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Characterization of root architecture in an applied core collection for phosphorus efficiency of soybean germplasm

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Abstract **In the present study, we constructed an "applied core collection" for phosphorus (P) efficiency of soybean germplasm using a GIS-assisted approach. Systematic characterization and comparative analysis of root architecture were conducted to evaluate the relationship between root architecture and P efficiency and its possible evolutionary pattern. Our results found that: i) root architecture was closely related to P efficiency in soybean. Shallow root architecture had better spatial configuration in the P-rich cultivated soil layer hence higher P efficiency and soybean yield; ii) there was a possible co-evolutionary pattern among shoot type, root architecture and P efficiency. The bush cultivated soybean had a shallow root architecture and high P efficiency, the climbing wild soybean had a deep root architecture and low P efficiency, while the root architecture and P efficiency of semi-wild soybean were intermediate between cultivated and wild soybean; iii) P availability regulated root architecture. Soybean roots became shallower with P addition to the topsoil, indicating that the co-evolutionary relationship between root architecture and P efficiency might be attributed to the long-term effects of topsoil fertilization. Our results could provide important theoretical basis for improving soybean root traits and P efficiency.**

Keywords: soybean, applied core collection, root architecture, P efficiency.

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Soybean (*Glycine max* (L.) Merr) originated in China, and now is the major protein source in the human food chain and an important component for food supplements and high-quality animal feed[1]. Since soybean consumption has increased rapidly in recent years, more soybean production is needed to meet the increasing demands in the world market. As one of the major soybean consuming and producing countries, China has had stagnant soybean production since 1993 with an annual soybean production around 1700 kg/ha in spite of increasing market demands[2]. Among the many limiting factors to soybean production, low phosphorus (P) availability in the soil is a major constraint to soybean growth in many areas[3]. Therefore, improving P efficiency is of great priority for the development of soybean production in our country.

China has abundant soybean germplasm resources that could be used for the genetic improvement of P efficiency[4]. Unfortunately, little has been done thus far on systematic characterization and utilization of soybean germplasm for P efficiency. Moreover, the reported characterization of soybean germplasm was mainly focused on aboveground (shoot) characters with little attention to the root system, possibly due to the technical difficulties in research and other reasons. But it is well known that root is the major plant organ for nutrient uptake from the soil, especially for immobile nutrients like P, whose acquisition by the plant would be greatly facilitated by increased soil volume explored by the roots and enhanced root activity[5,6]. It was reported that plants may have a series of adaptive changes in response to P deficiency, including altered root morphology and architecture, increased root exudation of proton and organic acids, enhanced activities of acid phosphatases and greater mycorrhizal symbioses, depending on various plant species[7—11]. Plant root architecture, or the spatial configuration of roots in the soil, determines to a great extent the soil volume explored by the roots, thus is very important to plant P acquisition and is the functional prerequisite of other root traits (such as root exudates)[12,13]. Evidence is being accumulated that plants may have adaptive mechanisms under P-deficient conditions by changing root morphology and architecture for better acquisition and utilization of P from the soil[14—17]. But our understanding of root architecture and its relationship to P efficiency is mostly based on the results from a limited amount of plant materials, and therefore should be verified by systematic studies with considerable amounts of germplasm materials.

Wild soybean (*Glycine. soja* L) is a closely related ancestor of the cultivated soybean, which gradually evolved into cultivated soybean by accumulating beneficial variations through a long-term process of natural selection and domestication. Compared with the cultivated soybean, wild soybean differs significantly in morphology, physiological biochemistry and quality chemistry, indicating an evolutionary process of continuous variation[18—23]. Nevertheless, in spite of its importance, information is scarce about the evolution of the root system, particularly in relation to root architecture and P efficiency.

In the present study, we constructed an "applied core collection" of soybean germplasm for P efficiency using a GIS-assisted approach, and selected 308 representative soybean genotypes for field study. Our objective was to evaluate the relationship between root traits (particularly root architecture) and P efficiency and the possible evolutionary pattern of these traits through screening, characterization and comparative analysis of germplasm materials from the applied core collection so as to provide important theoretical basis for improving soybean root traits and P efficiency.

1 Materials and methods

(i) Plant materials

This study included two experiments, one for screening and characterization of the "Applied Core Collection" of soybean germplasm (Experiment I) and one for comparative analysis of selected germplasm materials with different degree of evolution (Experiment II). In Experiment I, 308 soybean genotypes, including 278 cultivars (*Glycine max*) and 30 wild accessions (*Glycine soja*), were selected from an "applied core collection" of soybean germplasm in China that was formed based on a GIS-assisted approach as described as follows: a GIS map of China was divided into six areas, including the Lateritic Red Soil and Latosol Area in South China, the Red and Yellow Soil Area in Central China, the Yellow Brown Soil Area around Yellow River, Huai River and Hai River, the Brown Soil and Cinnamon Soil Area in North China, the Dark Brown Earth Area in Northeast China, and the Loess Soil Area in Northwest China based on information of soil types(including soil P status), agricultural divisions and distribution of soybean production using a GIS software. Then representative amounts of samples were selected for each region according to the biological characteristics of soybean, such as plant type, growth habits, seed weight, seed color, flower color, seed shape, etc. Totally 561 cultivated soybean genotypes were selected from more than 20000 cultivated soybean germplasm through cluster analysis to form a distribution map of the 'applied core collection' of soybean germplasm. Subsequently, 278 representative cultivated soybean genotypes were selected for field experimentation by screening out genotypes with a close kinship or similar morphological characters. The same method was used to select 202 representative genotypes from more than 5000 wild soybean genotypes to form an "applied core collection" of wild soybean germplasm, of which 30 wild or semi-wild genotypes were finally selected for field experiments. The cultivated soybean genotypes were provided by the Chinese Academy of Agricultural Sciences, and the wild (semi-wild) soybean genotypes were provided by the Jilin Academy of Agricultural Sciences.

