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Heterosis of maize photosynthetic performance

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Abstract Four maize inbred lines with different photosynthetic rates and their two hybrids were used as test materials, and the diurnal variations of their photosynthesis parameters in the silking stage were measured to study the heterosis of photosynthetic performance. Results showed that net photosynthetic rate (P_n), transpiration rate (Tr) and stomatal conductance (G_s) all presented an obvious single-peaked curve in a day, with the peak values occurring at 10:00–12:00, 12:00, 10:00–12:00 a.m., respectively, while water use efficiency (WUE) had a “V” type variant trend, with the lowest value appearing at 12:00. The diurnal variation of P_n and Tr was correlated markedly with G_s , suggesting that G_s played an important role in regulating the diurnal variation of P_n and Tr , and P_n , Tr and G_s had a higher heterosis in the afternoon than in the morning, while the WUE was in reverse, indicating that maize hybrid had higher resistance to the high temperature and dehydration in the afternoon, which provided a new path to select varieties with a high net photosynthetic rate.

Keywords maize (*Zea mays* L.), photosynthetic performance, heterosis, diurnal variation

1 Introduction

Maize is a typical C_4 crop with high photosynthetic efficiency and heterosis was widely utilized in maize breeding. It had been studied that the maize hybrid had higher heterosis than its parents in net photosynthetic rate, transpiration rate, chlorophyll fluorescence, activities of Hill reaction, photosynthetic phosphorylation activities and concentration of ATPase, chlorophyll fluorescence induction kinetics etc. Statistical analysis also revealed strong correlation between the net photosynthetic rate and the chlorophyll fluorescence

induction kinetics (Zhao et al., 1996). Besides, it had been reported on the maize diurnal variation of photosynthetic performance in net photosynthetic rate, assimilate export rate, metabolic intermediates of sucrose synthesis (Kalt-Torres et al., 1987; Usuda et al., 1987; Grammatikopoulos and Manetas, 1990). However, the diurnal variations of maize photosynthetic performance were still unclear. And it is important to further analyze the heterosis of photosynthetic performance and its adaptability to environment. The diurnal variance of photosynthetic performance actually is the adaptability of maize to an environment, and heterosis plays a significant role in it. Therefore, the diurnal variance of photosynthetic performance is one base of heterotic degrees. To determine the response of heterosis of photosynthetic performance to environment, the maize diurnal variance of photosynthetic performance was analyzed in this paper. It is to provide theoretical direction for breeding for the net high photosynthetic efficiency and cultivation management.

2 Materials and methods

2.1 Treatments and experimental design

This experiment was conducted at Shanjiao Village, Jiusuo Town, Hainan Province, China from January to February in 2005. The high photosynthetic efficient hybrid was 103 (Yinong 103) and its parents were 704 (70gao4) and 512. The low photosynthetic efficient hybrid was 7943 and its parents were 79 and 43.

A randomized blocks design was used in this experiment and there were three replications for each genotype. The rows were 5 m long and the plant spacing was 25 cm. Seeds were sown on November 10, 2004, heading in January 2005, harvesting in March 2005. Agronomic practices followed regional recommendations.

2.2 Methods

2.2.1 Measurement of photosynthetic performance parameters

Net photosynthetic rate (P_n), respiration rate (Tr), stomatal conductance (G_s) of ear-leaf were measured with a LI-6400

Translated from *Chinese Journal of Applied Ecology*, 2007, 18(5): 1049–1054 [译自: 应用生态学报]

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(LI-COR, USA) portable photosynthetic measuring system. The leaf chamber temperature was maintained at $(25 \pm 0.5)^\circ\text{C}$, Photon Flux Density Radiation (*PPFD*) was at $2\,800\ \mu\text{mol}/\text{m}^2\cdot\text{s}$, CO_2 concentrations was $350\ \mu\text{mol}/\text{mol}$. Three to five typical plants were selected per variety at five measuring time (8:00 a.m., 10:00 a.m., 12:00 a.m., 2:00 p.m. and 4:00 p.m.).

2.2.2 Measuring methods of light-response

Light-response was measured using *PPFD* set 100, 300, 600, 1 000, 1 500, 2 100, $2\,800\ \mu\text{mol}/\text{m}^2\cdot\text{s}$ besides the above measuring methods.

