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Agronomic and physiological contributions to the yield improvement of soybean cultivars released from 1950 to 2006 in Northeast China

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ABSTRACT

Increasing yield is a high priority in most breeding programs. Approximately 600 soybean cultivars had been released by the end of the last century in Northeast China. Understanding the agronomic and physiological changes is essential for planning further plant breeding strategies in soybean. In this study, 45 representative soybean cultivars, from maturity groups 00 and 0, released from 1950 to 2006 in Northeast China were compared in field conditions for 3 consecutive years. A positive correlation between seed yield and year of cultivar release was indicated with a 0.58% average annual increase. Seed number per plant was the most important contributor to yield gain, with a 0.41% increase per year. Pod number per plant and seed size varied slightly with the year of cultivar release. Although variation in protein was from 37.0% to 45.5%, and oil concentration was from 16.7% to 22.0%, their concentrations were not consistently related to year of cultivar release. A 33% increase in the photosynthetic rate, 10.6% increase in plant dry weight and 19.0% increase in harvest index (HI) were found, while leaf area index (LAI) decreased by 17.3%. Modern cultivars have higher photosynthetic rates than their predecessors. The reduced plant height gave increased resistance to lodging, with the lodging score dropping from 3.2 in 1951 to 1.0 in 2006. Seed resistances to disease and pest infestation were also improved. Yield stability was enhanced over years, which could be attributed to the stable pod production across different environments. A flow diagram to explain the contributors to genetic improvement of soybeans in Northeast China was developed.

1. Introduction

Cultivar selection is an important way to increase crop yield (Ustun et al., 2001). In the north central region of the USA, the yield increase attributed to soybean breeding was between 10 and 20 kg ha^{-1} per year from 1902 to 1977 in maturity groups 00 through IV (Specht and Williams, 1984). A similar trend was found in the mid-southern region of the USA. Soybean yield increased from 1972 kg ha^{-1} grown from ancestral lines to 2609 kg ha^{-1} from fifth generation cultivars, and the annual gain was 14 kg ha^{-1} (Ustun et al., 2001). Nearly 79% of the yield increase in the northern states was attributed to genetic improvement (Williams and Specht, 1979).

Using 21 cultivars spanning more than 50 years of breeding, Luedders (1977) observed a 1.0% per year yield improvement, partially attributed to increased lodging resistance. Investigating 10 cultivars released from 1920 to 1974, Wilcox et al. (1979) found a 0.5% yield improvement without an expected change in phenotypic stability or lodging resistance, but with linear decrease in protein with year of release, accompanied by an increase in oil concentration. With 28 cultivars from maturity groups VI, VII and VIII, Boerma (1979) reported a 0.7% per year yield gain for cultivars released from 1942 to 1973. The yield increase was correlated with increasing pod number, while seed size and seeds per pod did not change greatly over time. Plant height decreased in maturity group VIII but did not change in groups VI and VII. In Canada, Morrison et al. (2000) tested 41 cultivars released over seven decades of breeding and selection, and found that the yield improvement had an association with a decrease in protein concentration and some reduction in lodging. Recent cultivars, compared with older cultivars, had a lower maximum leaf area, and higher photosynthetic rate and stomatal

Abbreviations: HI, harvest index; LAI, leaf area index; CAP, canopy apparent photosynthesis; CV, coefficient of variability.

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conductance per unit area (Morrison et al., 1999, 2000). Further studies on population density revealed that recent cultivars were more tolerant of population stress than older ones (Cober et al., 2005). Most recently, Morrison et al. (2008) found that seed isoflavone concentration significantly increased over 58 years of soybean breeding for yield in the short-season region, and recent cultivars were more environmentally influenced for isoflavone concentration than older cultivars. Isoflavone was positively associated with N-fixation and disease resistance (Zhang and Smith, 1995; Dixon, 2001).

Northeast China is the main soybean producing area in China, where the average soybean yield per hectare in 1990s increased by 71.4%, compared with that of 1950s, and the annual yield increase averaged 13.4 kg ha^{-1} (Xue et al., 2006). Northeast China had released approximately 600 soybean cultivars by the end of the last century (Liu et al., 2008). However, no investigation has been conducted on the agronomic and physiological changes in the released cultivars. As agronomic and physiological performance is the direct expression of genotype's genetic traits, understanding these changes is essential for planning further plant breeding strategies in soybean.

The best way of estimating genetic progress over time is to evaluate the history of cultivars in common environments (Cox et al., 1988). For this purpose, the following conditions are required: (1) experiments must be conducted under field conditions, (2) measurement must be done on comparable field plots, (3) cultivars released at different times must be compared simultaneously (Slafer et al., 1994), and (4) cultivars of a given maturity group must be grown in their adapted region.

