Mol Breeding (2023) 43:55
https://doi.org/10.1007/s11032-023-01391-3

The genetic basis of shoot architecture in soybean

Chancelor B. Clark · Jianxin Ma

Received: 11 January 2023 / Accepted: 26 April 2023 / Published online: 20 June 2023

Abstract Shoot architecture refers to the three-dimensional body plan of the above ground organs of the plant. The patterning of this body plan results from the tight genetic control of the size and maintenance of meristems, the initiation of axillary growth, and the timing of developmental phase transition. Variation in shoot architecture can result in dramatic differences in plant productivity and/or grain yield due to their effects on light interception, photosynthetic efficiency, response to agronomic inputs, and environmental adaptation. The fine-tuning of shoot architecture has consequently been of great interest to plant breeders, driving the need for deeper understanding of the genes and molecular mechanisms governing these traits. In soybean, the world's most important oil and protein crop, major components of shoot architecture include stem growth habit, plant height, branch angle, branch number, leaf petiole angle, and the size and shape of leaves. Key genes underlying some of these traits have been identified to integrate hormonal, developmental, and environmental signals modulating the growth and orientation of shoot organs. Here we summarize the current knowledge and recent advances in the understanding of the genetic control of these important architectural traits in soybean.

Keywords Branch angle · Branch number · Ideotype · Leaf shape · Plant architecture · Stem growth habit · Soybean canopy

Introduction

The kingdom plantae presents an enormous range of shapes and sizes that allow plants to fill niches in their ecosystems. Various shoot body plans have evolved in plants to efficiently harvest light, convert it to biomass, and reproduce (Reinhardt and Kuhlemeier 2002). The spatial separation of meristematic zones of cell division and differentiation from zones of mature cells is a key factor in the proliferation of complex and diverse vascular plant body types from a comparatively simple common ancestor (Sussex and Kerk 2001). These apical, intercalary, axillary, and reproductive meristems produce the organs that define the plant body structure. The growth, positioning, and patterning of these organs are regulated by a series of networks of proteins, miRNAs, and hormones such as auxin, strigalactones (SLs), cytokinins (CKs), gibberellins (GAs), and brassinosteroids (BRs) (Guo et al. 2020b).

Shoot architecture in plants is inherently plastic, responding to available water and nutrient resources,

C. B. Clark · J. Ma
Department of Agronomy, Purdue University, 915 W Mitch Daniels Blvd, West Lafayette 47907, IN, USA

J. Ma (✉)
Center for Plant Biology, Purdue University,
West Lafayette, IN, USA
e-mail: maj@purdue.edu

competition from neighboring plants, herbivory, wind, and other environmental stresses (Wang et al. 2018). For example, plants may shift resources away from the shoot and towards the root in response to low water stress or reduce lateral branch growth in response to nutrient deficiency or competition for sunlight (Tiechmann and Muhr 2015; Wang et al. 2018). Despite this plasticity, a substantial proportion of the observed variation in shoot architecture between and within species is driven by genetic differences (Reinhardt and Kuhlemeier 2002). Plant breeders have exploited such genetic differences to increase yields or modify plant body types to suit modern agricultural practices and technologies. One of the most notable examples is the "green revolution" spurred by the development of high-yielding semi-dwarf wheat (*Triticum* spp. L.) and rice (*Oryza sativa* L.) varieties by Norman Borlaug and other plant breeders. The sturdier stems of the semi-dwarf wheat and rice varieties did not lodge after the application of synthetic fertilizers and allowed for dramatic gains in yield (Khush 2001). The semi-dwarf varieties also could be planted at higher densities without succumbing to disease (Liu et al. 2020). The semi-dwarf phenotype results from allelic variation in GA signal transduction and biosynthesis genes in wheat and rice, respectively (Hedden 2003). GA is a naturally occurring plant growth regulator most notable for its role in promoting shoot elongation (Marth et al. 1956). In hexaploid bread wheat, additive change-of-function alleles of homoeologous genes, *Rht-B1b* and *Rht-D1d*, cause insensitivity to GA (Hedden 2003). In rice, multiple recessive, loss-of-function alleles in a single gene, *Sd1*, impair GA biosynthesis (Hedden 2003). This landmark event in the history of agriculture has averted potentially catastrophic famine and demonstrates the impact that modifying plant shoot architecture can have on crop production (Pingali 2012).

