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Evaluation by grafting technique of changes in the contribution of root-to-shoot development and biomass production in soybean (*Glycine max*) cultivars released from 1929 to 2006 in China

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Abstract. Root traits are essential for optimising nutrient and water absorption and anchorage. However, changes in root traits and the contribution of root-to-shoot growth and development of soybean (*Glycine max* (L.) Merr.) across a century of breeding are poorly documented. In this study, we adopted a grafting technique, using 55 cultivars released in the three main soybean-production regions in China as rootstocks in a pot experiment and 24 cultivars from the Yellow-Huai-Hai Valley (YHH) region as rootstocks in a field experiment, with cv. Zigongdongdou as the common scion. Changes in soybean roots, including dry weight (DW) of roots, lateral root number (LRN) and taproot length (TRL), and their contribution to shoot development and biomass formation, including shoot DW, plant height and node number, were evaluated under optimal conditions in 2011. Aboveground traits declined with year of release in the YHH region and did not vary over time in the northern Heilongjiang province and mid-south Heilongjiang region except for shoot DW. The root traits root DW, LRN and TRL were similar over years of release in the pot and field experiments. The results suggest that the newer cultivars have lesser shoot growth and root capacity but the same amount of root growth as older cultivars. Root traits did not change during selection, suggesting that improvement in soybean root traits should be an aim in future breeding.

Additional keywords: evolutionary change, root traits, shoot, soybean.

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Introduction

Root traits are essential for optimising nutrient and water absorption, and for anchorage (Laplaze *et al.* 2007; Manavalan *et al.* 2010). The soybean (*Glycine max* (L.) Merr.) root system includes primary roots (taproot) and lateral branches (lateral roots). The taproot plays an important role in deep rooting ability (Kaspar *et al.* 1984); increased root length can delay drought stress and other abiotic stresses (Fenta *et al.* 2014). Root architecture determines the spatial distribution of roots in soil, including their shape and structure. Roots are quantified by measurements such as root length, lateral root numbers and root depth (Hodge *et al.* 2009).

Photosynthesis in the shoots and water and nutrient absorption in the roots are integrated processes for crop growth, such that the shoot and root systems interact during plant growth (Yan 2007). Differences in root traits between cultivars may result from differences in shoot capacity and vice versa. In a study by Liang *et al.* (2009), total root length, root surface area, root dry weight and root phosphorus (P) content of two contrasting soybean genotypes, cv. BD2 and cv. BX10, and their 106 F_9-derived recombinant inbred lines (RILs) were closely associated with aboveground biomass and yield. Cardwell and Polson (1972) grafted a single cultivar to rootstocks of a diverse collection of genotypes

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and showed that the scion played an important role in determining seed weight, oil and protein content, and maturity whereas the root had a determinant role in lodging, height and seed yield.

Numerous methods have been developed for studying root systems, including phenotypic root scoring, hydraulic soil excavation, automatic root-volume location method, soil core sampling, root box method, volumetric method, and isotope tracer method (Gross 1995; Lindsey *et al.* 1995; Pantalone *et al.* 1996; Liao *et al.* 2001, 2004; Lontoc-Roy *et al.* 2005; Yan 2007; Pivetta *et al.* 2011). However, excavation of roots is labour-intensive and time-consuming, and finding a non-destructive and large-scale technique remains challenging for the assessment of root traits (Fenta *et al.* 2014). Measuring soil-water content by using buried sensors and probes can infer root activity, and has been adapted in many studies (Han *et al.* 2012; Shanahan *et al.* 2015; White *et al.* 2015; Whalley *et al.* 2017). Establishing a method for phenotyping the root system is a prerequisite for root research, and phenotyping root function rather than root morphology has a promising future. The intact soybean root system has been used in studies of different aspects of root gene function and nutrient uptake. Liao *et al.* (2006) applied a uniform hydroponic medium to the entire root system to study P and aluminium (Al) interactions in soybean. Intact soybean roots were also studied in the overexpression and knockdown of a homogeneous transformation system for gene (*GmEXPB2*) function in root growth and P uptake in response to inorganic P deficiency (Guo *et al.* 2011). In addition, the intact root system was used for studying kinetics of potassium (K) and magnesium (Mg) uptake (Joseph and Hai 1976*a*) and phosphate uptake (Joseph and Hai 1976*b*) in soybean, as well as for studying the degradation and utilisation of exogenous allantoin in a hydroponic growth system (Imsande 1986).