In this study, 45 cultivars (maturity groups 00 and 0) that were released over the past 56 years in Northeast China were collected, and grown for 3 consecutive years to examine (1) the contribution of soybean breeding programs to yield increase, (2) what agronomic and physiological changes occurred which might be associated with yield improvement, and (3) whether the yield stability was related to genetic change over time.

2. Materials and methods

2.1. Culture practices and experimental design

Field experiments were conducted in 2006, 2007 and 2008 at Hailun Agroecological Experimental Station (47°26′N, 126°38′E, altitude 240 m), Chinese Academy of Sciences, Heilongjiang Province, China. Annual average sunshine at the research site is around 2600–2800 h, and growing degree days (GDD) (Dwyer et al., 1999) is 1362. The soil is the typical Mollisol (Black soil). The textural class of the black soil is silty clay loam or silty clay. Chemical characteristics were: soil organic matter of 50.77 g kg^{-1}, total nitrogen of 2.14 g kg^{-1}, total phosphorus of 0.98 g kg^{-1}, total potassium of 22.0 g kg^{-1}, alkali-hydrolysable N of 167.6 mg kg^{-1}, available P (Olsen et al., 1954) of 40.2 mg kg^{-1}, ammonium acetate extractable K of 140 mg kg^{-1}, and pH of 7.31 (1:5 v/v) in 2006.

Forty-five cultivars released over a 56-year period from 1950 to 2006 were chosen representing maturity groups 00 and 0 in Northeast China (Table 1). These cultivars were grown in a randomized complete block design with three replications at the station. Each plot consisted of 5 rows 5 m long with an inter-row spacing of 0.67 m. The seeds were sown on May 6, 2006, May 8, 2007 and May 4, 2008. The plants were thinned to a uniform stand of 27 plants m^{-2} after emergence. Di-ammonium phosphate of 50 kg ha^{-1} (N 18%, P_2O_5 46%), and composite fertilizer of 150 kg ha^{-1} (N 18%, P_2O_5 16%, K_2O 16%) were applied before sowing.

Table 1
Cultivar name, year of release, maturity group and days to maturity for the chosen 45 soybean cultivars.

Cultivar name	Year of release	Maturity group	Days to maturity
Xiaohuangjin	1951	MG0	128
Zihua 4 hao	1952	MG0	127
Yuanbaojin	1953	MG0	127
Ke 4430-20	1959	MG0	120
Fengshou6hao	1960	MG0	115
Hejiao 6 hao	1962	MG0	118
Keshansilijia	1962	MG0	118
Dongnong 4 hao	1963	MG0	125
Fengshou 10	1966	MG0	115
Xiaolidou 9 hao	1967	MG0	127
Heinong10	1969	MG0	118
Heinong16	1970	MG0	118
Mufeng 5 hao	1972	MG0	120
Nenfeng 1 hao	1972	MG00	113
Suinong 3 hao	1973	MG0	115
Hefeng 22	1974	MG0	115
Nenfeng 4 hao	1975	MG00	113
Hefeng 23	1977	MG0	118
Fengshou 17	1977	MG0	117
Hongfeng 2 hao	1977	MG00	110
Nenfeng 9 hao	1980	MG00	111
Suinong 4 hao	1981	MG0	115
Heinong 27	1983	MG0	120
Suinong 5 hao	1984	MG0	115
Dongnong 37	1984	MG00	113
Beifeng 3 hao	1984	MG00	108
Hefeng 25	1984	MG0	120
Beifeng 5 hao	1986	MG00	108
Suinong 8 hao	1989	MG0	120
Heinong 35	1990	MG0	120
Suinong 9 hao	1991	MG0	118
Kenong 4 hao	1992	MG0	118
Suinong 10	1994	MG0	125
Suinong 11	1995	MG0	117
Beifeng 11	1995	MG00	110
Suinong 12	1996	MG0	120
Suinong 14	1996	MG0	125
Suinong 15	1998	MG0	123
Heinong 45	2003	MG0	115
Kefeng 12	2004	MG0	117
Suinong 21	2004	MG0	120
Hefeng 47	2004	MG0	120
Suinong 22	2005	MG0	118
Hai 635	2006	MG0	123
Hai 5052	2006	MG0	125