In Experiment II, 18 soybean genotypes were chosen, including 6 cultivated soybeans: GD5142, GD5865, GD5078, GD3580, GD5587 and Jiqing 1, 6 semi-wild soybeans: ZYD01825, ZYD01506, ZYD01792, ZYD-01505, GD5602 and GD5584 and 6 wild soybeans: GYD01472, GYD01396, GYD01480, GYD01467, GYD-1395 and GYD1420. The biological characters of the above genotypes were further verified in a preliminary trial prior to the field experiment.

(ii) Field experiments

(1) Experiment I. The experiment was carried out at a field site in Boluo County, Guangdong Province, the P. R. China in 2002. The total experimental area was 12000 m^2. The soil for experiment was a typical acid red soil (lateritic red earth) deficient in P. Some basic physical and chemical properties of the soil are summarized in Table 1. The experiment was run for both spring and summer seasons; Two factors were studied at both seasons: genotype and P treatments. 308 soybean genotypes were used as plant materials (because of the bad germination rates of some genotypes, 277 genotypes were sampled in the spring and 288 in the summer season). There were two P levels, including one with P supply (160 kg P/ha added as calcium superphosphate to the topsoil) and another without P supply (no P added). Each treatment had 4 replicates in a randomized complete-block design. Each plot had an area of 1.5 m^2 and the planting density was 30 cm × 10 cm. There were two harvests for each growth season. One representative plant for each genotype was harvested for

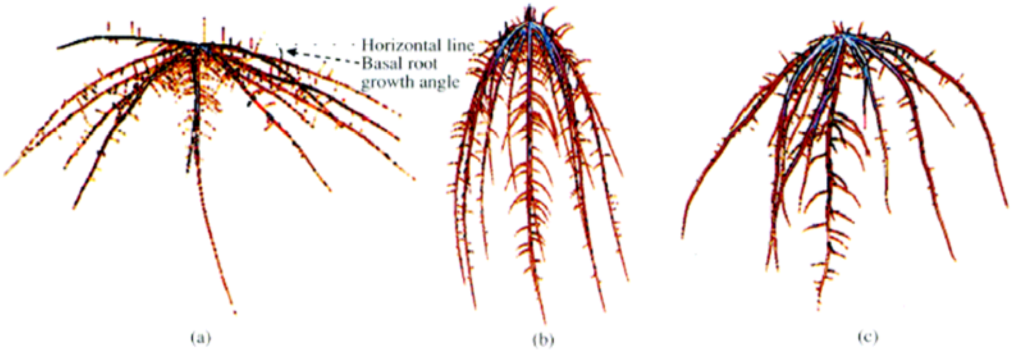

Fig. 1. Three representative root architectures of soybean in lateritic red earth. (a), (b) and (c) represents shallow, deep and intermediate root architecture, respectively (the images were the results of computer simulation using the data from the field experiment).

Table 1 Soil physical-chemical properties in the experimental field sites*

Soil type	pH	Organic matter /g • kg^{-1}	Total N /g • kg^{-1}	Total P /g • kg^{-1}	Total K /g • kg^{-1}	Available N /mg • kg^{-1}	Available P/mg • kg^{-1}			Available K /mg • kg^{-1}
							0—20 cm	20—40 cm	40—60 cm	
Lateritic red earth	5.88	15.6	0.91	0.53	15.41	87.64	17.18	4.32	0.00	93.14
Dark brown earth	7.13	32.07	0.99	0.69	25.74	87.42	17.30	6.90	0.10	129.37

* pH value: 2.5∶1 (water/soil); organic matter: $K_2Cr_2O_7$-H_2SO_4 digestion; total N content: Kjedahl method; total P content: H_2SO_4-$HClO_4$ digestion; total K content: NaOH fusion; available N content: alkaline diffusion; available P content: Bray Ⅱ method; available K content; 1 mol/L neutral NH_4OAc extraction[24].

every replicate. The first harvest was at vegetative stage in one month after sowing. All plants were divided into shoots and roots at harvest, and then the parameters of growth and P efficiency were analyzed. The second harvest was at maturity stage. The plants were harvested according to their maturity time, and then were used to estimate the yield based on the plot yield.

(2) Experiment Ⅱ. The experiment was performed at the experimental station of the Jilin Academy of Agricultural Sciences in 2003. Soil physical and chemical properties were shown in Table 1. Same as Experiment Ⅰ, there were two treatmental factors including genotype and P level in this study. The P treatments included P addition (same amount as Experiment Ⅰ) in topsoil and no P addition. There were 18 soybean genotypes with four replications in a randomized complete-block design. Plants were harvested at 100 d after sowing (flowering stage).

