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Selection of soybean elite cultivars based on phenotypic and genomic characters related to lodging tolerance

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Abstract

Soybean lodging can result in serious yield reduction. Detecting the quantitative trait loci (QTL) associated with lodging tolerance for their further application in marker-assisted selection (MAS) has the potential to enhance soybean breeding efficiency. In this study, a genome-wide association analysis (GWAS) was performed to identify soybean accessions that could potentially be used to produce lodging-tolerant varieties, based on the comprehensive evaluation of lodging scores (LS) obtained for the parental cultivar "Tokachi nagaha" and its 137 derived cultivars. Results showed that genotype, environment and genotype × environment interaction significantly influenced LS. Of the 31 significant SNPs identified, 22 were consistently detected in two or more environments and 27 SNPs were located in or close to agronomically important QTL mapped by linkage analysis. Best linear unbiased predictors (BLUPs) of LS tend to decrease with the elite alleles contained by accessions increasing. Some excellent accessions, with lower BLUPs and D_i (stability coefficients) values and more elite alleles, were selected. This study contributed to understand the genetic mechanism of lodging, providing genetic and phenotypic information for MAS.

KEYWORDS
additive main effects and multiplicative interaction model, genome-wide association analysis, lodging scores, lodging tolerance, soybean

1 | INTRODUCTION

Lodging is a common and severe threat to soybean [*Glycine max* (L.) Merr.] production. Lodging degree and yield were significantly

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correlated, with yield loss increasing 198 kg hm^{-2} for each lodging degree increase (Board, 2001). A yield reduction >22% has been attributed to lodging during the seed filling period (Mancuso & Caviness, 1991; Noor & Caviness, 1980; Wilcox & Sediyama, 1981). Lodging also increases the difficulty of field production management and combined harvesting and reduces seed appearance and quality (Fan et al., 2012; Noor & Caviness, 1980; Uchikawa, Miyazaki, & Tanaka, 2006). The highest yield-record registered worldwide revealed that controlling lodging is crucial to obtain high soybean yields (Alliprandini & Vello, 2004; Zhao, Gai, Li, Xing, & Qiu, 2006).

Lodging is a complex trait involving multiple genes and their interactions with the environment (Lee, Bailey, Mian, Carter, et al., 1996; Lee, Bailey, Mian, Shipe, et al., 1996; Liu et al., 2013; Orf et al., 1999; Panthee, Pantalone, Saxton, West, & Sams, 2007). Its severity has been closely related to population density, as plants tend to be prostrate as population density increases (Cooper, 1971), and it is correlated with both aboveground (e.g., plant height and stem strength) and underground (e.g., root weight and root length) traits (Inoue, Gao, & Cai, 2004; Keller et al., 1999; Menchey & Aycock, 1998; Tar'an et al., 2003). Although the low efficiency of phenotypic selection for complex traits is a major limitation for plant breeding, biotechnological advances have allowed identifying genetic variations associated with lodging tolerance and enhancing the efficiency of lodging selection in soybean breeding using marker-assisted selection (MAS). Thus far, 82 quantitative trait loci (QTL) associated with lodging score (LS) and 11 QTL related to the ratio of plant height to lodging have been deposited in Soybase (http://www.soybase.org/). These QTL were mainly distributed on the linkage groups L, C2, F, and G (Liu et al., 2013; Orf et al., 1999; Panthee et al., 2007; Wang, Graef, Procopiuk, & Diers, 2004; Zhang et al., 2004), and most were identified by linkage mapping based on biparental populations.

Since the publication of the soybean genome based on the cultivar "Williams 82" (Schmutz et al., 2010), millions of single nucleotide polymorphisms (SNPs) and insertion/deletions (indels) have been identified (Kim, Lee, et al., 2010; Lam et al., 2010; Li et al., 2013). With the development of high-throughput genotyping technology, SNPs are now widely applied to dissect complex traits in soybean through linkage analysis (Lee, Jun, Michel, & Mian, 2015; Nguyen et al., 2012) and association mapping (Hwang et al., 2014; Wen, Boyse, Song, Cregan, & Wang, 2015). However, SNPs have so far been underutilized to dissect the genetic variation of lodging, particularly based on genome-wide association analysis.

In China, soybean is a very important crop. The sown acreage and total yield in north-east China account for 42.6% and 42.8%, respectively, of the nation's sown acreage and yield (http://zzys.agri.gov.cn). To ensure high and stable yields of soybean in north-east China, it is critical to select elite cultivars with high lodging tolerance, either as commercial cultivars or as parent lineages to breed new cultivars. Therefore, this study aimed to (i) evaluate lodging performance and the stability of lodging tolerance in 138 soybean cultivars; (ii) explore the genetic architecture of soybean lodging tolerance under two planting densities, using genome-wide association mapping based on SNP markers explored by Illumina SoySNP6k iSelect BeadChip (Illumina, San Diego, CA, USA); and (iii) select elite cultivars from the 138 soybean cultivars analysed, based on their phenotypic and genomic characters associated with lodging tolerance. These results will enrich our genomic understandings of lodging tolerance, and provide molecular and material support for MAS in soybean breeding.

2 | MATERIALS AND METHODS

2.1 | Plant germplasm, phenotyping and genotyping

The parent lineage "Tokachi nagaha" and the 137 cultivars deriving from it were selected to construct the association mapping panel. Fifty-four of these cultivars originated from Heilongjiang Province, 80 from Jilin Province, two from Liaoning Province and one from Beijing. Detailed information on the 138 accessions used in this study is shown in Table S1.