2.2. Data collection and measurements

Phenological dates were recorded using the Fehr and Caviness (1977) growth stage key. During the period of maximum leaf area, i.e. full pod (R4) to beginning seed (R5) stage, a random 0.5 m^2 area in each plot was selected for sampling. The plants were cut at the soil surface, and were separated into stems, leaves, and pods. Leaf area per sample was measured by CI-203 portable laser leaf area analyzer (CID, USA). The leaf area was used to determine LAI that is the ratio between leaf area and the corresponding land area. The components were dried at 70 °C for at least 72 h before weighing. During the same period, a portable photosynthesis system (LI-6400; Li-COR Biosciences Inc.) was used to measure photosynthetic rate on penultimate fully expanded leaves. Measurements were done between 9:00 AM and noon on days with full sunlight. Lodging score was rated on a 1–5 scale (erect [1] to prostrate [5]) at the R5 to R6 stage (Morrison et al., 2000).

At full maturity (R8), plants in the central 4 m^2 of each plot were taken for seed yield measurement, and the yields were adjusted to 135 g kg^{-1} moisture content. Fifteen plants were selected for measurements of height, weight, seed number per plant, pod number per plant, seed size, and seed percentage with diseases and pests. Seed protein and oil concentrations were determined by near infrared transmittance spectroscope (Infratec 1241; FOSS, Eden Prairie, MN).

2.3. Data analysis

To facilitate analysis and presentation, data were combined across years, and means of each trait investigated were plotted against the year of cultivar release to illustrate the changes in plant characteristics over time. A straight line was fitted through the points using linear regression. The regression coefficients were examined for significance using $n-2$ degrees of freedom.

Pearson correlations among measured characteristics were calculated to establish relationships. Using SAS, the significance for these correlations was evaluated by Student's t test at 0.05 probability level unless otherwise indicated (SAS, 1994).

Phenotypic stability of the different characteristics was determined by calculating the coefficient of variability (CV) of cultivar means from 2006 to 2008 (Francis and Kannenberg, 1978). The smaller the CV during that period, the more stable the cultivar was to observe the changes in phenotypic characteristics' stability across time, the cultivar CVs of each characteristic were regressed on the year of release using linear regression (Morrison et al., 2000).

3. Results

The yields varied significantly among the 45 cultivars, ranging from 145 g m^{-2} to 270 g m^{-2} (Fig. 1A). A linear regression equation showed the relationship between yield and year of release was highly significant ($P < 0.001$). Across 56 years of soybean breeding and selection, 32.5% improvement of yield had been achieved, or the yield increased by 0.58% per year. Correspondently, the seed number per plant had a positive correlation with year of release ($P < 0.05$) (Fig. 1B), with a 0.41% increase per year observed. The pod number per plant, however, did not show a significant increase across the 56-year period (Fig. 1C), whereas the seed number per pod increased from 1.9 to 2.3 seeds per pod during the same period (Fig. 1D). Although significant differences in seed size among cultivars existed, there was no consistent relationship between seed size and year of cultivar release (Fig. 1E). Unlike the large increase in yield over the 56-year period, seed protein and oil concentrations did not have a significant change or relationship to year of release during the same period (Fig. 2). The variations of protein and oil concentrations were from 37.0% to 45.5% (Fig. 2A), and from 16.7% to 22.0% (Fig. 2B), respectively.

The average plant weight increase of 0.19% per year across the 56-year period not only differed among cultivars, but also had a significant association with the year of release (Fig. 3A). The harvest index (HI) increased significantly with year of release, averaging 0.40% per year, rising from 0.31 to 0.38 (Fig. 3B). Since the R4 to R5 stage is the crucial period for soybean yield formation, two yield-related physiological characteristics were investigated at these stages in the study. The LAI decreased linearly from 1951 to 2006 by 0.31% per year (Fig. 4A), while photosynthetic rate increased 0.59% per year with year of release (Fig. 4B).

Plant height decreased by 13.8% from 1951 to 2006 (Fig. 5A), and the lodging score went down from 3.2 in 1951 to 1.0 in 2006, a linear decline of 1.22% per year during the period (Fig. 5B). Seeds exhibiting disease decreased 55.1% from 1951 to 2006 or 0.98% per year (Fig. 5C) and pest infestation decreased 75.4% or 1.35% per year over the 56-year period (Fig. 5D).