As the centre of origin for soybean, China is also a primary centre for modern soybean breeding. In the past century through to 2015, more than 2400 soybean cultivars were developed in China (Wang *et al.* 2016). During this time, yield, agronomic and phenological traits of soybean have markedly improved (Zheng *et al.* 2006; Tian *et al.* 2007; Zhao *et al.* 2008, 2012; Xu *et al.* 2011; Wang *et al.* 2015; Wu *et al.* 2015; Qin *et al.* 2017). Modern soybean varieties tend to have greater root weight, root volume, root surface and lateral root length than older varieties (Yang *et al.* 2001). The weight of root exudates has also increased with year of release (Sun *et al.* 2012). However, few studies have documented the improvements in root features that contribute to shoot growth and development, and biomass production.

In this study, we adopted a grafting system to examine the overall capacity of roots to contribute to shoot growth, using the same scion to exclude genetic differences in performance, for a range of soybean cultivars released from 1929 to 2006 in China. The objectives of this study were: (*i*) to establish a method for studying the intact root system by using the same scion in a grafting technique; and (*ii*) to evaluate changes in soybean root traits and their contribution to shoot development and biomass formation during the last century of breeding in China. Our results will provide theoretical and technical support for the improvement of soybean varieties.

Materials and methods

Plant materials

Fifty-five widely grown soybean cultivars released from 1929 to 2006 in China were used as rootstocks (Table 1). These cultivars originated from three major soybean-producing regions in China: northern Heilongjiang province (NH) (13 cultivars), mid-south Heilongjiang region (MSH) (18 cultivars), and Yellow-Huai-Hai Valley region (YHH) (24 cultivars) (Wang *et al.* 2013, 2015, 2016). A late-maturing cultivar, Zigongdongdou (ZGDD), from South China (maturity group (MG) X) (Wu *et al.* 2006; Jia *et al.* 2011), was used as the common scion (Supplementary Materials fig. S1, available at the journal's website). ZGDD could retain vegetative growth throughout the experiment, and could therefore uniformly reflect biomass production without the influence of energy consumption of the reproductive period, as well as avoiding interference from aboveground differences, thereby accurately reflecting the function of root system.

Cut-in grafting method

The cut-in grafting method has been documented previously (Pantalone *et al.* 1999; Cao *et al.* 2013). After the cotyledons of the rootstock had expanded, the apical meristem of the seedlings was removed, and a bamboo toothpick was inserted into the hypocotyl of the young stem to 2 cm to make a hole (Supplementary Materials fig. S2*a*–*c*). A section of scion cultivar stem 1.5–2.0 cm long with a wedge-shaped end (Supplementary Materials fig. S2*d*–*e*) was inserted into the top centre of the rootstock. The grafting joint zone was wrapped with laboratory film (Parafilm; Beamis, Neenah, WI, USA) (Supplementary Materials fig. S2*f*), and the grafted seedlings were covered with plastic bags to recover for 3–4 days. The mean survival rate of cut-in grafts was >90% (Supplementary Materials fig. S3*a*, *b*) (Cao *et al.* 2013). After recovery, the grafted seedlings were transplanted into larger pots or the field.

Experimental design

Pot experiment

A pot experiment was performed at the Chinese Academy of Agricultural Sciences (CAAS) campus and followed a randomised complete block design with three replications. Five seeds for the scion and rootstock plants were sown in pots (9 cm top diameter, 9 cm height) filled with vermiculite on 5 May and 9 May 2011, respectively. After the grafting process and recovery, five grafted plants with uniform height and establishment from each pot were transplanted to larger pots (21 cm top diameter, 18 cm height) (Supplementary Materials fig. S3). The soil volume was uniform from pot to pot. The plants were managed routinely to prevent water stress and pest attack. The experiment was concluded on 18 August 2011, when the scion was still in vegetative growth. At that time, the aboveground and belowground parts of the grafting union were cut and separated.

Field experiment

The field experiment was carried out at the Changping Experimental Station of the Institute of Crop Sciences,

Table 1. Region, year of cultivar release, and maturity group of soybean cultivars in this study
NH, Northern Heilongjiang region; MSH, mid-south Heilongjiang region; YHH, Yellow-Huang-Huai-Hai Valley region