Soybean (*Glycine max* (L.) Merr.) is the most valuable oil crop in the world, with a production value of more than $120 billion in 2020, the most recent year for which data is available (Food and Agricultural Organization of the United Nations (FAO), 2020). It is an indispensable crop for meeting the oil and protein meal needs of a growing global population. As with other crops, the processes of domestication and selection have sculpted the shoot architecture of soybean. Wild soybean, *Glycine soja*, grows prostrate along the ground, always or nearly always displays indeterminate stem growth, and has comparatively small leaves, flowers, pods, and seeds. Along with other characteristic domestication syndrome traits including loss of shattering and increased seed coat permeability, domesticated soybean presents upright, gravitropic growth, variability in its main stem growth habit, and larger vegetative and floral organs (Sedivy et al. 2017).

Despite impressive gains achieved by the green revolution and other modifications to plant architectural traits in maize (*Zea mays* L.), wheat, and rice, research into the genetic basis of these traits in soybean has been comparatively limited. Although soybean yields have steadily increased over the past 9 decades, with an estimated two-thirds of the increase coming from genetic improvement of cultivars (Specht et al. 2014), there has been no great yield breakthrough on par with the green revolution. Nonetheless, key soybean architectural traits such as stem growth habit (i.e., determinacy), plant height, branch number, branch angle (compactness), leaf petiole angle, and leaf size and shape have been genetically dissected. The remainder of this review will describe the current knowledge of the genetic control of soybean shoot architecture, providing a foundation for researchers seeking to understand and improve upon these traits using modern molecular breeding techniques.

Stem growth habit

Flowering plants can be classified according to the timing of their transition from vegetative to reproductive growth. Plants with discreet reproductive and vegetative growth stages are described as having a determinate growth habit. In determinate plants the shoot apical meristems lose their undifferentiated status and differentiate into a terminal inflorescence (McGarry and Ayre 2012). Plants with indeterminate growth habits in contrast maintain undifferentiated shoot apical meristems that continue vegetative growth even after the induction of flowering elsewhere on the plant. There are both indeterminate and determinate domesticated soybean varieties, as well as those which are classified as semideterminate (Fig. 1). Semideterminate soybeans constitute an intermediate phenotype where vegetative growth at the shoot apical meristems continues for some period of time while flowering is occurring on axillary meristems before shifting to floral growth. Determinate soybean varieties have been found to produce more flowers at a time but over a shorter total period of flowering than indeterminate varieties (Kuroda et al. 1998; Yoshida et al. 1983). Determinate and semideterminate varieties possess characteristic terminal clusters of pods in contrast to indeterminate varieties which have main stems that gradually become thinner and produce fewer pods per node as the growing season progresses (Heatherly and Smith 2004). Determinate and semideterminate varieties normally have shorter, thicker stems with less nodes but more pods per node than indeterminate varieties grown in the same environments (Heatherly and Smith 2004). Stem growth habit is a major contributor to soybean height, with determinate and semideterminate varieties being respectively 45 to 60% and 12 to 15% shorter than indeterminate varieties when grown in the same environments (Bernard 1972).

Fig. 1 Exemplification of three categories of stem growth habit in soybean: indeterminate (**a**), semideterminate (**b**), and determinate (**c**)

