Theor Appl Genet (2014) 127:2127–2137
DOI 10.1007/s00122-014-2366-z

ORIGINAL PAPER

# Inheritance and QTL mapping of related root traits in soybean at the seedling stage

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Received: 14 February 2014 / Accepted: 15 July 2014 / Published online: 22 August 2014


**Abstract**

***Key message*** **This study provides a foundation for further research on root genetic regulation and molecular breeding with emphasis on correlations among root traits to ensure robust root growth and well-developed root systems.**

*Abstract* A set of 447 recombinant inbred lines (RILs) derived from a cross between Jingdou23 (cultivar, female parent) and ZDD2315 (semi-wild, male parent) were used to analyze inheritance and detect QTLs related to root traits at the seedling stage using major gene plus polygene mixed inheritance analysis and composite interval mapping. The results showed that maximum root length (MRL) was controlled by three equivalent major genes, lateral root number (LRN) was controlled by two overlapping major genes, root weight (RW) and volume (RV) were controlled by four equivalent major genes. Hypocotyl length (HL) was controlled by four additive main genes, and hypocotyl weight (HW) was controlled by four additive and additive × additive epistatic, major genes; however, polygene effects were not detected in these traits. Shoot weight (SW) was controlled by multi-gene effects, but major gene effects were not detected. Twenty-four QTLs for MRL, LRN, RW, RV, SW, HL, HW were mapped on LG A1 (chromosome 5), LG A2 (chromosome 8), LG B1 (chromosome 11), LG B2 (chromosome 14), LG C2 (chromosome 6), LG D1b (chromosome 2), LG F_1 (chromosome 13), LG G (chromosome 18), LG H_1 (chromosome 12), LG H_2 (chromosome 12), LG I (chromosome 20), LG K_2 (chromosome 9), LG L (chromosome 19), LG M (chromosome 7), LG N (chromosome 3), LG O (chromosome 10), separately. Root traits were shown to have complex genetic mechanisms at the seedling stage, SW was controlled by multi-gene effects, and the other six traits were controlled by major gene effects. It is concluded that correlations among root traits must be considered to improve the development of beneficial root traits.

Communicated by David A. Lightfoot.

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**Abbreviations**

| | |
|---|---|
| MRL | Maximum root length |
| RW | Root weight |
| LRN | Lateral root number |
| SW | Shoot weight |
| RV | Root volume |
| HL | Hypocotyl length |
| HW | Hypocotyl weight |

## Introduction

Soybean is a main legume crop, which provides most of the plant protein and oil for human; hence, it is very important

to improve the yield and quality of soybean. Roots as main components of plants would imbibe water for the plant and take up dissolved minerals, which have helped increase yields and improve stress resistance to adverse environmental condition (Hyten et al. 2004; Funatsuki et al. 2005; Guo et al. 2005; Walker et al. 2004; Tian 1984; Pantalone et al. 1996; Liao and Yan 2000; Yang et al. 2001). To improve soybean germplasm, it is crucial to study root characters and the relationship between roots and their environment. Roots provide nutrition and impact crop yields. Adversity stress can affect root morphology, volume and weight, leading to diminished yields.

Root traits are believed to be complex and controlled by many genes, which show stability in different environments and present higher heritability (Tar'an et al. 2003; Liu et al. 2004; Zhou et al. 2009). One of the most effective ways to improve stress resistance is to promote physiological functions and activities in soybean by improving the absorption and fixed functions of roots. Sun et al. (1996) suggested that soybean plants with good root systems have improved yield during the early growth stage, when high resistance to adversity stress is associated with early and fast root growth, long main roots, and more extensive lateral roots. Study of such traits by QTL mapping of roots at the seedling stage is needed for effective heredity breeding in soybean.

Ways to promote yield and increase quality through the development of new crop strains with improved root traits are sought. At present, root traits have been mainly studied in crops, such as rice (Kamoshita et al. 2002a, b), wheat (Hao et al. 2003; Dhanda et al. 2004; Zhou et al. 2005), and maize (Price et al. 2000; Zhang 2005), and many quantitative trait loci (QTLs) underlying root traits have been mapped in rice and wheat. Pertinent findings have been reported for physiological characteristics (King et al. 2009), morphology (Liu et al. 2005) and root mass in response to various abiotic/biotic stresses (Liu et al. 2007), but the QTLs related to root traits have not been studied extensively in soybean. Zhou et al. (2011) adopted RILs derived from a cross between zhongdou29 and zhongdou32 to detect the QTLs related to root traits, including maximum root length, lateral root number, root weight, root volume, root–shoot ratio, plant weight, shoot weight and hypocotyl weight in seedlings, twenty QTLs were detected, of which nine major QTLs were mapped on chromosomes 11 and 14. Because the roots grow underground in a more complex living environment resulted in less study on the root traits in the present. So far the QTLs for root traits at seedling stage in soybean were relatively less. The objectives of this study to identify QTL(s) were associated with root traits in soybean at the seedling stage based on a recombinant inbred lines (RILs) population developed from a cross of Jingdou23 (cultivar, female parent) and ZDD2315 (semi-wild, male parent) using WinQTLCart2.5 (http://statgen.ncsu.edu/qtlcart/WQTLCart.htm) with composite interval mapping (Wang et al. 2005; Gai et al. 2001). We also have analyzed the genetic laws related to root traits in soybean by major gene plus polygene mixed inheritance analysis, which is the premise for the development of marker-assisted selection (MAS) strategies in the selection of soybean varieties with stress resistance.