Region	Cultivar	Year of release	Province	Maturity group	Region	Cultivar	Year of release	Province	Maturity group
NH	Zihua 4	1941	Heilongjiang	0	YHH	Haiyang pawanqing	1929	Shandong	IV
NH	Heilongjiang 41	1958	Heilongjiang	0	YHH	Shangcaiercaopingdingshi	1940	Henan	IV
NH	Kexi 283	1956	Heilongjiang	0	YHH	Hezeniumaohuang	1950	Shandong	IV
NH	Heihe 3	1966	Heilongjiang	00	YHH	Yidupingdinghuang	1951	Shandong	IV
NH	Fengshou 10	1966	Heilongjiang	00	YHH	Xinhuangdou	1952	Shandong	IV
NH	Fengshou 12	1969	Heilongjiang	0	YHH	Juxuan23	1963	Shandong	IV
NH	Fengshou 17	1977	Heilongjiang	00	YHH	Qihuang10	1966	Shandong	III
NH	Beifeng 2	1983	Heilongjiang	000	YHH	Yanhuang 1	1973	Shandong	IV
NH	Fengshou 19	1985	Heilongjiang	0	YHH	Fengshouhuang	1971	Shandong	IV
NH	Heihe 9	1990	Heilongjiang	0	YHH	Wenfeng 7	1971	Shandong	IV
NH	Beifeng 9	1995	Heilongjiang	0	YHH	Yejin 5	1975	Shandong	IV
NH	Heihe 38	2005	Heilongjiang	0	YHH	Youbian 30	1983	Beijing	IV
NH	Beidou 5	2006	Heilongjiang	0	YHH	Jidou 4	1984	Hebei	III
MSH	Jinyuan 2	1941	Heilongjiang	0	YHH	Ludou4	1985	Shandong	III
MSH	Mancangjin	1941	Heilongjiang	0	YHH	Yudou 2	1985	Henan	IV
MSH	Jingshanpu	1958	Heilongjiang	0	YHH	Zhongdou 19	1987	Hebei	IV
MSH	Zhi 2	1958	Heilongjiang	0	YHH	Kefeng 6	1988	Beijing	III
MSH	Dongnong 4	1959	Heilongjiang	0	YHH	Ludou 11	1995	Shandong	III
MSH	Hejiao 6	1963	Heilongjiang	I	YHH	Jidou 7	1992	Hebei	III
MSH	Suinong 3	1973	Heilongjiang	0	YHH	Yudou 22	1997	Henan	IV
MSH	Hefeng 22	1974	Heilongjiang	0	YHH	Jidou 12	2001	Hebei	III
MSH	Heinong 26	1975	Heilongjiang	I	YHH	Zhonghuang13	2001	Beijing	III
MSH	Suinong 4	1981	Heilongjiang	0	YHH	Zheng 92116	2001	Beijing	IV
MSH	Hefeng 25	1984	Heilongjiang	0	YHH	Handou 5	2004	Hebei	III
MSH	Heinong 33	1988	Heilongjiang	0					
MSH	Heinong 35	1990	Heilongjiang	0					
MSH	Hefeng 35	1994	Heilongjiang	0					
MSH	Suinong 14	1996	Heilongjiang	I					
MSH	Heinong 44	2002	Heilongjiang	0					
MSH	Hefeng 45	2003	Heilongjiang	0					
MSH	Hefeng 50	2006	Heilongjiang	0					

CAAS, in a completely randomised design with three replications. Twenty-four cultivars from the YHH region were used as rootstocks (Table 1). The soil type in Changping is fluvo-aquic (Avery 1973). Eight seeds of the scion cultivar and five seeds of each rootstock plant were sown in each pot (replication) on 22 May and 26 May 2011, respectively. After the grafting process and recovery, uniform plants were transplanted to the field on 18 June 2011, with a row spacing of 0.9 m and hill spacing of 0.9 m, with five plants in each hill (Supplementary Materials fig. S3d). Plants were harvested on 19 September 2011.

Data collection and measurements

At the end of each experiment, all plants in each pot in the pot experiment or in the field experiment were harvested for measurement of plant height (PH), node number (NN) and shoot dry weight (SDW). PH referred to the height of the grafted part from the cotyledonary node to the terminal growing point, and NN was the number of nodes between the grafting cotyledon node and the top of the terminal growing point. All aboveground parts were collected, and a subset of samples was taken for measuring SDW (biomass) after oven drying at 80°C for 48 h to a constant weight. In the pot experiment, roots were soaked for 2 h in a basin, and soil and impurities were carefully removed from roots by rinsing with clean water. In the field experiment, the roots of five plants in each hill were excavated in a soil block 90 cm in diameter and 45 cm deep for washing and drying. Taproot length (TRL) was measured from the cotyledonary node of stock to the end of the main root tip; lateral root number (LRN) was determined by counting the branched roots emerging from tap and $\geq$3 cm in length; and root dry weight (RDW) was determined after oven drying at 80°C for 48 h (Pantalone *et al.* 1996; Fenta *et al.* 2014).

Data analyses

All measured traits were analysed by analysis of variance (ANOVA), using the GLM model. In the pot experiment, region and cultivar nested within each region were considered fixed factors, and replication a random factor. In the field experiment, cultivar was considered a fixed factor and replication a random factor. A linear regression analysis of trait means with their respective year of stock cultivar release was performed within each region from the pot and field experiments. Pearson's correlation coefficients were estimated for the aboveground and belowground traits. Data were analysed using SAS version 9.2 (SAS Institute, Cary, NC, USA).

