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Full Length Article

Adaptive Variations for Salt Tolerance in Mineral Content and Photosynthetic Characteristics in Different Evolutionary Types of Soybean

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Abstract

This study was conducted to determine the differences and changes in trends of physiological metabolism in the process of adaptation to saline environments and artificial domestication among the subgenus *Soja*. *Glycine max*, *Glycine gracilis* and *Glycine soja* were used as the experimental material. The determination of mineral contents during different growth periods and the photosynthetic pigments, gas exchange parameters and soluble carbohydrate contents in the initial bloom stage were investigated. The results showed that, NO_3^-, $H_2PO_4^-$, Cu, Zn and B contents and the photosynthetic pigments, gas exchange parameters and photosynthetic product were significantly higher in salt-tolerant wild soybean than in common wild soybean. NO_3^-, $H_2PO_4^-$, SO_4^{2-}, K, Mg, Fe, Cu, Mo and Mn contents were significantly lower in cultivated soybean than in common wild soybean; and Ca and B were significantly higher. The photosynthetic pigments, gas exchange parameters and photosynthetic product at the initial bloom stage in cultivated soybean were significant higher than in common wild soybean and semi-wild soybean. The correlations of $H_2PO_4^-$, SO_4^{2-}, K, Mg, Mo and Mn with photosynthetic characteristic parameters significantly differed among members of *Soja*. Our study confirmed that mineral contents and photosynthetic characteristics among *Soja* had evolved towards the different environments and human requirements during long-term natural selection and artificial domestication. These findings will contribute to understanding the evolutionary trend of soybean.

Keywords: Correlation analysis; Mineral elements content; Photosynthesis characteristics; *Soja*
Abbreviations: Chl *a* - Chlorophyll *a*; Chl *b* - Chlorophyll *b*; Chl (*a*+*b*) - Chlorophyll *a*+*b*; Chl *a*/*b* - Chlorophyll *a*/*b*; Car - Carotenoid; p_N - Net photosynthetic rate; g_s - Stomatal conductance; *E* - Transpiration rate; C_i/C_a - Intercellular CO_2 concentration; Ss - Soluble carbohydrate; *WUE* - Water use efficiency

Introduction

The subgenus *Soja* includes *Glycine max*, *Glycine gracilis* and *Glycine soja*. Cultivated soybean (*G. max*), one of the most economically important crops and an oil crop, is rich in protein and fatty acids and a major source of protein for humans and animals. Previous studies have confirmed that the wild soybean (*G. soja*) is the close ancestor of cultivated soybean and *G. gracilis* is the transitional species between them in terms of morphological structure and physiological metabolism (Shi *et al*., 2015). After long-term artificial selection, and then genetic differentiation, wild soybean evolved extremely slowly into various cultivated soybeans through a primitive cultivation type (Wang and Li, 2012; Li *et al*., 2013). This genetic differentiation emerged not only among *Soja*, but also occurred in different ecotypes of wild soybean. In order to adapt to different habitats, wild soybean has evolved various ecotypes with corresponding resistance due to genetic differentiation, such as salt-tolerant wild soybean (Wang *et al*., 2001; 2011). Studies on soybean evolution, a fundamental question in basic biology, are also an important aspect of soybean germplasm resources. Study of soybean evolution can provide a clear understanding of the genetic characteristics of *Soja* and provide a theoretical basis for protecting resources and breeding new soybean varieties. There have been previous studies on the genetic differences and laws of evolution at the anatomical, cytological and molecular levels (Singh and Hymowitz, 1988; Abe *et al*., 1999; Chen and Nelson, 2004). Plant breeders have tried to confer salt-sensitive plants with salt tolerance used classical plant breeding and molecular biology techniques (Blumwald, 2003), and utilization of excellent wild resources can help to achieve this goal. The exploration of metabolic differences and evolutionary trends in *Soja* in relation to plant life activities will help in protection and utilization of *Soja*.

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Mineral nutrition plays a vital role in plant growth and directly or indirectly affects plant growth, and metabolism. Depending on the requirements during the plant's life, mineral elements can be divided into microelements and macroelements. The essential elements are also divided into 4 groups according to their biochemical action and functions (Mengel and Kirkby, 1987). The various mineral elements perform significantly different functions in soybean. The proportion and homeostasis of various elements in plants not only reflect the nutritional status of plants, but are also an index of plant resistance to environmental stress, especially salt stress (Wang *et al*., 2004; Liao *et al*., 2006; Wang *et al*., 2006). Photosynthesis, the most important chemical reaction and the most basic metabolism in plants, is directly related to plant growth and biomass (Gowik and Westhoff, 2011). Previous studies on photosynthetic characteristics of *Soja*, especially cultivated soybean, have mainly focused on yield formation (Cooper and Qualls, 1967; Buttery *et al*., 1981; Li *et al*., 2006). Studies on the combination of mineral elements and photosynthetic characteristics in soybean have mainly concentrated on the rational use of fertilizer and the regulation of special elements for photosynthesis (Wang *et al*., 2006; Huang *et al*., 2009). Little research has been reported from the perspective of photosynthetic characteristics and mineral nutrition and their correlation, and adaptation mechanisms and evolutionary trends of *Soja*.