## Materials and methods

### Plant materials and the hydroponic experiment

The RILs population study was derived from the cross between Jingdou23 (cultivar) as the female and ZDD2315 (semi-wild cultivar) as the male (Sun et al. 1996; McCouch et al. 1997). The population consisted of 447 lines. Glycine max Merr. cv. Jingdou23 is a high yield cultivar, which is tolerant to drought and planted in Shanxi Province. Glycine max Merr. cv. ZDD2315 is a farm variety that is woven into the country's germplasm resources and numbered ZDD2315. Thirty seeds from each of the RILs and their parents were covered with pasteurized paper, and cultivated in clean water at 20–28 °C on 27 May, 2013 and 28 June, 2013, and a complete random design with three replications was used in this study; the experiment was finished on 8 June, 2013 and 8 July 2013. The data derived from data in 8 June and 8 July, 2013 as two environmental factors. Root traits were measured on 8 June and 8 July at the V2 stage.

### Root trait measurement and phenotypic data processing

Five plants of each RILs and parents group were sampled at the growth-V2 stage (Zhou et al. 2011). Root characters of maximum root length (MRL), root weight (RW), lateral root number (LRN), shoot weight (SW), root volume (RV), hypocotyl length (HL) and hypocotyl weight (HW) were measured, and the phenotypic data were analyzed using DPS (Tang and Zhang 2013).

### Major gene plus polygene mixed inheritance analysis

The dataset of root traits in soybeans from a RILs population was analyzed by major gene plus polygene mixed inheritance analysis (McCouch et al. 1997). Component parameters were estimated using the maximum likelihood method based on the IECM (Iterated Expectation and Conditional Maximization) algorithm. Among the possible models, the best one was chosen according to AIC (Akaike's information criterion) and a set of tests for goodness of fit. Then the genetic parameters of the optimal model were estimated using the least squares method.

Major gene and polygene heritability are calculated as $h^2_{mg}(\%) = \sigma^2_{mg}/\sigma^2_{mg} \cdot \sigma^2_p$ and $h^2_{pg}(\%) = \sigma^2_{pg}/\sigma^2_{pg} \cdot \sigma^2_p$, respectively; where $\sigma^2_p$ is the variance of phenotype traits, and $\sigma^2_e$ is the genetic variance under multiple environments, $\sigma^2_{pg}$ is the genetic variance of multiple genes, and $\sigma^2_{mg}$ is genetic variance of the major gene. Relationships among the genetic variances above were estimated by $\sigma^2_P = \sigma^2_{mg} + \sigma^2_{pg} + \sigma^2_e$, $h^2_{mg}(\%)$, $h^2_{pg}(\%)$ and $h^2_e(\%)$, representing heritability of the major gene, multi-genes and the environment, respectively.

### Construction of the genetic linkage map and QTL mapping

Wang (2004) integrated a genetic linkage map containing 227 SSR markers in soybean using the RILs population developed from a cross between Jingdou23 (cultivar) as the female and ZDD2315 (semi-wild cultivar) as the male. Liang (2006) integrated a new map spanning 2047.6 cM across 27 linkage groups that contained 232 markers, which were based on the SSR marker map and the public soybean SSR markers. The current study used the genetic linkage map constructed by Liang (2006) to detect QTLs at the seedling stage. QTL analysis was performed using Zmapqtl on composite interval mapping (CIM) from WinQTLCart 2.5 (Liang 2006). Model 6 was adopted, and the control marker number and window size were 2 cM. The markers were first grouped at an LOD of 2.0 and then ordered to construct core linkage groups. Other markers were added using the insert command as the LOD score was decreased to 2.0. LOD score peaks greater than 2.0 served to indicate the existence of QTLs. A map distance less than 5 cM between adjacent markers indicated existence of QTLs. Linkage groups were named with designations from the consensus map of McCouch et al. (1997).

## Results

### Segregation laws and phenotypic analysis of root traits

Segregation and genetic characters of root traits of MRL, RW, LRN, SW, RV, HL and HW were studied in a RILs population derived from a cross between Jindou23 and ZDD2315 (Table 1). Substantial segregation was observed for seven traits in the RILs population and the differences between the minimum and maximum values in the RILs population were significant, which indicated that the heritability was significantly greater and provided a better genetic background for QTL analysis. The heritability values for MRL, RW, LRN, SW, RV, HL, and HW were 32.78, 33.13, 22.23, 35.01, 19.24, 20.32 and 22.75 %, respectively. Phenotypic variation coefficients for RW, RV, SW and HW were less than 2 % in two environments, demonstrating that these four traits had the greatest stability and were less affected by environmental conditions. The LRN phenotypic variation coefficients were 0.73 and 0.96 in two environments, which suggested the LRN had high variation and was easily affected by environmental factors. This finding was similar to that of Sun et al. (1996). Deviation and kurtosis for the seven traits above were relatively low, and mean values of the RILs population were close to the value of medium parents. These traits were approximately