2.2.3 Calculation of the heterosis rate of photosynthetic performance

Heterosis rate of photosynthetic performance = (photosynthetic performance value of hybrid – photosynthetic performance average value of parents) $\times 100\%$ / photosynthetic performance average value of parents.

The efficiency of water application was calculated according to the method of Bierhuizen and Slatyer (1965): $WUE = Pn/Tr$.

2.3 Data statistical analysis

Presented data were the mean values and standard deviations of four replicates for all measured traits. Analysis of correlation for main photosynthetic performance parameters was carried out by the PERSON procedure in SPSS. An obvious single-peaked curve in a day was presented, with the peak value occurring at 10:00–12:00 a.m.

3 Result

3.1 Diurnal variance and heterosis rate of net photosynthetic rate in different genotypes

Results in Fig. 1 indicated that the net photosynthetic rate presented an obvious single-peaked curve with the peak values occurred at 10:00–12:00 a.m. in all genotypes. P_n of 103 and its parents were comparably higher than 7943 and its parents in every period of a day. P_n of 704, the male parent of 103, was significantly higher than that of the other inbred lines. There was an increasing trend of heterosis rate of P_n in the two maize varieties in a day. Moreover, the average P_n values and heterosis rates of all the genotypes during 12:00 a.m.–4:00 p.m. were higher than those during 8:00–12:00 a.m.. Summarily, 103 had high P_n in a day especially in the afternoon. Although 7943 had higher heterosis rate of P_n than 103, the parents of 7943 had lower P_n , so P_n of 7943 was lower than that of 103. Consequently, when we combine high P_n variety, we should select parent materials with high P_n and pay attention to the characteristic in the morning and afternoon.

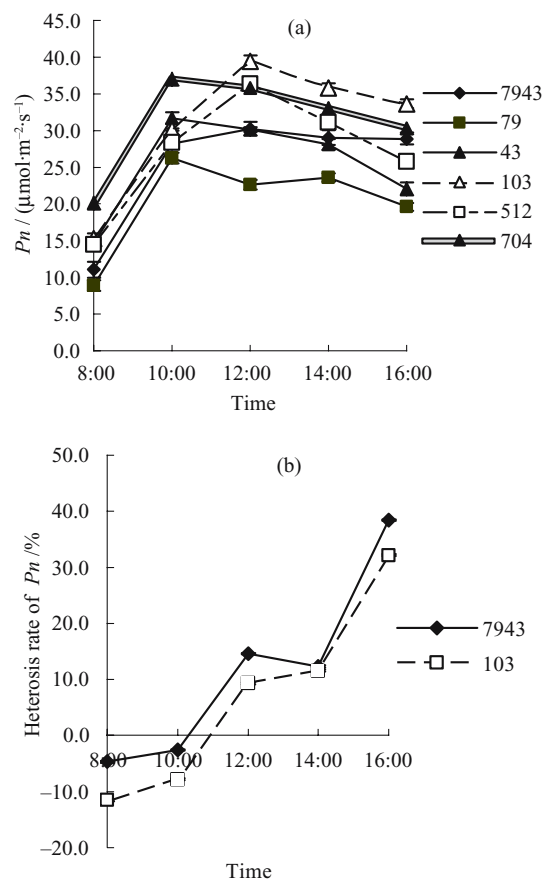


Fig. 1 Diurnal variance of P_n and its heterosis rate in different genotypes

3.2 Diurnal variance and heterosis rate of respiration rate in different genotypes

Transpiration rate (Tr) exhibited an obvious single-peaked curve in a day, and the time of arising peak value was 12:00 a.m. (Fig. 2). 103 and its parents had higher Tr and heterosis rate than 7943 and its parents, indicating that 103 was a hybrid with high Tr and high heterosis rate. Tr and heterosis rate of different genotypes in the afternoon were higher than in the morning, which had the same trend as P_n . However, the time that the peak value appeared was posterior to P_n . Thus, it could be seen that the diurnal variance of P_n and Tr had a synergistic relationship.

