (measured at harvest) calculated from different plants should be similar to the correlation calculated from same plant, because genetically uniform F_1 hybrids were used for this study and genetic basis for different F_1 plants at seedling stage and mature stage was the same. The correlation analyses identified five physiological traits (i.e., Gs_{20},Tr_{20}, Pn_{20}, Fv/Fm_{40}, $\phi PSII_{40}$ that greatly impacted dry matter at later growth stages, DM_{Silk} and DM_{end}. These results suggested that these five physiological traits at earlier stages could be used as indicator for greater dry matter at later growing stages. Interestingly, the two dry matter variables, $DW_{Shoot40}$ and DW_{Root40}, were not significantly correlated with none of the four dry matter variables at later growth stages, suggesting that dry matter at earlier growth stage would not be useful for predicting dry matter at later growth stages.

The results from Table 2 also showed that 13 out of the 35 physiological traits studied were statistically significantly correlated with either GY or at least one of the YCs. Among them, PH_{20}, PH_{40}, LA_{40}, $DW_{Shoot40}$ were positively correlated with KRATE; $C_{Water40}$, $Pmax_{40}$, $F'm_{40}$, and Fs_{40} were positively correlated with EL and KR; Tr_{20} and $Pmax_{40}$ had negative relationship with RE; Fv/Fm_{20} had a negative relationship with EL and KR, but was positively correlated with ED; and LSP_{40} had negative and positive relationship with RE and KR, respectively. Fm_{20} was only negatively correlated with KR and $F'm_{20}$ was the sole trait that was negatively correlated with three agronomic traits, i.e., GY, KW, and KRATE.

Conflicting results (Evans and Dunstone, 1970; Borrás et al, 2004) or untested theoretical analyses (Sinclair et al, 2004; Long et al, 2006) have been reported on whether improvement in photosynthesis can increase crop yield. Some physiological traits were found to be positively correlated to GY, and some physiological traits were significantly negatively correlated with GY (Watanabeet al, 1994; Hirel et al, 2001). By comprehensively reviewing recent experiments on impacts of current and future projected elevated (CO_2) environments on plant growth, Long et al (2006) indicated that an increase in leaf photosynthesis was closely associated with increases in yield; there are six potential routes of increasing biomass by improving photosynthetic efficiency (Long et al, 2006). Here, our results further confirmed that some physiological traits, including those related to canopy architecture traits (i.e., PH, LA, DW_{Shoot}) and/or leaf photosynthetic rate (i.e., Ci, Gs, Tr, LSP, Pmax, F'm, Fs) should be directly related to photosynthetic efficiency, and, in turn, related to the GY or YCs. Thus, the above-noted physiological traits could be used as selection criteria in breeding programs aimed at improving GY or YCs.

Combining ability analyses on 13 traits correlated to GY or yield components

Table 4 - Specific combining ability effects for thirteen physiological traits related to YCs with significant variance in hybrids.

Hybrids	PH_{20} †	PH_{40}	LA_{40}	$DW_{Shoot40}$	$C_{Water40}$	Tr_{20}	Fv/Fm_{20}	LSP_{40}	$Pmax_{40}$	Fm_{20}	$F'm_{20}$	$F'm_{40}$	Fs_{40}
KI 50×YML46	0.37	-0.41	-0.03**	-0.42**	-1.5**	0.1**	0	-35.09	-1.38	-1.4	17.21	-17.77	-8.95
KI 50×MON 2	-0.21	-2.04	-0.02**	-0.38*	0.15	-0.2**	0	184.88*	2.27**	0.52	-1.54	20.98	13.24*
KI 50×87-1	-0.15	-0.59	0.01	0.04	0.91*	0.06	0	-116.57	-2.99**	-34.23	-8	-7.62	4.07
KI 50×YML1218	-0.67	3.59*	0.03**	0.48**	-0.06	0.12**	0	-31.97	1.73*	83.73**	-7.38	-2.04	-8.95
KI 50×Xin9101-1/o2	0.66	-0.54	0.02**	0.28	0.5	-0.08*	0	-1.26	0.37	-48.63	-0.29	6.44	0.59
YML46×MON 2	0.26	3.31*	0.02**	0.56**	0.31	-0.16**	0	-72.82	-0.86	-24.29	-4.08	-4.81	-1.68
YML46×87-1	-0.8	-4.21**	0	-0.27	0.57	-0.13**	0	-17.87	0.64	62.88*	6.88	13.42	7.57
YML46×YML1218	-0.57	-1.18	0	-0.21	0.96**	0.13**	0	93.14	1.74*	-30.67	-19.33	6.75	-1.12
YML46×Xin9101-1/o2	0.73	2.49	0.01	0.35*	-0.35	0.06	0	32.64	-0.14	-6.52	-0.67	2.4	4.18
MON 2×87-1	0.05	2.9	0	0.13	-1.00**	0.06	0	66.24	2.09*	-26.04	-8.21	-10.41	-7.58
MON 2×YML1218	0.68	-2.88	-0.01	-0.41**	0.52	-0.01	0	-134.5	-3.62**	1.83	13.75	-4.08	-0.68
MON2×Xin9101-1/o2	-0.78	-1.29	0.01	0.11	0.01	0.31**	0	-43.79	0.13	47.98	0.08	-1.68	-3.3
87-1×YML1218	1.03*	1.51	0.01	0.49**	-0.87*	0.03	0	64.56	0.39	-32.33	10.71	5.57	4.07
87-1×Xin9101-1/o2	-0.13	0.38	-0.01	-0.39*	0.39	-0.02	0	3.64	-0.12	29.73	-1.38	-0.95	-8.14
YML1218×Xin9101-1/o2	-0.48	-1.04	-0.03**	-0.35*	-0.55	-0.27**	0	8.77	-0.24	-22.56	2.25	-6.2	6.68