Results

Changes in aboveground traits of the scion with year of release of rootstock cultivars from different regions

The ANOVA showed significant differences among the rootstock cultivars for aboveground and below-ground traits in both the pot and field experiments (Supplementary Materials table S1). From the histograms in Fig. 1, node number and plant height showed in a right-skewed distribution, whereas other traits showed approximately normal distribution with a slightly left skew; the self-grafted control ranked in the upper half of each trait. To investigate the effect of rootstock cultivars on aboveground biomass accumulation and genetic improvement over time, the SDW of the common scion ZGDD was regressed against the release year of stock cultivars. In the pot experiment, SDW declined significantly with release year of stock cultivars from the NH region (R^2 = 0.41*), with an annual decrease of 0.14 g plant^{-1} (Fig. 2*a*). From this region, SDW ranged from 9.67 g (cv. Fengshou19, released 1985) to 25.45 g (cv. Zihua 4, 1941). From the MSH and YHH regions, SDW did not vary over time. In the field experiment, SDW declined with year of release of cultivars from the YHH region (R^2 = 0.18*), with an annual decrease of 0.35 g plant^{-1} (Fig. 2*b*). From this region, SDW ranged from 29.09 g (cv. Ludou 4, 1985) to 89.32 g (cv. Juxuan 23, 1963).

In the pot experiment, PH ranged from 52.13 cm (cv. Beifeng 2, released 1983) to 88.80 cm (cv. Fengshou 19, 1985) from the NH region; 18.00 cm (cv. Heinong 44, 2002) to 85.75 cm (cv. Hejiao 6, 1963) from the MSH region; and 61.37 cm (cv. Zhongdou 19, 1987) to 97.83 cm (cv. Wenfeng 7, 1971) from the YHH region. However, the trends with year of release were not significant for any region. In the field, PH ranged from 57.25 cm (cv. Jidou7, 1992) to 93.63 cm (cv. Hezeniumaohuang, 1950) from the YHH region and decreased with year of release of rootstock cultivar (R^2 = 0.44**), with an annual decrease of 0.32 cm (Fig. 3), indicating that older cultivars were taller than newer ones.

In the pot experiment, NN ranged from 9.25 (cv. Beifeng 2, released 1983) to 19.13 (cv. Fengshou 10, 1966) from the NH region; 5.00 (cv. Heinong 44, 2002) to 22.50 (cv. Hejiao 6, 1963, and cv. Hefeng 45, 2002) from the MSH region; and 15.80 (cv. Shangcaiercaopingdingshi, 1940) to 20.65 (cv. Kefeng 6, 1988) from the YHH region. However, the trends with year of release were not significant in any region. In the field experiment, NN ranged from 14.4 (cv. Fengshouhuang, 1971) to 21.8 (cv. Haiyangpawanqing, 1929) from the YHH region, and decreased significantly with year of release (R^2 = 0.23*), with an annual decrease of 0.04 (Fig. 4), suggesting that older cultivars have more nodes than newer ones.

Changes in root traits of rootstock cultivars with year of release

Root traits were regressed against the release year of the rootstock cultivar. The traits TRL, LRN and RDW did not change significantly with year of release in the pot or field