**Table 1** Statistical results for seven traits of the parent and RIL populations

| Trait | MRL | LRN | RW | RV | SW | HL | HW |
|---|---|---|---|---|---|---|---|
| Parents Jindou23 | 16.47 | 38.58 | 0.67 | 0.68 | 1.38 | 9.93 | 0.54 |
| Parents ZDD2315 | 14.58 | 35.50 | 0.40 | 0.43 | 0.75 | 12.20 | 0.47 |
| 2013.05.27 RIL population | | | | | | | |
| Mean | 14.46 | 33.75 | 0.48 | 0.50 | 0.93 | 12.17 | 0.51 |
| SD | 1.53 | 7.08 | 0.09 | 0.11 | 0.16 | 1.89 | 0.10 |
| Variance | 0.16 | 0.73 | 0.01 | 0.01 | 0.02 | 0.19 | 0.01 |
| Min | 8.67 | 9.00 | 0.18 | 0.25 | 0.38 | 6.10 | 0.32 |
| Max | 18.00 | 48.60 | 0.69 | 0.75 | 1.27 | 19.00 | 0.86 |
| Skewness | −0.71 | −0.21 | −0.75 | −0.21 | −0.18 | −0.05 | 0.77 |
| Kurtosis | 0.87 | 0.59 | 0.88 | −0.06 | 0.75 | 0.88 | 0.72 |
| 2013.06.27 RIL population | | | | | | | |
| Mean | 13.81 | 40.56 | 0.42 | 0.44 | 0.97 | 11.54 | 0.52 |
| SD | 2.34 | 9.96 | 0.11 | 0.12 | 0.19 | 1.68 | 0.10 |
| Variance | 0.23 | 0.96 | 0.01 | 0.01 | 0.02 | 0.16 | 0.01 |
| Min | 4.70 | 10.00 | 0.09 | 0.10 | 0.48 | 7.43 | 0.32 |
| Max | 19.00 | 66.50 | 0.68 | 0.92 | 1.50 | 15.10 | 0.89 |
| Skewness | −0.84 | −0.27 | −0.01 | 0.55 | −0.04 | −0.11 | 0.80 |
| Kurtosis | 0.85 | 0.33 | 0.25 | 0.86 | −0.20 | −0.33 | 1.47 |

*MRL* maximum root length, *RW* root weight, *LRN* lateral root number, *SW* shoot weight, *RV* root volume, *HL* hypocotyl length, *HW* hypocotyl weight

normally distributed (Fig. 1), meeting the requirements of QTL analysis.

## Correlation among root traits in soybean

Correlations among root traits based upon 447 RILs population means are given in the top right and bottom left corner in Table 2. There was a significant positive correlation between any two traits among root traits (MRL, LRN, RW, RV, SW) in a simple correlation analysis. In the partial correlation analysis, significant positive correlations for SW and HW, HW and SW (or HL) were observed. Root traits showed mutual influence and restriction, laying the foundation for selection of phenotypic traits.

## The major gene plus polygene mixed inheritance analysis for root traits

Among the possible models, the best one was chosen according to AIC (Akaike's information criterion), a set of tests for homogeneity, and the Kolmogorov–Smirnov test. Then the genetic parameters were estimated through the least squares method based on weight arithmetic and weighted harmonic mean derived from the optimal model (Table 3).

The three pairs of the equivalent major gene genetic model (3MG-CEA) were used in analysis of inheritance for MRL. The results suggested that the MRL was controlled by three pairs of major genes, which had an additive effect of 0.7522. Heritability of the main gene was 37.93 %, but a multi-gene effect was not detected in the population. We tested the inheritance of LRN using two pairs of the overlapping major gene genetic model (2MG-Dup). The results showed that the epistatic effect from interaction between two major genes was 4.7639. Heritability of the major gene was 19.89 %, but a multi-gene effect was not detected in the population. We tested the inheritance of RW and RV using four pairs of the equivalent major gene genetic model (4MG-CEA), it was determined that the additive effects among four major genes were 0.0250 and 0.0249, and heritability levels of the major genes were 14.98 and 8.25 %, but a multi-gene effect was not detected in the population. The inheritance of SW was detected by an additive multi-genes genetic model (PG-A), it showed that the additive effect among genes was 0.2683, and heritability of the polygene was 1.13 %, but a major gene effect was not detected in the population. The inheritance of HL was detected by four pairs of an additive major genes genetic model (4MG-A), it suggested that the additive effects among four major genes were −0.0797, −0.1153, 0.1928 and −1.0024. Heritability of the major genes was 91.06 %, but a polygene effect was not detected in this population. We tested the inheritance of HW using an additive × additive epistatic genetic model containing four pairs of major genes (4MG-AI), it was determined that the additive effects among four major genes were −0.0606, −0.0070, 0.0386 and 0.0058, and epistatic effects among four major genes were 0.0564, −0.0492, 0.0327, −0.0263, 0.0106, −0.0219, heritability of the major genes was 94.25 %, but a polygene effect was not detected.

## QTL mapping for root traits

Twenty-four QTLs were detected for MRL, LRN, RW, RV, SW, HL and HW in the study (Table 4; Fig. 2). Five QTLs for MRL were identified on LG B1 (chromosome 11), LG L (chromosome 19), LG N (chromosome 3) and LG O (chromosome 10), respectively; the variation accounted by each of these five QTLs ranged from 7.05 to 13.18 %. q*MRL1-b1-1* was one of the five QTLs to be located in the interval between satt519 and satt597 of LG B1 (chromosome 11), which explained 13.18 % of the phenotype variation and showed the greatest effects.

Four QTLs for LRN were identified on LG A1 (chromosome 5), LG D1b (chromosome 2), LG I (chromosome 20), LG L (chromosome 19).The phenotype variation accounted for by each of these four QTLs ranged from 8.21 to 16.43 %. q*LRN1-a1-1* was one of the four QTL to be located in the interval between satt267 and satt364 of LG A1 (chromosome 5), which explained 16.43 % of the phenotype variation and showed a relatively high effect.

Three QTLs for RW were identified on LG F_1 (chromosome 13), LG G (chromosome 18), LG N (chromosome 3), respectively; the phenotype variation accounted by each of these three QTLs ranged from 7.55 to 10.85 %. q*RW2-f_1-1* was one of the three QTLs to be located in the interval between satt193 and GMRUBP of LG F_1 (chromosome 13), which explained 10.85 % of the phenotype variation and showed the largest effects of the three QTLs.