*, ** statistically significant at 0.05 and 0.01 probability levels, respectively. †See abbreviations of all physiological traits in Supplementary Table 1.

Because GYYCs are final targets that we would like to improve, we need to figure out which lines to be used or what crosses to be made for improving the final target traits. To complete this task, first we identified physiological traits that significant correlated with one of GYYCs; then computed the combining ability (GCA, SCA, and REC) effects of individual lines on the physiological traits; and finally, figure out how to use these lines in a cross to improve GYYCs. To facilitate such analysis, GCA effects of six parental lines and their significance levels for the 13 physiological traits related to GY or YCs are given in Table 3. The SCA and REC effects from the 30 crosses for these 13 physiological traits are given in Tables 4 and 5, respectively. In addition, to help breeders identify potential lines for improving corresponding target traits, the GCA effects and the correlation coefficients between the 13 physiological traits and GYYCs are given in Table 6. The detail discussions for GY and one of the YCs will be given in following different sectors.

GY improvement

Among the 13 traits, $F'm_{20}$ was the only physiological trait that was correlated to GY with a significantly negative correlation coefficient (r = -0.446, Table 2). This result suggested that to improve GY, a line with lower $F'm_{20}$ value and/or a negative significant GCA effect for $F'm_{20}$ should be selected as a parent. From Table 3, we can see that the GCA effect of line YML1218 (-16.028) was significantly negative. Thus, it should be a good parent to lower F'm in a cross. Though, no significant SCA effect (Table 4) was detected in all 30 crosses for $F'm_{20}$, the REC effects for F'm20 in KI 50 × YML1218 and KI 50 × Xin9101-1/o2 crosses were significantly negative (both = -40.67, Table 5). By considering both GCA effects of YML1218 and REC effect of above two crosses, we can conclude that use of YML1218 as male parent will effectively lower $F'm_{20}$ and increase GY.

EL improvement

The EL was positively correlated with four physiological traits i.e., $C_{Water40}$ (0.389), $Pmax_{40}$ (0.418), $F'm_{40}$ (0.478), and Fs_{40} (0.486) and negatively correlated with Fv/Fm_{20} (-0.385) (Tables 2 and 6). These results suggested that any lines that had positive GCA, SCA, and REC effects for $C_{Water40}$, $Pmax_{40}$, $F'm_{40}$ and Fs_{40} or negative GCA, SCA, and REC effects for Fv/Fm_{20} may be used to improve EL. Based on this information, MON2 can be used to increase $C_{Water40}$, $Pmax_{40}$, and Fs_{40} (Table 6); KI 50 can be used to lower Fv/Fm_{20}; Xin9101-1/o2 can be used to increase both $Pmax_{40}$ and Fs_{40} but may negatively affect $C_{Water40}$; YML1218 and 87-1 may not be used in any crosses because both lines had negative effects on most of positively related physiological traits affecting EL.