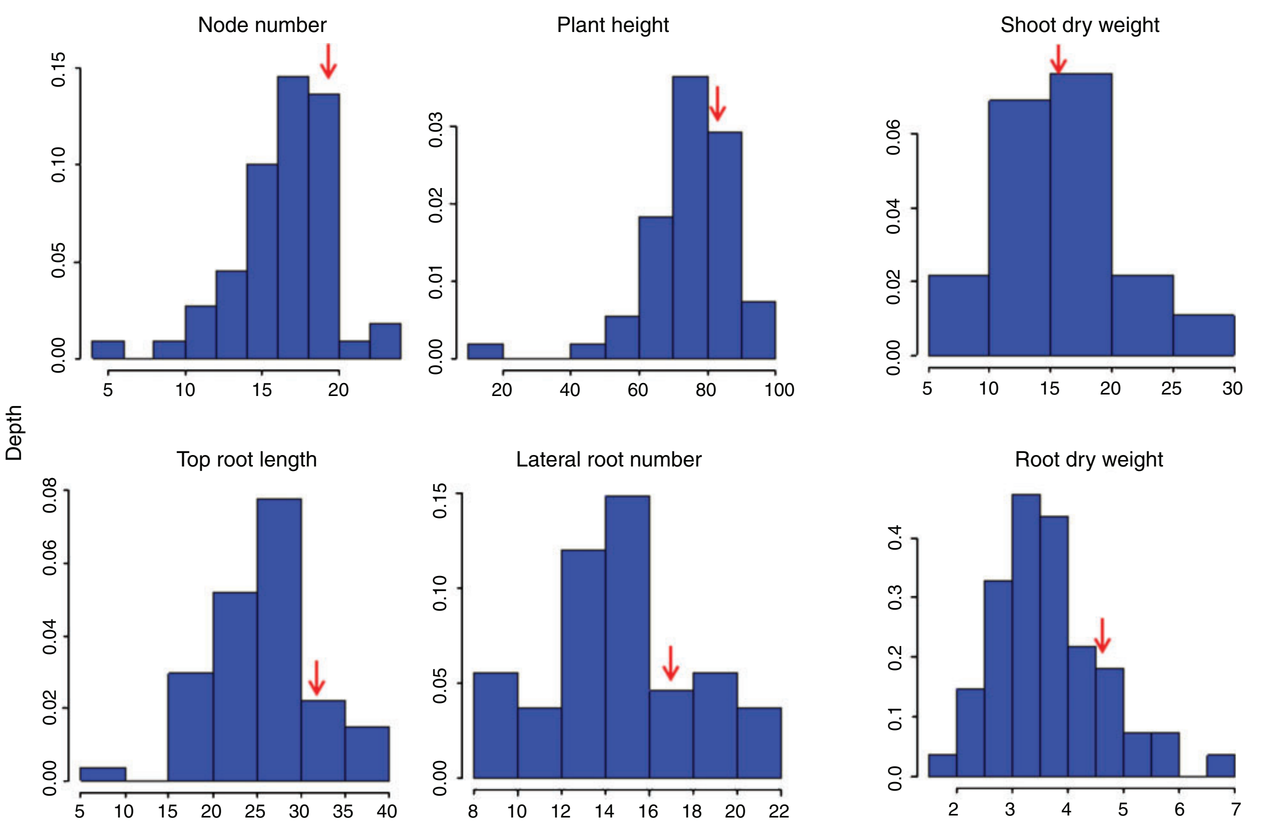

Fig. 1. Histograms of six measured traits. Red arrow indicates values of self-grafted control.

