Identification and Molecular Mapping of a Major Quantitative Trait Locus Underlying Branch Angle in Soybean

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Abstract

Soybean branch angle is a critical architectural trait that affects many other traits of agronomic importance associated with the plant's productivity and grain yield, and is thus a vital consideration in soybean breeding. However, the genetic basis for modulating this important trait in soybean and many other crops remain unknown. Previously, we developed a recombinant inbred line (RIL) population derived from a cross between a domesticated soybean (*Glycine max*) variety, Williams 82, and a wild soybean (*Glycine soja*) accession, PI 479752, and observed drastic variation in plant architecture including branch angle among individual RILs. In this study, one of the RILs possessing extremely wide branch angle (WBA) was crossed with an elite soybean cultivar (LD00-3309) possessing narrow branch angle (NBA) to produce an F_2 population composed of 147 plants and F_2-derived F_3 families for inheritance analysis and QTL mapping. We found that branch angle is controlled by a major QTL located on chromosome 19, designated q*GmBa1*, and that WBA – derived from the wild soybean accession – is dominant over NBA. This locus was also detected as a major one underlying branch angle by QTL mapping using a subset of the soybean nested association mapping (SoyNAM) population composed of 140 RILs, which were derived from a cross between a landrace, PI 437169B, possessing WBA and an elite variety, IA3023, possessing NBA. Molecular markers located in the QTL region defined by both mapping populations can be used for marker-assisted selection of branch angle in soybean breeding.

Key Message

A major quantitative trait locus (QTL) modulating soybean (*Glycine max*) branch angle was identified by linkage analysis using two bi-parental mapping populations with and without pedigree from wild soybean (*Glycine soja*).

Introduction

Plant architecture is defined as the three-dimensional organization of the plant body. For above-ground plant parts, this includes plant height, branch/tiller pattern, and the shape and position of leaves and reproductive organs (Reinhardt and Kuhlemeier, 2002). Among these architectural traits, branch, tiller, and/or leaf angles are key determinants of canopy structure which directly affects light interception, photosynthetic efficiency, planting density, and ultimately plant productivity and grain yield in many crops (Burgess, 2019). Consequently, the optimization of these traits for enhanced ability of the plant to capture light energy and efficiently convert it into biomass over the course of the growing season has been a major goal in plant breeding (Tollenaar and Lee, 2002, Zhu et al. 2008).

Canopy architecture is often determined by distinct factors among different species. In cereal crops such as maize, sorghum, rice, and wheat, the canopy structure is primarily determined by leaf angle – the inclination between the leaf blade midrib and the vertical stem, and upright plant architecture with erect leaves has been identified to be a key component in the development of high-yielding cultivars (Pendelton et al. 1968; Lu et al. 2007; Khush, 2013; Truong et al. 2015; Mantilla-Perez et al. 2017). In legume species

such as soybean, common bean, and pea, canopy architecture is mainly determined by branch angle – the inclination between the main stem and lateral branches (Agudamu et al. 2016). In the past few decades, several major quantitative trait loci (QTLs) modulating leaf angles in cereals have been identified, cloned, and used to optimize plant architecture for enhancement of grain yields (Yu et al. 2007; Li et al. 2007; Ku et al. 2011; Wu et al. 2013; Zhang et al. 2014; Dong et al. 2016; Zhang et al. 2018; Tian et al. 2019; Li et al. 2019). By contrast, little is known regarding how branch angles are genetically controlled in legumes. Given that the genetic mechanisms underlying branch/tiller/leaf angles differ greatly among different crops as revealed in the cereals, it is essential to understand the genetic basis of these traits in individual crops.

Soybean (*Glycine* max), with global production greater than 100 billion US dollars (FAOSTAT, 2018), is the most valuable legume crop, playing a key role in meeting the protein and oil needs of a growing population. It is believed that soybean was domesticated from its wild relative, *Glycine soja*, approximately 5,000 ~ 9,000 years ago (Carter et al. 2004; Kim et al. 2012; Wang et al. 2019), resulting in drastic morphological and physiological modifications such as the transition from the procumbent growth without upright branches/stems in *G. soja* to the upright stem growth found in cultivated soybeans. The domestication process was followed by varietal diversification, resulting in a multitude of soybean landraces with variable branch angle widths. Some of the landraces were subsequently used worldwide to develop elite cultivars through modern breeding (Carter et al. 2004; Li et al. 2008). Although branch angle is a quantitative trait, most soybean varieties can be roughly classified into three categories – compact with a narrow branch angle (NBA), spread-out with a wide branch angle (WBA), or semi-compact with an intermediate branch angle (IBA). In general, WBA is primarily seen in landraces, NBA is mainly observed in elite cultivars, and IBA is found in both landraces and elite cultivars (The U.S. National Plant Germplasm System).