Pearson correlations (Table 2) among agronomic and physiological characteristics showed that photosynthetic rate had a positive correlation with yield, as well as plant dry weight and HI, which were also positively and significantly associated with seed number and yield. Yield, plant height, and HI were all negatively correlated with lodging score. Yield was also negatively correlated

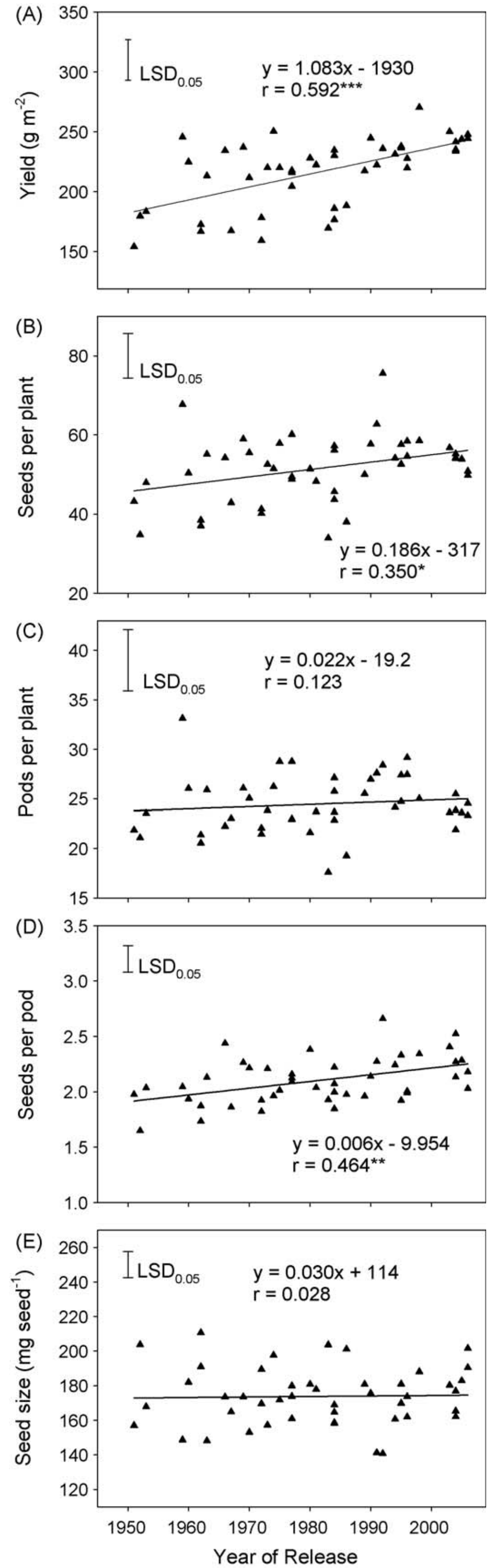

Fig. 1. Relationship between the year of cultivar release and (A) seed yield, (B) seeds per plant, (C) pods per plant, (D) seeds per pod and (E) seed size. The bar represents statistically significant differences among cultivars, LSD (0.05). Note: *, ** and *** indicate linear correlation coefficient significant at the 0.05, 0.01 and 0.001 probability levels, respectively.

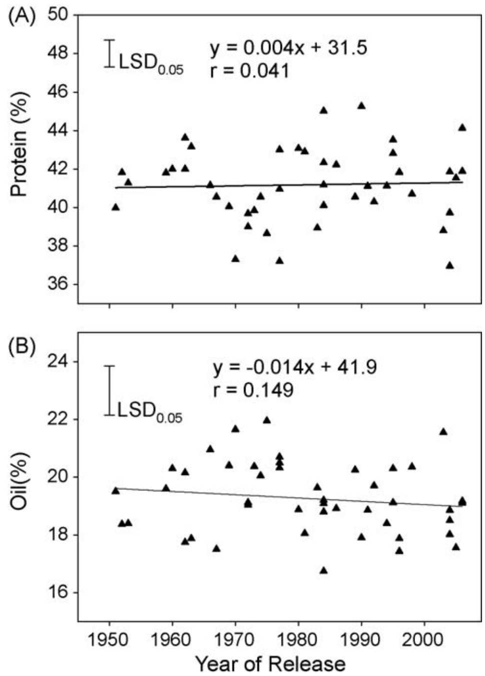

Fig. 2. Relationship between the year of cultivar release and (A) protein and (B) oil concentration in seed.

with prevalence of diseased and pest infested seed. The largest CV among these characteristics was in the pest infested seed percentage, followed by diseased seed percentage, lodging, yield, seed number per plant, and pod number per plant (Table 3). Among them, the yield and the pod number per plant had a significantly negative association with year of cultivar release. The CVs for yield and pod number per plant in newer cultivars were lower than for older cultivars. The oil and protein concentration, and seed size had lower CV than other characteristics.