3.3 Diurnal variance and heterosis rate of stomatal conductance in different maize varieties

Stomatal conductance (G_s) presented an obvious single-peaked curve in a day, and the time that the peak value arose was at 10:00–12:00 a.m. (Fig. 3) which was simultaneous with P_n and earlier than that of Tr . In contrast with 7943 and its parents, 103 and its parents maintained higher G_s values all day. G_s and its heterosis rates of all varieties were higher in the afternoon than in the morning. The G_s of 103 was positive heterosis, while that of 7943 was negative heterosis.

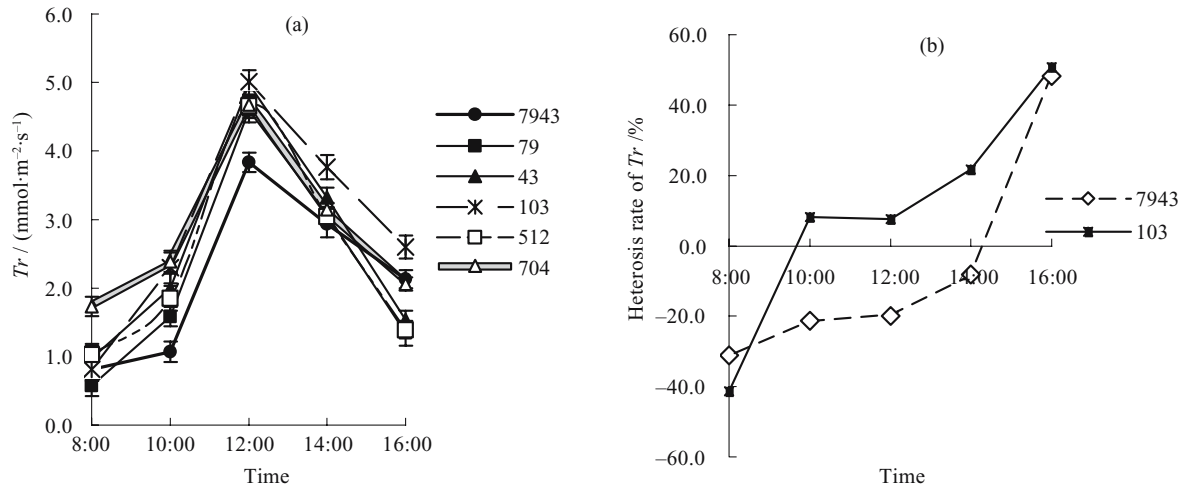


Fig. 2 Diurnal variance of Tr and its heterosis rate in different genotype

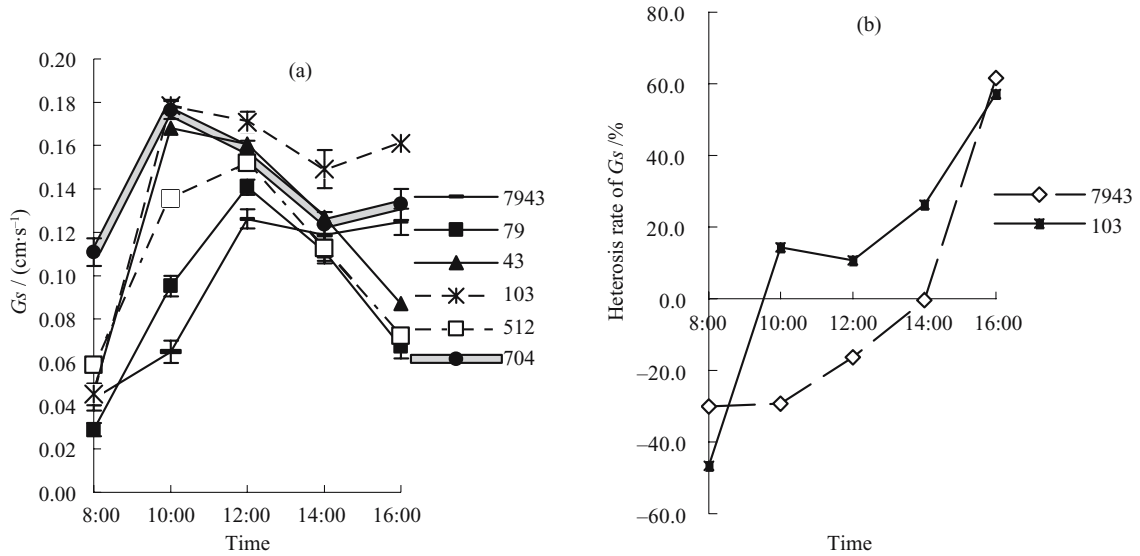


Fig. 3 Diurnal variance of G_s and its heterosis rate in different genotypes

The diurnal variance of G_s and P_n was simultaneous and the variant trend of heterosis rate of G_s was in accordance with Tr , which suggested the G_s was one of the important factors in regulating the diurnal variance of P_n and Tr .