Increases in soybean yield through breeding in the past few decades has been slower than growers have expected, primarily due to the narrow genetic base of ancestral lines used in soybean breeding programs (Hyten et al. 2006). To widen the genetic base of elite cultivars, it is important to bring new and diverse landraces into soybean breeding programs. However, given the wide range of phenotypic variation in branch angle among different varieties, as well as the plasticity of the trait under short photoperiod and adverse growing conditions such as greenhouse and winter nursery routinely used for accelerating soybean breeding, developing soybean cultivars with optimized branch angles for improved grain yields remains challenging. There is therefore a critical need to understand the genetic control of branch angle in soybean. Here, we report the identification and mapping of a major QTL modulating soybean branch angle using two distinct bi-parental populations.

Methods

Plant materials

Two bi-parental populations were employed in this study for inheritance analysis and mapping of QTL underlying branch angle. One population is composed of 147 F_2 plants and F_3 families derived from a cross between an NBA high-yielding soybean line LD00-3309 – one of the founder lines used to develop the soybean nested association mapping (SoyNAM) population (soybase.org/NAM), and a typical WBA recombinant inbred line 1890 (RIL1890) selected from a RIL population derived from a cross between a *G. soja* accession PI 479752 and an IBA soybean cultivar Williams 82 (Swarm et al. 2019). The other population is composed of 140 RILs as a subset of the SoyNAM population derived from a cross between an NBA high-yielding soybean line IA3023 and a WBA soybean landrace PI 437169B.

Branch angle phenotyping

The 147 (LD00-3309 × RIL1890) F_2 individuals and the two parental lines were grown in the field at the Agronomy Centre for Research and Education (ACRE) at Purdue University in West Lafayette, Indiana, United States, in 2015, and the F_2-derived F_3 families were grown in the field at ACRE in 2016 for branch angle evaluation. The 140 (IA3023 × PI 437169B) RILs were grown in the field at ACRE. Photos were taken of the parental lines from representative individuals selected at 6, 8, 11, and 20 weeks post planting to show the phenotypic differences across growth stages. The angles between two branches growing in opposite directions near the base of 20 fully mature individuals from each parental line were measured with a protractor; average branch angles were calculated and compared. Branch angles of individual plants in the mapping populations were classified into two groups: “NBA” when the average branch angle was less than 90° and ‘WBA’ when the average branch angle was greater than 90°. Individuals with less than 5 branches were not evaluated. Because NBA is dominant over WBA as described in the Results below, most individuals in the mapping populations show parental-type branch angles and were easily classified. Photos were also taken from 20 randomly selected F_3 individuals for each of the three genotypes (homozygous for each parental allele and heterozygous) at the mapping region and merged together with 95% transparency to display the phenotypic differences among the three genotypes.

DNA isolation and genotyping

DNA of each F_2 individual of the mapping population were extracted by mixing hypocotyls from 15–20 germinating $F_{2:3}$ seeds. DNA of each RIL of the mapping population were extracted directly from the mixed leaf tissues of each RIL. DNA isolation was performed using a CTAB based method modified from Mace et al. (2013). The DNA samples of the (LD00-3309 × RIL1890) F_2 mapping population and the parental lines were genotyped using the soybean 6K single nucleotide polymorphism (SNP) chip (BARCSoySNP6K) (Song et al, 2020, TPJ). The genotypic data of the 140 (IA3023 × PI437169B) RILs and the two parental lines were downloaded from SoyBase (www.soybase.org).