(iii) Root sampling and measurements

(1) Root architecture evaluation and root length measurement. A representative plant was selected in the field. A square block of soil (40cm×40cm) with the plant base at the center was dug to reach the end of tap root to get the complete plant root system (one meter was the maximum depth for the soil block if the depth of tap root was deeper than 1 m). In the field, root architecture was classified based on the initial growth angle of basal roots as described before[17,24]. The root system was defined as a shallow root architecture (type A) when the basal root growth angle of most basal roots was less than 40 degrees from horizontal, as a deep root architecture (type B) when more than 60 degrees from horizontal, and as an intermediate root architecture (type C) between type A and B (Fig. 1).

The roots were carefully cleaned before being scanned into the computer and the digital images were quantified with computer image analysis software (WinRhizo Pro, Régent Instruments, Québec, Canada) for root morphological parameters, such as root length, root surface area and average root diameter.

(2) Determination of biomass and P content. Shoots and roots were dried at 105℃ for 30 min, then kept at 75℃ until completely dry. The biomass was measured as dry weight. Phosphorus content was analyzed colorimeterically as described by Murphy and Riley after ash digestion[25].

(iv) Expression of P efficiency and criteria for its classification. Plant P efficiency is usually indicated by plant biomass, seed yield and P content under low P conditions[26,27]. According to the classification criteria for plant nutrient efficiency and its responsiveness to fertilization[28], the tested soybean genotypes were classified into four types using seed yield as an indicator: Ⅰ. P inefficient, low responsive; Ⅱ. P inefficient, high responsive; Ⅲ. P efficient, high responsive; Ⅳ. P efficient, low responsive. Type I represents the genotypes with a seed yield lower than the average yield of the whole collection under both high and low P additions; Type Ⅱ represents the genotypes with a seed yield lower than the average yield without P addition, but higher than the average yield with P addition; Type Ⅲ represents the genotypes with a seed yield higher than the average yield both with and without P additions; IV represents the genotypes with a seed yield higher than the average yield without P addition, but lower with phosphorus addition.

All the data were analyzed statistically using Microsoft® Excel 2000 (Microsoft Company, USA) for calculating mean and standard error and SAS (SAS Institute Inc., Cary, NC, USA) for Two-way ANOVA.

2 Results and analysis

(i) Experiment Ⅰ

(1) Genotypic variation for P efficiency and its relationship to biomass and P content at vegetative stage. Significant genotypic variation for P efficiency was observed among the tested soybean genotypes using seed yield as an indicator in both growth seasons (F_{spring} = 5.30***, F_{summer} = 6.27***) (Table 2). Without P addition, the highest seed yield was more than ten times as much as the lowest, showing a wide range of genotypic variance thus great genetic potential (Fig. 2). Phosphorus addition increased seed yield, but such response varied with genotypes. According to the classification method proposed by Lynch[28], the tested soybean genotypes were divided into the following four groups: Type Ⅰ: P inefficient, low responsive; Type Ⅱ: P inefficient, high responsive; Type Ⅲ: P efficient, high responsive; and Type Ⅳ: P efficient, low responsive (Table 3).

Significant genotypic variations among the tested soybean materials were also found for both biomass and P content at the vegetative stage in both seasons (Biomass:

Table 2　ANOVA results of plant biomass, phosphorus content, and yield in Experiment Ⅰ

	Spring season			Summer season		
	G	P	G×P	G	P	G×P
Biomass/g • plant^{-1}	2.20***	65.84**	0.98 ns	1.68***	18.77***	0.70 ns
P content/mg • plant^{-1}	1.98***	65.47***	0.81 ns	1.46**	87.19***	0.76 ns
Yield/g • plant^{-1}	5.30***	12.67***	0.64 ns	6.27**	3.80***	1.35**

Note: data in the table are F values from two-way ANOVA; G: genotype (the tested soybean materials); P: phosphorus level; G× P: interactions between genotype and P level; * $0.05 > P > 0.01$; ** $0.01 > P > 0.001$; *** $P < 0.001$; ns: not significant.

F_{spring} =2.20***, F_{summer} = 1.67***; P content: F_{spring} =1.98***, F_{summer} = 1.46***) (Table 2). Plant biomass and P content increased with P addition, but the extent of this response differed with genotypes (Table 2). Applying the same classification method to plant biomass and P content at the vegetative stage, we found that the distribution pattern of plants in the four efficiency classes using P content as an indicator was similar to that using biomass as an indicator, suggesting that P acquisition is closely related to plant biomass in the field (Table 3). Furthermore, both biomass and P content showed a similar pattern to seed yield, indicating P efficiency at maturity is also closely related to plant biomass and P content at the vegetative stage.

(2) Relationship between root architecture and biomass, P content, and yield in soybean. According to the classification criteria for root architecture (see above), three root types were defined in the field: Type A: shallow root, Type B: deep root, and Type C: intermediate root. In the spring season, type A, B and C accounted for 23.1%, 24.9% and 52.0% of the total genotypes, respectively. Because of the dry climate in the summer, the roots of soybean tended to be deeper. Type B increased to 44.0%, while type C decreased to 29.4%, but type A remained largely unchanged (26.6%) (Table 3).