Therefore, this experiment used *Soja* as the experimental material: *G. max*, *G. gracilis* and *G. soja* (common and salt-tolerant). We investigated the mineral element contents in the different growth stages and the chlorophyll content, gas exchange parameters and soluble carbohydrate content in the initial bloom stage. Then the correlations between the mineral element contents and photosynthetic characteristics under the two types of selective pressure were analyzed, in order to explore the evolutionary trend of physiological metabolism of *Soja* during the long-term adaptation to the natural environment and artificial domestication. This study showed crucial variations in mineral element contents and photosynthetic characteristics among *Soja* and will provide a theoretical basis for protection, screening and utilization of wild soybean and breeding new varieties of cultivated soybean.

Materials and Methods

Plant Materials

The common wild soybean (*G. soja*, Huinan06116), salt-tolerant wild soybean (*G. soja*, Tongyu06311), semi-wild soybean (*G. gracilis*) and cultivated soybean (*G. max*, JN24) were kindly provided by the Jilin Center of Germplasm Introduction and Breeding of Crops (denoted as W1, W2, S and M, respectively).

The soybean seeds were sown at the Jilin Center of Germplasm Introduction and Breeding of Crops experimental station in Gongzhuling city, Jilin Province. The plant materials were cultivated and managed according to general practices. The fully expanded leaves (the third node) of fresh samples were collected and immediately plunged into liquid nitrogen for further analysis. The collecting periods were in the seedling, initial bloom, full bloom, pod bearing and seed filling stages (expressed as S1, S2, S3, S4 and S5, respectively). The fresh samples were kept at 100°C for 10 min and then dried to constant weight at 80°C and thereafter stored for further determination of contents of nutrition elements, chlorophyll and soluble carbohydrate. The gas exchange parameters were determined at the initial bloom stage.

Experimental Methods

Dry samples of soybean leaves (0.1 g) were steeped in 65% (v/v) HNO_3 for 6 h then digested three times with 65% (v/v) HNO_3 at 120°C, and the extracts used to determine the content of mineral elements. An inductively coupled plasma emission spectrometer was used to measure the contents of K, Ca, Mg, Fe, Mn, Zn, Cu, B and Mo. Dry samples of soybean leaves (0.1 g) were treated with 4 mL of deionized water at 100°C for 40 min, and then centrifuged at 4000 × *g* for 15 min and the supernatant collected. After repeating this cycle twice, a 14 mL sample extract was used for determination the contents of anions. NO_3^-, SO_4^{2-} and $H_2PO_4^-$ were determined using ion chromatography (*DX-300 ion chromatographic system*, AS4A-SC chromatographic column, CDM-II electrical conductivity detector, mobile phase: Na_2CO_3/$NaHCO_3$ = 1.7/1.8 mM; Dionex, Sunnyvale, CA, USA) (Wang *et al*., 2004; Shi *et al*., 2009).

Gas exchange parameters of soybean leaves were determined using a portable open flow gas exchange system *LI-6400* (*LI-COR*, Lincoln, Nebraska, USA) at 10:00 AM. WUE was calculated as the ratio of P_N/E. The photosynthetically active radiation (PAR) was 1000 ± 12 μmol m^{-2} s^{-1}, CO_2 concentration was 350 ± 2 cm^3 m^{-3} and leaf temperature was 26.0 ± 0.8°C. Gas exchange was measured in fully expanded leaves from the same adult plants. There were five replications for each measurement, with three replications per plot and measurements were performed in 3 d in series during the initial bloom stage (Wang and Zhou, 2004).

Leaf dry sample (0.1 g) was dipped into 80% acetone/anhydrous ethanol mixture (1:1) to extract the photosynthetic pigments until the leaf became white. Photosynthetic pigments were determined by spectrophotometer (*SpectrUV-754*, Shanghai Accurate Scientific Instrument Co., China) at 440, 645 and 663 nm. Each sample was repeated three times. The calculation used the formulae of Holm (1954). Of each sample, 50 mg was dipped into 80% ethanol, placed in an 80°C water bath for 40 min, centrifuged at 3000 × *g* for 15 min and then the supernatant was collected. This course was repeated twice.

Unified supernatants were used to measure soluble carbohydrate (Liu *et al*., 2004). Each measurement was repeated three times.