QTL mapping

To clean up the genotypic data for QTL mapping, all non-polymorphic markers between the parental lines, LD00-3309 and RIL18990, were removed. Then, markers with missing values for more than 50% of the

individuals and markers with distorted segregation patterns in the (LD00-3309 × RIL18990) F_2 population were removed. The same filtering was applied to the (IA3023 × PI437169B) mapping population

QTL mapping was conducted separately using the two mapping populations described above and the R/qtl package (Broman et al. 2003). Composite interval mapping (CIM) was used to identify QTLs. 1000 permutations were performed for each population to determine the critical cutoff odds scores (LOD) at significance level α = 0.05. The 1.5 LOD drop method was applied to define the QTL confidence intervals and determine boundary markers.

Results

Branch angle variation in parent lines

The two parental lines, LD00-3309 and RIL1890 display clear distinction in branch angle (Fig. 1). The average branch angle of the NBA line LD00-3309, is 66.8° ± 2.2°, while the average branch angle of the WBA line RIL 1890 is 132.0° ± 2.4°. This large phenotypic difference developed over the course of the growing season, with no clear difference observed during the first six weeks after planting. The difference in branch angles between the two parental lines became apparent at 8 and 11 weeks after planting, and the phenotypic difference was most obvious at 20 weeks after planting when the leaves had fallen off and the plants were fully mature.

Mapping of the QTL, *qGmBa1*, modulating branch angle using a bi-parental F_2 population and F_3 progeny

The F_2 population derived from LD00-3309 and RIL 1890 also showed large variations in branch angle; nevertheless, the majority of the F_2 individuals appeared to possess branch angles similar to the two parent lines. Thus, we simply categorized the F_2 plants as either WBA or NBA, when they possessed branch angles greater or less than 90°, respectively. Of 147 F_2 plants, 101 were classified as WBA while 46 were classified as NBA (Fig. 2A). This fits a 3:1 phenotypic segregation ratio ($\chi^2 = 3.10$, $p = 0.08$), suggesting that a single major locus is responsible for the branch angle variation observed in this population.

QTL mapping for branch angle was conducted using the phenotypic data of the 147 F_2 plants and their genotypes at the 1,132 polymorphic SNP sites across the 20 soybean chromosomes. Consistent to the inheritance pattern, only a single major QTL modulate branch angle was detected (Fig. 2B). This QTL, designated *qGmBa1*, is located on the short arm of chromosome 19 and could explain 55% of the total phenotypic variation in the mapping population. SNP marker ss715633059 (physical position based on the version 2 assembly: chr19_1163245 (Chr19:1,163,245bp) had the highest LOD value, 30.72, while marker chr19_922646 (Chr19:922,646) and marker chr19_1855442 (Chr19:1,855,442) defined boundaries of this QTL based on the 1.5 LOD drop method (Fig. 2C).

We further compared the average branch angle scores of the F_3 families derived from the (LD00-3309 × RIL 1890) F_2 plants of the three genotypes at the peak marker chr19_1163245 (Fig. 3). F_3 plants with the LD00-3309 genotype (GG) had a score (66.8° ± 13.0°) that is very close to that (66.8° ± 2.2°) of LD00-3309, while F_3 plants with the RIL1890 genotype (AA) had a score (132.0° ± 15.5°) that is very close to that (132.0° ± 2.4°) of RIL1890. We did not measure the branch angles of (LD00-3309 × RIL 1890) F_1 plants as they were grown in the greenhouse, but the F_3 plants with the (A/G) genotype had a score (129.3 ° ± 26.5°) that was close to that of the F_3 plants with the (A/A) genotype. These observations further support the single-gene inheritance pattern of branch angle and that WBA is dominant over NBA.

qGmBa1 was also identified by QTL mapping using a bi-parental RIL population

To determine whether the phenotypic variation in branch angle among cultivated soybeans is also modulated by *qGmBa1*, we performed QTL mapping using 140 RILs derived from a WBA landrace, PI437169B, and an NBA elite cultivar, IA3023, which form one of 40 subpopulations of the SoyNAM population. The same criteria described above were used to phenotype branch angles of the (PI437169B × IA3023) RILs, and this phenotypic data was integrated with the available genotyping data for the 140 RILs and two parent lines (Soybase.org/SoyNAM/). This identified a single major QTL on chromosome 19, which is defined by marker chr19_1286696 (Chr19:1,286,696) at the left boundary. The next marker is Chr19_3291531, but LOD declines well before this, putting the right QTL boundary around 2 megabases. This QTL overlaps with the *qGmBa1* region defined by the (LD00-3309 · RIL1890) population, suggesting they are the same QTL.