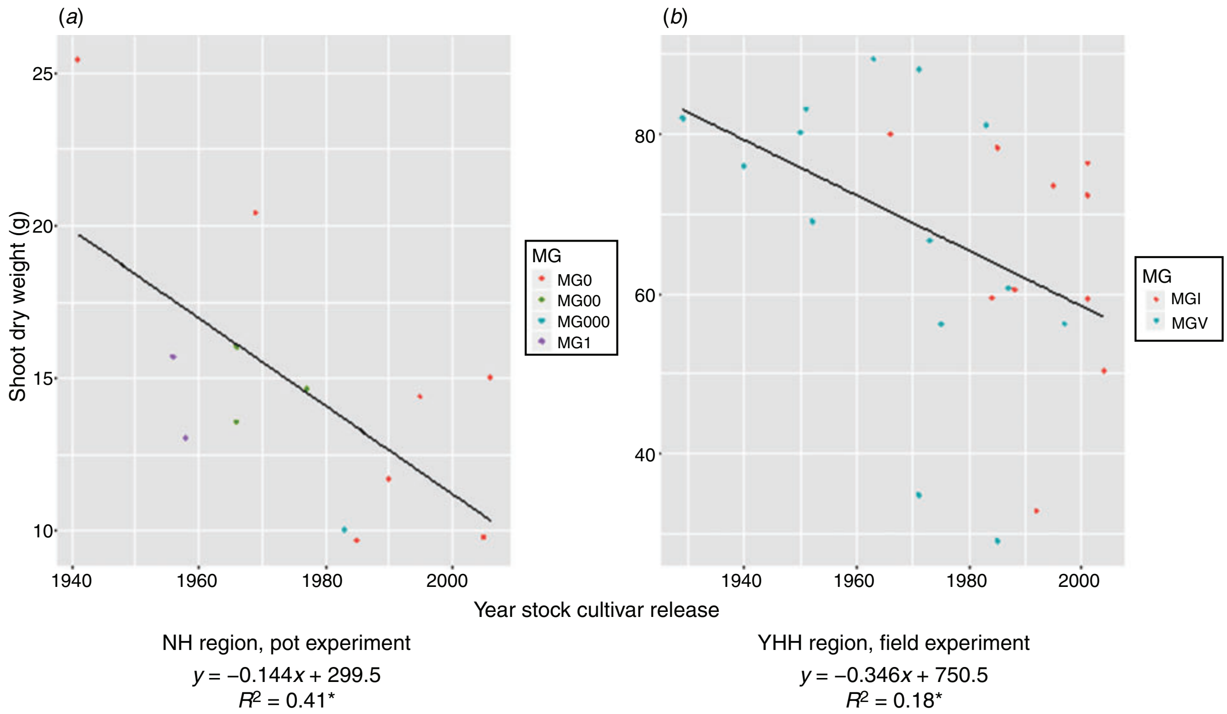

Fig. 2. Change in shoot dry weight (SDW) of the scion grafted onto rootstock cultivars released in different years from (*a*) Northern Heilongjiang (NH) region in the pot experiment, and (*b*) Yellow-Huai-Hai Valley (YHH) region in the field experiment. Lines, equations and their corresponding R^2 values are shown only for significant relationships. *$P < 0.05$; ** $P < 0.01$ for significance of linear correlation coefficient. Different-coloured symbols represent soybean rootstocks of different maturity groups.

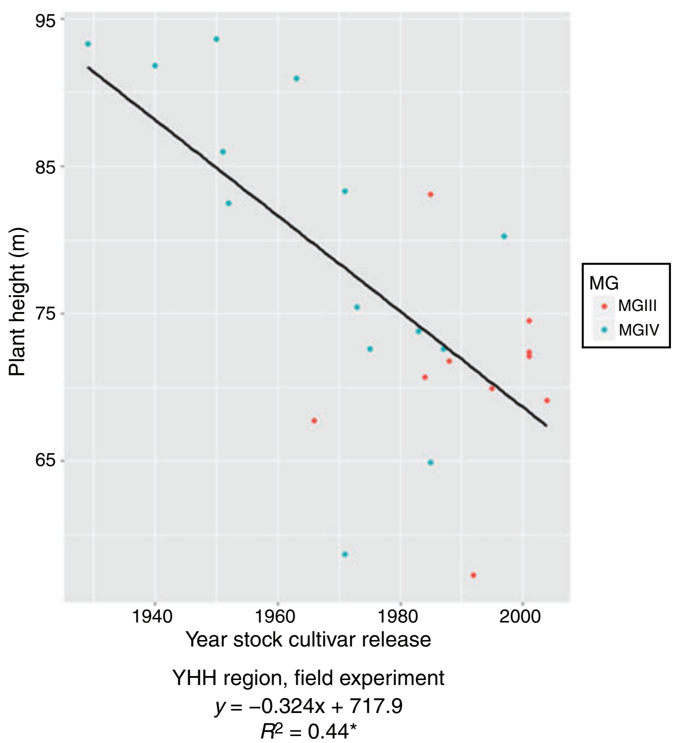

Fig. 3. Change in plant height (PH) of the scion grafted onto rootstock cultivars released in different years from Yellow-Huai-Hai Valley (YHH) region in the field experiment. Lines, equations and their corresponding R^2 values are shown only for significant relationships. *$P < 0.05$; **$P < 0.01$ for significance of linear correlation coefficient. Different coloured symbols represent soybean rootstocks of different maturity groups.

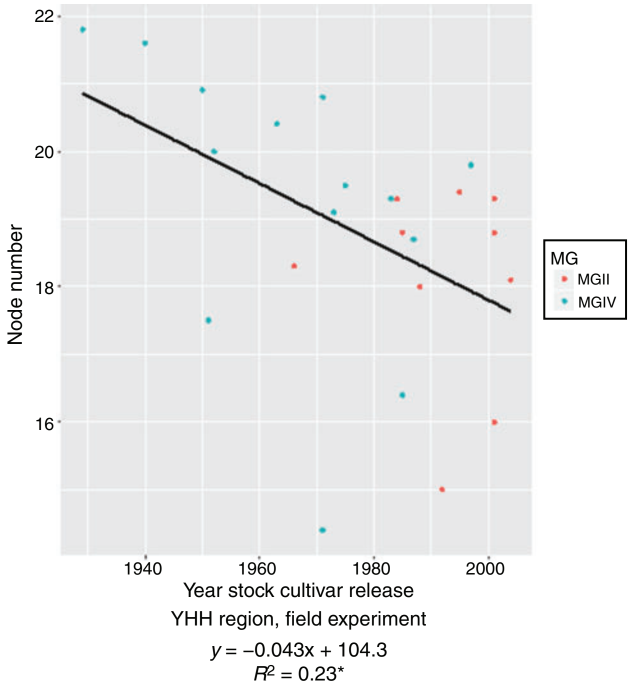

Fig. 4. Change in node number (NN) of the scion grafted onto rootstock cultivars released in different years from Yellow-Huai-Hai Valley (YHH) region in the field experiment. Lines, equations and their corresponding R^2 values are shown only for significant relationships. $^*P < 0.05$; $^{**}P < 0.01$ for significance of linear correlation coefficient. Different coloured symbols represent soybean rootstocks of different maturity groups.

experiment, indicating that these root traits have not been used as selection criteria in soybean breeding in China. This result emphasises the need to continue to improve the soybean root system.