Statistical Analysis

Data were analyzed by one-way analysis of variance (ANOVA) and Duncan's method to detect differences in physiological parameters using SPSS statistical software (Version 17.0 IBM, Chicago, IL, USA). All data were expressed as means ± standard error (SE). The term 'significant' indicates differences at $P \leq 0.05$. Figures were constructed using Sigma Plot software (Version 10.0 SSI, California, USA). Correlation analysis was performed using http://www.metaboanalyst.ca.

Results

The Changes in Nutrient Contents

There were significant changes and differences in coefficients of variation in leaf nutrients among *Soja* during different growth periods (Figs. 1 and 2; Table 1). The contents of NO_3^-, $H_2PO_4^-$ and Zn were higher in seedling and initial bloom stages than the other growth periods (Figs. 1A, B and 2C). Ca, Mn and B had gradually increasing trends along with soybean growth (Figs. 1C and 2E, F); in contrast, SO_4^{2-}, K, Fe and Cu showed declining trends (Figs. 1 D, E and 2A, B); and Mg and Mo showed declining trends in *G. soja* and *G. gracilis*, but increasing trends in *G. max* (Fig. 1D, F). $H_2PO_4^-$, Zn and Mn had their maxima of coefficients of variation in leaf mineral contents during the seedling stage; NO_3^-, SO_4^{2-} and Cu at full bloom; Fe and B at pod bearing; and K, Ca, Mg and Mo at seed filling stage. This showed that the plants had large requirement differences for different mineral elements during different growth stages among *Soja*. This difference had a close relationship to physiological metabolism and growth.

There were large differences in leaf mineral nutrient contents between the common and salt-tolerant wild soybean during different growth periods. SO_4^{2-}, Ca, Mg, Mo and Mn contents in salt-tolerant wild soybean were 6.05, 54.41, 20.45, 17.69 and 43.88% lower, respectively, than in common wild soybean at seedling stage; however, NO_3^-, $H_2PO_4^-$, Fe, Cu and Zn were 328.51, 53.51, 8.22, 73.01 and 28.56% higher, respectively, than in common wild soybean. NO_3^-, $H_2PO_4^-$, Ca, K and Fe contents were 54.37, 18.76, 11.81, 13.52 and 13.19% lower, respectively, in salt-tolerant than in common wild soybean at initial bloom stage; and SO_4^{2-}, Mg, Zn, Mo and B were 9.48, 19.46, 50.60, 11.70 and 24.92%, higher, respectively. SO_4^{2-}, Cu and Mn contents were 8.96, 30.46 and 16.80% lower, respectively, in salt-tolerant than in common wild soybean at full bloom stage; and Mg and Zn were 14.20 and 30.68% higher. NO_3^-, $H_2PO_4^-$, SO_4^{2-}, K, Mg, Mo and Mn contents were 55.49, 23.78, 18.44, 14.42, 11.49, 11.15 and 14.45% lower, respectively, in salt-tolerant than common wild soybean in the pod bearing period; but Cu content was 262.29% higher. $H_2PO_4^-$, Mg, Fe, Zn and Mo contents were 20.58, 9.46, 14.66, 15.01 and 9.47% lower, respectively, in salt-tolerant than common wild soybean in the seed filling period; and K and B contents were 14.19 and 13.07% higher.

There were regular changes in leaf mineral nutrient contents among the common wild soybean, semi-wild soybean and cultivated soybean during the different growth periods. SO_4^{2-}, Ca, Mg, Fe, Mo and Mn contents in semi-wild and cultivated soybean were 10.54, 39.36, 26.25, 7.30, 21.26 and 65.13% and 30.10, 32.33, 37.62, 20.46, 33.59 and 47.42% lower, respectively, than in common wild soybean; and NO_3^- and B were 229.75 and 62.27% higher in semi-wild and 340.91 and 85.47% higher in cultivated soybean, respectively, than in common wild soybean in the seedling stage. NO_3^-, SO_4^{2-}, Mg, Fe, Cu and Mo contents in semi-wild and cultivated soybean were 74.14, 16.41, 6.42, 22.07, 50.41 and 3.69% and 55.35, 20.48, 13.26, 36.31, 51.01 and 12.33% lower, respectively, than in common wild soybean; and Zn and B were 38.35 and 45.83% higher in semi-wild and 44.13 and 71.77% higher in cultivated soybean, respectively, than in common wild soybean at the initial bloom stage. NO_3^-, $H_2PO_4^-$, SO_4^{2-}, K, Fe and Cu contents in semi-wild and cultivated soybean were 63.69, 32.49, 27.49, 28.05, 11.98 and 76.48% and 78.31, 17.64, 46.33, 12.92, 21.79 and 73.20% lower, respectively, than in common wild soybean at the full bloom stage; and B was 132.82 and 135.48% higher, respectively. NO_3^-, $H_2PO_4^-$, SO_4^{2-}, K, Fe, Zn and Mn contents in semi-wild and cultivated soybean were 65.89, 24.35, 20.67, 22.76, 23.31, 18.99 and 35.07% and 59.34, 19.51, 22.77, 31.13, 38.43, 14.06 and 23.91% lower, respectively, than in common wild soybean in the pod bearing period; and Ca and B were 61.43 and 58.20% higher in semi-wild and 88.17 and 157.15% higher in cultivated soybean than in common wild soybean at the pod bearing period, respectively. $H_2PO_4^-$, Fe and Zn contents in semi-wild and cultivated soybean were 21.72, 22.97 and 13.73% and 18.63, 17.80 and 7.60% lower, respectively, than in common wild soybean in the seed filling period; and Ca, Mg, Mo and B were 110.21, 8.85, 9.13 and 75.62% and 171.10, 57.98, 46.37 and 150.92% higher, respectively. The contents and change trends of NO_3^-, SO_4^{2-}, Ca, K, Fe, Cu and B analysis showed that cultivated soybean was closer to the semi-wild and quite different to common wild soybean.