Genes in the QTL region

The *qGmBa1* region contains several genes which could be plausible candidates modulating lateral branch angle based upon the known functions of their *Arabidopsis* homologs. (Supplemental Table 3). *Glyma.19g010200* is the homolog of *ATMBD9*, a methyl-CpG binding protein which regulates flowering and shoot branching in *Arabidopsis* (Peng et al. 2006). *Glyma.19g010600* is homologous to *AtSLO*, a pentatricopeptide repeat protein, whose mutant shows branching defects (Hsieh et al. 2015). The homolog of *Glyma.19g012300* in Arabidopsis is *SUO*, which is required for the activity of miR156 (Yang et al. 2012) that directly cleaves SPL14 transcripts and regulates plant architecture in rice (Jiao et al. 2010). Additionally, the region contains several genes involved in the biosynthesis and modification of cell wall components. These include *Glyma.19g012100* and *Glyma.19g015700*, homologs of *AXY4L/TBL22* and *AXY8*, respectively, which are required for the O-acetylation of hemicellulose xyloglucan and the fine structure of cell wall polysaccharides in Arabidopsis (Gille et al. 2011; Gunl et al. 2011), and *Glyma.19g012700* and *Glyma.19g016100*, homologs of Arabidopsis *LGT8* and *CSLC4*, respectively (Cocuron et al. 2007; Kong et al. 2011). Fine mapping with a larger population is needed to pinpoint the candidate for *qGmBa1*.

Discussion

Soybean branch angle not only exhibits a great range of natural variation among different varieties, but is also influenced by planting date, planting density, and other environmental factors (Asanome and Ikeda 1998, Foroutan-pour et al. 1999; Schon and Blevins 1990; Settimi and Board 1998; Weaver et al 1991; Harder et al. 2007). As such, it is not easy to genetically dissect this trait and its inheritance pattern using a natural population through genome-wide association study (GWAS). By using two segregating populations each derived from two parental lines showing extreme difference in branch angle, we were able to reveal the inheritance pattern of the trait and demonstrate that this complex trait is modulated by a single major QTL, *qGmBa1*.

Although the same major QTL modulating branch angle was detected in both bi-parental populations, whether this QTL is the major one underlying natural variation in branch angle in natural soybean populations remains unknown. Nevertheless, a GWAS analysis of the SoyNAM population through high throughput phenotyping of canopy coverage using an unmanned aircraft system (UAS) identified a major QTL on soybean chromosome 19 responsible for phenotypic variation in canopy coverage, and this QTL overlaps with the *qGmBa1* region (Xavier et al. 2017). In addition, a more recent GWAS analysis of 399 diverse maturity group I soybean accessions reveals that branch angle and leaflet shape are major drivers of canopy coverage in soybean (Virdi et al. 2021). Together, these observations suggest that *qGmBa1* is most likely to be the major player responsible for the natural variation in branch angle in soybean germplasm.

The GWAS analysis by Xavier et al. (2017) also suggests that the QTL underlying canopy coverage contributes to soybean grain yield, providing an increase of 47.3 kg/ha^2. Their further variance analysis suggested that canopy coverage was a highly heritable trait with a promising genetic correlation with grain yield. If this QTL is indeed same as *qGmBa1*, soybean branch angle would be a major contributor to grain yield by shaping canopy structure and coverage that affects photosynthetic efficiency and ultimately grain yield. As most elite soybean cultivars possess narrower branch angles than those found in most landraces, it is apparent that narrower branch angles, which allow for higher planting densities for increased yield (Harder, 2007; Norman, 1989), have been the target for selection in modern soybean breeding. Marker-assisted selection for *qGmBa1 or qGmba1* alleles will facilitate development of soybean cultivars with desirable branch angles as part of optimized plant architecture for enhanced plant productivity and grain yield in soybean.

Declarations

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Conflict of interest: The authors declare no conflict of interest.

Availability of data and material: All data presented in this manuscript are included in the supplemental tables. All materials are available to the public upon request and under material transfer agreement.

Code Availability: Not applicable.

Author contributions: JM designed research, CBC, WW, YW, GJF, ZW, and BR performed research, CBC, DW, and BR analyzed data, CBC and JM wrote the manuscript.