Experiments were performed in three locations in Jilin Province, at Jilin City Station and Tonghua Station during four consecutive years from 2011 to 2014 (abbreviated as 2011J, 2012J, 2013J, 2014J, 2011T, 2012T, 2013T and 2014T), and at Fanjiatun Station in 2011 and 2014 (abbreviated as 2011F and 2014F). Accessions were planted in a randomized block design consisting of three rows per plot, each measuring 300 cm in length and 60 cm in width. Two planting densities were included in our experiments: low density (one seed/10 cm) and high density (two seeds/10 cm). All experiments were performed in duplicate. In this study, lodging scores were evaluated at plant maturity stage R8 (Fehr & Caviness, 1977). Hence, in each plot, lodging was scored as 0 (almost all plants erect), 1 (all plants slightly leaning, less than 15 degrees or a few plants down), 2 (all plants moderately leaning, from 15 to 45 degrees or 25%–50% of plants down), 3 (all plants considerably leaning, more than 45 degrees or 50–80% of plants down) and 4 (prostrate, almost all plants down) (Rossi, Orf, Liu, Dong, & Rajcan, 2013).

DNA samples were extracted from soybean seedlings and leaves following a previously described method (Kisha, Sneller, & Diers, 1997). All accessions were genotyped via the Illumina SoySNP6k iSelect BeadChip, which consisted of 5,361 SNPs (Akond et al., 2013). Chromosomal distributions, coding and quality controlling of these SNPs were followed as previously documented (Wen et al., 2014).

2.2 | Phenotypic data analyses

Each location × year combination was considered as an environment, totalizing 10 environments (2 locations × 4 years + 1 location × 2 years). Analyses of variance (ANOVAs) were conducted to test the statistical significance of the several sources of variation, and the stability of the LS was analysed based on the genotype × environment interaction, using additive main effects and multiplicative interaction (AMMI) model (Samonte Stanley Omar et al., 2005; Zhang, Lu, & Xiang, 1998). The ANOVA model used was,

$$y_{lijk} = \mu + D_l + R_{k/j} + G_i + E_j + GE_{ij} + \varepsilon_{lijk},$$

and the AMMI model was,

$$y_{lijk} = \mu + D_l + R_{k/j} + G_i + E_j + \sum_{m=1}^{M} \lambda_m \xi_{im} \eta_{jm} + \rho_{ij} + \varepsilon_{lijk},$$

where y_{lijk} was the observed value of a trait of interest for the ith accession (i = 1, 2, . . ., 138) in the kth replication (k = 1, 2) under the jth environment (i.e., location × year in this study; j = 1, 2, . . ., 10) and the lth density (l = 1, 2). Model parameters included m = 1, 2, 3, the number of singular value decomposition (SVD) axes retained in the model; μ, the overall mean of the whole population; D_l, the density effect of the lth density; $R_{k/j}$, the kth replication effect in the jth environment; G_i, the genotypic effect of the ith accession; E_j, the environmental effect of the jth environment; GE_{ij}, the interaction effect between the ith accession and the jth environment; λ_m, the singular value for the SVD axis m; ξ_{im}, the genotype singular vector values for the SVD axis m; η_{jm}, the environment singular vector values for the SVD axis m; ρ_{ij}, the AMMI residuals for the interaction; and ε_{lijk}, the random error effect which was assumed to be normally distributed with a mean of zero, that is, $\varepsilon_{lijk} \sim N(0, \sigma^2_\varepsilon)$. The AMMI model analysis of LS was performed using a SAS 9.1.3 (SAS Institute, Cary, NC, USA) program written by Hermandez and Crossa (2000).

Heritability in the abroad sense was estimated as:

$$H^2 = \frac{\sigma^2_G}{\sigma^2_G + \frac{1}{e}\sigma^2_{GE} + \frac{1}{er}\sigma^2_\varepsilon},$$

where $\sigma^2_G, \sigma^2_{GE}$ and σ^2_ε, and were the genetic variance, interaction variance and error variance, respectively; e was the number of environments (e = 10 in this study); and r was the number of replications (r = 2 in this study). $\sigma^2_G, \sigma^2_{GE}$ and σ^2_ε were calculated by the MIXED procedure in SAS 9.1.3 (SAS Institute).

Lodging stability, that is,

$$D_i = \sqrt{\sum_{m=1}^{M} \xi^2_{im}}$$

was evaluated as the distance from a genotype to the base point in the iPCA space. The lower D_i is, the higher the stability of the accession. Best linear unbiased predictors (BLUPs), excluding the variations among years and locations and experimental error, were calculated by the procedure MIXED in SAS software and used for statistical descriptions and to explore the genetic variation of lodging.

2.3 | Genotypic data analyses

Minor allele frequencies (MAFs), polymorphic information content (PIC), heterozygosity and gene diversity for each SNP locus were calculated in Powermarker 3.25 (Liu & Muse, 2005). A subset of 4,044 SNPs, all with missing rates lower than 0.25 and MAF higher than 0.05, was selected from the 5,361 SNPs obtained (Fig. S1), and used to determine the population structure, using the Bayesian Markov chain Monte Carlo (MCMC) algorithm incorporated in STRUCTURE 2.3 (Pritchard, Stephens, & Donnelly, 2000). Ten independent simulations based on 100,000 MCMC replications and 100,000 burn-ins were performed with the number of subpopulations (k) ranging from 1 to 15. The ancestry model used in STRUCTURE analysis allowed population admixture and correlated allele frequencies; the optimal k was determined by the log-likelihood of the Ln P(D) and an ad hoc statistic Δk based on the second-order rate of changes in Ln P(D) between successive ks (Evanno, Regnaut, & Goudet, 2005).

Nei's genetic distances (Nei & Feldman, 1972) among individual accessions were calculated in Powermarker and used to construct a neighbor-joining (NJ) phylogenetic tree based on 1,000 bootstraps. Genotypic similarity among the 138 accessions was evaluated in Flapjack (Milne et al., 2010). The kinship coefficient between each accession pair was estimated in the SPAGeDi package (Hardy & Vekemans, 2002) using the Loiselle algorithm (Loiselle, Sork, Nason, & Graham, 1995). All negative values between individuals were set to 0 (Yu et al., 2006). The linkage disequilibrium (LD) parameter r^2 was calculated between all SNP pairs in TASSEL 4.0 (Yu et al., 2006). The physical LD decay distance at r^2 = .1 was considered as the length of LD block.