The annual average contents of NO_3^-, $H_2PO_4^-$, Cu, Zn and B were significantly higher in salt-tolerant than in common wild soybean; but the annual average contents of SO_4^{2-}, Ca, K, Mg, Fe, Mo and Mn were significantly lower than in common wild soybean (Table 2, $P < 0.05$). This showed that the salt-tolerant wild soybean had a special nutrient absorption and accumulation mechanism adaptation to saline environments during the process of natural selection and evolution.

Table 1: Compared the coefficient of variation in leaves mineral contents among *Soja* during the different growth periods

	NO_3^-	$H_2PO_4^-$	SO_4^{2-}	Ca	K	Mg	Fe	Cu	Zn	Mo	Mn	B
The seedling stage	48.62	20.69	16.04	47.31	2.86	19.97	12.79	33.05	25.37	16.95	30.97	31.85
The initial bloom stage	59.15	17.90	15.07	17.55	11.05	14.10	18.59	38.47	17.06	10.07	28.59	22.50
The full bloom stage	63.21	18.41	25.93	39.52	15.19	16.04	10.27	66.62	13.47	12.29	28.21	41.78
The pod bearing period	55.49	13.81	12.38	33.09	16.01	7.80	21.68		11.45	8.00	18.20	45.49
The seed filling period	24.83	12.07	21.04	49.83	20.45	26.27	11.44		7.55	21.93	17.36	43.20

Table 2: Compared the annual average value in leaves mineral contents among *Soja*

	NO_3^-	$H_2PO_4^-$	SO_4^{2-}	Ca	K	Mg	Fe	Cu	Zn	Mo	Mn	B
W2-W1	*	*	A	AA	A	A	A	*	*	A	A	*
S-W1	AA	A	A	**	A	A	A	AA	*	A	A	***
M-W1	AA	A	AA	**	A	A	AA	AA	A	A	A	***

Decrease significance: A: 0%<(X-W1)/W1≤20%; AA: 20%<(X-W1)/W1≤50%; AAA: 50%<(X-W1)/W1. Increase significance: *:0%<(X-W1)/W1≤20%; **: 20%<(X-W1)/W1≤50%; ***: 50%<(X-W1)/W1.W1: the common wild soybean; W2: the salt-tolerance wild soybean; S: the semi-wild soybean; M: the cultivated soybean. X = W2, S, M