Ethics approval: Not applicable.

Consent to participate: Not applicable.

Consent for publication: Not applicable.

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Figures

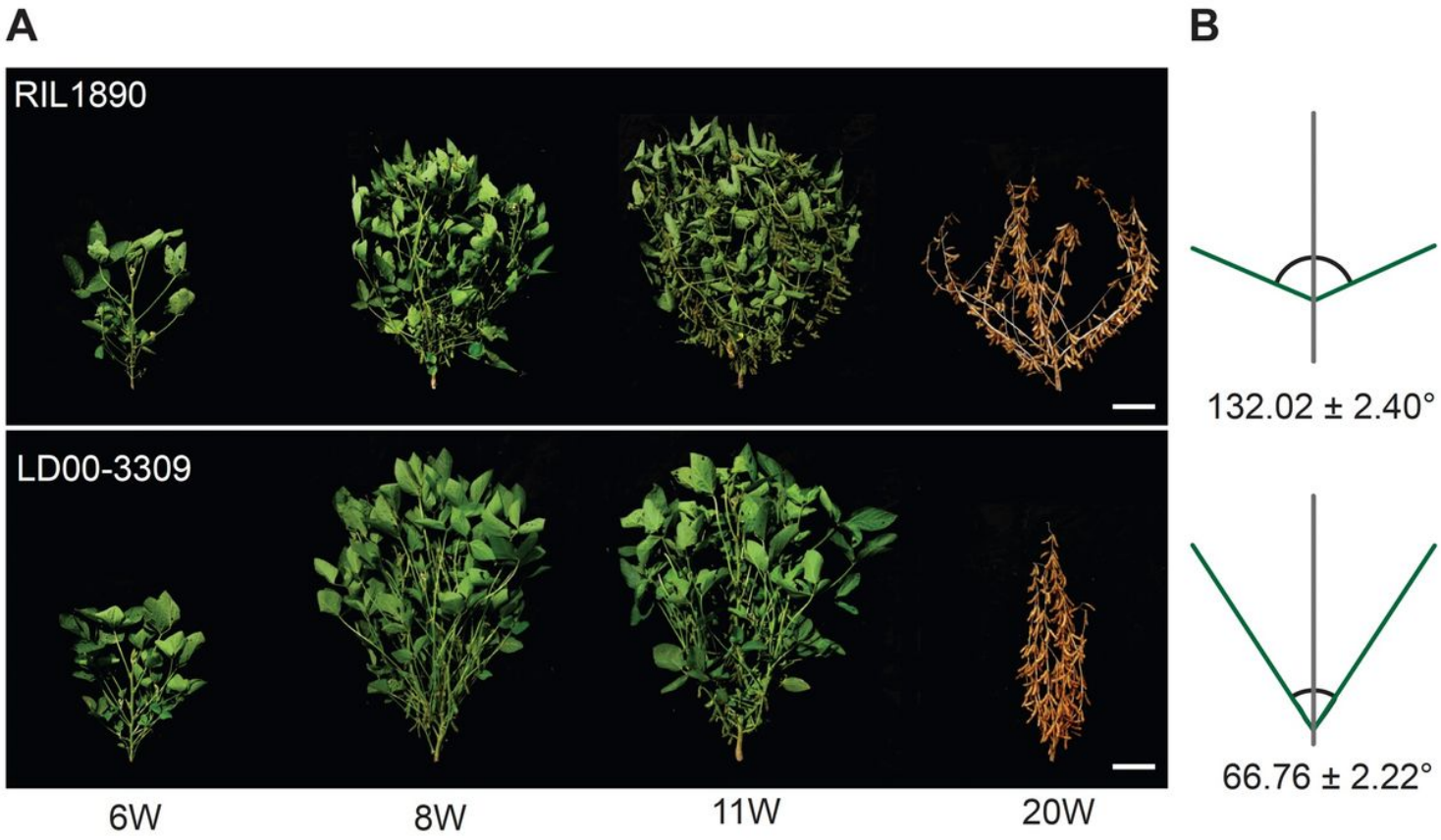

Figure 1

Phenotypic difference in branch angle between RIL1890 and LD00-3309 at different plant developmental stages. (A) RIL 1890 (top panel) and LD00-3309 (bottom panel) at 6, 8, 11, and 20 weeks after planting. (B) The green bars represent the branch angles of RIL1890 (top panel) and LD00-3309 (bottom panel) at 20 weeks after planting; 20 plants were measured for each line.

