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Development of yield and some photosynthetic characteristics during 82 years of genetic improvement of soybean genotypes in northeast China

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Abstract

The aim of this work was to investigate development of some photosynthetic characters and their relationship with seed yield during the genetic improvement of soybean. For this objective, we grew 38 soybean cultivars representing genetic improvement progress in northeast China, released from the period of 1923 to 2005 (82 years). The experiment was performed in 2005 and 2006. Some photosynthetic characteristics such as leaf area, chlorophyll content and specific leaf weight (SLW) were measured at R2 stage (flowering stage). Days to maturity and yield were measured in each plot. The results of two years study showed that number of days to maturity decreased from 140.3d to 125.6d depends on the year of release, but soybean seed yield increased significantly from 1282.3 Kg to 2310.7 Kg during the 82 years of breeding. The net photosynthetic rate (Pn), stomatal conductance (Gs), apparent mesophyll conductance (Pn/Ci), transpiration (Tr), chlorophyll content and SLW all increased in bred cultivars during the improvement, but contrastingly the leaf area and ratio of Ci/Ca (intercellular CO_2 concentration, Ci; ambient CO_2 concentration, Ca) decreased in the same time. Yield was positively correlated with Pn, Tr, Gs, Pn/Ci, chlorophyll content and SLW, whereas the leaf area, Ci/Ca and WUE were negatively correlated. Our results revealed that Pn and Pn/Ci are the effective selection indexes for seed yield and can be used in future soybean breeding programs. We also found that the increase of Tr is higher than Pn. As a result, WUE is decreased as the increase of yield with year of release. Therefore, the main cost of high yield in new cultivars is water expense.

Keywords: soybean, genetic improvement, yield, photosynthesis, water usage efficiency.
Abbreviations: Ci–intercellular CO_2 concentration, Ca–ambient CO_2 concentration, Chl–chlorophyll content, Pn–net photosynthetic rate (Pn), Pn/Ci–apparent mesophyll conductance, Gs–stomatal conductance, Tr–transpiration, WUE–water usage efficiency, SLW–specific leaf weight; R2 stage- flowering stage.

Introduction

Soybean production has increased sharply in post several decades (Specht et al., 1999; Wilcox, 2001; Zhao et al., 2006). The yield increase per unit area is the main goal of cultural practices and genetic improvement of soybean cultivars. Cox et al. (1988) pointed out that the comparisons of cultivars in test environments were the most direct estimate of genetic progress. There were many researches showed that soybean yield was increased linearly with the progress of release year (Luedders, 1977; Karmaker and Bhatnagar, 1996). At the same time, agronomic characteristics (Volgeng et al., 1997; Ustun et al., 2001), growth features (Kumudini, 2001; Zhen et al., 2006; Jin et al., 2004) and physiological traits (Gay et al., 1980, Morrison et al., 1999; Kumidini et al., 2001; Zhu et al., 2002; Wang et al., 2006) were assayed to examine the reason why at same cultural and management environment the yield of different soybean cultivars differed.

Leaf photosynthesis is a basis of yield formation in crops. A number of researchers have demonstrated that there are great differences in photosynthesis level of cultivars (Dornhoff and Shibles, 1970; Buttery et al., 1981; Ashley and Boerma, 1989; Richards, 2000). Morrison et al. (1999) grew 14 soybean cultivars representing the genetic improvement of 58 years (1934-1992) to investigate the physiological changes associated with yield. They found that the increase of yield with year of release was significantly correlated with the harvest index, photosynthesis and stomatal conductance. Specht et al. (1999) and Ustun et al. (2001) suggested that soybean yield increase was linear in post several decenniums. This linear increase demonstrated that a yield plateau has not been reached. However, the yield of new soybean cultivars did not show linear increase in recent years in China (Zhao et al., 2006). This may be due to the fact that there are not effective physiological indices for selection of high yield soybean cultivars (Zhu et al., 2002; Jin et al., 2004; Zhao et al., 2006).

In this study, we grew 38 soybean cultivars representing genetic improvement progress in northeast China during the period of 1923 to 2005 (82 years) under field trials in 2005 and 2006 (Zhao et al., 2006). The objective of this research was to investigate the effect of breeding programs on photosynthetic characters and their relationship with seed yield of soybean cultivars.