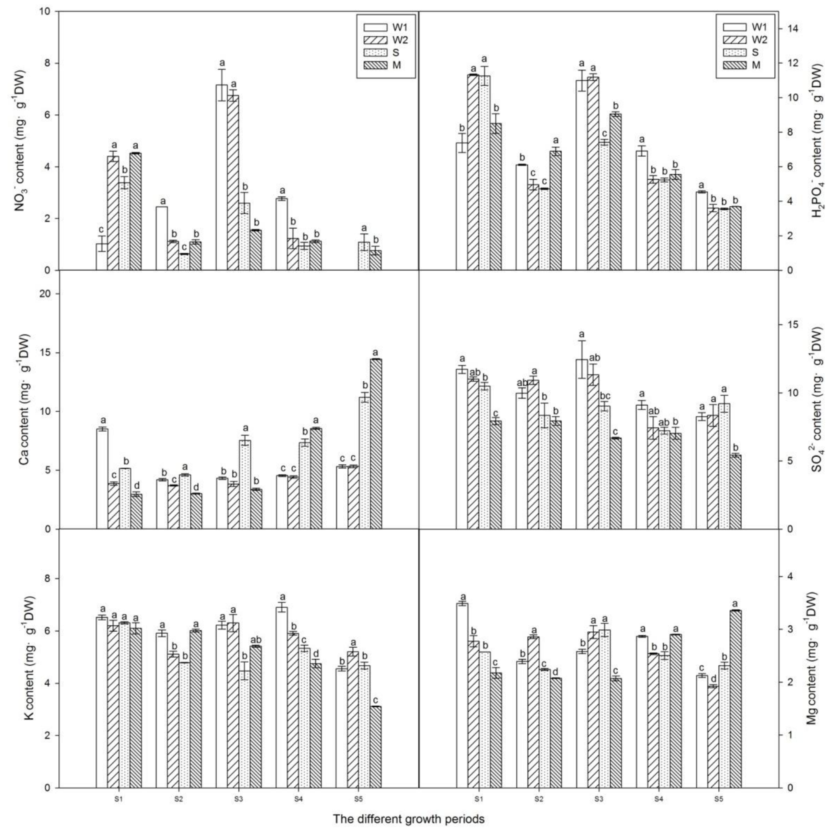

Fig. 1: The contents of macronutrients changes of *Soja* in different growth periods

The values are the means of three replicates. Means followed by different letters in the same growth periods are significantly different at $P<0.05$ according to Duncan's method. NO_3^-: A; $H_2PO_4^-$: B; Ca: C; SO_4^{2-}: D; K: E; Mg: F. W1: The common wild soybean; W2: The salt-tolerant wild soybean; S: The semi-wild soybean; M: The cultivated soybean. S1: The seedling stage; S2: The initial bloom stage; S3: The full bloom stage; S4: The pod bearing period; S5: The seed filling period

The annual average contents of NO_3^-, $H_2PO_4^-$, SO_4^{2-}, K, Mg, Fe, Cu, Mo and Mn in semi-wild and cultivated soybean were significantly lower than in common wild soybean; and Ca and B were significantly higher (Table 2, $P < 0.05$). This may be related to artificial domestication and cultivation management.

Changes in Photosynthetic Characteristics

The nutrition absorption and photosynthetic assimilation ability in salt-tolerant wild soybean have changed significantly during adaptation to saline habitats. With the enhanced ability to adapt to salt stress, there were specific

Table 3: Compared the chlorophyll contents, gas exchange parameters and soluble carbohydrate contents of *soja* in the initial bloom stage

	The common wild soybean	The salt-tolerance wild soybean	The semi-wild soybean	The cultivated soybean
Chl *a* (mg g^{-1}. DW)	3.61±0.03 c	4.85±0.02 a	3.68±0.04 c	4.65±0.06 b
Chl *b* (mg g^{-1}. DW)	1.44±0.01 d	1.98±0.00 a	1.48±0.01 c	1.91±0.01 b
Chl (*a*+*b*) (mg g^{-1}. DW)	5.04±0.02 c	6.83±0.02 a	5.15±0.05 c	6.56±0.07 b
Chl a/b	2.51±0.03 a	2.45±0.01 ab	2.49±0.01 ab	2.43±0.01 a
Car (mg g^{-1}. DW)	1.03±0.00 c	1.36±0.01 a	1.11±0.01 b	1.36±0.02 a
p_N (μmol m^{-2} s^{-1})	17.73±1.86 c	27.85±0.81 a	23.94±0.57 b	29.00±0.51 a
g_s (mol m^{-2} s^{-1})	0.53±0.07 b	0.83±0.01 a	0.89±0.07 a	0.91±0.04 a
E (mol m^{-2} s^{-1})	12.70±0.98 c	15.60±0.08 ab	14.17±0.28 bc	15.86±0.19 a
C_i/C_a (cm^3 m^{-3})	0.77±0.01 b	0.79±0.01 ab	0.81±0.01 a	0.78±0.01 b
WUE (p_N/E)	1.39±0.07 b	1.79±0.05 a	1.69±0.03 a	1.83±0.05 a
Soluble carbohydrate (mg g^{-1}. DW)	83.41±0.78 ab	91.56±3.04 a	81.95±4.38 b	91.68±0.73 a

The values are the means of three replicates. Means followed by different letters in the same line are significantly different at P<0.05 according to Duncan's method