3.4 Diurnal variance and heterosis rate of WUE in different maize varieties

Results in Fig. 3 showed that the diurnal variance of water use efficiency (WUE) had a “V” type variant trend with the peak value arising at 10:00 a.m. and the lowest value appeared at 12:00 a.m.. The WUE values of 103 with high P_n and Tr were distinctly lower than 7943 which had low P_n and Tr . The WUE values of all genotypes were higher in the morning than in the afternoon without exception. The phenomenon likely related to strong Tr caused by higher temperature in the afternoon and relative lower humidity. The heterosis rate of

WUE was also higher in the morning than in the afternoon. But different hybrids had different heterosis rates, and the negative heterosis rate of 103 was lower than that of 7943. Hence 7943 was a low Tr and water-saving hybrid, while 103 was a high P_n , high Tr and water consumptive hybrid. It was suggested that we should pay much attention to parent material with higher WUE in the water-saving and high P_n breeding.

3.5 Correlation analysis of diurnal variance of gas exchange parameters

Correlation analysis for gas exchange parameters indicated that the diurnal variance of P_n and Tr in all genotypes was positively correlated with G_s , and negative correlated with WUE (Tables 1, 2). This indicated that the diurnal variance of P_n and Tr was mainly caused by the different responses of G_s

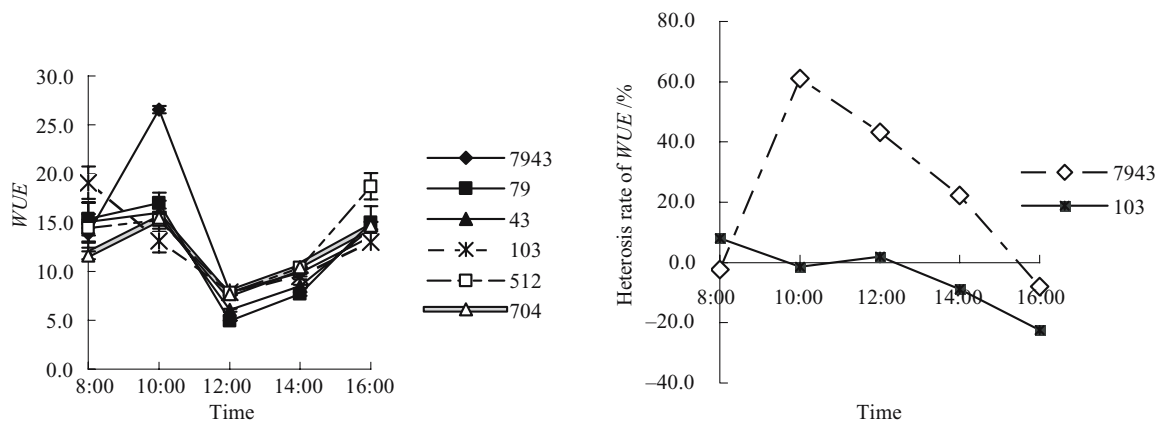


Fig. 4 Diurnal variance of *WUE* and its heterosis rate in different genotypes

to the environment, and resulted in changes of *WUE*. But the *G_s* of different genotypes had different influences on *WUE*. The *G_s* of 7943 with high *WUE* value was significantly and negatively correlated with *WUE*, while for 103, a low *WUE* variety, its *WUE* was negatively correlated with *G_s*, yet not significant. The results showed that the *G_s* of water-saving variety had a definite regulating effect on *WUE*, while the water-consumed variety was opposite. The water-consumed variety could be double influenced by the stomatal conductance and non-stomatal conductance regulation. The correlation for the diurnal variance of main photosynthetic performance parameters was also an important index for high *P_n* and high *WUE* breeding.