Using seed yield as an indicator, a large percentage of the type A (shallow root) genotypes (46.9% in the spring season and 54.7% in the summer season) were classified as type Ⅲ (P efficient, high responsive) (Fig. 2; Table 3), showing that shallow root plants had higher P efficiency and greater yield potentials. Another considerable portion of shallow root genotypes also distributed in type Ⅳ (P efficient, low responsive), indicating that plants with shallower root architecture generally had higher P efficiency. Moreover, genotypes with deep root architecture were mainly classified as type Ⅰ (P inefficient, low responsive) (Table 3), showing relatively low P efficiency and less yield potential. Similar patterns were found for genotypes in the summer season.

Such a tendency was also observed for the relationship between root architecture and biomass or P content at the vegetative stage. Shallow root genotypes were mostly classified into type III (with biomass as an index, 43.7% in the spring season and 41.3% in the summer season; with P content as an index, 51.6% in the spring season and 38.7% in the summer season). On the other hand, type B genotypes with deep root architecture were mainly classified as type I (Table 3), indicating that the relationship between plant growth and root architecture at the vegetative stage may resemble that at maturity stage.

(3) Relationship between root architecture and total root length. It was found that most shallow root genotypes have longer total root length than the deep root genotypes. Taking the root length in the spring season as an example: without P addition, the average root length of shallow root genotypes was 728 cm, but that of deep root genotypes was only 433 cm. With P added to the topsoil layer, the roots of the tested genotypes tended to be shallower and longer, and the average root length of the shallow root genotypes was 752 cm, contrasting to that of only 529 cm for the deep root genotypes, showing the general tendency that shallow root genotypes have longer root length. It is worthy to mention that under both low and high P conditions, total root length was significantly correlated with P content at the vegetative stage in the spring season, indicating that the total root length significantly contributed to P uptake (Fig. 3). But in the summer, the correlation between root length and P content became less significant, probably due to some other factors rather than P availability, such as drought (Figs. 3(b) and (d)).

(ii) Experiment Ⅱ

(1) Relationship between shoot architecture and root architecture in soybean genotypes differing in the degree of evolution. Based on the phenotypic characters, the tested soybean genotypes were divided into the following 3 types with decreasing degree of evolution: cultivated, semi-wild and wild type. Each type differed in shoot architecture. The cultivated type had a bush shoot architecture with shorter shoot height, the wild type had a climbing shoot architecture with taller shoots, and the semi-wild type had an intermediate shoot architecture and shoot height in between the above two. Our results indicated that there was a close relationship between root architecture and shoot architecture in the tested soybean genotypes. Without P addition, most cultivated genotypes had shallower roots and most wild genotypes had deeper roots, and the semi-wild genotypes were mostly intermediate, indicating that the evolutionary pathway of soybean root architecture could be from deep to shallow. However, some semi-wild genotypes became shallow-rooted when P was applied to the topsoil, indicating a preferred proliferation of roots to the P fertilizer zone (Fig. 4). This sug-