Results

Changes in number of days to maturity and seed yield

Data from two years showed that there was significant difference ($P<0.01$) in days to maturity among cultivars. Days to maturity decreased significantly with year of release (Fig. 1a). The calculated result from the regression equation showed that days to maturity were shortened by 14.7d from 1923 to 2005. The differences of seed yield among cultivars were significant (Fig. 1b), and soybean seed yield were elevated during the genetic improvement. The yield was

Table 1. The name, year of release, days to maturity and origination of soybean cultivars.

Cultivar	Year of release	Days to maturity	Origination
Huangbaozhu	1923	140	JAAS
Mancangjin	1929	135	JAAS
Yuanbaojin	1929	131	JAAS
Jinyuan No.1	1941	133	JAAS
Jilin No.5	1956	134	JAAS
Jilin No.1	1963	140	JAAS
Jilin No.3	1963	135	JAAS
Jilin No.4	1963	135	JAAS
Jilin No.5	1963	145	JAAS
Jilin No.6	1963	140	JAAS
Jilin No. 8	1971	134	JAAS
Jilin No.9	1971	135	JAAS
Jilin No.10	1971	128	JAAS
Jilin No.12	1971	130	JAAS
Jilin No.15	1978	128	JAAS
Jilin No.16	1978	142	JAAS
Jilin No.18	1982	125	JAAS
Jilin No.20	1984	123	JAAS
Jilin No.22	1989	116	JAAS
Jilin No.23	1990	120	JAAS
Jilin No.26	1991	118	JAAS
Jinong No.4	1992	128	JLAU
Jilin No.30	1995	132	JAAS
Jilin No.35	1995	126	JAAS
Jiunong No.21	1995	129	JLAC
Jilin No.36	1996	131	JAAS
Jilin No.38	1998	135	JAAS
Jilin No.43	1998	116	JAAS
Jilin No.47	1999	115	JAAS
Jinong No.7	1999	129	JLAU
Jilin No.45	2000	128	JAAS
Jilin No.55	2001	119	JAAS
Jilin No.58	2001	115	JAAS
Jinong No.11	2002	132	JLAU
Jinong No.12	2002	130	JAAS
Jiyu No.66	2002	126	JAAS
Jinong No.15	2004	130	JLAU
Jinong No.16	2005	132	JLAU

JAAS- Jilin Academy of Agricultural Sciences; JLAU- Jilin agricultural University; JLAC- Jilin Agricultural College.

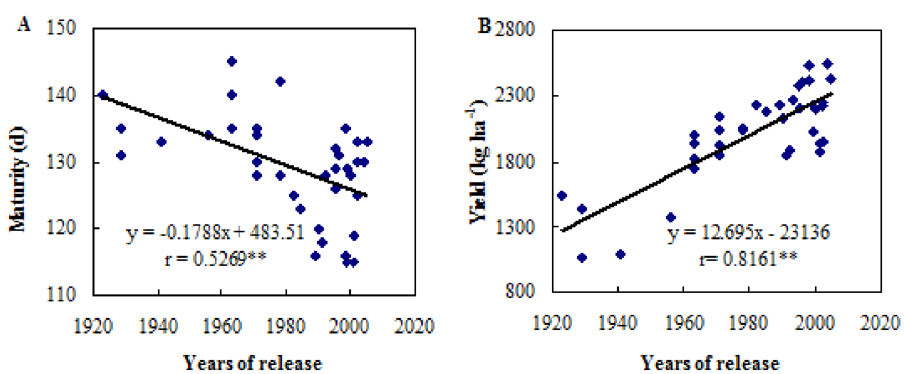

Fig 1. Thirty eight soybean cultivars representing progress of genetic improvement in northeast China during the period of 1923 to 2005 (82 years). (A) Changes of days to maturity and (B) yield in the years of release. The experiment was performed in 2005 and 2006. The values are the means of 2005 and 2006.

positively correlated (P<0.01) with year of release. The results of the regression equations showed that soybean yield increased from 1084.0 Kg ha^{-1} (1923) to 2188.3 Kg ha^{-1} (2005) in 2005 experiment and from 1398.0 Kg ha^{-1} (1923) to 2391.6 Kg ha^{-1} (2005) in 2006 (Table 2), respectively. The increase of 1028.3 Kg ha^{-1} (12.5 Kg ha^{-1} per year) or 80.25% per hectare (0.98% ha^{-1} per year) in the past 82 year was achieved from 1923 to 2005 in mean of two-year in northeast China.