After a physiological trait is selected according to correlation between a physiological trait and YCs, information on GCA, SCA and REC effects is further needed for determining which inbred line should be used and which line should be used as female or male parent. For example, there were five physiological traits correlated with EL and $C_{Water40}$ is one of those traits. To improve EL, we need to have a line with positive GCA, to have a cross with both positive SCA and REC effects. Take Pmax40 for an example. From Table 2 and Table 6, we can see that $Pmax_{40}$ has significantly positive correlation with EL and significantly positive GCA effects are found for MON2 (1.010) and Xin 9101-1/o2 (1.172). Significant positive SCA effects were observed for the following crosses: KI 50 × MON2 (2.27), KI 50 × YML1218 (1.73), YML46 × YML1218 (1.74) and MON2 × 87-1 (2.09); and significant negative REC effects were detected for KI 50 × YML1218 (-2.58) and 87-1 × Xin9101-1/o2 (-3.77) (Tables 4 and 5). Results on GCA, SCA, and REC effects suggested that EL could be effectively improved by Pmax40 by using KI 50 as male parent, Xing9101-1/o2 as female parent, and MON2 as either male or female parent in the crosses. Results for other physiological traits are similar to those described for $Pmax_{40}$.

ED improvement

In this study, Fv/Fm_{20} was the sole physiological trait that was positively correlated with ED and line 87-1 was the only line that showed a positive GCA effect for Fv/Fm_{20}. Because information on SCA and

Table 5 - Reciprocal effects for thirteen physiological traits related to YCs with significant variance in hybrids.

Hybrids	PH_{20}†	PH_{40}	LA_{40}	$DW_{Shoot40}$	$C_{Water40}$	Tr_{20}	Fv/Fm_{20}	LSP_{40}	$Pmax_{40}$	Fm_{20}	$F'm_{20}$	$F'm_{40}$	Fs_{40}
KI 50×YML46	-1.03	-4.85*	0	-0.08	0	-0.12*	0	59.4	-0.36	38	16.83	1	-5.17
KI 50×MON 2	-0.24	-3.33	0.03**	0.6**	0.24	-0.19**	0	211.8*	1.96	7.08	15.5	-18	8.17
KI 50×87-1	-0.86	-2.08	0.01	0.11	0.38	-0.04	0	80.4	0.94	-7.92	-7.58	7.58	-4
KI 50×YML1218	-2.02**	-0.75	0.01	-0.49*	1.14*	0.32**	0	-18.6	-2.58*	-60.17	-40.67**	-3.25	3.83
KI 50×Xin9101-1/o2	-0.74	-4.06*	-0.02**	-0.43*	0.03	0.15**	0	203.4*	1.95	35.83	-40.67**	9.58	23.8**
YML46×MON 2	1.41**	2.73	-0.01	-0.22	0.18	0.12*	0	63.6	2.05	-26.67	8.58	25	10.58
YML46×87-1	0.77	2.44	0	0.09	-0.08	0.32**	0	149.4	1.64	-100.42**	3.25	5.08	-0.83
YML46×YML1218	0.62	-4.34*	-0.01	-0.19	0.47	0.45**	0	-85.2	-1.94	69.17	12.5	-3.18	0.33
YML46×Xin9101-1/o2	0.32	1.29	-0.01	-0.12	0.71	0.4**	-0.01	15.6	0.51	34.67	23.92	9	18.67*
MON 2×87-1	-0.65	0.73	0.02**	0.43*	0.7	0.02	0	72.33	-0.15	6.33	-3.58	-30.3*	-18.17*
MON 2×YML1218	-0.28	5.18*	-0.01	-0.16	0.36	0.1*	0	24	1.1	40.17	29.17*	18.08	5.58
MON2×Xin9101-1/o2	0.41	5.62**	0.01	0.55**	-1.22*	0.13**	0	-126	-0.27	-7.5	-10.75	-10.67	3.33
87-1×YML1218	1.68**	-1.54	0.01	0.06	-0.21	-0.16**	0	-56.9	-1.09	-66.25	-14.67	26.58	5.17
87-1×Xin9101-1/o2	0.76	0.57	0.01	0.44*	-0.36	0.21**	0	-98.67	-3.77**	31.67	27.5*	28.08	4.67
YML1218×Xin9101-1/o2	0.09	-6.31**	0	-0.18	1.17*	-0.12*	0	-97.8	-1.69	54	9.42	12.92	9

*, ** statistically significant at 0.05 and 0.01 probability levels, respectively. †See abbreviations of all physiological traits in Supplementary Table 1.