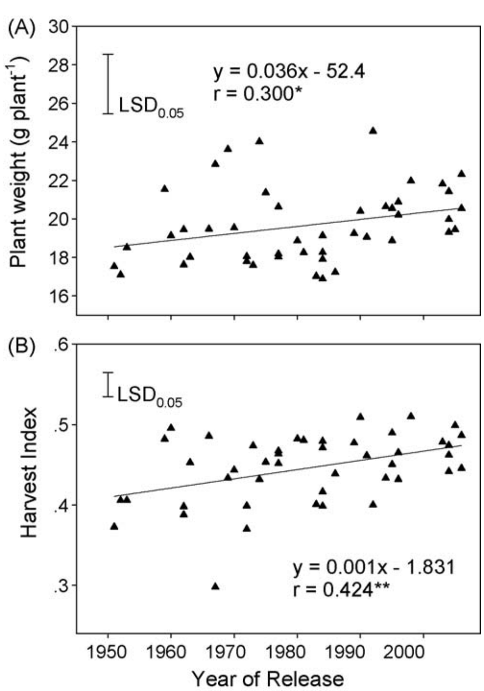

Fig. 3. Relationship between the year of cultivar release and (A) plant weight and (B) harvest index. Note: * and ** indicate linear correlation coefficient significant at the 0.05 and 0.01 probability levels, respectively.

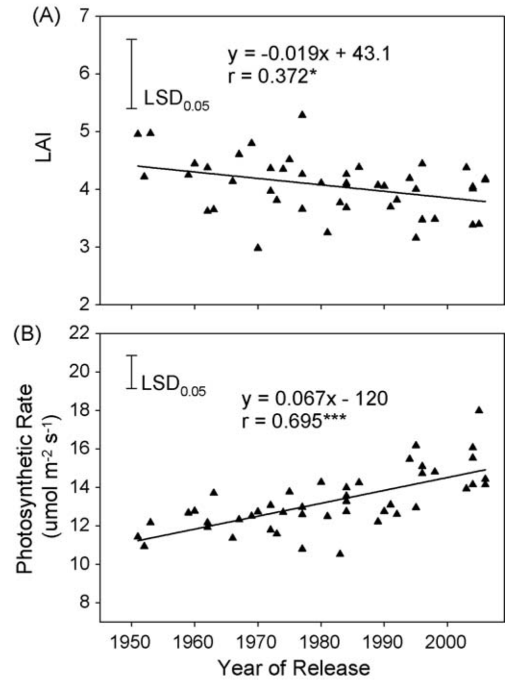

Fig. 4. Relationship between the year of cultivar release and (A) LAI and (B) photosynthetic rate. Note: * and *** indicate linear correlation coefficient significant at the 0.05 and 0.001 probability levels, respectively.

4. Discussion

The present study shows that during the past 56 years of plant breeding and selection in Northeast China, the genetic yield gain has averaged 0.58% per year, which is similar to reports of 0.5% annual increase in Canada (Voldeng et al., 1997) and 0.5–1.0% in the USA (Luedders, 1977; Wilcox et al., 1979; Boerma, 1979; Boyer et al., 1980). This indicates that nearly equal contribution of breeding for the yield improvement has occurred in soybean production regions where the maturity group and latitude are similar. Although variations in protein and oil concentration existed among cultivars released during the past 56 years, there has been no great improvement in these traits associated with year of release, which suggests that soybean breeders focused much more on selection of high-yielding cultivars, rather than genetic improvement in these quality traits. In this study, we found that the largest contributor to soybean yield increase over the last 56 years in Northeast China was the seed number per plant, not the seed size, which was consistent with short-season cultivars in Canada (Morrison et al., 2000). Yield was correlated with seed number per plant and not seed size (Egli et al., 1978). Since there was a smaller relationship between the year of release and pod number per plant in the present study, some of the yield gain across time comes from the increase in seed number per pod.

Pod production and seed number in soybean respond to changes in photosynthesis during the entire flowering and pod set period or just a portion of the period (Egli and Zhen-Wen, 1991; Jiang and Egli, 1993; Egli and Bruening, 2005). Across over 50 years of soybean breeding, photosynthetic rate increased gradually and was associated with increased seed number and yield. This suggests that by selecting for higher yield, soybean breeders have also selected higher photosynthetic rate. Since soybean cultivars differ in photosynthetic rate, and since positive correlation between canopy apparent photosynthesis (CAP) and yield were found (Dornhoff and Shibles, 1970; Wells et al., 1982), breeding and selection for higher yield soybean cultivars are associated with