The rootstock soybean cultivars, encompassing 55 widely grown soybean cultivars from three regions in China, had normal root growth at harvest (Fig. 5). Interestingly, root longevity did not differ when using cultivars ranging from MG 000 to MG IV as rootstock. For instance, Beifeng 2 (MG 000), an extremely early-maturing and spring-planting cultivar survived and grew for as long as Yuejin 5 (MG IV), a summer-planting cultivar from the YHH region (Fig. 5*a*, *f*).

Correlation between aboveground and belowground traits

The correlations between shoot and root traits in both the pot and field experiments were positive for all traits (Table 2). In the pot experiment, SDW had significant positive correlations with TRL (0.45, $P < 0.01$), LRN (0.48, $P < 0.01$) and RDW (0.75, $P < 0.01$), suggesting that greater dry weights of shoots are associated with longer taproot, more lateral roots and greater dry weights of roots. RDW was positively correlated with NN (0.37, $P < 0.01$), TRL (0.48, $P < 0.01$), LRN (0.53, $P < 0.01$), indicating that greater dry weights of roots are associated with more nodes, longer taproot and more lateral roots.

The field experiment produced associations similar to, but less significant than, the pot experiment. SDW had significant positive relationships with TRL (0.50, $P < 0.05$) and RDW (0.53, $P < 0.01$), and TRL was positively correlated with NN (Table 2). Our results indicate that root growth is highly associated with shoot growth.

In both the pot and field experiments, SDW was positively and highly correlated with RDW. Therefore, breeding programs can concurrently select RDW and SDW, and RDW can be evaluated by measuring SDW without destroying the root system.

Discussion

Advantages of grafting technique for studying crop root function

The grafting technique is a satisfactory means for assessing the effects of scion and rootstock factors on several physiological aspects of plant growth and development (Lawn *et al.* 1974; Lawn and William 1974; Lawn and Bushby 1982; Abd-alla *et al.* 1998). For soybean, grafting technology has been used to assess photoperiod responses (Borthwick and Parker 1938; Przepiorkowski and Martin 2003) and interactions between shoots and roots (Balatti and Pueppke 1990; Ookawa *et al.* 2001). Grafting techniques have shown that shoots and roots play different roles in the nodulation process (Kleese and Smith 1970; Delves *et al.* 1986). Grafting has also been used to study the influence of rootstocks on the scion and the scion on rootstocks in inducing flowering in soybean (Hamner 1969).

In the present study, the seedling cut-in grafting technique was used as a platform for different rootstocks with the same scion to exclude interference caused by different shoots on the root system. By grafting, we can directly observe the overall function of roots and evaluate the contribution of the root to the shoot as an entity. Grafting provides a non-destructive and highly efficient approach for large-scale phenotyping of the soybean root system and has advantages for evaluating root features and capacities.

Evolutionary changes in the supporting capacity of the root system for aboveground parts in widely grown soybean cultivars

In the present study, scion SDW—a good indicator of the comprehensive capability of a root system—was negatively correlated with the year of release of rootstock cultivars from the NH region in the pot experiment and the YHH region in the field experiment. Less dependence of shoot biomass on the root system in these cultivars may explain the reduced contribution of roots.

According to our results, plant height and node number of the scion cultivar (cv. Zigongdongdou) decreased when grafted to newer cultivars than to older cultivars of soybean. Communication between rootstock and scion is bidirectional. The rootstock affects scion growth through transmissible substances (water, nutrient and hormone) and the effect of scion on rootstock is dependent on supply of photosynthates and signals (Albacete *et al.* 2015).

Evolutionary trends of root traits in widely grown soybean cultivars

From all three regions, TRL, LRN and RDW of soybean rootstocks did not change significantly with year of cultivar release. For the NH and MSH regions, in the northern part of

Fig. 5. Root systems of different maturity groups (MG) of soybean: (*a*) Beifeng 2 (MG 000), (*b*) Fengshou10 (MG 00), (*c*) Beifeng9 (MG 0), (*d*) Heilongjiang41 (MG I), (*e*) Jidou12 (MG III), and (*f*) Yuejin5 (MG IV).