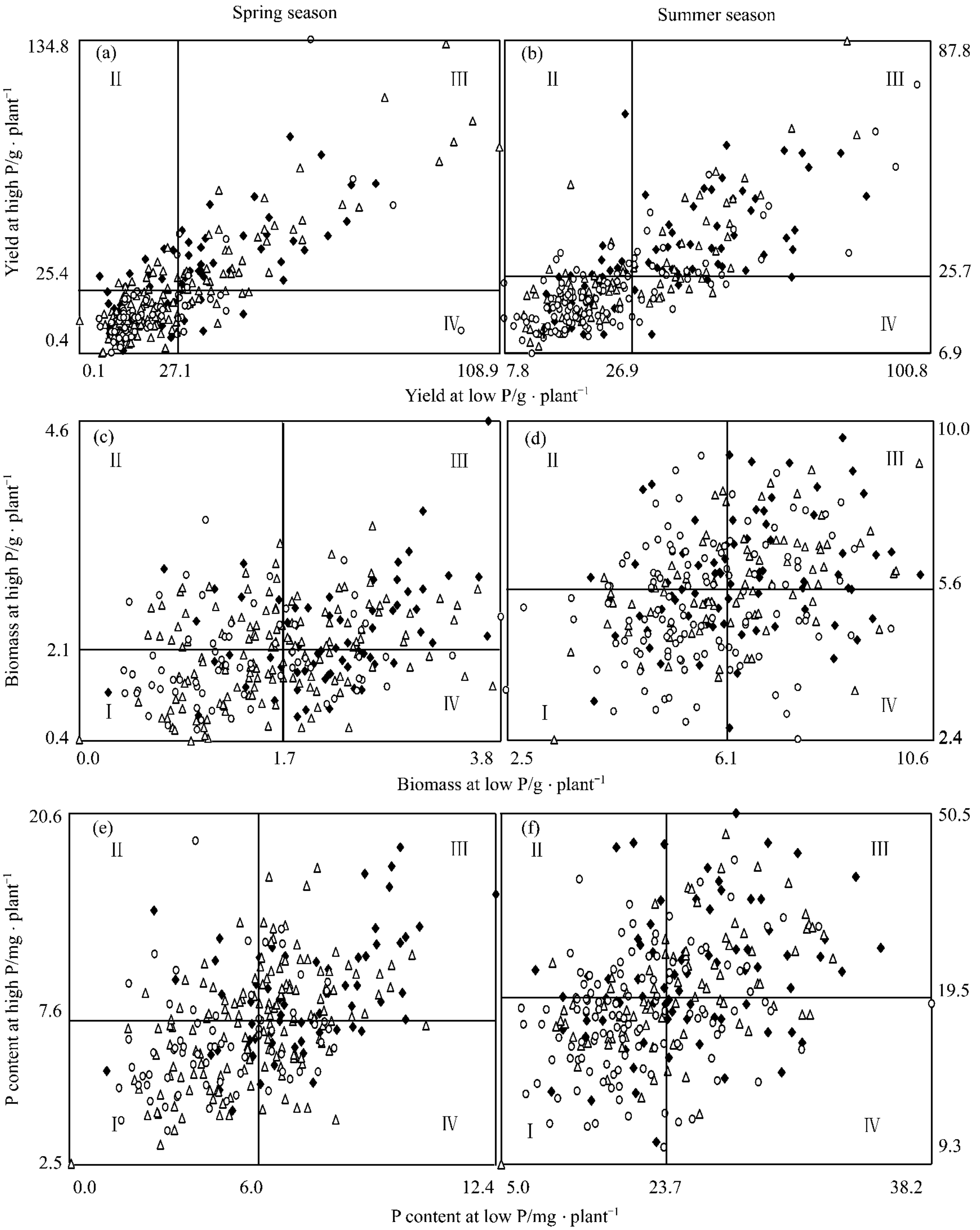

Fig. 2. Relationship between root architecture and P efficiency using yield, biomass and P content as indicators in the applied core germplasm experiment. (a)—(f) is yield, biomass and P content in spring and summer season, respectively. ◆, △, and ○ represents shallow, intermediate and deep root architecture. The dividing lines are the means of the corresponding data at the same P level. Each point is the mean of four replicates.

gested that root architecture could vary with changing soil conditions.

(2) Relationship between root length and root architecture in soybean genotypes differing in the degree of evolution. The total root length differed significantly among three evolutionary types (F = 13.22***), showing a general rank of the cultivated type > the semi-wild type > the wild type (Table 4 and Fig. 5). Similar to Experiment I, genotypes with shallow root architecture had longer root length than genotypes with deep root architecture.

Table 3 Distribution of different root architecture types in different P efficiency classes as measured by biomass, P content and yield

	Root architecture	P Efficiency									
		Spring					Summer				
		I	II	III	IV	Total	I	II	III	IV	Total
Biomass	Type A	9(14.1%)*	8(12.5%)	33(51. 6%)	14(21.9%)	64(23.1%)	16(21.3%)	15(20.0%)	29(38.7%)	15(20.0%)	75(26.6%)
	Type B	38(55.1%)	9(13.0%)	9(13.0%)	13(18.8%)	69(24.9%)	64(51.6%)	23(18.6%)	18(14.5%)	19(15.3%)	124(44.0%)
	Type C	46(31.9%)	21(14.6%)	52(36.1%)	25(17.4%)	144(52.0%)	30(36.1%)	9(10.8%)	31(37.4%)	13(15.7%)	83(29.4%)
	Total	93(33.6%)	38(13.7%)	94(33.9%)	52(18.8%)		110(39.0%)	47(16.7%)	78(27.7%)	47(16.7%)	
P content	Type A	8(12.5%)	6(9.4 %)	28(43.7%)	22(34.4%)	64(23.1%)	19(25.3%)	13(17.3%)	31(41.3%)	12(16.0%)	75(26.6%)
	Type B	33(47.8%)	14(20.3%)	8(11.6%)	14(20.3%)	69(24.9%)	50(40.3%)	31(25.0%)	22(17.7%)	21(16.9%)	124(44.0%)
	Type C	47(32.6%)	35(24.3%)	36(25.0%)	26(18.1%)	144(52.9%)	25(30.1%)	13(15.7%)	31(37.3%)	14(16.9%)	83(29.4%)
	Total	88(31.8%)	55(19.9%)	72(26.0%)	62(22.4%)		94(33.3%)	57(20.2%)	84(29.8%)	47(16.7%)	
Yield	Type A	21(32.8%)	9(14.1%)	30(46.9%)	4(6.3%)	64(23.1%)	20(26.7%)	9(12.0%)	41(54.7%)	5(6.7%)	75(26.6%)
	Type B	49(71.0%)	1(1.4%)	7(10.1%)	12(17.4%)	69(24.9%)	85(68.5%)	7(5.6%)	22(17.7%)	10(8.1%)	124(44.0%)
	Type C	81(56.6%)	12(8.4%)	42(29.4%)	8(5.6%)	143(51.6%)	42(50.6%)	7(8.4%)	23(27.7%)	11(13.3%)	83(29.4%)
	Total	151(54.5%)	22(7.9%)	79(28.5%)	24(8.6%)		147(52.1%)	23(8.2%)	86(30.5%)	26(9.2%)	

Note: 1) the number in the table represents the number of genotypes with different root architecture distributed in different P efficiency classes as measured by biomass, P content and yield. Numbers in parentheses represent its relative percentage to the total genotypes tested. 2) A, B and C represent shallow, deep and intermediate root architecture, respectively. 3) I, II, III and IV represent P inefficient, low responsive; P inefficient, high responsive; P efficient, high responsive; and P efficient, low responsive, respectively.