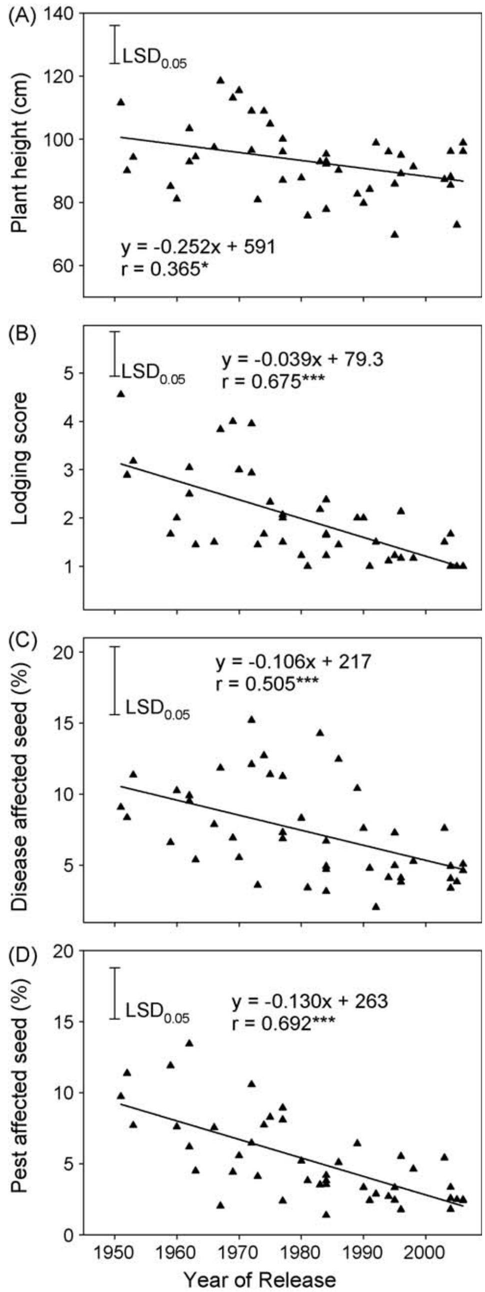

Fig. 5. Relationship between the year of cultivar release and (A) plant height, (B) lodging score, (C) disease affected seed and (D) pest affected seed. Note: * and *** indicate linear correlation coefficient significant at the 0.05 and 0.001 probability levels, respectively.

the greater leaf photosynthetic rate (Ojima, 1972). With 14 short-season soybean cultivars developed across 58 years of breeding, Morrison et al. (1999) concluded that newer cultivars had higher photosynthetic rate than older ones. Ford et al. (1983) also observed variations in photosynthetic rate in 20 lines after seven generations of selection for the characteristic. A positive correlation existed between CAP during seed fill and yield from F3-derived lines from two crosses (Ashley and Boerma, 1989).

The LAI plays an important role in yield formation due to light interception by leaves when other environmental factors are not limiting (Jin et al., 2004; Liu et al., 2008). Our data revealed that LAI had a negative correlation with year of cultivar release, but no significant relationship to yield, whereas two other yield-related characteristics, plant weight and HI, increased with later year of release. Thus, recently released cultivars have higher efficiency in producing and allocating carbon resources than their predecessors. Buttery et al. (1981) proposed that cultivars with higher photosynthetic rate may have better photosynthetic storage and translocation mechanisms as well. The higher photosynthetic rates are probably the result of reduced leaf area and increased sink demand (Morrison et al., 1999). Increasing seeding density or population has been widely adopted as an effective way to optimize seed yield because of the shorter season and cold climate in Northeast China (Liu et al., 2007). Cober et al. (2005) has found that seed yield differences between new and old short-season cultivars of soybean were greater at high plant populations than at commercial plant density. Therefore, the need for the higher population density in cold area might contribute to the selection of cultivars with lower leaf area. Soybean has a large leaf area and short plant height, thus a more closed canopy than crops like corn, causing soybean an uneven distribution of light on the surface of leaves within the canopy (Liu et al., 2008). Shading negatively impacts yield, especially in a high-density canopy (Egli, 1988). Egli and Bruening (2005) have shown that diminished light within the canopy increases the abortion of flowers and pods. Normal development of pod and/or seed requires a minimum flux of assimilates; if the minimum levels were not met, the pod or seed aborted (Egli, 2005). Therefore, a lower LAI but higher leaf photosynthetic rate enables new cultivars to tolerate greater plant densities before mutual shading reduces photosynthetic rate to a point that would impact yield (Cober et al., 2005). Thus, for high-density populations, having a lower leaf area with a higher photosynthetic rate is the efficient way to achieve higher yield. On the other hand, the horizontal orientation and inclination angle of foliage are the morphological characteristics which influence the light penetration into canopy, and subsequently influence photosynthesis and yield (Jin et al., 2004). However, the interaction of LAI, photosynthetic rate and plant density in cultivars, and whether there exist differences in leaf horizontal orientation and inclination angle of foliage between new and old cultivars in Northeast of China remain unknown and need to be evaluated in future research.