2.4 | Genome-wide association analysis

For marker–trait associations, a mixed linear regression model controlling both population structure and kinship matrices (denoted as Q + K model) was applied to data using TASSEL 4.0. The phenotypic variance explained by each SNP was calculated from the coefficient of determination R^2 of the mixed linear model in TASSEL. Quantile–quantile plots of estimated vs. observed p values from marker–trait associations were also produced and deviations from the expectation demonstrated that statistical analysis might cause spurious associations. Bonferroni corrections were applied, and a p-value of 1×10^{-4} was defined as the significance of marker–trait associations threshold. SNPs with p-values in the range of 1×10^{-3}-1×10^{-4} for one trait and p-values $<1 \times 10^{-4}$ for another trait were also reported. The LD decay distance at r^2 = .1 was used as the support interval to avoid multiple significance within one LD block.

3 | RESULTS

3.1 | Phenotypic variation

The averaged LS of BLUPs in the low density, high density and in the combination of the two treatments were 1.01 (0.09–2.10), 1.33 (0.12–2.26) and 1.17 (0.06–2.16), respectively (Table 1). Thus, lodging tends to increase with increasing population density, as the means increased from 1.01 (low density) to 1.33 (high density) (Table 1). LS varied greatly within populations (Fig. S2) and the phenotypes of LS were highly correlated between the two planting densities (R^2 = .85; Figure 1). The heritability of the lodging score was estimated as 87.0%.

3.2 | Stability analysis based on the AMMI model

According to the ANOVAs for the 138 accessions across the 10 environments in the two planting densities, all genotypes,

TABLE 1 Variation in the best linear unbiased predictions (BLUPs) of lodging scores across low, high and combined planting densities

Density	Mean	Min	Max	SD	CV
Low	1.01	0.09	2.10	0.56	55.54
High	1.33	0.12	2.26	0.62	46.70
Combination	1.17	0.06	2.16	0.61	51.87

SD, standard deviation; CV, coefficient of variation.

environments, and genotype × environment interactions were significantly different (Table 2), indicating that the environment (locations) influenced the experiments and that the genotype × environment interaction significantly affected lodging tolerance. Therefore, stability evaluation was necessary. There were nine iPCAs at the 1% significant level (Table 2), which explained up to 85.19% of the variation in the genotype × environment interaction.

Stability of the LS of the 138 accessions was analysed based on the D_i value, that is, on the distance from those nine iPCAs to ordinate origin in multidimensional space (Table S1). D_i values of the whole population ranged from 0.49 to 1.37, with an average value of 0.82 and standard deviation of 0.17. D_i values were positively correlated with the BLUPs of the LS. Compared to other accessions, those presented in the dotted box in Figure 2 have lower BLUPs and D_i values with small variation range, indicating that accessions with stronger lodging tolerance also showed higher stability.

"Jinong 14" had the lowest D_i value (0.49), while "Jiyu 301" had the highest (1.37). Some accessions, such as "Heihe 25," "Dongda 1," "Heihe 19," "Kenjiandou 14," "Kenjiandou 15" and "Beidou 1," had low D_i values and average LS, whereas other accessions, namely "Jinong 15," "Haodou 2000," "Jiyu 57," "Bainong 8" and "Bainong 6," were susceptible to lodging although presenting high stability (Table S1).

3.3 | Genetic diversity of the 138 accessions based on 4,044 SNPs

Genotypes comprising 4,044 SNPs were analysed using STRUCTURE, NJ trees and PCA to evaluate the relatedness among the 138 accessions. The likelihood of Δk values obtained in STRUCTURE analysis showed that $k = 2$ was the optimal population subdivision, indicating that accessions formed two major clusters, and the results are in accordance with Liu et al. (2017). There were 64 accessions in subpopulation 1, including "Tokachi nagaha," and 74 accessions in subpopulation 2. Fifty accessions in subpopulation 1 were from Heilongjiang Province, and 68 accessions in subpopulation 2 were from Jilin Province. These results were consistent with the geographical origin of the 138 accessions. The significant pairwise F_{ST} found between the two subpopulations (0.17, $p < .001$) further confirmed the existence of two subpopulations for the 138 accessions. Therefore, the Q matrix with $k = 2$ and the K matrix estimated were used in the subsequent genome-wide association analysis.

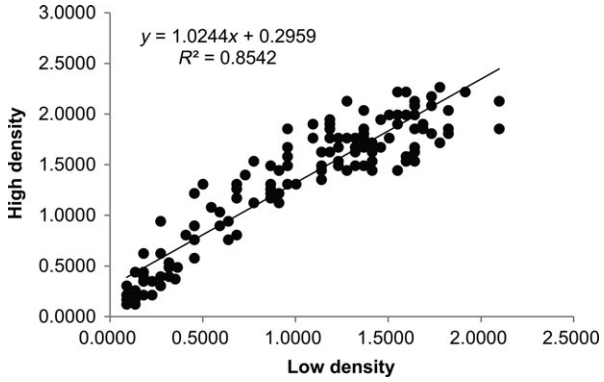

FIGURE 1 Scatter plot of lodging scores under low and high planting densities

Average LD of the whole-genome was $r^2 = .23$. When the LD decay distance was around 2,000 kb, r^2 decreased to half of its maximum value and when the decay distance was about 8,000 kb, r^2 was below .1 (Figure S3), suggesting a strong LD in this population. Average marker density was 232.63 kb in the whole population, and therefore, it was expected to have an adequate power to detect the major QTL related to LS in the 138 soybean accessions tested. To avoid false positives due to the strong LD, LD blocks were determined based on the LD decay distance at $r^2 = .1$, which was used as the support interval to declare significant SNPs associated with the target trait.

3.4 | Genome-wide association analysis

Using 4,044 SNPs, we conducted a genome-wide association analysis for soybean LS across 10 trials by Q + K model to correct for population structure and genetic relatedness (Figures S4 and S5). Thirty-one SNPs, distributed across 16 soybean chromosomes, were significantly associated with LS and explained 8.79% of the phenotypic variation on average (sum of genetic contribution of significant SNPs/the number of SNP; Table 3, Figures 3 and 4). There were three SNPs on each of chromosomes 6, 8, 11 and 13, and one SNP on each of chromosomes 7, 14, 16, 17 and 20 (Table 3, Figures 3 and 4).