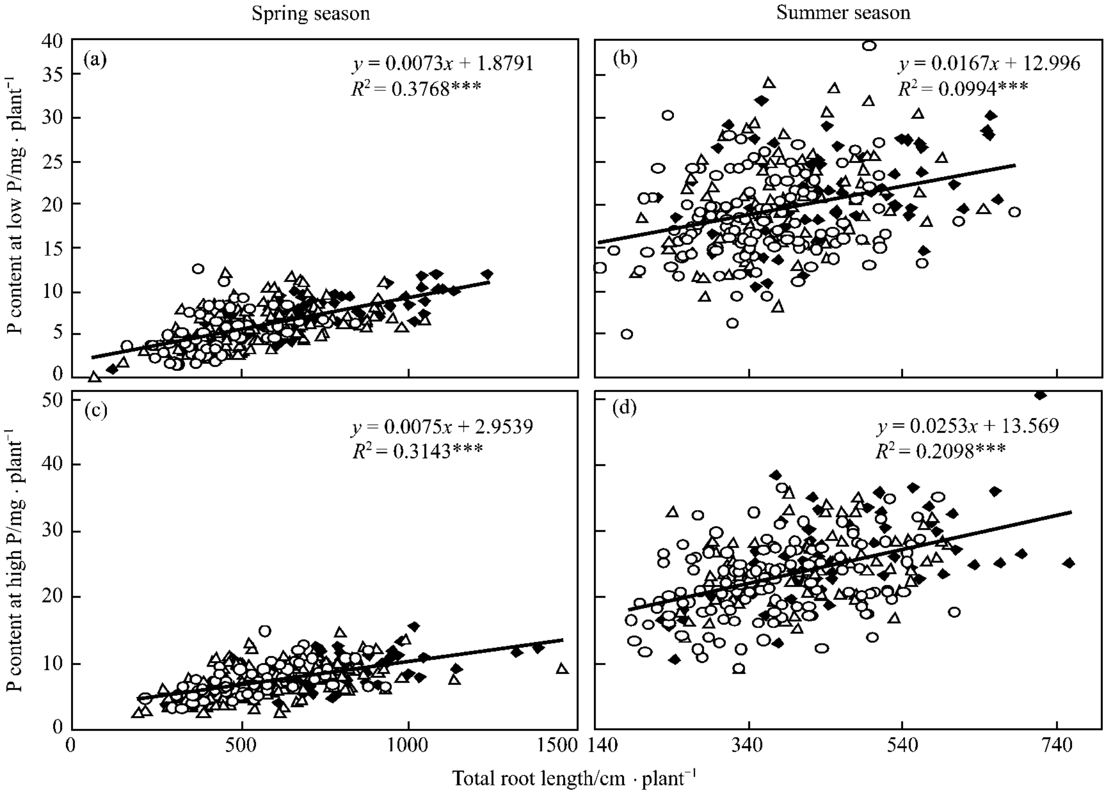

Fig. 3. Correlation between P uptake efficiency and root length in the applied core germplasm experiment (experiment I). (a) and (b) represent the correlation between P content and root length at low P level in spring and summer, respectively; (c) and (d) for the correlation at high P level. ◆, △ and ○ represents shallow, intermediate and deep architecture, respectively. Each point is the mean of four replicates.

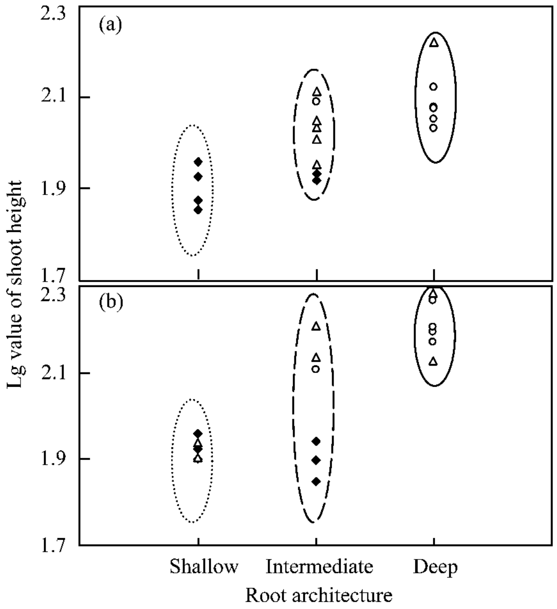

Fig. 4. Relationship between root architecture and shoot height (Lg value) in the Experiment Ⅱ. (a) and (b) are the treatments without P and with P addition in the topsoil. Each point is the mean of four replicates. ◆, Cultivated; △, semi-wild; ○, wild.

Phosphorus availability significantly affected biomass and P content but not total root length of the tested soybean genotypes based on in-group analysis, indicating that total root length might not be directly related to the increased biomass and P content caused by P treatment. Instead, the increased biomass and P content could be attributed to the altered spatial configuration of roots (or root architecture), resulting in more root distribution in the P-rich topsoil and thus higher P acquisition.