Changes in leaf photosynthetic characteristics

Leaf net photosynthetic rate (Pn), stomatal conductance (Gs), apparent mesophyll conductance (Pn/Ci) and transpiration (Tr) increased significantly with the progress in year of release, according to mean of two stages in two years. Among the above mentioned physiological traits, increase of Tr (57.7%) was higher than Pn (17.6%). As result, WUE was reduced (by 23.6%) significantly with year of release. The increase of Pn/Ci (50.7%) was more than Gs (22.3%) during the 82 years. Despite of increase of Gs, ratios of Ci/Ca was reduced significantly with year of release (Fig. 2 and Table 2). Leaf area decreased significantly with the year of release (Fig. 3a). The SLW and chlorophyll content increased significantly with the year of release (Fig. 3b and Fig. 3c). According to regression equation, leaf area was reduced by 32.14%, and SLW and chlorophyll content were increased by 20.7% and 17.5% in the past 82 years, respectively.

The relationships between yield and some photosynthetic characteristics

Yield was positively correlated with Pn, Gs, Pn/Ci, Tr, chlorophyll content and SLW. In contrast, yield was negatively correlated with ratios of Ci/Ca and WUE based on mean of two years (Tables 3 and 4). However, there were significantly positive correlations between yield and Pn, Pn/Ci and Tr (P< 0.01), while a significantly negative correlation observed between yield and WUE in consistent results of two years. For other photosynthetic traits, there were significant correlations between yield with Gs and SLW in mean of two year and in 2005, while no significant correlation was observed in 2006. Also, there was significant correlation between yield and chlorophyll content in 2006, while no significant correlation observed in mean of two year and in 2005. Except in 2005, there was significant negative correlation between yield and ratios of Ci/Ca in mean of two years and in 2006. Leaf area had slight negative correlation with yield and Pn, but it was not statistically significant.

Discussion

Seed yield

Our research indicates that short-season soybean cultivars have been selected by soybean breeders in northeast China. This result is consistent with Ustun et al. (2001), while it contradicts with the result of Morrison et al. (1999). They found there were no significant relationships between year of cultivars release and the number of days to maturity. This selection was related to demand of farmers, because farmers of northeast China are accustomed to later sowing and early harvest in soybean production calendar. Using this calendar will help soybean producers to be able to adjust the required labor. However, the yield did not decrease by shortening of days to maturity. The yield has been elevated by 12.5 Kg ha^{-1} or 0.98% ha^{-1} per year in past 82 years by means of two years (Fig. 1 and Table 2). Our result is consistent with the estimate of Wilcox (2001) in sixty years of soybean genetic improvement, and is nearly in agreement with the results from Boerma (1979), Volgeng et al. (1997), Kumudini et al. (2001) and Ustun et al. (2001). They found that the yield increase was in the range of 0.5 to 1% per year in the genetic improvement of soybean. However, the yield increase per year in our work is lower than yield increase of 1.5 to 2.0% per year during nearly one century of the genetic improvement of soybean in China as reported by Zhao et al. (2006). This difference may be related to the estimates of yield in soybean genetic improvement. Zhao et al. (2006) recorded the yield of released cultivars under field conditions but did not include the effect of management advancements and practices in their yield increase calculations through the years of study.

Photosynthesis

Pn, Gs, Pn/Ci and Tr increased through the year of release, and the selection for high-yield cultivars led to higher photosynthetic ability. Pn, Gs, Pn/Ci and Tr were positively correlated with yield, while the ratio of Ci/Ca was negatively correlated with yield at R2 and R4 stages in soybean cultivars released from 82 years. The results also showed that the correlations between Pn/Ci with yield and Pn were closer than the correlations between Gs with yield and Pn. Similar result also was found by Koc et al. (2003) in durum wheat. Their result showed that mesophyll conductance has an effect on Pn variation rather than Gs. Increase of Pn and Pn/Ci caused a decrease on Ci/Ca, indicating that although modern cultivars had higher Gs, they still have some limitation in stomatal characteristics.