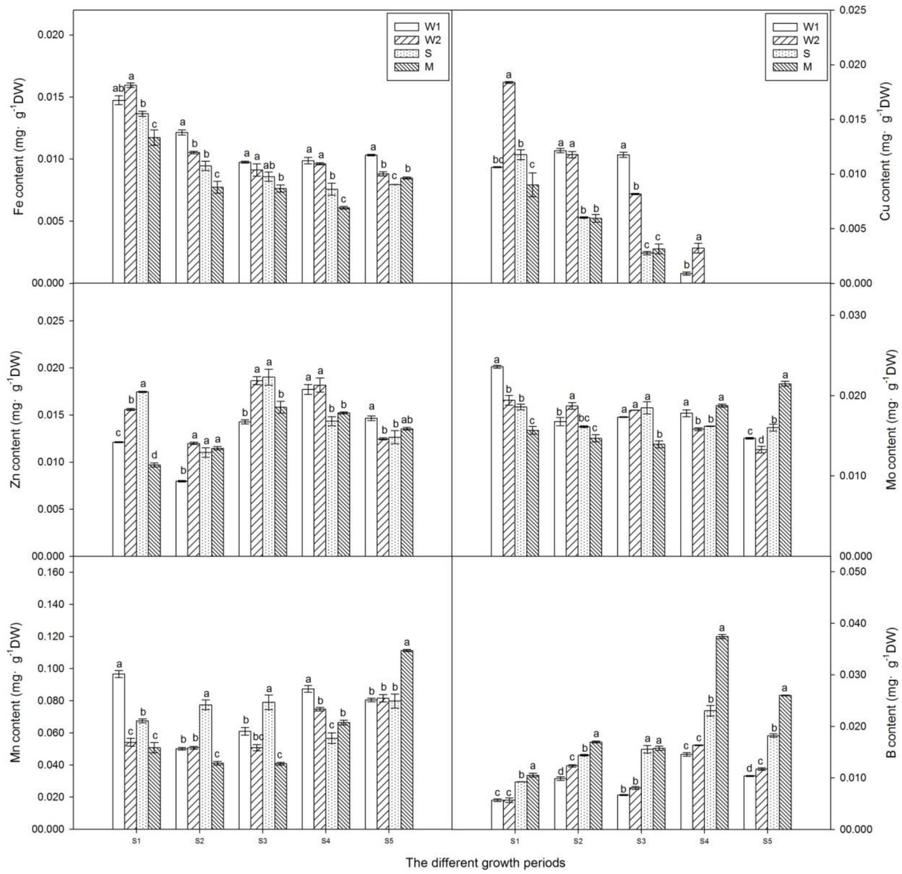

Fig. 2: The contents of micronutrients changes of *Soja* in different growth periods

The values are the means of three replicates. Means followed by different letters in the same growth periods are significantly different at P<0.05 according to Duncan's method. Fe: A; Cu: B; Zn: C; Mo: D; Mn: E; B: F. W1: The common wild soybean; W2: The salt-tolerant wild soybean; S: The semi-wild soybean; M: The cultivated soybean. S1: The seedling stage; S2: The initial bloom stage; S3: The full bloom stage; S4: The pod bearing period; S5: The seed filling period

correlations between different mineral elements and photosynthetic parameters of wild soybean at the initial bloom stage (Table 3). Photosynthetic pigments, gas exchange and photosynthetic products showed significant differences between common and salt-tolerant wild soybean. Photosynthetic pigment contents were significantly higher in salt-tolerant than in common wild soybean. Chl *a*, *b*, Chl (*a*+*b*) and Car content were 34.40, 37.70, 35.40 and 31.90% higher, respectively. Gas exchange and photosynthetic products, p_N, g_s, E, C_i/C_a and *WUE* and soluble carbohydrate content in salt-tolerant wild soybean were significantly higher by 57.10, 55.20, 22.80, 2.30, 28.50

and 9.80%, respectively, than in common wild soybean. At the same time, Chl *a*/*b* was 2.40% lower. The relative greater contents of Chl *b* in salt-tolerant wild soybean were likely beneficial to avoid damage from adverse environmental factors.

Leaf photosynthetic characteristics showed regular changes among common wild soybean, semi-wild soybean and cultivated soybean at initial bloom stage (Table 3). Chl *b*, Car, p_N, g_s, *E*, C_i/C_a, and *WUE* in *G. gracilis* were 2.80, 8.00, 35.00, 67.70, 11.60, 5.60 and 21.60% higher, respectively, than in common wild soybean. Chl *a*, *b*, Chl (*a*+*b*), Car, p_N, g_s, *E*, *WUE* and soluble carbohydrate content in cultivated soybean were 28.80, 33.20, 30.10, 31.40, 63.50, 71.50, 24.90, 31.80 and 9.90% higher, respectively, than in common wild soybean. The Chl *a*/*b* was 3.19% lower in cultivated than in common wild soybean. This may be conducive to close planting of cultivated soybean because Chl *b* mainly absorbs scattered light.

Correlation Analysis of Mineral Content and Photosynthetic Characteristics

Significant correlations of mineral contents and photosynthetic characteristics were detected between common and salt-tolerant wild soybean at the initial bloom stage (Fig. 3). There were significant positive correlations between SO_4^{2-}, Mg, Zn, Mo, Mn and B and Chl *a*, Chl *b*, Chl (*a*+*b*), Car, p_N, g_s, *E*, C_i/C_a, *WUE* and soluble carbohydrate; and significant negative correlations with Chl *a*/*b*. There were significant positive correlations between NO_3^-, $H_2PO_4^-$, Ca, K, Fe and Cu and Chl *a*/*b*, but significant negative correlations with Chl *a*, Chl *b*, Chl (*a*+*b*), Car, p_N, g_s, *E*, C_i/C_a, *WUE* and soluble carbohydrate.