Three QTLs for RV were identified on LG K_2 (chromosome 9) and LG M (chromosome 7) based on the data from 27 May 2013. The phenotype variation accounted by each of these three QTLs ranged from 8.44 to 12.39 %. q*RV1-k_2-1* was one of the three QTLs to be located in the interval between satt337 and satt167 of LG K_2 (chromosome 9), which explained 12.39 % of the phenotype variation and showed a relatively high effect in three QTLs, but the main QTL was not detected in the experiment on 28 June, 2013.

Five QTLs for SW were identified on LG A1 (chromosome 5), LG A2 (chromosome 8) and LG N (chromosome 3). They accounted for phenotype variation ranged from 11.43 to 38.91 %, of q*SW1-a2-1* and q*SW2-a2-2* were located on LG A2 (chromosome 8), q*SW2-a2-2* was located in the interval between satt333 and satt327 of LG A2 (chromosome 8), which explained 38.91 % of the phenotype variation and showed the greatest effects among the five QTLs.

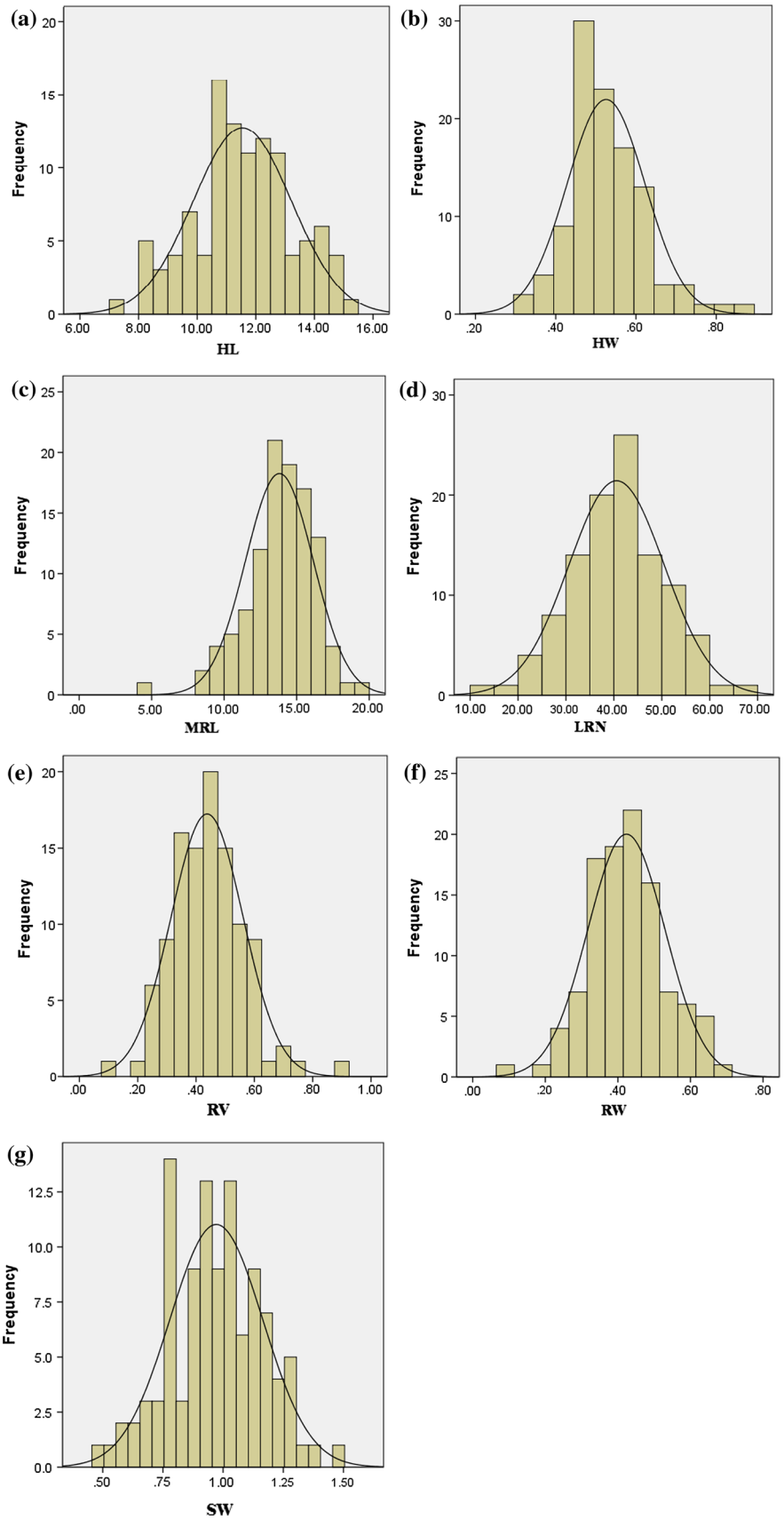


**Fig. 1** Frequency distribution on the basis of an average of two environments for **a** HL (cm), **b** HW (cm), **c** MRL (cm), **d** LRN (cm), **e** RV (cm), **f** RW (cm) and **g** SW (cm) in $F_{21}$-derived soybean population in developed from ZDD2315 × Jingdou23