Of the 31 identified SNPs controlling LS, nine were detected in a single environment, five in two, four and five environments, seven in three environments and none in six or more environments (Table 3). Twenty-two SNPs were detected in low planting density, 25 SNPs in high planting density and 16 SNPs in both planting densities. Nine SNPs, including ss250480419 on chromosome 20 and ss249841514 on chromosome 18, were identified in both planting densities, in the same trial. The SNP ss247050193 on chromosome 9, which was detected in low planting density in the 2012J environment, explained up to 15.86% of the phenotypic variance, whereas SNP ss247400714 on chromosome 11, which was detected in high planting density in the 2011T environment, explained only 6.68% of the phenotypic variance (Table 3).

3.5 | Elite alleles

The distributions of elite alleles across the 31 SNPs and 138 accessions are shown in Tables 4 and S1, respectively. The

TABLE 2 Analysis of variance (ANOVA) for the additive main effects and multiplicative interaction (AMMI) model of lodging scores

Variance source	Sum of Square	Mean Square	*F*-value	Percentage (%)	Accumulated percentage (%)
Model	7467.77	2.71	6.33**		
Geno	2182.83	15.93	37.27**		
Env	2397.58	126.19	295.15**		
Geno × Env	2884.92	1.11	2.59**		
IPCA1	902.62	5.82	13.62**	31.29	31.29
IPCA2	433.92	2.84	6.63**	15.04	46.33
IPCA3	283.04	1.87	4.38**	9.81	56.14
IPCA4	207.07	1.39	3.25**	7.18	63.32
IPCA5	173.53	1.18	2.76**	6.02	69.33
IPCA6	144.20	0.99	2.33**	5.00	74.33
IPCA7	135.39	0.95	2.21**	4.69	79.02
IPCA8	99.03	0.70	1.64**	3.43	82.46
IPCA9	78.85	0.57	1.33**	2.73	85.19

Env, environment; Geno, genotype; Geno × Env, genotype × environment interaction; IPCA, interaction principal component axis.
**Significant difference at $p < .01$.

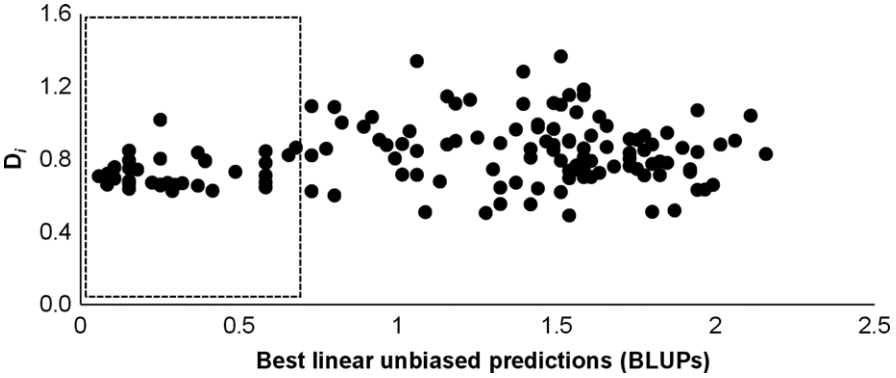

FIGURE 2 Scatter plot of lodging stability (D_i) vs. the best linear unbiased predictions (BLUPs) of the lodging scores obtained for the 138 accessions included in the present study. The dotted box indicates accessions with both low BLUPs and D_i values

number of elite alleles harboured by the 138 accessions ranged from 7 to 27 and averaged at 18.05 (Table S1). "Heihe 32" harboured the largest number of elite alleles, while "Jilin 47" the lowest. The popular and widely grown cultivars "Heihe 19," "Heinong 44," "Heinong 43" and "Beifeng 11" harboured more than 20 elite alleles for soybean lodging. "Tokachi nagaha," the founder lineage for soybean cultivars in north-east China, also harboured 20 elite alleles for lodging.

Of the 30 accessions with the smallest BLUPs, 19 accessions contained at least 20 elite alleles (Table S1). The BLUPs and the number of elite alleles within accessions present opposite trends (Figure 5), as BLUPs tended to decrease with increasing elite alleles. Thus, the higher the number of elite alleles within an accession, the stronger its lodging tolerance.

3.6 | Selection of excellent germplasm

Excellent accessions were screened based on the BLUPs of LS, D_i values and elite alleles (Table S1). There were large variations among these three parameters. Some accessions presented strong tolerance, high stability and large number of elite alleles, including "Heihe 25," "Heihe 19," "Dongda 1," "Kenjiandou 15," "Beidou 1," "Heihe 30" and "Tokachi nagaha," whereas others had multiple elite alleles, strong tolerance, but comparatively low stability (e.g., "Kenjiandou 27," "Heihe 17," "Kenjiandou 1," "Jiufeng 8" and "Kenjiandou 31"). Although the poor stability for "Heihe 32," "Beifeng 11" and "Kenfeng 6," they harbour multiple elite alleles for lodging tolerance and thus still have the high potential to be used as the founder parents in soybean breeding in particular area.

4 | DISCUSSION

4.1 | Multienvironmental trials are critical to study lodging tolerance

The genotype × environment interactions from ANOVA explained a significant proportion of phenotypic variance, suggesting that lodging is seriously affected by environmental factors. Moreover, nine of the 31 QTL, only detected in a specific environment, constituted 29.03%

TABLE 3 Single nucleotide polymorphism (SNP) markers significantly associated with lodging score