REC effects on Fv/Fm_{20} is largely unavailable, we concluded that though 87-1 could be used as a parent to improve ED by enhancing Fv/Fm_{20}, it would be difficult to decide if 87-1 should be used as male or female parent.

The results for RE, KR, KW, and KRATE were similar to what we have reported for EL and ED. To reduce redundancy, we will only report which lines and which crosses need to be used for ED, RE, KR, KW, and KRATE in the following sub-sections.

RE improvement

Correlation coefficient and combining ability effect results (Table 6) for RE indicated that Tr_{20}, LSP_{40}, $Pmax_{40}$ were three physiological traits that could be used for improving RE by usingYML1218 as female parent and YML46 as male parent in a cross to decrease Tr_{20}. This conclusion was confirmed by REC effects for YML1218 × Xin9101-1/o2 (-0.12), KI 50 × YML46 (-0.12), KI 50 × YML1218 (0.32), YML46 × MON2 (0.12), YML46 × 87-1 (0.32), and YML46 × Xin9101-1/02 (0.40). However, 87-1 × YML1218 had a negative REC effect (-0.16) that would reduce Tr_{20} when YML1218 was used as male parent. This may be because of a specific interaction between the cytoplasm of 87-1 and nuclear genes of YML1218.

KR improvement

Seven physiological traits were significantly correlated with KR. Among them, five, i.e., $C_{Water40}$, LSP_{40}, $Pmax_{40}$, $F'm_{40}$, and Fs_{40}, had positive and two, i.e., Fv/Fm_{20} and Fm_{20}, had negative correlation with KR (Table 6). MON2 may be a preferred parent for improving KR because it exhibited significantly positive GCA effects for $C_{Water40}$ (1.254), LSP_{40} (160.825), $Pmax_{40}$ (1.010), and Fs_{40} (12.118), which were positively correlated with KR. In contrast, MON2 had negatively significant GCA effects for Fm_{20} (-36.049) and did not show a significant GCA effect for Fv/Fm_{20} (Table 6). Xin9101-1/o2, which had significantly positive GCA effects for $Pmax_{40}$ (1.172) and for Fs_{40} (11.847), could be another good line for improving KR, as these two traits were positively correlated with KR.

In summary, to improve KR, one should select crosses with positive SCA effects for $C_{Water40}$, LSp_{40}, $Pmax_{40}$, $F'm_{40}$, and Fs_{40} and/or crosses with negative SCA effects for Fv/Fm_{20} and Fm_{20}. According to correlation between the seven physiological traits and GYYCs, SCA effect (Table 4) and REC effect (Table 5) directions (i.e., positive or negative), MON2 and Xin91-1-1/o2 would be better as male parents to improve $C_{Water40}$ and Fs_{40} and better female parent to improve LSP_{40} and $Pmax_{40}$.

KW improvement

KW was negatively correlated (-0.460) with $F'm_{20}$ (Tables 2 and 6). YML1218 would seem to be a good inbred line for improving KW because it displayed negative GCA effect for $F'm_{20}$. Because no SCA effect was detected in all 30 crosses for $F'm_{20}$, we focused on REC effect analysis for $F'm_{20}$. Significant REC effects (Table 5) were observed for $F'm_{20}$ in four crosses: KI 50 × YML1218 (-40.67), KI 50 × Xin9101-1/o2 (-40.67), MON2 × YML1218 (29.17), and 87-1 × Xin9101 (27.5). Because negative REC effect was needed for obtaining negative $F'm_{20}$, YML1218 should be used as male parent when it is crossed with KI 50 and it should be used as female parent when it is crossed with MON2.

KRATE improvement

Five physiological traits were significantly correlated with KRATE. Among them, four had positive and one had negative correlation with KRATE (Table 6). According to correlation coefficient and GCA effects, YML1218, MON2, and Xin9101-1/o2 should be good candidates for improving KRATE. YML1218 might be the best line because it showed significantly positive GCA effects for these four traits: PH20 (1.547), PH_{40} (2.114), LA_{40} (0.022), and $DW_{Shoot40}$ (0.402) and significantly negative GCA for $F'm_{20}$ (-16.028) that was negatively correlated with KRATE (-0.37). MON2 was considered the second best line for improving KRATE because it had significantly positive GCA effects for these three traits: PH_{20} (1.733), LA_{40} (0.013) and $DW_{Shoot40}$ (0.190) even with its GCA effect on $F'm_{20}$ being unfavorable.