**Table 2** Phenotypic correlation coefficients among root traits in parent and RIL populations

| Trait | MRL | LRN | RW | RV | SW | HL | HW |
|---|---|---|---|---|---|---|---|
| MRL | 1 | 0.54** | 0.61** | 0.47** | 0.44** | 0.07 | 0.00 |
| LRN | 0.49** | 1 | 0.50** | 0.44** | 0.40** | 0.13 | 0.11 |
| RW | 0.50** | 0.39** | 1 | 0.78** | 0.66** | −0.12 | −0.01 |
| RV | 0.42** | 0.49** | 0.76** | 1 | 0.59** | −0.05 | 0.03 |
| SW | 0.45** | 0.48** | 0.51** | 0.46** | 1 | 0.11 | 0.21* |
| HL | 0.06 | −0.19 | 0.00 | −0.06 | 0.16 | 1 | 0.58** |
| HW | −0.03 | −0.17 | 0.15 | 0.08 | 0.24* | 0.68** | 1 |

*,** significance at 0.05 and 0.01 probability levels, respectively. The data in the upper right corner of Table 2 were collected on 28 June, the data in the lower left corner of Table 2 were collected on 27 May

*MRL* maximum root length, *RW* root weight, *LRN* lateral root number, *SW* shoot weight, *RV* root volume, *HL* hypocotyl length, *HW* hypocotyl weight

**Table 3** Analysis of the best models and genetic parameters for root traits

| Traits | MRL | LRN | RW | RV | SW | HL | HW |
|---|---|---|---|---|---|---|---|
| Genetic model | 3MG-CEA | 2MG-Dup | 4MG-CEA | 4MG-CEA | PG-A | 4MG-A | 4MG-AI |
| First-order parameter | | | | | | | |
| M | 13.4972 | 38.1738 | 0.4224 | 0.4362 | 0.9732 | 11.4197 | 0.5373 |
| d(da) | 0.7552 | – | 0.0250 | 0.0249 | – | −0.0797 | −0.0606 |
| db | 0.7552 | – | 0.0250 | 0.0249 | – | −0.1153 | −0.0070 |
| dc | 0.7552 | – | 0.0250 | 0.0249 | – | 0.1928 | 0.0386 |
| dd | – | – | 0.0250 | 0.0249 | – | −1.0024 | 0.0058 |
| iab (i*) | – | 4.7639 | – | – | – | – | 0.0564 |
| iac | – | – | – | – | – | – | −0.0492 |
| iad | – | – | – | – | – | – | 0.0327 |
| ibc | – | – | – | – | – | – | −0.0263 |
| ibd | – | – | – | – | – | – | 0.0106 |
| icd | – | – | – | – | – | – | −0.0219 |
| iabc | – | – | – | – | – | – | – |
| [d] | – | – | – | – | 0.2683 | – | – |
| Second-order parameter | | | | | | | |
| $\sigma_p^2$ | 5.4624 | 99.1825 | 0.0113 | 0.1576 | 0.0354 | 2.809 | 0.0094 |
| $\sigma_{mg}^2$ | 2.0719 | 19.7274 | 0.0017 | 0.0013 | – | 2.5579 | 0.0089 |
| $\sigma_{pg}^2$ | – | – | – | – | 0.0004 | – | – |
| $h_{mg}^2(\%)$ | 37.93 | 19.89 | 14.98 | 8.25 | – | 91.06 | 94.25 |
| $h_{pg}^2(\%)$ | – | – | – | – | 1.13 | – | – |

$\sigma_p^2$ is the variance of phenotype traits, and $\sigma_e^2$ is the genetic variance under multiple environments, $\sigma_{pg}^2$ is the genetic variance of multiple genes, and $\sigma_{mg}^2$ is genetic variance of the major gene. $h_{mg}^2(\%)$, $h_{pg}^2(\%)$ and $h_e^2(\%)$, representing heritability of the major gene, multi-genes, and the environment, respectively. 3MG-CEA, 2MG-Dup, 4MG-CEA, PG-A, 4MG-A, 4MG-AI were genetic model

*MRL* maximum root length, *RW* root weight, *LRN* lateral root number, *SW* shoot weight, *RV* root volume, *HL* hypocotyl length, *HW* hypocotyl weight

Based on the data for HL on 27 May, the QTL was located in linkage group H_1 (chromosome 12). It explained 7.86 % of the phenotype variation, but the main QTL was not found on 28 June. Three QTLs for HW were identified on linkage groups LG B2 (chromosome 14), LG C2 (chromosome 6) and LG H_2 (chromosome 12). They accounted for phenotype variation ranged from 7.70 to 12.48 %. q*HW1-h_2-1* was one of the three QTLs to be located in the interval between satt181 and satt343 of LG H_2 (chromosome 12), which explained 12.48 % of the phenotype variation and showed the largest effects of these three QTLs.

## Discussion

The main purpose of this study was to identify genetic law associated with root traits, and verify previously identified genetic laws. QTL mapping has become increasingly important in molecular breeding by marker-assisted selection (MAS) and gene discovery, which can enhance disease resistance in plants (Price 2006; Su et al. 2002; Zuo et al. 2007; Beaver and Osorno 2009; Swarbrick et al. 2009) and improve crop quality (Blair et al. 2009; Sabouri 2009). Great progress has been made in understanding