Markers	Chr	Position	Associated traits (R^2%)[a]	−log(P)	Reported QTL/genes
ss244345772	1	2600388	2014J (7.91)	3.02	
ss244599352	1	53493422	2011T (8.16)	2.91	Seed weight (Kim, Kim, et al., 2010; Liu et al., 2011; Panthee, Pantalone, West, Saxton, & Sams, 2005); whitefly resistance (Zhang et al., 2013)
ss244675917	2	6954614	2011F (7.90), 2013T (8.52), 2011T (8.36), 2012T (8.78), 2013T (7.83)	3.19	Flower number (Zhang et al., 2007); pod number (Zhang et al., 2007)
ss244864280	2	47205688	2014F (7.58), 2012T (10.27)	3.11	Seed weight (Sun et al., 2012); seed oil (Qi et al., 2011)
ss245908019	6	16669687	2011J (8.84)	2.95	Seed yield (Du et al., 2009); pod, beginning (R3 beginning pod) (Tasma et al., 2001); pod maturity, beginning (R7 beginning maturity) (Tasma et al., 2001)
ss245962646	6	24441282	2012T (10.95), 2013T (7.08), 2014J (7.66), 2013T (9.35)	3.53	Plant height (Guzman et al. 2007); seed weight (Han et al., 2012); seed yield (Guzman et al. 2007; Zhang et al., 2004); seed protein (Liang et al., 2010); first flower (Githiri et al., 2007); pod maturity (Guzman et al. 2007; Specht et al., 2001)
ss246105366	6	47801398	2012T (10.18), 2014J (9.13), 2014T (7.40)	3.45	Plant height (Liu et al., 2011); seed weight (Han et al., 2012); seed yield (Reinprecht et al., 2006); seed oil plus protein (Chen et al., 2007)
ss246280747	7	14892282	2013J (7.83), 2012T (11.82)	3.85	Plant height (Guzman et al. 2007); seed yield (Du et al., 2009); seed oleic (Bachlava et al., 2009); pod maturity (Bachlava et al., 2009); reproductive stage length (Cheng et al., 2011)
ss246501414	8	9866660	2011J (9.93), 2011J (8.07), 2012T (8.12)	3.13	Internode length (Alcivar et al., 2007); seed protein (Lu et al., 2013); seed oil (Liang et al., 2010)
ss246573652	8	17927603	2014J (7.68), 2011J (10.98), 2014J (7.48)	3.47	
ss246741845	8	44466061	2011T (8.71), 2012T (14.84), 2013T (10.93)	4.12	Seed weight (Han et al., 2012); seed linolenic (Bachlava et al., 2009)
ss246828821	9	7144227	2014J (8.55)	3.01	Lodging (Wang et al., 2004); plant height (Wang et al., 2004); seed yield (Wang et al., 2004)
ss247050193	9	45254305	2011T (7.35), 2012J (15.86)	4.96	Seed yield (Du et al., 2009); seed palmitic (Li et al., 2011)
ss247348244	11	414393	2012T (8.08), 2013J (8.178)	2.77	
ss247400714	11	8088818	2011F (7.72), 2011J (8.59), 2011T (6.68), 2014F (7.978), 2014T (7.09)	2.89	Plant height (Chen et al., 2007); node number (Chen et al., 2007); branching (Chen et al., 2007); pod number (Sun et al., 2006); pod maturity (Bachlava et al., 2009)
ss247434650	11	14586934	2012J (8.75), 2012T (8.95), 2011J (10.55), 2012T (7.90)	3.35	Lodging (Reinprecht et al., 2006); seed weight (Han et al., 2012)
ss247589563	12	446667	2011T (7.41)	2.90	Seed weight (Funatsuki, Kawaguchi, Matsuba, Sato, & Ishimoto, 2005)
ss247790225	12	34375177	2011J (9.56)	3.20	
ss247892318	13	5779023	2012J (8.86), 2013T (8.18)	3.09	Node number (Zhang et al., 2004); seed weight (Sun et al., 2012); seed abortion (Tischner, Allphin, Chase, Orf, & Lark, 2003); seed oil (Qi et al., 2011; Wang et al., 2012); seed linoleic (Bachlava et al., 2009); seed oleic (Bachlava et al., 2009); seed palmitic (Wang et al., 2012)
ss247955863	13	12142087	2011F (8.73), 2011J (9.47), 2012T (12.39)	3.94	Plant height (Sun et al., 2006)
ss248143039	13	36633721	2011T (7.07), 2013T (8.53), 2011T (8.23), 2013J (8.82)	3.14	Stem strength (Chen et al., 2011); seed yield-to-plant height ratio (Orf et al., 1999; Reyna & Sneller, 2001); seed yield (Orf et al., 1999; Reyna & Sneller, 2001)
ss248496931	14	47211704	2011F (7.31), 2014J (10.94), 2013J (9.44)	3.05	Seed linoleic (Xie et al., 2012)

(Continues)

TABLE 3 (Continued)

Markers	Chr	Position	Associated traits (R^2%)[a]	−log(P)	Reported QTL/genes
ss248590521	15	9194711	2011F (8.25), 2013J (10.68), 2014F (8.01), 2014T (7.96), 2013J (7.46)	3.06	Plant height (Liu et al., 2011); seed weight (Liu et al., 2011); seed oil (Reinprecht et al., 2006)
ss248926633	15	50561379	2012T (8.09)	2.76	Plant height (Specht et al., 2001; Sun et al., 2006); pod number (Zhang et al., 2007)
ss249201608	16	33854136	2014T (8.22)	2.92	Plant height (Guzman et al. 2007; Kabelka et al., 2004; Sun et al., 2006); seed yield (Guzman et al. 2007; Kabelka et al., 2004)
ss249303877	17	8508412	2011F (7.35), 2012J (10.12), 2013T (10.52)	3.50	Seed yield-to-plant height ratio (Orf et al., 1999); seed yield (Orf et al., 1999; Reinprecht et al., 2006; Reyna & Sneller, 2001); seed weight (Hoeck et al., 2003; Panthee et al., 2005); seed oil (Hyten et al., 2004); seed linoleic (Bachlava et al., 2009); seed palmitic plus stearic (Kim, Kim, et al., 2010); seed palmitic (Reinprecht et al., 2006)
ss249523637	18	2788739	2011T (7.18), 2012T (9.86), 2013T (7.06), 2013J (10.80)	3.71	Lodging (Reinprecht et al., 2006); plant height-to-lodging ratio (Orf et al., 1999); plant height (Reinprecht et al., 2006); internode length (Alcivar et al., 2007); branching (Sayama et al., 2010); seed yield (Reinprecht et al., 2006); seed protein (Panthee et al., 2005)
ss249841514	18	52310546	2011F (7.63), 2013T (7.34), 2011F (7.88), 2012T (10.05), 2013T (9.13)	3.20	Seed yield (Du et al., 2009); seed protein (Lu et al., 2013); seed oil (Qi et al., 2011); reproductive stage length (Cheng et al., 2011)
ss250062395	19	8778142	2011J (8.77)	2.86	Plant height (Li et al., 2008); seed oil (Qi et al., 2011)
ss250201579	19	38390845	2014T (9.28), 2011F (8.04)	2.73	Plant height (Orf et al., 1999); seed yield-to-plant height ratio (Orf et al., 1999); seed yield (Du et al., 2009); seed weight (Hyten et al., 2004); pod number (Zhang et al., 2007); seed protein (Tajuddin, Watanabe, Yamanaka, & Harada, 2003); seed oil (Hyten et al., 2004)
ss250480419	20	34222629	2011T (7.71), 2011F (6.79), 2011T (9.91), 2012J (7.30), 2013J (8.61)	3.73	Lodging (Palomeque et al., 2009b, 2010); plant height (Palomeque et al., 2010); pods per node (Palomeque et al., 2009b); pod number (Zhang et al., 2007); flower number (Zhang et al., 2007); seed weight (Palomeque et al., 2009b); seed yield (Du et al., 2009; Palomeque et al., 2009a; Rossi et al., 2013); seed oil (Palomeque et al., 2009b; Qi et al., 2011; Reinprecht et al., 2006); seed oleic (Bachlava et al., 2009; Li et al., 2011); seed linoleic (Bachlava et al., 2009)