There are many reports (Buttery and Buzzell, 1972; Ojima, 1972; Secor et al., 1982; Ashley and Boerma, 1989) showed that breeding and selecting for higher soybean yield resulted in greater leaf photosynthetic rate. The Canadian soybean breeders have also selected the higher photosynthetic rate as index of higher yield in soybean cultivars (Morrison et al., 1999). In northeast China, leaf photosynthesis has not been effectively used as a selection index of high yield cultivars mainly due to limitation in photosynthetic measurement conditions. Although soybean breeders have not considered photosynthesis and related traits as a selection indexes for high yield cultivars, our study showed that yield is positively correlated with Pn during the genetic improvement (82 years) of soybean cultivars. This indicates that photosynthesis has been used as a selective index in actual fact. So, our results indicated that Pn and Pn/Ci are available in future soybean high yield breeding as a selective index.

Leaf area, SLW, leaf thickness and chlorophyll content are important measures for yield and photosynthesis (Wiebold et al., 1981; Xu and Miao, 1983; Fischer et al., 1998; Haile et al., 1998). They are often used as selection indexes of high yield soybean cultivars probably due to their easily measurements and low costs. Many researches have revealed that leaf area, leaf thickness and chlorophyll content are positively correlated with yield and photosynthesis (Buttery and buzzell, 1972; Buttery et al., 1981; Bhagsari and brown, 1986; Ma et al., 1995). In our results, leaf area was decreased with year of release, and SLW and chlorophyll content increased significantly with year of release. We also found that leaf area was negatively correlated with yield and Pn, and SLW and chlorophyll content were positive correlation with yield and Pn.

Table 2. The changes of yield, days to maturity and some photosynthetic characteristics with year of release. 38 soybean cultivars representing genetic improvement progress in northeast China during the period of 1923 to 2005 (82 years). The experiment was performed in 2005 and 2006.

Traits	Units	Year of trial	Regression equation	Increase or Decrease (%)	R value
Yield	Kg ha^{-1}	2005	13.467x-24813	101.80	0.7431**
		2006	12.121x-21911	71.00	0.8438**
Pn	µmol $CO_2.m^{-2}.s^{-1}$	2005	0.0469x-67.921	17.27	0.5260**
		2006	0.0395x-54.204	15.07	0.4997**
Ci/Ca		2005	-0.0004x+1.3515	-5.63	0.2292
		2006	-0.0007x+2.1765	-7.00	0.4647**
Gs	mol $H_2O.m^{-2}.s^{-1}$	2005	0.0009x-1.1849	13.52	0.2363
		2006	0.003x-4.5572	20.55	0.2480
Pn/Ci		2005	0.0003x-0.4705	23.12	0.6193**
		2006	0.0001x0.1294	13.20	0.2927
Tr	mmol $H_2O.m^{-2}.s^{-1}$	2005	0.0271x-47.637	49.64	0.6856**
		2006	0.0378x-66.995	55.10	0.6897**
WUE	µmolCO_2.mmolH_2O	2005	-0.0123x+28.569	-20.52	0.6824**
		2006	-0.0142x+31.226	-29.71	0.6705**
Chlorophyll content	mg.dm^{-2}	2005	0.0098x-13.253	14.37	0.3506*
		2006	0.0119x-17.473	18.25	0.3768*
SLW	mg.dm^{-2}	2005	0.9543x-1514.9	24.44	0.5085**
		2006	1.0066x-1535	20.60	0.4354**

Analysis of linear regression between each photosynthetic index and year of release were performed. Statistically significant of regression equations were marked as * (P < 0.05) and ** (P < 0.01). Ci, intercellular CO_2 concentration; Ca, ambient CO_2 concentration; Pn, net photosynthetic rate (Pn); Pn/Ci, apparent mesophyll conductance; Gs, stomatal conductance; Tr, transpiration; WUE, water usage efficiency; SLW, specific leaf weight.