**Table 4** QTL analysis for root traits

| Traits (cm) | QTL | Chr. | Marker interval | Position | LOD | Additive (%) | $R^2$ (%) |
|---|---|---|---|---|---|---|---|
| MRL | | | | | | | |
| 05.27 | q*MRL1-b1-1* | B1 | satt519–satt597 | 106.34 | 2.7012 | 0.5648 | 13.18 |
| | q*MRL1-n-1* | N | satt152–satt521 | 30.61 | 2.7183 | −0.4856 | 9.83 |
| 06.28 | q*MRL2-l-1* | L | satt388–satt182 | 18.02 | 2.0450 | 0.8116 | 9.65 |
| | q*MRL2-l-2* | L | satt232–satt446 | 21.90 | 2.1247 | 0.6886 | 7.05 |
| | q*MRL2-o-1* | O | satt345–satt466 | 54.22 | 2.1584 | 0.6623 | 8.01 |
| LRN | | | | | | | |
| 05.27 | q*LRN1-a1-1* | A1 | satt267–satt364 | 4.01 | 2.9132 | 2.9277 | 16.43 |
| | q*LRN1-D1b-1* | D1b | satt274–satt271 | 59.20 | 2.3118 | 2.0540 | 8.21 |
| | q*LRN1-i-1* | I | satt239–satt292 | 20.94 | 2.8042 | 2.6685 | 9.52 |
| 06.28 | q*LRN2-l-1* | L | satt232–satt446 | 28.07 | 3.2417 | 3.4008 | 10.96 |
| RW | | | | | | | |
| 05.27 | q*RW1-n-1* | N | satt152–satt521 | 30.61 | 2.1537 | −0.0280 | 8.32 |
| 06.28 | q*RW2-f_1-1* | F_1 | satt193–GMRUBP | 2.01 | 2.3957 | 0.0356 | 10.85 |
| | q*RW2-g-1* | G | satt570–satt356 | 59.89 | 2.1138 | −0.0344 | 7.55 |
| RV | | | | | | | |
| 05.27 | q*RV1-k_2-1* | K_2 | satt337–satt167 | 16.01 | 2.2036 | 0.0391 | 12.39 |
| | q*RV1-m-1* | M | satt220–satt323 | 73.14 | 2.2104 | 0.0320 | 8.44 |
| | q*RV1-m-2* | M | satt323–satt175 | 81.57 | 2.0139 | 0.0343 | 9.38 |
| SW | | | | | | | |
| 05.27 | q*SW1-a1-1* | A1 | satt267–satt364 | 4.01 | 2.0067 | 0.0559 | 11.43 |
| | q*SW1-a2-1* | A2 | satt333–satt327 | 94.12 | 2.0572 | 0.0744 | 20.16 |
| | q*SW1-n-1* | N | satt152–satt521 | 30.61 | 3.6744 | −0.0594 | 12.79 |
| 06.28 | q*SW2-a2-1* | A2 | satt329–satt333 | 78.49 | 3.5923 | 0.0948 | 23.17 |
| | q*SW2-a2-2* | A2 | satt333–satt327 | 88.12 | 3.9155 | 0.1230 | 38.91 |
| HL | | | | | | | |
| 05.27 | q*HL1-h_1-1* | H_1 | Satt353–satt568 | 0.01 | 2.1367 | 0.5411 | 7.86 |
| HW | | | | | | | |
| 05.27 | q*HW1-b2-1* | B2 | satt272–satt063 | 31.17 | 2.0833 | −0.0283 | 7.70 |
| | q*HW1-h_2-1* | H_2 | satt181–satt343 | 38.07 | 2.0201 | 0.0350 | 12.48 |
| 06.28 | q*HW2-c2-1* | C2 | satt100–satt134 | 108.47 | 3.2875 | −0.0336 | 11.32 |

*Chr.* means chromosomes, $R^2$ means percentage of phenotypic variation explained, *Additive* means additive effect. The marker underline mean significant relatively

*MRL* maximum root length, *RW* root weight, *LRN* lateral root number, *SW* shoot weight, *RV* root volume, *HL* hypocotyl length, *HW* hypocotyl weight

the genetic regulation of root traits (Liu et al. 2005, 2007; Yang et al. 2005). Several QTLs for root traits have been detected recently (Zhou et al. 2011; Williams et al. 2012; Liang et al. 2010). In this study, MRL was controlled by three equivalent major genes, LRN was controlled by two overlapping major genes, and RW and RV were controlled by four equivalent major genes, HL was controlled by four additive main genes, and HW was controlled by four additive and additive × additive epistatic major genes, SW was controlled by multi-gene effects, the result was similar to Liu et al. (2005), Yang et al. (2005) and Liu et al. (2007), but unlike lü et al. (2010). Liu et al. (2005) using The RILs population derived from Kefeng1 × Nannong1138-2 found the relative values of dry root weight, total root length and root volume were, respectively, controlled by two major genes plus polygene. Yang et al. (2005) suggested that total root length, maximum root length, root dry weight and drought tolerance are controlled by the two pairs of major genes model and have multi-gene effects at the seedling stage, which demonstrates that heritability of the major gene is low and heritability of the polygene is relatively high. Liu et al. (2007) identified the inheritance of total root length, root dry weight ratio and root volume, which follows the two pairs of major and polygene genetic model. But lü et al. (2010) used the $F_2$ population of the cross Bare × PI416937 demonstrated that root dry weight was found to be mainly controlled by minor-effect polygene under both routine irrigation and drought stress conditions; the root dry weight and root volume in the segregating populations of the cross Fengshouhuang × PI471938 were mainly controlled by polygene. Clearly, further research in this area is needed.