(3) Variation for P efficiency in three evolutionary types. Both plant biomass and P content showed the pattern of the cultivated type > the semi-wild type > the wild type with or without P addition ($F_{\text{biomass}}=89.76^{***}$ and $F_{\text{P content}}=72.99^{***}$) (Table 4 and Fig. 6). Based on the classification method by Lynch[28], the cultivated genotypes with shallow roots were mainly distributed in type Ⅲ (P efficient, high responsive), while the wild genotypes with deep roots were mainly in type Ⅰ (P inefficient,

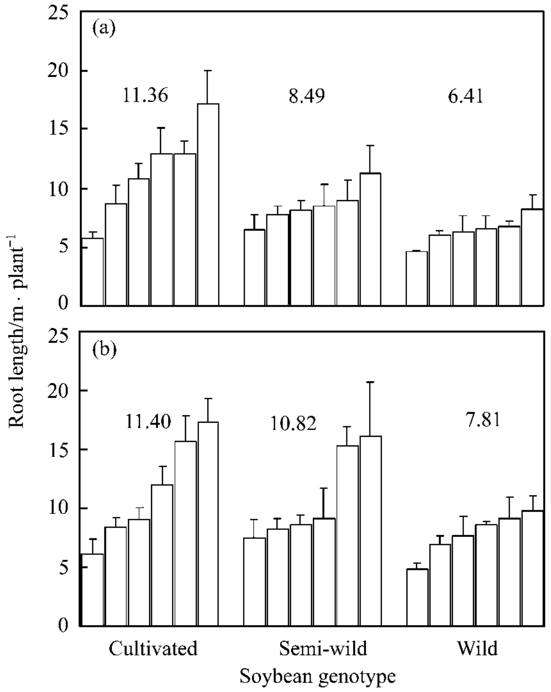

Fig. 5. Root length at two P levels in the Experiment Ⅱ. (a) and (b) are the treatments without P and with P addition in the topsoil. Data on the top of each group of bars are the means of root length of genotypes in each evolutionary type. Each point is the mean of four replicates with standard error.

Table 4 ANOVA results of the growth parameters through in-group and between-group analysis in Experiment II

			Shoot height	Root length	Biomass	P content
Between-group		G	42.91^{***}	13.22^{***}	89.76^{***}	72.99^{***}
		P	12.49^{***}	3.42 ns	33.27^{***}	42.84^{***}
		G × P	5.21^{**}	0.94 ns	1.03 ns	1.35 ns
In-group	G1	V	0.38 ns	10.82^{***}	2.91^{*}	2.60^{*}
		P	0.01 ns	0 ns	11.42^{**}	15.93^{***}
		V × P	1.02 ns	1.33 ns	0.50 ns	0.26 ns
	G2	V	2.62^{*}	2.26 ns	3.36^{*}	3.21^{*}
		P	1.63 ns	3.96 ns	17.99^{**}	19.37^{***}
		V × P	0.30 ns	1.99 ns	0.83 ns	0.86 ns
	G3	V	1.19 ns	2.14 ns	2.21 ns	1.91 ns
		P	21.00^{***}	5.24^{*}	15.16^{***}	17.65^{***}
		V × P	0.46 ns	1.91 ns	0.94 ns	0.98 ns

Note: Data in the table are F values from two-way ANOVA; Between-group analysis: G, P and G × P represent genotype, P level and interaction between genotype and P level, respectively; In-group analysis: G represents soybean genotypes with different evolutionary degree. G1, G2 and G3 represents cultivated, semi-wild and wild type, respectively; V, P and V×P represent genotype, P level and interactions between genotype and P level, respectively; *, $0.05 > P > 0.01$; **, $0.01 > P > 0.001$; ***, $P < 0.001$; ns means not significant.

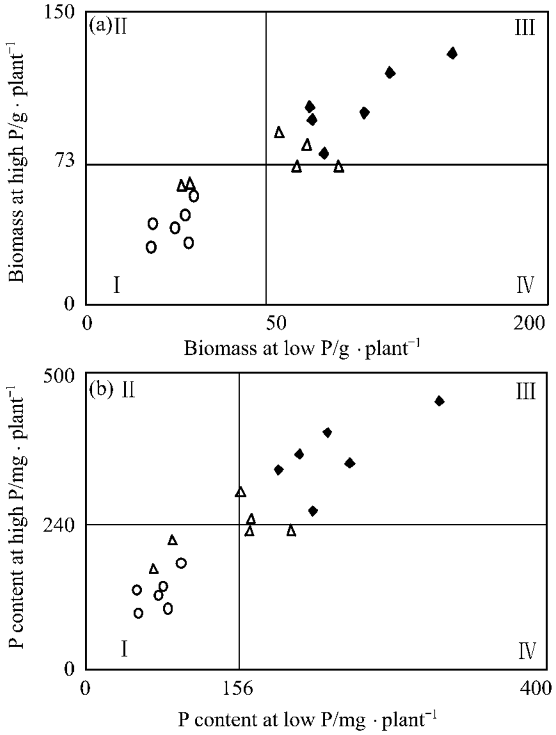

Fig. 6. Relationship between P efficiency and root architecture in the Experiment II. (a) and (b) are biomass and P content. ◆, △ and ○ represents the cultivated, semi-wild and wild type, respectively. Each point is the mean of four replicates.

low responsive), and the semi-wild genotypes were distributed everywhere in type I, III and IV. Such a tendency was similar to that in Experiment I.