Our study also showed that over the past 56 years in Northeast China, the resistance to stress has been much improved by plant breeders with reduced plant height, enhanced lodging resistance, and decreased levels of disease and pest infested seed in more recently released cultivars. A tendency toward decreased lodging with year of cultivar release was reported by Wilcox et al. (1979) and Voldeng et al. (1997). The correlation between disease and pest infested seed with the lodging scores (Table 2) suggests that there might be several coordinated ways or endo-mechanisms regulating the resistance at the whole plant level. A possible mechanism could be related to the variations in length and density of pod trichomes (glandular hairs), fiber concentration, and potassium and other nutrients absorption, as well as direct contact of lodged plants with the soil, a source of disease inoculums (Kono, 1995; Reuveni and Reuveni, 1998; Lam and Pedigo, 2001; Edwards and Singh, 2006).

High production of soybean requires not only high yield in a unique environment, but also the stability of relatively high yield across varied environments. The data from this experiment revealed a trend toward improved seed yield stability, as evidenced by the lower CV values for seed yield and pod number of the newly released cultivars. This indicates that the key strategies for yield stability improvement are most likely to be the pod production, improved seed number per pod, and breeding higher yield cultivars. While the mechanism for pod survival in different environments has been improved genetically in the past 56 years, the pod setting stage is of crucial importance for yield formation, some studies did not find a significant association of

Table 2
Correlation coefficients of agronomic and physiological characteristics of soybean cultivars ($n = 45$) released in the past 56 years in Northeast China.

	Yield	Seed number	Pod number	Seed size	Protein	Oil	Plant weight	Harvest index	LAI	Photosynthetic rate	Height	Lodging score	Disease seed percentage
Seed number	0.756***												
Pod number	0.563***	0.813***											
Seed size	−0.109	−0.642***	−0.529***										
Protein	0.189	0.023	0.124	0.170									
Oil	0.131	0.137	0.064	0.069	−0.461**								
Plant weight	0.593***	0.616***	0.537***	−0.090	−0.046	0.165							
Harvest index	0.793***	0.512***	0.388**	−0.016	0.251	0.170	0.054						
LAI	−0.250	−0.088	−0.006	0.019	0.036	0.084	0.138	−0.306*					
Photosynthetic rate	0.537***	0.336*	0.246	−0.037	0.230	−0.280	0.393**	0.416**	−0.257				
Height	−0.367*	−0.161	−0.154	−0.028	−0.365*	0.262	0.303	−0.650***	0.425**	−0.325*			
Lodging score	−0.698***	−0.443**	−0.270	0.022	−0.273	0.109	−0.119	−0.717***	0.414**	−0.541***	0.641***		
Disease seed percentage	−0.571***	−0.609***	−0.413**	0.466**	−0.237	0.259	−0.203	−0.449**	0.379*	−0.494***	0.348*	0.581***	
Pest seed percentage	−0.393**	−0.263	−0.038	0.199	−0.211	0.351*	−0.151	−0.201	0.358*	−0.513***	0.264	0.441**	0.536***

[*] Significant at the 0.05 probability level.
[**] Significant at the 0.01 probability level.
[***] Significant at the 0.001 probability level.

Table 3
Phenotypic stability of agronomic and physiological characteristics for cultivars as measured by the coefficient of variability (CV) of the means across 3 years (2006–2008), and regression of the stability against year of release.