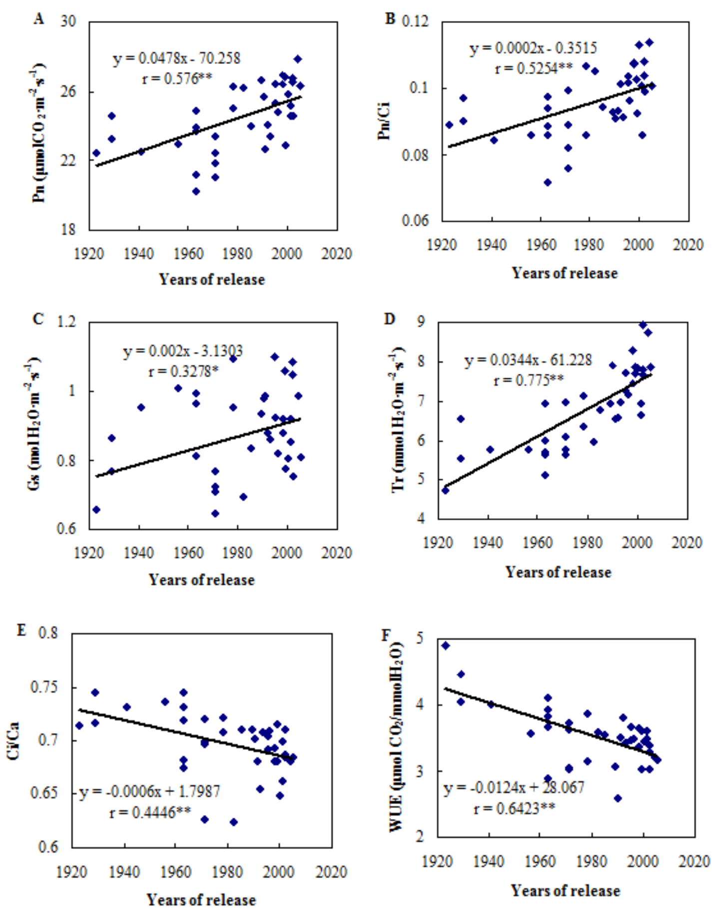

Fig 2. Changes of (A) net photosynthetic rate (Pn), (B) apparent mesophyll conductance (Pn/Ci), (C) stomatal conductance (Gs), (D) transpiration (Tr), (E) ratio of Ci/Ca, and (F) water usage efficiency (WUE) with years of release. 38 soybean cultivars representing genetic improvement progress in northeast China during the period of 1923 to 2005 (82 years). The experiment was performed in 2005 and 2006. The values are the means of 2005 and 2006. Ci, intercellular CO2 concentration; Ca, ambient CO2 concentration.

Table 3. Correlation coefficients between yield and Pn, Gs, Ci/Ca, Pn/Ci Tr, chlorophyll content and SLW of 38 soybean cultivars with means of 2005 and 2006. 38 soybean cultivars representing genetic improvement progress in northeast China during the period of 1923 to 2005 (82 years). The experiment was performed in 2005 and 2006.

	yield	Pn	SLW	Chlo	Gs	Ci	Ci/Ca	Pn/Ci	Tr
Pn	0.6102**								
SLW	0.4464**	0.446**							
Chlo	0.3075	0.5127**	0.4939**						
Gs	0.1613	0.5644**	0.2981	0.4444**					
Ci	-0.2821	-0.011	-0.0199	-0.1171	0.3122				
Ci/Ca	-0.3493*	-0.2047	-0.2442	-0.327	0.1206	0.9151**			
Pn/Ci	0.5211**	0.7919**	0.4996**	0.5985**	0.4035*	-0.3629*	-0.5484**		
Tr	0.6277**	0.6715**	0.4836**	0.3716*	0.4739**	-0.044	-0.2292	0.6587**	
WUE	-0.5166**	-0.2067	-0.1645	-0.0032	-0.1254	0.0926	0.075	0.0606	-0.4996**

Analysis of correlation were performed according to the means of 2005 and 2006. Ci, intercellular CO_2 concentration; Ca, ambient CO_2 concentration; Chl, chlorophyll content; Pn, net photosynthetic rate (Pn); Pn/Ci, apparent mesophyll conductance; Gs, stomatal conductance; Tr, transpiration; WUE, water usage efficiency; SLW, specific leaf weight. Statistically significant of correlation analysis were marked as * ($P < 0.05$) and ** ($P < 0.01$).