Table 6 - General combining ability effects of different lines with physiological traits significantly correlated with GY or its components.

Target Trait[§]	Physiology Traits[†]	r[‡]	Lines: KI 50	YML 146	MON 2	87-1	YML 1218	Xin 9101-1/o2
GY	$F'm_{20}$	-0.446**			24.806**		-16.028**	
EL	$C_{Water40}$	0.389**			1.254**	-0.438*	3	-0.481*
	Fv/Fm_{20}	-0.385*	-0.002*			0.003*		
	$Pmax_{40}$	0.418*		-1.662**	1.010*			1.172*
	$F'm_{40}$	0.478**					-30.028**	
	Fs_{40}	0.486**			12.118**	-7.715*	-12.028**	11.847**
ED	Fv/Fm_{20}	0.498**	-0.002*			0.003*		
RE	Tr_{20}	-0.398*	0.084**	-0.183**	0.088**	0.091**	-0.152**	0.071**
	LSP_{40}	-0.478**		-155.608**	160.825**			
	$Pmax_{40}$	-0.448*		-1.662**	1.010*			1.172*
KR	$C_{Water40}$	0.453*			1.254**	-0.438*	-0.481*	
	Fv/Fm_{20}	-0.380*	-0.002*			0.003*		
	LSP_{40}	0.509**		-155.608**	160.825**			
	$Pmax_{40}$	0.519**		-1.662**	1.010*			1.172*
	Fm_{20}	-0.425*			-36.049*		37.660*	
	$F'm_{40}$	0.414*					-30.028**	
	Fs_{40}	0.466**			12.118**	-7.715*	-12.028**	11.847**
KW	$F'm_{20}$	-0.460*			24.806**		-16.028**	
KRATE	PH_{20}	0.663**	-0.689**	-2.453**	1.733**	-0.756*	1.547**	0.578**
	PH_{40}	0.527**	-3.824**			-2.088*	2.114*	2.985**
	LA_{40}	0.395*	0.008*		0.013**	-0.016**	0.022**	
	$DW_{Shoot40}$	0.393*			0.190*	-0.383**	0.402**	
	$F'm_{20}$	-0.370*			24.806**		-16.028**	

*, ** statistically significant at 0.05 and 0.01 probability levels, respectively. [†]See abbreviations of all physiological traits in Supplementary Table 1.

Because PH_{20}, PH_{40}, LA_{40}, and $DW_{Shoot40}$ had positive correlation coefficients with KRATE and $F'm_{20}$ had a negative correlation coefficient with KRATE (Table 6), any crosses with positive SCA effects for the foregoing four traits and/or with negative SCA effects for $F'm_{20}$ could be selected for improving KRATE. The information from SCA and REC effects further confirmed that YML1218, MON2, and Xin9101-1/o2 were good parental candidates for improving KRATE. To decide whether these three lines should be used as female or male parent, REC effects in the crosses with the three lines involved should be considered (Table 5).

In summary, for diallel analysis, even when the entry mean square is not significant, partition of the genetic components from the entry might still be needed due to canceling our of GCA, SCA, and REC effects that constitutes entry mean square. Plant height (PH_{40}, PH_{20}) and leave area (LA_{40}) at seedling stage may be used as indicators for both shoot ($DW_{Shoot40}$) and root dry matter (DW_{Root40}) at the same stages. However, the two dry matter variables of $DW_{Shoot40}$ and DW_{Root40} were not significantly correlated with none of the four dry matter variables at later growth stages, suggesting that dry matter at earlier growth stage would not be useful for predicting dry matter at later growth stages. By considering results from both combining ability and correlation analyses, authors found YML1218 can directly be used for improving GY as male parent; lines of KI 50 (as male parent), Xing9101-1/o2 (as female parent), and MON2 (as either male or female parent) in the crosses can be used for improving EL. No best inbred line was identified for improving ED from studied materials; lines of YML1218 (as female parent) and YML46 (as male parent) in a cross can enhance RE; lines of MON2 and Xin91-1-1/o2 would be better as male parents to improve KR. Line YML1218 seems to be a good inbred line for improving KW and lines YML1218, MON2, and Xin9101-1/o2 should be good parental candidates for improving KRATE.

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