Table 1 Correlation for diurnal variance of gas exchange parameters among two hybrids and its parents

	<i>P_n</i>	<i>G_s</i>	<i>Tr</i>	<i>WUE</i>
<i>P_n</i>		0.86**	0.83**	-0.48
<i>G_s</i>	0.90**		0.66**	-0.41
<i>Tr</i>	0.64**	0.81**		-0.86**
<i>WUE</i>	-0.35	-0.57*	-0.89**	

Note: Row indicates 103, and column indicates 7943.

Table 2 Correlation for gas exchange parameters of two hybrids and its parents among morning and afternoon

	<i>P_n</i>	<i>Tr</i>	<i>WUE</i>	<i>G_s</i>
<i>P_n</i>		0.75**	-0.39	0.92**
<i>Tr</i>	0.58*		-0.87**	0.74**
<i>WUE</i>	-0.31	-0.91**		-0.48
<i>G_s</i>	0.78**	0.82**	-0.65**	

Note: Row indicates morning, column indicates afternoon.

3.6 Light-response curve of gas exchange parameters

Of the main ecological factors in measuring period, the temperature out of leaf chamber varied from 23°C to 28°C, which had a minor impact on maize photosynthesis. Moreover, the CO₂ concentration outside ranging from 300 to 330 μmol/mol also could not affect photosynthesis. Therefore, the emphasis

of this experiment was to analyze the regulating effect of photo-synthetically active radiation (*PAR*) on the photosynthetic performance of different genotypes (Fig. 5). Results showed that there was an obvious liner relationship between *P_n* and *PAR*. The *P_n* could be improved with the increasing of *PAR*. But different genotypes had different variant ranges, especially *P_n* of 103 and its parents had an evident advantage when *PAR* was greater than 600 μmol/m²·s. So the variant ranges of 103 and its parents were larger than those of 7943 and their parents. The trend of light-response curve of *Tr* and *G_s* was consistent, but the response of different genotypes was different. The light-response curves of *Tr* and *G_s* of 7943 and its parents were not distinct with the variance of *PAR*. However, the same curve of 103 and its parents presented a “V” type trend, and the lowest value appeared in *PAR* 300 μmol/m²·s. Different genotypes had different light-response curves of *WUE*. The *WUE* of 103 and its parents appeared an obvious single-peaked curve, and the highest value appeared in *PAR* 300 μmol/m²·s. But the *WUE* of 7943 and its parents exhibited liner variance with the increasing of *PAR*. The above result instructed that *PAR* was an important ecological factor to affect main photosynthetic performance and was crucial to photosynthesis.

4 Discussion

4.1 Dynamic characteristic of the diurnal variance of maize photosynthetic performance, its heterosis rate and environmental, ecological factors

There was a close correlation between maize photosynthetic performance, heterosis rate and ecological condition. Because main environmental factors: *PAR*, temperature (*T_a*), relative humidity (*RH*) and CO₂ concentration (*C_a*) exhibit an obvious diurnal variant regularity, the photosynthetic performance also presented a diurnal variant characteristic. Moreover this variant characteristic was different because of different carbon metabolic paths and environmental factors. The difference of