After long periods of artificial domestication, cultivated soybeans could meet the needs of mankind. The correlations between mineral elements and the photosynthetic parameters during the process of artificial domestication significantly differed from those of wild soybean (Fig. 4). There were significant positive correlations between $H_2PO_4^-$, K, Zn, B and photosynthetic pigments and products; and between Zn, B and gas exchange parameters. There were significant negative correlations between $H_2PO_4^-$, K, Zn, B and Chl *a*/*b*. There were significant positive correlations between NO_3^-, SO_4^{2-}, Ca, Mg, Fe, Cu, Mo, Mn and Chl *a*/*b*; and opposite with photosynthetic pigments, gas exchange parameters, products.

Discussion

After long-term adaptation to saline environments and artificial domestication, *Soja* diverged from a common ancestor species, with significant differences in nutritional and photosynthesis physiology and their correlations with each other.

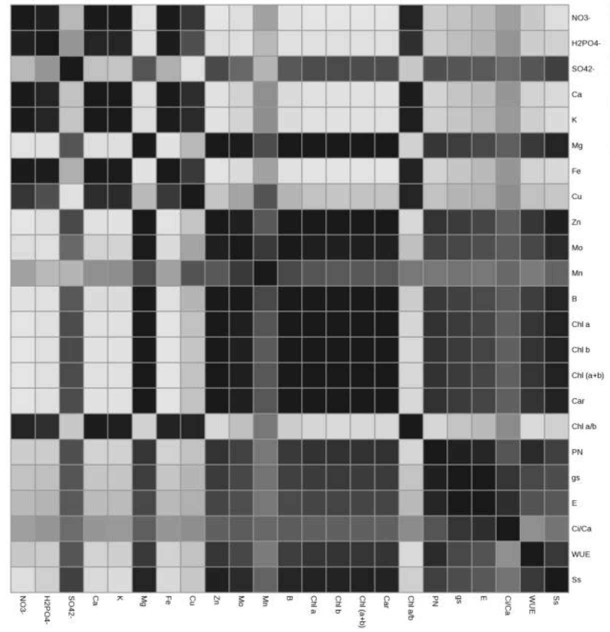

Fig. 3: The correlations analysis between the mineral elements contents and the photosynthetic parameters as the enhancement of the ability to adapt to salt stress

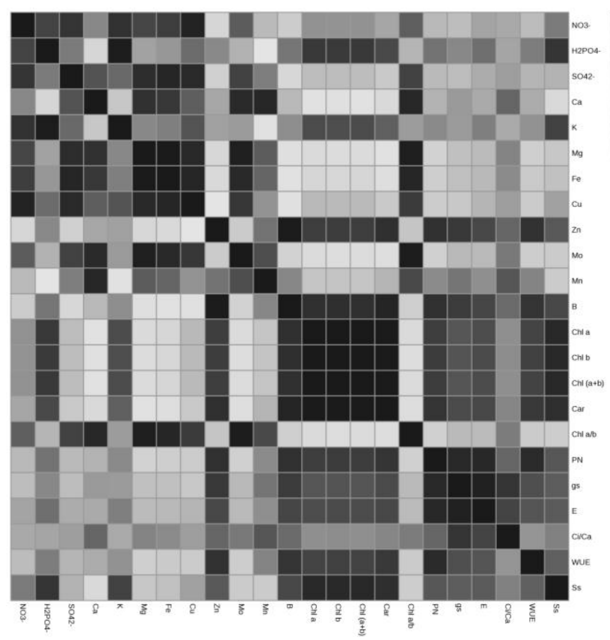

Fig. 4: The correlations analysis between the mineral element contents and the photosynthetic parameters during the process of artificial breeding

In the absorption and accumulation of mineral elements, NO_3^-, $H_2PO_4^-$, Cu, Zn and B contents were significantly higher in salt-tolerant than in common wild soybean. Cu and Zn are important components of plant antioxidant enzymes. Moderate exogenous Cu and Zn could significantly increase activity of antioxidant enzymes and maintain stability of enzymes, while reducing oxyradical content and improving plant resistance to salt stress (Yao *et al*., 2002). B is closely related to structural stability of plant cells and various physiological metabolisms, especially the ability of plant resistance to adverse environment (Sharma and Ramchandra, 1991; Silva *et al*., 2008). This showed that in order to endure the stress of highly saline environments, salt-tolerant wild soybean could alleviate the toxic effect of high levels of salt ions or improve the function of self-repairing by adjusting the amount absorbed of various mineral elements. Our experiments confirmed that the contents of Cu, Zn and B in leaves were an important indicator of salt resistance of wild soybean. During long-term evolution, plants can adjust their photosynthesis metabolism in the minimum degree and achieve an optimal state, thus adapting to changes in diverse environments and needs of breeding (Luo *et al*., 2009; Gurmani *et al.,* 2014). Gas exchange ability, photosynthetic pigment contents and photosynthetic product accumulation were significantly higher in salt-tolerant than in common wild soybean. The stronger photosynthesis assimilation ability and more photosynthetic products did not result in significant differences in plant height and biomass between the two types of wild soybean (Shu *et al*., 1986). This showed that salt-tolerant wild soybean consumes much energy to improve their resistance to stress in a saline environment, and consequently photosynthetic products would not be effectively transported and applied to the growth and seed organs. Photosynthetic gas exchange capacity is an important physiological marker of salt-tolerant wild soybean, and effective distribution of photosynthetic products might be an important factor in growth and formation of yield in soybean.