Table 2. Correlation coefficients between root and shoot traits in the pot and field experiments

PH, Plant height; NN, node number; SDW, shoot dry weight; TRL, taproot length; LRN, lateral root number; RDW, root dry weight. *P < 0.05; **P < 0.01

Traits	NN	SDW	TRL	LRN	RDW
			Pot experiment		
PH	0.81**	0.54**	0.17	0.21	0.24
NN		0.62**	0.17	0.35**	0.37**
SDW			0.45**	0.48**	0.75**
TRL				0.26	0.48**
LRN					0.53**
			Field experiment		
PH	0.79**	0.75**	0.38	0.2	0.18
NN		0.73**	0.47*	0.12	0.21
SDW			0.50*	0.26	0.53**
TRL				–0.18	0.21
LRN					0.33

North East China, this finding could be attributed to the narrow-row planting technique and machinery widely used in North East China, particularly in the NH region (Hu 2008; Hang *et al.* 2009*a*, 2009*b*). Consequently, the cultivars are characterised by narrow leaves, few branches and small seeds, as well as small root volume and RDW, and yield increase is mainly attributed to high plant density (Yang 1982; Du and Lyu 2011). The governmental policy of a family-contract responsibility system was applied in the early 1980s, which enhanced the level of field management (increase in plant density and fertiliser application) (Wang 1993). We suggest that the increased fertiliser application provides adequate nutrition to topsoil roots and attenuates the absorbing capacity and root depth of modern soybean cultivars (Zheng *et al.* 2015); thus, no large root system for new soybean cultivars.

In the YHH region, innovations in field management techniques and increased fertiliser application provide adequate nutrition to topsoil roots and attenuate the absorbing capacity and root depth of modern soybean cultivars. Because seed yield is the primary target in soybean breeding, more upright and shorter plants with higher yields over time were observed in our previous study (Wang *et al.* 2016). Genetic selection of cultivars with smaller shoot and root systems may align with modern breeding objectives of high-plant-density cultivation. For instance, Jidou 7, released in the 1990s in Hebei province (YHH region), has a compact plant architecture (PH 57.25 cm, NN 15.0, SDW 32.93 g) and small root system (TRL 10.83 cm, LRN 15.0, RDW 4.00 g in the field experiment). By contrast, Haiyangpawanqing, an obsolete cultivar developed in 1929 in Shandong province (YHH region), has an extensive plant architecture (PH 93.63 cm, NN 21.8, SDW 81.97 g) and large root system (TRL 14.90 cm, LRN 19.8, RDW 4.91 g in the field experiment). In the present study, lower shoot biomass and relatively smaller root systems in the newer cultivars as rootstocks than the older cultivars is indicative of attenuated root functionality. Enhanced field-management techniques (increased plant density and fertiliser application) since the 1980s in China have dramatically improved topsoil nutrition, which may have led to a shallower rooting system in the modern cultivars (Wang 1993). Previous studies in rice (*Oryza sativa* L.) showed that redundant root growth may utilise excess energy source and thus cause yield loss (Wang *et al*. 2004). Appropriate pruning or cutting is effective to inhibit redundant root growth and reduce unnecessary consumption of carbohydrates in wheat (*Triticum aestivum* L.) and soybean (Shi *et al.* 1999, 2000; Ma *et al.* 2008). In the present study, root longevity did not differ among rootstocks of different maturity groups, suggesting that the scion plays a key role in the determination of root longevity. A similar result was found in the study of Li *et al.* (2017) with 11 scion cultivars of different maturity groups released in different years and two rootstock cultivars, in which agronomic traits such as pod numbers, seed numbers, 100-seed mass and yield were correlated with release years of scion cultivars.

Suggestions for root-trait improvement in soybean breeding

Our previous studies on changing trends in agronomic traits in these widely grown soybean cultivars indicated that, in North East China, newer cultivars had earlier flowering, shorter plants with fewer branches, higher lodging resistance and higher yields per plant than older cultivars, and in the YHH region, modern cultivars had shorter plants, fewer nodes, higher lodging resistance, more seeds per pod and heavier seeds than older cultivars (Wu *et al.* 2015; Wang *et al.* 2016). These results may shed light on strategies for soybean root improvement in different production regions. Because root longevity is mainly controlled by the shoots, the growing environments for the shoot and root systems need to improve through cultivation and farming practices to prevent premature senescence of roots and improve yield. Improvement of soybean root features, using conventional breeding and marker-assisted selection, has the potential to improve yield significantly. This study demonstrated the genetic progress in root traits and root contributions to shoots during a century-long breeding process. It also offers a methodology for studying intact root systems by observing aboveground growth, which will facilitate breeding for improved soybean root traits to boost soybean production.

Conflicts of interest

The authors declare that no competing or conflicts of interest exist.

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