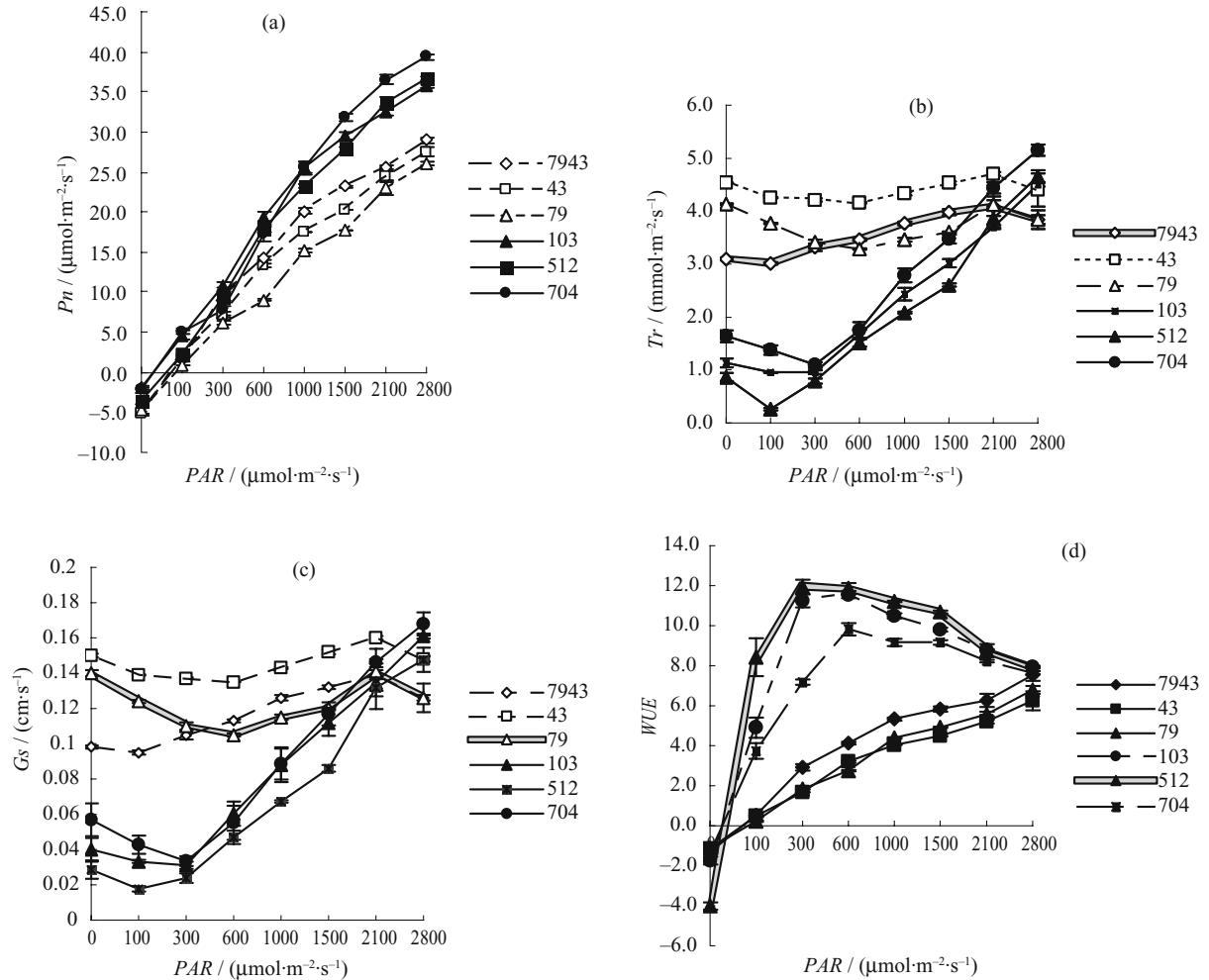


Fig. 5 Light-response of gas exchange parameters in different genotypes

diurnal variance of photosynthetic efficiency between C_3 and C_4 plants was significant. In the field without deficient RH , T_a , nutrition, the diurnal variance of P_n of C_4 plants presented a single-peaked curve, which suggested the photosynthetic efficiency at noon was not depressed but slightly elevated (Zhang et al., 1998a; Wang et al., 2004). However, the diurnal variance of P_n of C_3 plants exhibited the double-peaked curve and the lowest value appeared at noon. In the main environmental factors, the PAR was determinative, and the main limiting factor was air temperature (Liu et al., 2006). The PAR decided the P_n . The trend of PAR and P_n was consistent, namely the P_n could be enhanced basically with the increasing of PAR (Wang and Liu, 2003). The experiment was measured in the adequate temperature of maize leaf photosynthesis, so the influence of temperature on photosynthesis could be neglected. The photosynthetic performance values measured were mainly impacted on the PAR outside. Although main ecological factors are controlled in the experiment, the uncontrolled PAR out of leaf chambers also affect photosynthesis of position measured. So it appeared that the diurnal variance of photosynthesis in the controlled condition, namely the diurnal

variance of photosynthesis intensively depended on the diurnal variance PAR outside.