In the progression from wild soybean to *G. gracilis* to cultivated soybean under long-term artificial domestication, the change trends of *G. gracilis* have become close concern the absorption of mineral elements with the cultivated soybean. The average contents of Ca and B were higher in cultivated soybean than in common wild soybean, but $NO_3^–$, $H_2PO_4^–$, $SO_4^{2–}$, K, Mg, Fe, Cu, Mo and Mn contents were lower. Ca and B were more closely related to vertical growth and lower pod shedding rate in cultivated soybean (Zhou and Dong, 2007). Obviously, the other elements are associated with the functions and physiological effects in cultivated soybean (Zhou and Dong, 2007). The gas exchange ability, photosynthetic pigment contents and accumulation of photosynthetic products all showed gradual increasing trends proceeding from wild soybean to *G. gracilis* to cultivated soybean. Previous studies confirmed obvious differences in their external morphology, and the resistance to adverse environment of cultivated soybean was significantly reduced (Shu *et al*., 1986). Due to better plant conditions and cultivation techniques, especially constant breeding, the cultivated soybean genetic characteristics have changed and the photosynthetic products transported and accumulated in a direction to satisfy human requirements (Wells *et al*., 1982). However, these are not conducive to resistance of cultivated soybean to environmental stress. Our results confirmed that the photosynthetic characteristics and mineral nutrition of *G. gracilis* were mostly close to those of cultivated soybean, and distant from those of wild soybean.

Some elements are essential for biosynthesis of chlorophyll, and some involved in the process of photosynthetic electron transport and water-splitting. Some take part in the transformation and transportation of photosynthetic products, which indirectly affect photosynthesis. In fact, a variety of mineral elements in plants directly or indirectly affect photosynthesis. Research on the correlation between mineral elements and photosynthetic parameters is not only conducive to understanding the function and role of mineral elements, but also has important reference value for determining the co-evolutionary history of two types of physiological processes among *Soja*. Our results showed that, in the adaptation process of wild soybean to saline environments, the contents of $SO_4^{2–}$, Mg, Zn, Mo, Mn and B had the same change trends as Chl *a*, Chl *b*, Chl (*a*+*b*), Car, p_N, g_s, E, C_i/C_a, *WUE* and carbohydrate content, meaning that all showed a gradual increase; and had opposite change trends to Chl *a*/*b*. The contents of $NO_3^–$, $H_2PO_4^–$, Ca, K, Fe and Cu had the same change trends as Chl *a*/*b*; and had opposite change trends to Chl *a*, Chl *b*, Chl (*a*+*b*), Car, p_N, g_s, E, C_i/C_a, *WUE* and carbohydrate contents; that is, with decreasing contents of these ions, the other characteristics increased. Significantly different, during the process of adapting to human needs and artificial domestication of soybean, the contents of $H_2PO_4^–$, K, Zn and B had the same change trends as Chl *a*, Chl *b*, Chl (*a*+*b*), Car and carbohydrate content. The contents of Zn and B had the same change trends as p_N, g_s, E, C_i/C_a and *WUE*. The contents of $NO_3^–$, $SO_4^{2–}$, Ca, Mg, Fe, Cu, Mo and Mn had opposite change trends to Chl *a*, Chl *b*, Chl (*a*+*b*) , Car, p_N, g_s, E, *WUE* and carbohydrate content; and the same change trend as Chl *a*/*b*. There were significant differences between the changes in $H_2PO_4^–$, $SO_4^{2–}$, K, Mg, Mo and Mn and the evolutionary trends of photosynthetic parameters during the process of adaptation to saline environments and artificial domestication among *Soja*. This has important significance for protection and making use of *Soja*.

Conclusion

Our experimental results showed that nutrient contents, photosynthetic physiology and their correlations with each other had crucial variations among *Soja*, likely due to long-term adaptation to natural saline environments and to artificial domestication. The main change trends were increasing the assimilation ability of salt-tolerant wild soybean and cultivated soybean. At the same time, our results showed that the photosynthetic characteristics of semi-wild soybean and cultivated soybean were closer. This will help in understanding the evolutionary relationships among *Soja*.

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