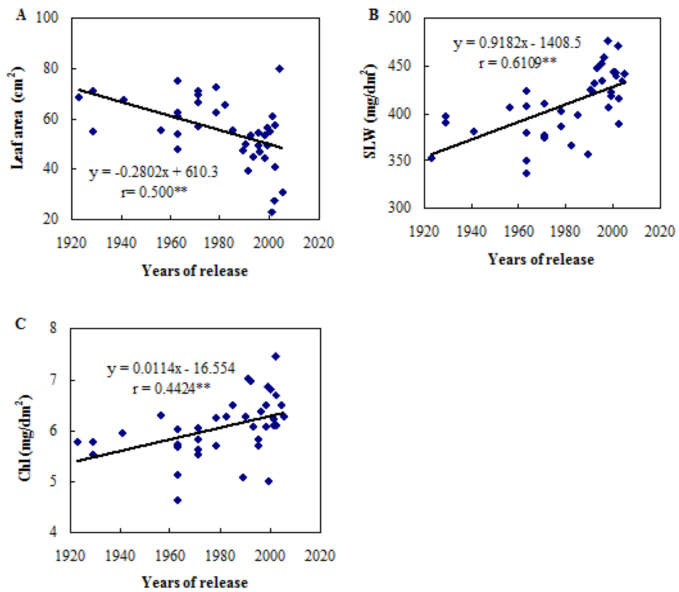

Fig 3. Changes of leaf area (A), specific leaf weight (SLW) (B) and chlorophyll content (chl) (C) with years of release. 38 soybean cultivars representing genetic improvement progress in northeast China during the period of 1923 to 2005 (82 years). The experiment was performed in 2005 and 2006. The values are the means of 2005 and 2006.

However, the relationships of leaf area, SLW and chlorophyll content with yield were not significant like the relationships of Pn and Pn/Ci with yield. Morrison et al. (1999) showed the increase of yield with year of release was significantly correlated with photosynthesis and stomatal conductance, and the relationship between Pn and year of release were more close than chlorophyll content and specific leaf area (leaf area/leaf dry weight, 1/SLW). We suggest that leaf area, SLW and chlorophyll content should be comprehensively further evaluated as potential selection criteria for yield.

Our data revealed that increase of Tr was greater than Pn, while water usage efficiency (WUE) decreased with the year of release. Frederick et al. (1990 and 1991) compared two old and two modern soybean cultivars under drought stress and irrigated conditions. They found that older and lower-yielding cultivars are more efficient in conserving water under drought condition. Our result also showed old cultivars have higher WUE than new ones. Soybean breeders did not consider WUE as the selective index. This is possibly due to the fact that modern and high-yield cultivars were bred under high water and fertilizer availability. Therefore, WUE should be considered as the stressing of water deficit in further soybean breeding.

Materials and methods

Plant materials

Research work was conducted at experimental station of Jilin Agricultural University, Changchun city, Jilin Province, P.R. of China (125.10E Longitude, 43.53N Latitude) in 2005 and 2006. The annual average precipitation was 567 mm. The accumulated temperature is 2860 °C and annual average temperature was 4.6 °C in Changchun region. 38 cultivars were chosen for this research. Three of most old ancestral soybean cultivars were Huangbaozhu (released in 1923), Yuanbaojin (released in 1929) and Mancanjin (released in 1929), respectively (Zhao et al., 2006). The latest new cultivar in the experiment was Jinong No 16 (released in 2005). The time span of release was 82 years (Table 1). 38 soybean cultivars used in this work were all main soybean cultivars with excellent agronomic character at their released time point (1923-2005). These soybean cultivars able to

Table 4. Correlation coefficients between yield, Pn, Gs, Tr, chlorophyll content and SLW in each year. 38 soybean cultivars representing genetic improvement progress in northeast China during the period of 1923 to 2005 (82 years). The experiment was performed in 2005 and 2006.