3 Discussion

Our study was the first attempt to systematically evaluate an “applied core collection” of soybean germplasm for root architecture, an important root character. We found a close relationship between soybean root architecture and P efficiency: shallow root architecture had an optimal three-dimension distribution in the soil, which might facilitate soybean to absorb P from soil thus leading to a higher P efficiency and yield. Root architecture determines the distribution of the whole root system in the different soil layers, hence may affect soil exploration and exploitation of nutrients (especially for nutrients with low mobility, such as P) and in the end affect plant nutrient acquisition efficiency, biomass and yield[12,13]. It is well known that available P mainly concentrates in the topsoil (cultivated layer) because of soil weathering, organic residue accumulation and long-term fertilization[29—32]. The soil chemical analyses in our two experimental field sites also showed that the available P content in the cultivated layer is much higher than that in the subsoil (Table 1). It is worth mentioning that although the available P of the cultivated layer in the field site was about 17 mg/kg, the plants still suffered from P deficiency. As was reported in ref. [5], the nutrient concentration in the soil from chemical extraction may not exactly represent the real soil nutrient status because of the differences in soil physical and chemical properties, and therefore only the actual plant response can really represent soil nutrient status. In fact, soybean yield was significantly increased by P addition (Table 2), showing that the soil in our experimental field site was still P deficient. If the soil is P deficient, but the cultivated layer with relatively more available P, it is reasonable to assume that the more the roots in the topsoil (shallower root system), the more P would be absorbed by plants from the cultivated layer. This has previously been shown in both theoretical and experimental work. Through computer simulation, Rubio et al.[33,34] demonstrated that among different types of root architectures, the shallow root architecture was more beneficial for plant to absorb nutrient in the cultivated soil. With systematic studies in paper pouch, stratified soil and sand culture, it was found that shallow root architecture improved the adaptation of common bean to low P availability[15,17]. The results of our field experiments also showed that soybean with shallow root architecture had higher P efficiency than that with deep root architecture or intermediate root architecture (Figs. 2 and. 6). Shallow root architecture would allow soybean plants to absorb more P in the cultivated soil layer, resulting in higher P efficiency and better growth hence higher yield. On the other hand, deep root system might be disadvantageous for P uptake from the cultivated soil layer, resulting in low P acquisition efficiency hence low yield. Taken together, these results showed that root architecture is an important agronomic trait that should not be neglected in the future breeding work. The plant materials used in the experiment were selected from an applied core collection of soybean germplasm from more than 20000 accessions. Therefore, they are highly representative of the soybean genetic diversity in China. If different plant materials were used, the dividing lines in Fig. 2 might be changed, but the distribution pattern of soybean root architecture as related to P efficiency would not necessarily change.

Another major finding of this study was that root architecture might be closely related to shoot architecture. Based on the evolutionary degree, soybean could be divided into 3 types, including cultivated, semi-wild and wild soybean with corresponding shoot architectures (bush, climbing and semi-climbing). Interestingly, there was a close relationship between root architecture and shoot architecture among different evolutionary types. The bush, climbing and semi-climbing genotypes had shallow, deep and intermediate root architecture, respectively. This indicates that a co-evolutionary relationship might exist between shoot architecture, root architecture and P efficiency. The bush cultivated soybean generally had shallow root architecture and high P efficiency, the climbing wild soybean had deep root architecture and low P efficiency, and the semi-wild soybean had intermediate root architecture and P efficiency. From the evolutionary point of view, wild soybean had climbing growth habit with deep root architecture in order to acquire enough light, water and essential elements[22,23]. Nevertheless, in the evolutionary process from wild type to cultivar, root architecture became shallower and P efficiency higher. This might have resulted from a long-term human domestication and fertilization to the topsoil. Plant root growth might preferentially proliferate to upper fertilizer zone and root architecture evolves gradually from deep to shallow. Our results also support this point. Based on biomass and P content, no significant variations were observed in the wild genotypes, but significant variations existed in both semi-wild and cultivated genotypes (Table 4), suggesting that the direction of evolution for root architecture and P efficiency might have resulted from human selection. Under natural soil conditions, although the nutrient content in the topsoil could be higher than that in the subsoil, root architecture might not be changed without the effects of concentrated fertilizers supplied in the topsoil. On the other hand, some cultivated genotypes might have deep root architecture if they had a long-term growth in the less cultivated soils with little fertilization or no fertilization, or in the drought or semi-drought areas where water became the primary constraints to soybean growth.

From the view of germplasm resource utilization, deep root architecture would be helpful for improving plant drought resistance, in which case wild species and some cultivars with deep root architecture would be useful genetic resources. On the other hand, shallow root architecture can facilitate plant to absorb nutrients mainly distributed in the topsoil, and therefore cultivars with shallow root architecture could be used for improving plant nutrient (particularly P) efficiency. Combining those two types of root architecture, we might develop an ideal root architecture—“umbrella-shape” root system, which could facilitate not only nutrient uptake in the topsoil, but also water uptake in the subsoil[30]. In our study, drought was an important limiting factor to soybean growth in the dry summer season, and the tested genotypes tended to grow deeper for water uptake. Therefore, the percentage of type C (intermediate root type) genotypes dropped from 52.0% in the spring to 29.4% in the summer and that of type B increased from 24.9% in the spring to 44.0% in the summer (Table 3), indicating that beside genetic effects, the root growth environment could also influence soybean root architecture. Moreover, since large yearly or seasonal variations might exist in the field trials, results of some genotypes might vary from year to year, as demonstrated by our different results between spring and summer seasons in Table 3. Therefore, some of the present results need to be further verified.

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