2011J, 2012J, 2013J and 2014J denoted the experimental trials at Jilin Station in Jilin Province from 2011 to 2014, respectively; 2011T, 2012T, 2013T and 2014T denoted the experimental trials at Tonghua Station in Jilin Province from 2011 to 2014, respectively; and 2011F and 2014F denoted the experimental trials at Fanjiatun Station in Jilin Province in 2011 and 2014, respectively.

[a]Underlined markers were associated with lodging under high density.

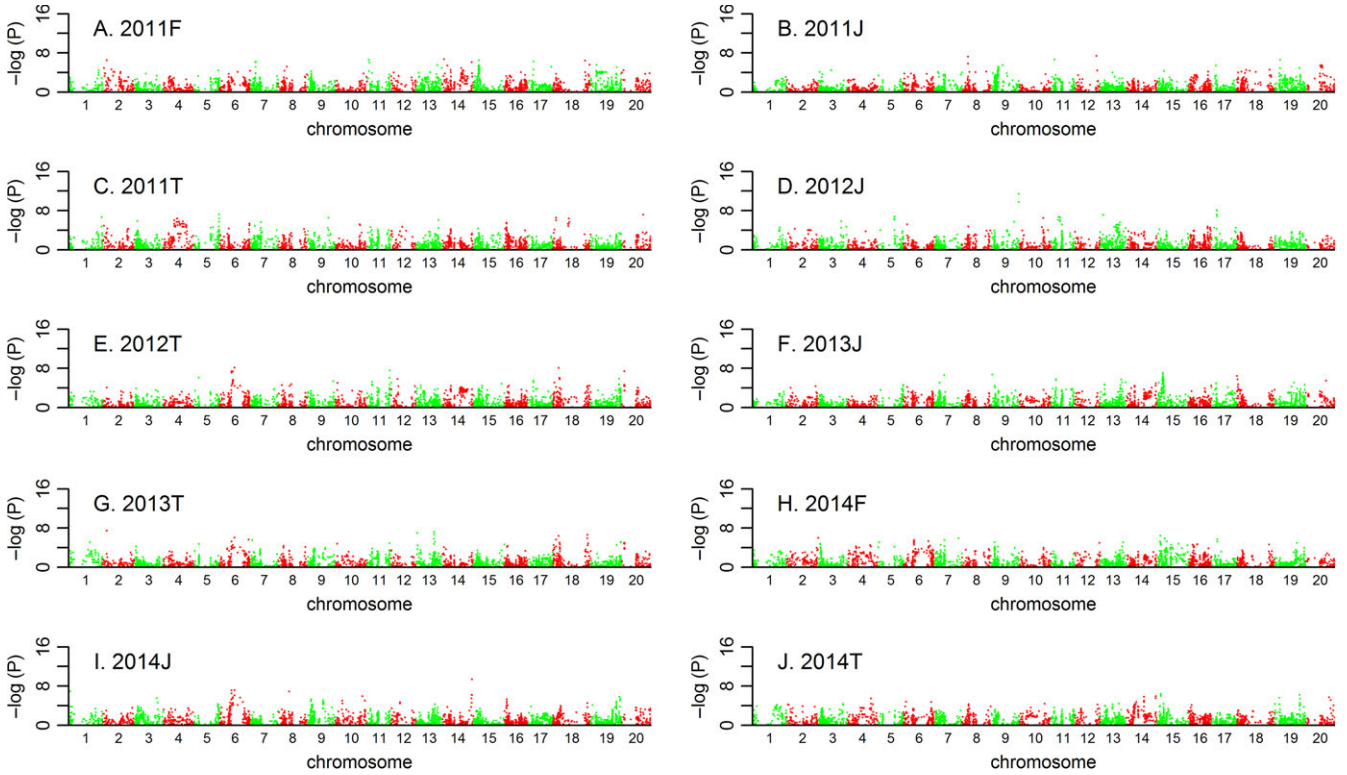

FIGURE 3 Manhattan plots of the marker–trait associations along the 20 chromosomes under low planting density in the 10 environments. Environments are denoted using four digits corresponding to year (2011–2014) followed by a letter indicating locations: F, Fanjiatun; J, Jilin; and T, Tonghua [Colour figure can be viewed at wileyonlinelibrary.com]

of the phenotypic variance, indicating that lodging is controlled by multiple QTL and is sensitive to the environment. Therefore, evaluation of lodging in multienvironmental trials was critical to understand its phenotypic variation and facilitated the subsequent investigation of the genetic variation of lodging.