2005	Yield	Pn	Gs	Ci	Ci/Ca	Pn/Ci	Tr	WUE	SLW	Chl	leaf area	2006
Yield		0.52**	0.14	-0.15	-0.49**	0.41**	0.52**	-0.42**	0.26	0.45**	-0.44**	Yield
Pn	0.68**		0.44**	-0.04	-0.34*	0.75**	0.48**	-0.25	0.52**	0.46**	-0.25	Pn
Gs	0.40*	0.66**		0.28	0.15	0.20	0.32*	-0.39*	0.15	0.38*	-0.22	Gs
Ci	-0.24	0.05	0.58**		0.87**	-0.40*	-0.04	0.03	-0.18	-0.03	-0.13	Ci
Ci/Ca	-0.07	0.16	0.66**	0.97**		-0.56**	-0.29	0.23	-0.38*	-0.27	0.05	Ci/Ca
Pn/Ci	0.66**	0.80**	0.21	-0.55	-0.45*		0.42**	-0.03	0.36*	0.34*	0.14	Pn/Ci
Tr	0.67**	0.75**	0.56**	0.01	0.11	0.64**		-0.66**	0.33*	0.08	-0.22	Tr
WUE	-0.49**	-0.35	-0.29	0.07	-0.04	-0.36	-0.86**		-0.44**	-0.18	0.34*	WUE
SLW	0.60**	0.35	0.27	-0.29	-0.12	0.41*	0.39*	-0.34		0.34*	-0.2	SLW
Chl	0.34	0.52**	0.32	-0.15	-0.13	0.53**	0.45*	-0.24	0.28		-0.28	Chlo

Ci, intercellular CO_2 concentration; Ca, ambient CO_2 concentration; Chl, chlorophyll content; Pn, net photosynthetic rate (Pn); Pn/Ci, apparent mesophyll conductance; Gs, stomatal conductance; Tr, transpiration; WUE, water usage efficiency; SLW, specific leaf weight. Statistically significant of correlation analysis were marked as * ($P < 0.05$) and ** ($P < 0.01$).

represent the technical level of crop breeding from their released periods (Zhao et al., 2006).

Plant Growth Conditions

Seeds were sown on 28 April in 2005 and 29 April in 2006, respectively. The experiment was in a randomized complete block design with three replications. The stand was thinned to 25 plants m^2 after planting for about three weeks. Cultivars were in five rows of 5 m in length and 0.65 m in width between the rows.

Measurements of physiological indices

Net photosynthesis rate (Pn), stomatal conductance (Gs), ratio of Ci/Ca (intercellular CO_2 concentration, Ci; ambient CO_2 concentration, Ca) and transpiration (Tr) were measured with a portable photosynthesis system (model Li—6400, LI—COR., Inc., Lincoln, NE). In order to estimate the relative importance of the mosophyll limitation to Pn, apparent mesophyll conductance (the conductance of CO2 from the stomatal cavity to the chloroplast, Pn/Ci) was calculated from the ratio of Pn to Ci according to Fischer et al. (1998). Because the ambient CO_2 concentration always changed during measurement, we used Ci/Ca ratios to estimate the limitation of stomatal rather than Ci. Water usage efficiency (WUE) was calculated according the ratio of mean of Pn to mean of Tr. Measurement works were done at 9:00-11:30h with stable red-blue light source under field condition, photo flux density is 1200 uEm^{-2} s^{-1}. All data are the means of three days measurement at each grow stage.

Specific leaf weight (SLW, dry weight per unit leaf area) was measured with leaf disk taken by fiercer. Materials were killed at 110 ºC for 10 min, then were dried at 80 ºC for at least 48h of oven. Dry weight was recorded. Chlorophyll content was determined on fresh leaves. Chlorophyll was extracted using a mixture liquid of 50% acetone and 50% ethanol, then the absorption value at 645 nm and 663 nm were read using a TU-1810 spectrophotometer. The results were calculated according the equations of Arnon (1949). The leaf area (middle leaflet on penultimate) was measured with a Leaf Area Meter (Model Li—3100). Days to maturity were recorded from sowing to the seed mature when approximately 95% of plants reached mature pod color during the growth season. Seed yield was calculated based on per unit area. Measurement was done from the three center rows of each plot after 50cm were discarded at the end of the rows at maturing stage.

Statistical Analysis

The experiment design was randomized complete block design with three replications. Statistical analysis including linear regressions and analysis of variance for regression of the data was performed using the statistical program SPSS 13.0 (SPSS, Chicago, USA).

Conclusions

During the genetic improvement of soybean cultivars, the increase of yield led to the increase of SLW and chlorophyll content, Pn, Gs, Pn/Ci, Tr, and the decrease of WUE, leaf area and Ci/Ca with year of release. Considering the relationships between yield and such leaf photosynthetic traits, the correlations of yield with Pn and Pn/Ci were the closest in two years results. We suggested that Pn and Pn/Ci are also suitable as selection criteria for yield. The result also showed that WUE was decreased as the increase of yield with year of release.

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