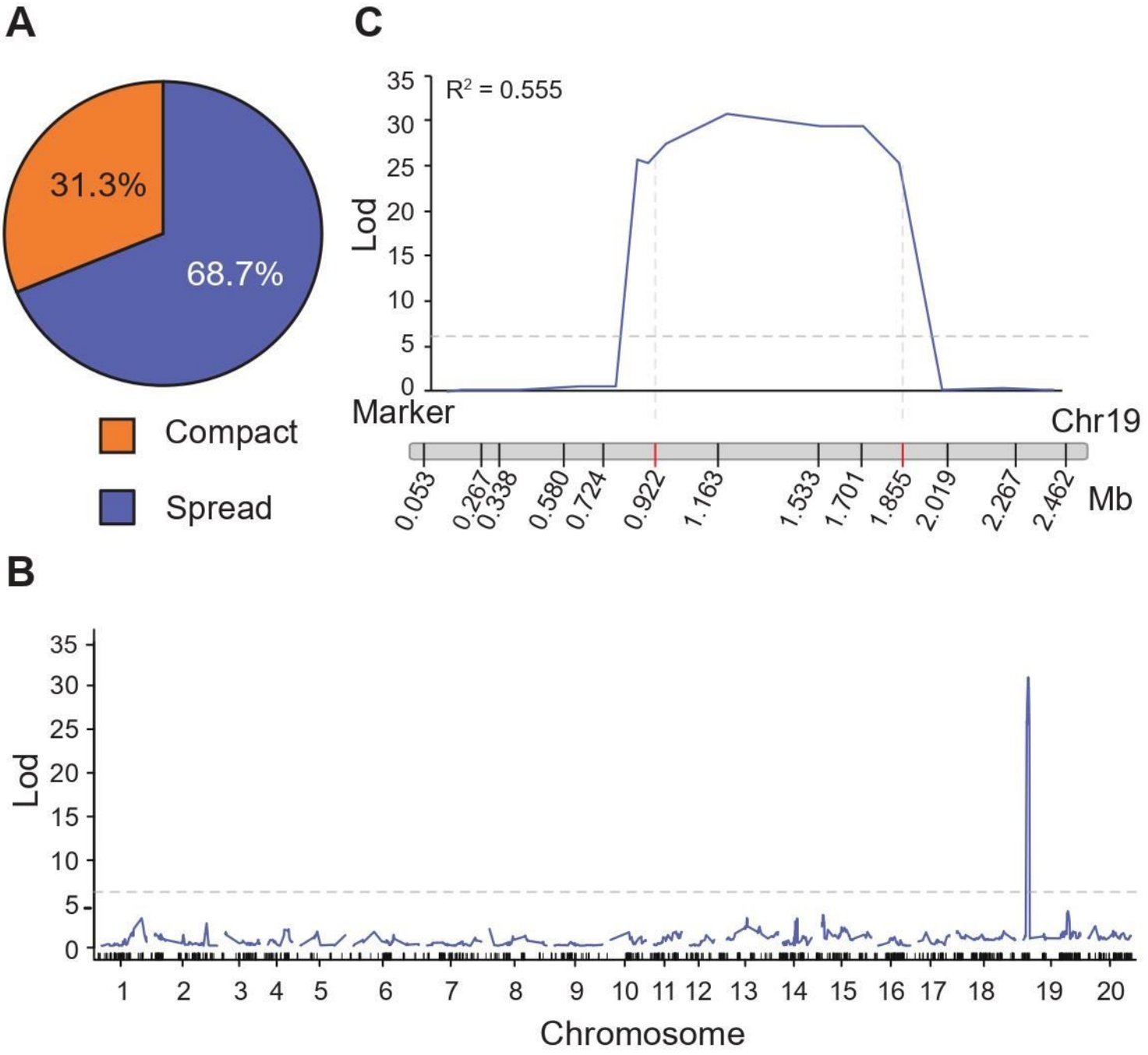

Figure 2

Phenotypic segregation of branch angles and QTL mapping using an F2 population derived from RIL1890 and LD00-3309. (A) Frequencies of F2 plants showing WBA and NBA that fits a 3:1 ratio ($\chi 2$ = 3.10, p = 0.08). (B) Genome-wide QTL mapping detects a single major QTL modulating branch angle. The x-axis represents the 20 chromosomes of soybean, the y-axis shows the Lod scores, and the horizontal line is the cutoff LOD value at the significance level α = 0.05 from 1000 permutations. (C) The major QTL identified on chromosome 19 and physical positions of the markers. The vertical dashed lines define the boundaries of the QTL using the 1.5 LOD rule.