4.2 | SNPs repeatedly detected or located in or close to reported QTLs

QTL detected in different genetic backgrounds and environments is considered more useful than those identified in a specific environment with high phenotypic variation contributions, as in the first case QTL are more helpful for breeding with broad adaptability to different environments (Fulton et al., 1997; Lee, Jun, et al., 2015). Four significantly signalled QTL, namely ss246828821 on chromosome 9, ss247434650 on chromosome 11, ss249523637 on chromosome 18 and ss250480419 on chromosome 20, were located in or close to previously reported lodging-related QTL (Orf et al., 1999; Palomeque et al., 2009b, 2010; Reinprecht et al., 2006; Wang et al., 2004). For example, ss246828821 was only 192.3 kb away from previously reported QTL Satt178 (Wang et al., 2004). In addition, lodging was positively correlated with stem strength (Matsukawa & Banba, 1986), the quantitative locus Sat_197 located on chromosome 13 was related to stem strength (Chen et al., 2011), and the distance between Sat_197 and ss248143039 detected in the present study was 231.9 kb. In this study, 22 QTLs can be identified in two or more environments simultaneously, of which, five QTLs detected in four and five environments, respectively. These results suggested that some casual gene/genes might be present in those genome regions and their associated markers might be well useful for soybean breeding with broad adaptability to various environments.

4.3 | SNPs colocated or near agronomic QTL

It was reported that QTLs controlling lodging, and other agronomic traits, including plant height, maximum internode length, flowering date and branch number, occurred in the same genomic region (Lee, Bailey, Mian, Shipe, et al., 1996; Liu et al., 2007; Mansur, Lark, Kross, & Oliveira, 1993; Orf et al., 1999; Sayama et al., 2010; Specht et al., 2001). The similar results were observed in the present study (Table 3). Of the 31 QTL, 13 were located in or near regions where QTL was related to plant height (Chen et al., 2007; Guzman et al., 2007; Kabelka et al., 2004; Li, Pfeiffer, & Cornelius, 2008; Liu et al., 2011; Orf et al., 1999; Palomeque et al., 2010; Reinprecht et al., 2006; Specht et al., 2001; Sun et al., 2006; Wang et al., 2004). Five LS-related markers were located in or adjacent to regions associated with growth period (Bachlava, Dewey, Burton, & Cardinal, 2009; Cheng et al., 2011; Githiri et al., 2007; Guzman et al. 2007, Specht et al., 2001; Tasma, Lorenzen, Green, & Shoemaker, 2001). For example, ss246280747 on chromosome 7 was close to QTL related to pod maturity (Bachlava et al., 2009) and

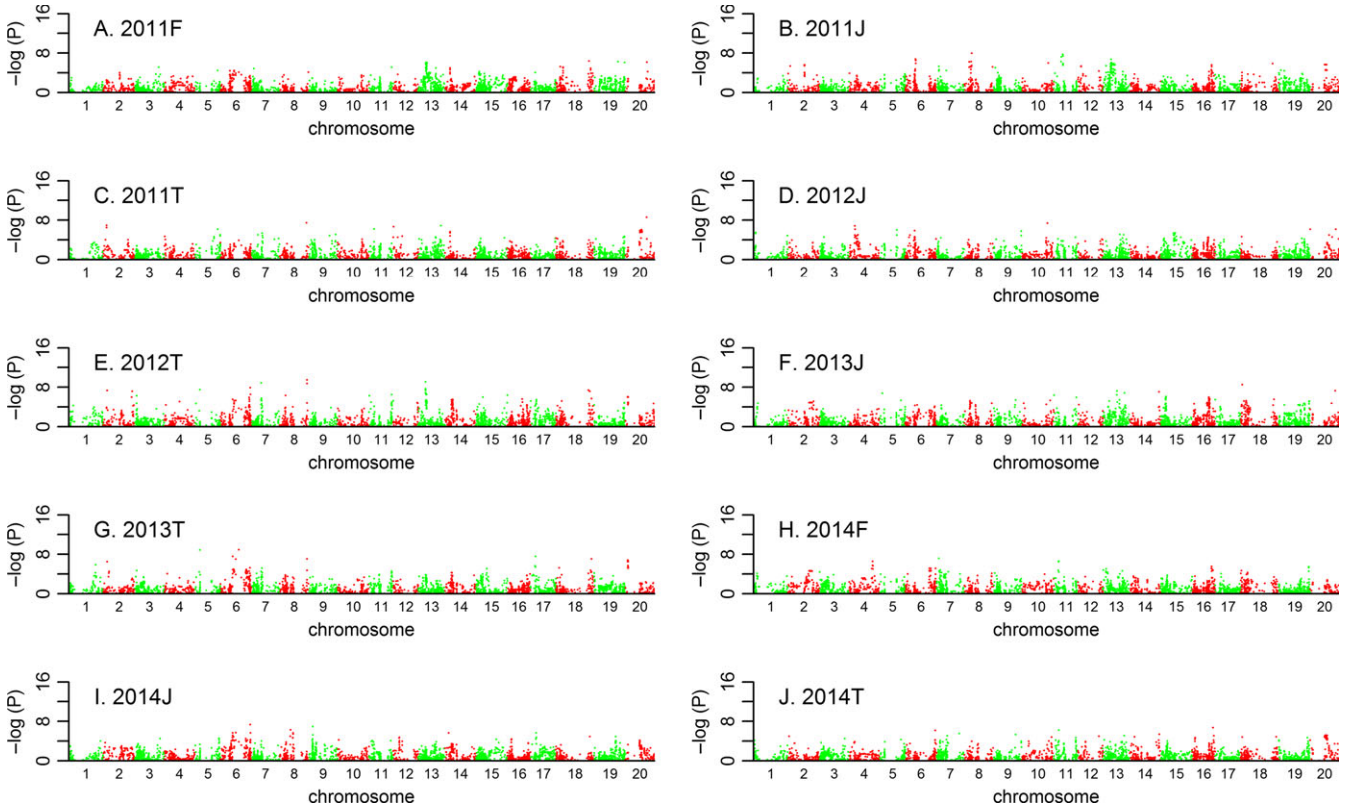

FIGURE 4 Manhattan plots of the marker–trait associations along the 20 chromosomes, under high planting density in the 10 environments. Environments are denoted using four digits corresponding to year (2011–2014) followed by a letter indicating locations: F, Fanjiatun; J, Jilin; and T, Tonghua [Colour figure can be viewed at wileyonlinelibrary.com]

reproductive stage duration (Cheng et al., 2011), and ss245962646 located on chromosome 6 was close to QTL determining pod maturity (Guzman et al. 2007; Specht et al., 2001) and first flowering (Githiri et al., 2007).