The another main purpose of this study was to identify new QTL associated with root traits, and verify previously

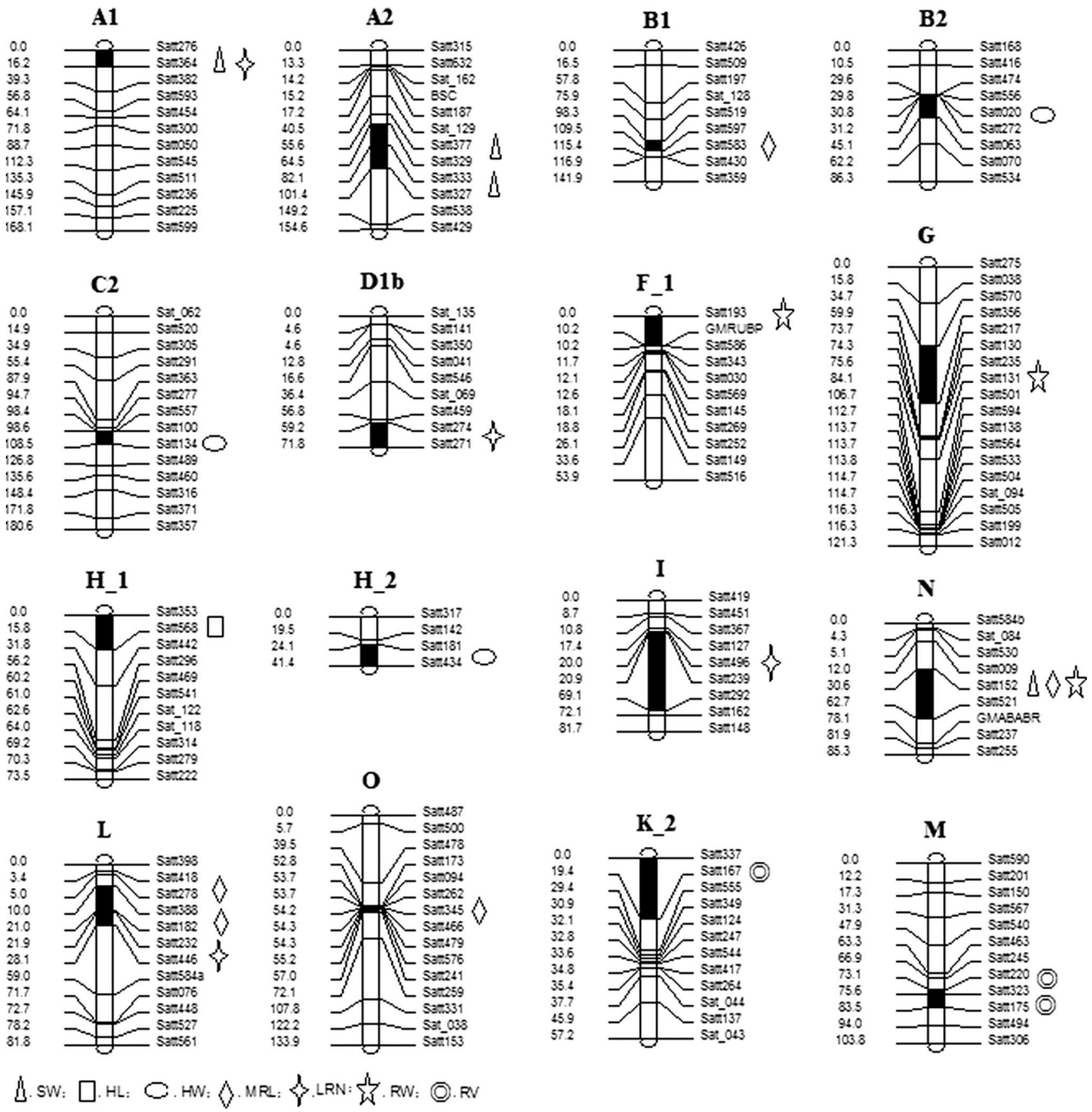


**Fig. 2** The QTL map and additive effects of QTLs distributed on different linkages

identified QTLs (Williams et al. 2012; Zhou et al. 2011; Liang et al. 2010). Some new QTLs were detected in this study. We tried to compare the QTLs between the present study and previous studies (Table 5). Twenty-four QTLs for seven root traits (MRL, LRN, RW, RV, SW, HL and HW) were detected in the study (Table 4; Fig. 2). Five QTLs for MRL were identified on LG B1 (chromosome 11), LG L (chromosome 19), LG N (chromosome 3) and LG O (chromosome 10), respectively; Two new LG of L and O were detected in present study, except LG B1 (Liang et al. 2000), LG N (Williams et al. 2012), but LG C2 (Williams et al. 2012; Zhou et al. 2011) and D1a (Liang et al. 2010) were not detected in present study. Four QTLs for LRN were identified on LGs A1, D1b, I and L. Four new QTLs for LRN were identified on LG A1 (chromosome 5), LG D1b (chromosome 2), LG I (chromosome 20), LG L (chromosome 19), and unlike previous studies which located on LG G, LG B2, LG F_1 (Williams et al. 2012; Zhou et al. 2011).

**Table 5** Comparison of QTL detected in this population with other researches

| Authors | Parents | Traits | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | MRL | LRN | RW | RV | SW | HL | HW |
| Liang et al. (the result from the paper) | Jindou23 × ZDD2315 | B1, N, L, O | A1, D1b, I L | N, G, F_1 | M, K_2 | A1, A2, N | H_1 | B2, C2, H_2 |
| Williams et al. (2012) | Essex × Forrest | C2, N | G | A2, N | | A2, C2, N, D1a | | |
| Zhou et al. (2011) | Zhongdou29 × Zhongzhou32 | C2, E | B2, G, F_1 | G, F_1 | D1a, F_1, G | G | | B2, E, H_1 |
| Liang et al. (2010) | BD2 × BX10 | B1, D1a | | B1 | | B1 | | |