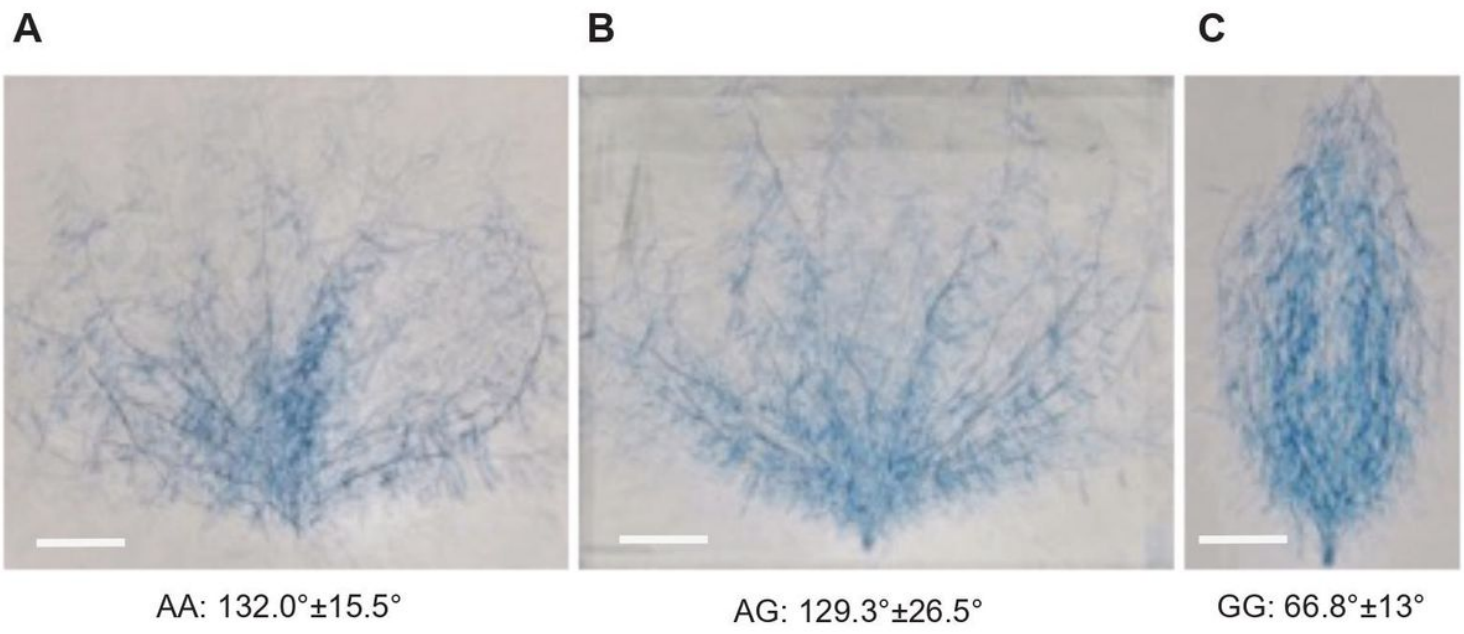

Figure 3

Display of the branch angles of the three genotypes of F3 plants derived from RIL1890 and LD00-3309 at marker chr19_1163245 that defines the peak of the qGmBa1 region. (A) RIL1890-type genotype AA. (B) heterozygous genotype AG. (C) L00-3309-type genotype GG. For each genotype, 20 images were taken from 20 randomly selected individuals from the individual F3 families and merged together with 95% transparency.