The significant correlations between lodging and yield-related soybean traits have also been proposed in several studies (Board, 2001; Mancuso & Caviness, 1991; Noor & Caviness, 1980; Wilcox & Sediyama, 1981). In the present study, 23 SNPs were located in or near regions for which QTL related to yield and yield-related traits have been reported (Table 3). For example, ss250480419 located on chromosome 20 was close to the QTL determining pods per node (Palomeque et al., 2009b), pod number (Zhang et al., 2007), seed weight (Palomeque et al., 2009b), seed yield (Du, Wang, Fu, & Yu, 2009; Palomeque et al., 2009a; Rossi et al., 2013) and flower number (Zhang et al., 2007).

Totally, there are 27 SNPs repeatedly detected or located in or close to agronomically important QTL mapped by linkage analysis. Thumma et al. (2001) suggested a cause–effect relationship among different traits if the QTL controlling such traits were colocated. Genomic regions where multiple traits were coassociated or colocated indicated pleiotropy of a single causal gene or a tight linkage among multiple causal genes. Thus, using pleiotropic or closely linked markers in MAS could simultaneously improve multiple traits, enhancing breeding efficiency. In condition, there are four novel SNPs identified in the present study, which could increase our understanding of the genetic mechanisms of lodging tolerance in soybean.

4.4 | MAS of lodging-tolerant accessions

MAS has been widely applied in crop improvement. SNPs are currently the most efficient and preferred molecular markers in most plant species, including soybean (Lee, Jun, et al., 2015). The newly available SNP180K (Lee, Jeong, et al., 2015) and SNP355K (Wang et al., 2016) chips would provide new opportunities to discover more genetic variations of soybean. The present study revealed that many loci are involved in lodging tolerance and that different loci have different effects (Table 3). There could be complex gene interactions besides additive effects, and therefore, comprising multiple loci does not necessarily indicate that the accession has high lodging tolerance. However, in the present study, it was found that the more elite alleles one accession contains, the stronger lodging tolerance the accession tends to have. The D_i value tended to decrease and the stability of lodging tolerance tended to increase with decreasing BLUPs and increasing lodging tolerance, all suggesting that elite germplasms with strong and stable lodging tolerance might be selected through MAS, and the genetic bases of these elite accessions were the large number of elite alleles in their genome. By combing the phenotypic value, D_i and the elite alleles contained in the accessions, it was possible to select elite germplasms, including

TABLE 4 Elite alleles of the 31 identified single nucleotide polymorphisms (SNPs) associated with lodging scores and the number of accessions carrying each elite allele

Markers	Chr.	Position	SNP biallele	Elite allele	Number of carrier accessions
ss244345772	1	2600388	C/T	T	73
ss244599352	1	53493422	A/G	A	117
ss244675917	2	6954614	C/T	C	110
ss244864280	2	47205688	C/T	T	74
ss245908019	6	16669687	A/G	G	28
ss245962646	6	24441282	A/G	G	41
ss246105366	6	47801398	G/T	T	53
ss246280747	7	14892282	G/T	G	29
ss246501414	8	9866660	C/T	C	75
ss246573652	8	17927603	G/T	T	43
ss246741845	8	44466061	C/T	C	98
ss246828821	9	7144227	A/G	G	13
ss247050193	9	45254305	C/T	T	121
ss247348244	11	414393	C/T	T	98
ss247400714	11	8088818	A/G	G	116
ss247434650	11	14586934	A/C	C	31
ss247589563	12	446667	C/T	C	99
ss247790225	12	34375177	A/G	G	125
ss247892318	13	5779023	A/C	A	125
ss247955863	13	12142087	A/G	G	103
ss248143039	13	36633721	A/G	A	51
ss248496931	14	47211704	A/G	G	90
ss248590521	15	9194711	A/C	A	78
ss248926633	15	50561379	C/T	T	81
ss249201608	16	33854136	C/T	C	53
ss249303877	17	8508412	A/G	G	125
ss249523637	18	2788739	A/G	G	109
ss249841514	18	52310546	A/G	G	23
ss250062395	19	8778142	C/T	T	118
ss250201579	19	38390845	C/T	C	109
ss250480419	20	34222629	A/G	A	66

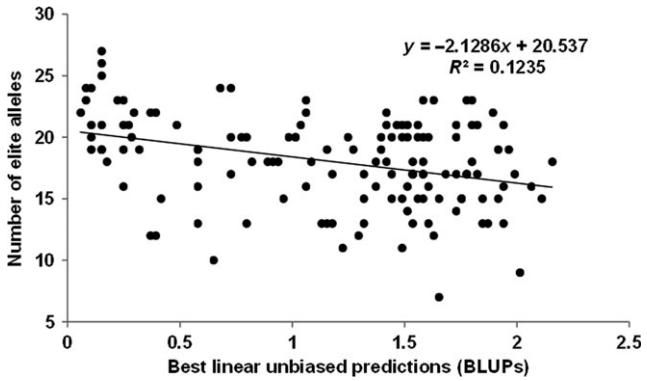

FIGURE 5 Scatter plot of the number of elite alleles vs. the best linear unbiased predictions (BLUPs) of the lodging scores for the 138 accessions included in the present study

"Heihe 25" and "Kenjiandou 15," which may provide the required phenotypic and molecular backgrounds for soybean lodging improvement.

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CONFLICT OF INTERESTS

The authors have declared that no competing interests exist.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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