*MRL* maximum root length, *RW* root weight, *LRN* lateral root number, *SW* shoot weight, *RV* root volume, *HL* hypocotyl length, *HW* hypocotyl weight

Three QTLs for RW were identified on LG F_1 (chromosome 13), LG G (chromosome 18), LG N (chromosome 3), which were reported by Williams et al. (2012) and Zhou et al. (2011). Three QTLs for RV were identified on LG K_2 (chromosome 9) and LG M (chromosome 7), which was not different of previous studies (Zhou et al. 2011). Five QTLs for SW were identified on LG A1 (chromosome 5), LG A2 (chromosome 8) and LG N (chromosome 3), LG A2 and LG N were reported by Williams et al. (2012). A new QTL for HL was located in linkage group H_1 (chromosome 12). Three QTLs for HW were identified on LG B2 (chromosome 14), LG C2 (chromosome 6) and LG H_2 (chromosome 12), of LG B2 was reported by Zhou et al. (2011).

In the previous studies, the numerous disease resistance loci are clustered on LG D1b and LG F (Rector et al. 1999; Hayes et al. 2000). The phenomenon was also evident in present study, the QTLs for seven root traits were distributed on chromosomes 16, but majority of the QTLs were clustered in five chromosomal intervals (Fig. 1; Table 4), the five internals located on LGs A1, A2, N, L, M were found to be involved in the control of two or more of the root traits. The QTLs for SW, MRL and RW were direction of both negative additive and dominant effect involved novel alleles from the same parent, ZDD2315, they were located in satt152-satt521 interval on chromosome 3 (LG N). The QTLs for MRL and LRN were located in the satt232–satt446 interval on chromosome 19 (LG L) on 28 June, shared the same direction of both positive additive and dominant effects and involved novel alleles from the same parent, Jindou23. The QTLs for SW and LRN were located in satt267–satt364 interval on chromosome 5 (LG A1), shared the same direction if both positive additive and dominant effects and involved novel alleles from the same parent, Jindou23. The QTLs for RW, RV were located in sat_360–satt415 on chromosome 11, and they exhibited the same phenomenon found by Zhou et al. (2011) that some QTLs for RW, RV, SW were clustered between sat_287and sct_034 on chromosome 14. The QTLs for MRL, RW and SW were clustered between satt519 and sat_128 on chromosome 11, and they exhibited the same phenomenon found by Liang et al. (2012). The reason why QTLs clustering has been studied by Qin et al. (2008) is that may be the high correlation between some traits, coupling tight linkage could better the data.

Certain traits and QTLs were inconsistent with previous results and genetic models. For example, the PG-A equal additive equated multi-gene genetic model was suited to SW; two or three major QTLs were detected in two groups of experiments, and the results differed between segregation analysis and QTL analysis. There were at least three reasons for this result. Firstly, the four pairs of major plus polygene mixed inheritance analysis, which does not consider linkage among major genes, was adopted in this study. In future work, the model needs to include linkage relationships among major genes. Secondly, the genetic model was affected by constitutive parameters and estimated parameters, which offer accuracy parameters and estimated methods. Thirdly, the difference may be associated with genetic map type. Development of integrated mapping may lead to improved QTL analysis.

## Conclusion

This work serves as a reference in root inheritance and molecular investigation. A set of 447 recombinant inbred lines (RILs) derived from a cross between Jingdou23 and ZDD2315 served to detect QTLs for root traits at the seedling stage using major gene plus polygene mixed inheritance analysis and the composite interval mapping method. MRL was controlled by three pairs of equivalent major genes, and LRN was controlled by two pairs of overlapping main genes, and RW and RV root were controlled by four pairs of equivalent major genes. HL was controlled by four pairs of additive main genes, HW was controlled by four pairs of additive and additive × additive epistatic main genes, but a polygene effect was not detected in these traits. SW was controlled by multi-genes, while these effects

were not detected in the population. Twenty-four QTLs for MRL, RW, LRN, SW, RV, HL, HW were mapped on LG A1 (chromosome 5), LG A2 (chromosome 8), LG B1 (chromosome 11), LG B2 (chromosome 14), LG C2 (chromosome 6), LG D1b (chromosome 2), LG F_1 (chromosome 13), LG G (chromosome 18), LG H_1 (chromosome 12), LG H_2 (chromosome 12), LG I (chromosome 20), LG K_2 (chromosome 9), LG L (chromosome 19), LG M (chromosome 7), LG N (chromosome 3), LG O (chromosome 10). Root traits have complex genetic mechanisms at the seedling stage. This study provides a foundation for further research on root genetic regulation and molecular breeding with emphasis on correlations among root traits to ensure robust root growth and well-developed root systems.

**Author contributions** Huizhen Liang led the experimental design and experimental research in the study. Yongliang Yu completed the data analysis. Hongqi Yang, Wei Dong, Lanjie Xu and Weiwen Cui collaborated on the experimental design and analysis. Huizhen Liang and HaiYang Zhang oversaw the project; they guided the experimental design, data analysis, writing and editing.

**Acknowledgments** This project was financially supported by the Foundation for Distinguished Young Scholars of Henan Province (114200510002) and the grants from Key Project of National Plant Transgenic Genes of China (2009ZX08018-001B, 2011ZX08004-005). The authors thank Dr. Xuanjun Fang from the Hainan Institute of Tropical Agricultural Resources and Xueyi Liu from the Shanxi Academy of Agricultural Sciences for kindly providing the RIL population and Dr. Yuanming Zhang from Nanjing Agricultural University for kindly providing the major gene plus polygene mixed inheritance analysis software and for assistance in data analysis.

**Conflict of interest** The authors declare that they have no conflict of interest.

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