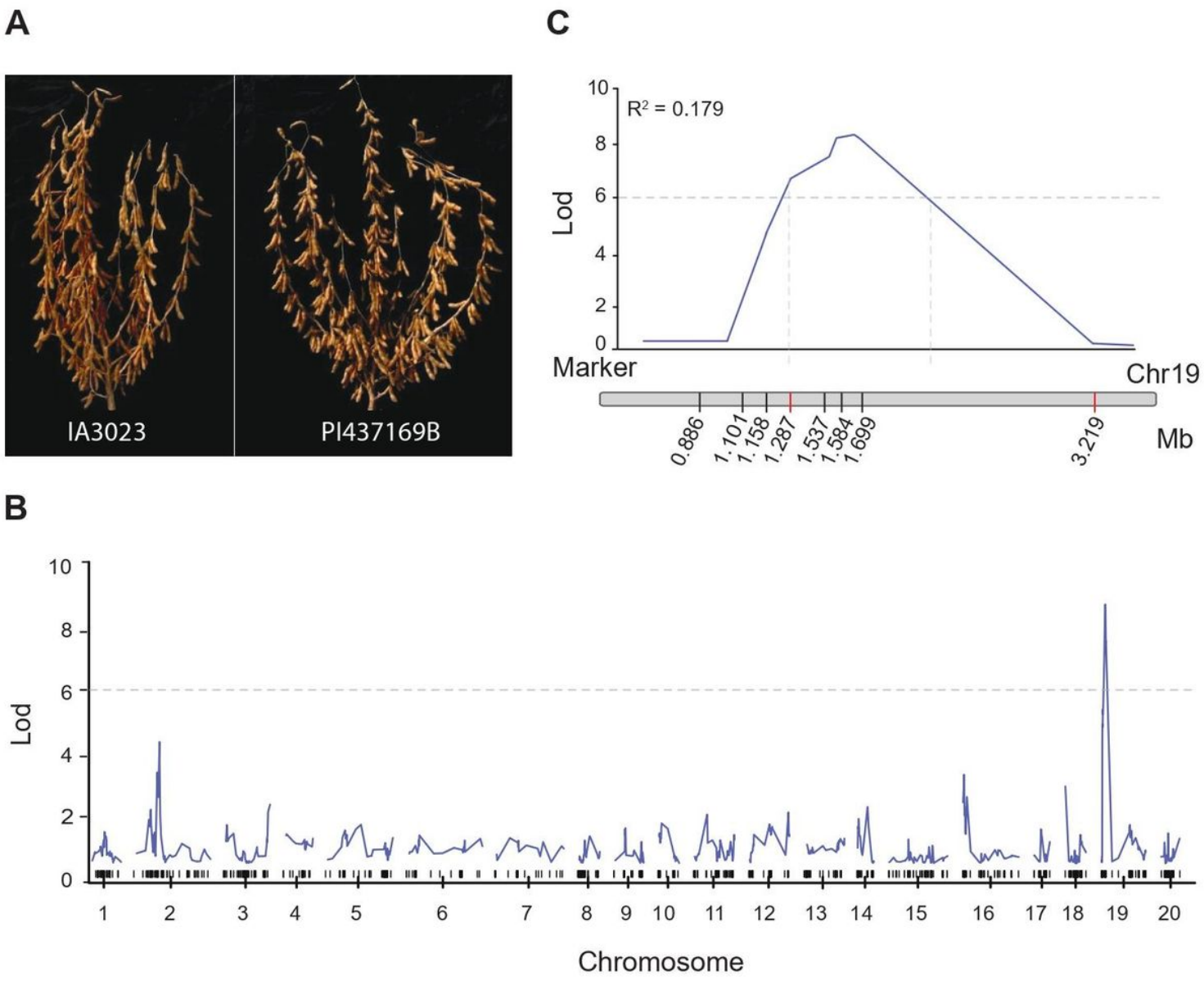

Figure 4

QTL mapping using the RIL population derived from IA3023 and PI437169B. (A) Phenotypic difference in branch angle between IA3023 and PI437169B. (B) Genome-wide QTL mapping. The x-axis represents the 20 chromosomes of soybean, the y-axis is the LOD score, and the horizontal line is the cutoff LOD score at the significance level α = 0.05 from 1000 permutations. (C) The major QTL on chromosome 19 and physical positions of the markers. The vertical dashed lines define the boundaries of the QTL using the 1.5 LOD rule.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- ClarkSupplementalTable1.csv

- ClarkSupplementalTable2.csv
- ClarkSupplementalTable3.pdf