In the study, hybrids had an obvious time difference in the diurnal variance of photosynthetic performance including P_n , T_r , G_s . Namely, the P_n of maize presented a single-peaked curve in a day and its heterosis rate was higher in the afternoon than in the morning. The advantage of afternoon mainly was because the ecological environment (T_a , RH , PAR) in the morning and afternoon had differences which led to the physiological metabolic variance in plants. Accordingly, the heterosis rate of photosynthetic performance improved markedly in the afternoon. That also indicated that the hybrid had a better adaptability to environmental variation, and the hybrid root system was developed, with highly insensitive responses to the circumstances in the afternoon. Sequentially, the hybrid maintained higher P_n . But for C_3 plants such as rice and wheat, the environment in the morning could make full use of advantages, while the high temperature with the depression of RH and deficient CO_2 concentration in the afternoon could bring P_n to a valley called noon sleep phenomenon. After that, P_n gradually recovered.

The heterosis of photosynthetic performance is a complicated process controlled by hereditary factors and restricted by circumstance. Therefore, it was suggested that the heterosis rate value of photosynthetic performance in the afternoon was a reference index to evaluate the high photosynthetic efficient heterosis rate under the stress and screen the high photosynthetic efficiency variety.

4.2 Selection for maize high photosynthetic efficient breeding index and combining high P_n variety

Photosynthetic performance is the foundation for substantial yield, and 95% of crop yield comes from the photosynthetic performance. The positive correlation between P_n and yield was significant ($r = 0.868$) (Li and Zhao, 1999). The heterosis is an important foundation for high photosynthetic efficient breeding and high yielding cultivation. The hybrid had a multiform heterosis in the photosynthetic performance. Generally, hybrid had a distinct super-parental heterosis (Zhao et al., 1997; Li and Zhao, 1999). Experimentally, the hybrid had a positive heterosis in P_n than its parents, ranging from 3.1%–23.4%, with superhigh parents at 2.4%–9.3%. The heterosis of P_n was related to the content of chlorophyll (Zhao et al., 1997). But it was also reported that the hybrid had no or negative heterosis in P_n (Zhang et al., 1998b).

Different maize varieties had different photosynthetic performance characteristics (Li and Zhao, 1999; Li et al., 1999). It could be divided into different types by the clustering analysis according to the different elements of photosynthetic performance (Zhao et al., 1999). The heterosis of photosynthetic performance was related to the characters of varieties. However, circumstances were also important factors to affect heterosis. Looking at the aspect from developmental physiology, certain photosynthetic characteristic was formed under the given ecological condition. It was the result of phylogenetic development (Deng et al., 1995). Additionally, the P_n varied with the condition changing, which suggested that it could not make the full heterosis of photosynthetic performance until being adapted to climates in a place.

In the study, the main characters of 103, as a high photosynthetic efficient variety, were higher P_n of its parents and lower heterosis rate, while the parents' P_n of 7943, as a low photosynthetic efficient variety, was lower than that of 103 but its heterosis rate was higher than that of 103. Hence, the reason for the lower P_n of 7943 was mainly the lower P_n of parents, followed by the heterosis rate. In comparison with the main photosynthetic performance indexes, 103 was distinguished from 7943 in the characteristics of higher P_n , higher Tr and lower WUE . And the characteristics of 103 were correlated with the G_s . On the contrary, 7943 had lower P_n and Tr due to the lower G_s , but gained higher WUE , indicating that improving G_s may elevate P_n and Tr , but require more water consumption. It proved that stomatal modulation

may play an important controlling role in the photosynthesis. Therefore, high G_s is viewed as a significant index for high photosynthetic efficient breeding.

In the breeding for the high photosynthetic efficient variety, we should give priority to select high photosynthetic efficient parents, and pay attention to making full use of heterosis along with the effect of circumstance on P_n and heterosis rate. Our result suggests that we should select feasible varieties under different conditions. In the fertile land, 103 can realize the full use of high yield potential. While in the droughty soil, we can select varieties with higher P_n , lower Tr and higher WUE to increase production under the stress.

This experiment only researched two maize genotypes under the special condition, and the responses of different genotype's heterosis need to be further discussed under the multiple conditions.

Acknowledgements This work was supported by the Science and Technology Project of Food Production Enhance, China (No. 2004BA520A12) and the Technology Plan Project of Beijing (No. H022020030130-4).

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