	Yield	Seed number	Pod number	Seed size	Protein	Oil	Weight	Harvest index	LAI	Photosynthetic rate	Height	Lodging score	Disease seed percentage	Pest seed percentage
Mean across cultivars	26.9	23.9	25.1	5.12	3.36	8.11	17.2	6.54	22.7	9.36	12.3	31.2	41.9	53.3
Range[a]	0.764–65.4	2.02–48.4	4.74–48.3	0.399–18.7	0.019–7.09	0–20.9	16.9–24.6	0.163–23.4	1.02–50.9	0.685–32.5	0.039–24.8	0–70.7	1.00–109	1.03–127
Slope[b]	−0.312	−0.111	−0.198	−0.014	−0.013	0.009	−0.008	−0.078	−0.096	0.029	0.046	−0.250	0.051	0.178
SE of slope[c]	0.159	0.105	0.084	0.035	0.026	0.062	0.083	0.053	0.103	0.069	0.047	0.202	0.248	0.256
r values[d]	−0.304*	−0.159	−0.337*	−0.063	−0.078	0.023	−0.015	−0.219	−0.142	0.064	0.149	−0.185	0.031	0.105

[a] The range of CV value among cultivars (from minimum to maximum).
[b] The slope of linear regression equation (characteristics against year of release).
[c] Standard error of slope.
[d] r values: linear correlation coefficient of cultivar plotted against year of release.
[*] Significant at the 0.05 probability level.

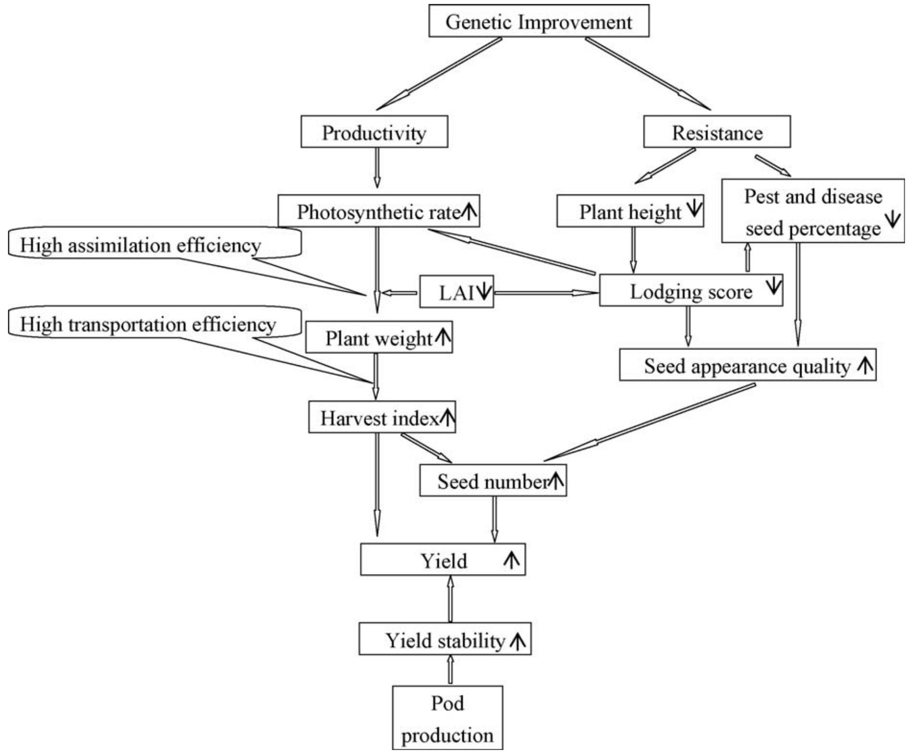

Fig. 6. A diagram of the traits associated with the genetic improvements in yield and yield stability during the years from 1950 to 2006. Note: the thin upward or downward arrows indicate the characteristics increasing or decreasing over time.

phenotypic stability for yield with year of release in North American cultivars (Morrison et al., 2000; Wilcox et al., 1979; Voldeng et al., 1997). The reason for the difference is probably due to the broader genetic base of breeding in China. Cui et al. (2002a,b) reported that Chinese cultivars were derived from a far greater number of ancestors than were North American cultivars (339 vs. 80 ancestors). Wide genetic diversity may reduce vulnerability to environmental stresses and accelerate breeding progress for higher yield (Cui et al., 2001).

A diagram to illustrate the genetic contributors to yield gain was developed and is shown in Fig. 6. The genetic improvement in soybean during the past 56 years in Northeast China, reduced the LAI, while the photosynthetic rate was increased, which contributed to more plant biomass accumulation and greater assimilate translocation to seeds, and thus higher HI. Seed number per plant is the most important contributor to the yield gain genetically. The decrease in plant height leads to an improvement of lodging resistance, and the seed tolerance to disease and pests is of benefit in improving seed number and seed appearance quality. Newer cultivars were less affected by the varied environments as demonstrated by their greater yield stability. High efficiency in photosynthesis and assimilate translocation are crucial factors for soybean yield improvement. An examination of the efficiency of assimilated carbon supply systems in the developing pods and seeds might explain the differences between new and old cultivars, and will be a potential topic for research to be addressed in the future studies.

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