These differences in main stem growth habit constitute an important factor in adaptation to regional environments. Determinate soybeans are often preferred in regions with long growing seasons, such as the southern USA or southern China. Indeterminate and semideterminate soybeans meanwhile are grown in higher latitudes where less time is available for separate vegetative and floral stages. Commercial soybean cultivars in the midwestern corn belt of the United States are primarily indeterminate, while farmers in Northeastern China have transitioned to growing semideterminate varieties (McWilliams et al. 1999; Liu et al. 2008). Studies comparing seed yield between determinate, semideterminate, and indeterminate varieties have shown significant results based upon geographic location and genetic background, with each growth habit type conferring advantages and disadvantages in different scenarios (Beaver et al., 1985; Chang et al., 1982; Cooper 1981; Foley et al., 1986). Determinate and semideterminate lines have been consistently found to lodge less than indeterminate varieties (Foley et al., 1986; Hicks et al., 1969; Wilcox and Sediyama 1981). It has been suggested that tall, later flowering or faster growing determinate soybeans which produce more nodes before flowering possess a yield advantage because they combine the pods per node and lodging advantages of determinate cultivars without a reduction in node number (Cober and Tanner 1995; Maw and Nelson, 1988), while others have hypothesized that semideterminate varieties could achieve this ideal balance (Ping et al. 2014). Some studies have reported that indeterminate cultivars are able to recover more fully from low water stress (Villalobos-Rodriquez and Shibles, 1985) and defoliation (Fehr et al. 1977; Goli and Weaver 1986). In contrast, Schug et al. (2022) found no difference in response to defoliation by feeding from the lepidopteran pest *Helicoverpa zea* between determinate and indeterminate varieties, and Neyshabouri and Hatfield (1986) found that semideterminate varieties performed better under drought stress than indeterminate varieties.

Classical genetic analysis determined that two major genes are responsible for the variation in soybean main stem growth habit (Bernard 1972). The first, *Dt1,* specifies determinate or indeterminate growth in soybean and the indeterminate allele *Dt1* is completely or incompletely dominant over the determinate allele *dt1* (Bernard 1972; Woodworth 1932). Another allele of *Dt1*, *dt1-t,* results in determinate plants which are taller and look more like those classified as semideterminate (Thompson et al. 1997). At least four recessive loss-of-function mutations (*dt1-ta, dt1-bb, dt1-tb, and dt1-ab)* result in determinate growth, and were selected for by early farmers during or soon after domestication (Tian et al. 2010). Analysis of Chinese soybean landraces revealed that the dominant functional allele was favored in northern China and the loss of function alleles were favored in southern China, while both alleles are roughly equally distributed in central China (Tian et al. 2010).

Dt1 was identified to be the ortholog of *Arabidopsis thaliana TERMINAL FLOWERING 1 (TFL1)* and encodes a phosphatidyl ethanolamine-binding protein (PEBP) that maintains indeterminate growth at the shoot apical meristems (Liu et al. 2010; Tian et al. 2010). PEBPs are a large and ancient plant protein family that includes homologs of *TFL1* as well as homologs of *Arabidopsis FLOWERING LOCUS T (FT)* and *MOTHER OF FT AND TFL1 (MFT)* (Wang et al. 2015). The role of *TFL1* in maintaining indeterminate stem growth is highly conserved, and mutations in its homologs are the source of determinate growth habits in many species from diverse families including cucumber (*Cucumis sativus* L.*)*, pea (*Pisum sativum* L.), rapeseed (*Brassica napus* L.), and tomato (*Solanum lycopersicum* L.) (Liu et al. 2021; Njogu et al. 2020; Foucher et al. 2003; Jia et al. 2019; Pnueli et al. 1998). *Dt1* can complement *Arabidopsis tfl1* mutants (Tian et al. 2010).

A series of experiments have been conducted to understand how *Dt1* functions at the molecular level. Yue et al. (2021) found that *Dt1* functions to repress floral identity genes in shoot apical meristems including homologs of *Arabidopsis AGAMOUS (AG), AP1, LEAFY (LFY),* and *PISTILLATA (PI),* among others, while *dt1* is nonfunctional and cannot repress these genes. In *Arabidopsis, TFL1* maintains indeterminate main stem growth as a transcriptional cofactor to *FD,* a bzip transcription factor. Yeast two-hybrid screening demonstrated that *Dt1* directly interacts with the *FD* homolog *GmFDc1*, and not any other *FD* homologs in soybean. Another PEBP, GmFT5a, encoded by an ortholog of *Arabidopsis Flowering Time (FT)* which acts as a mobile florigen moving from leaves to shoot apical meristems to promote floral transition, also binds to GmFDc1, but has the opposite effect of Dt1, increasing the expression of floral identity genes. *Dt1* also forms a feedback loop with the MADS-Domain floral integrator *GmAP1* whereby the Dt1-FDc1 complex directly binds to and downregulates expression of *GmAP1* which in turn can directly bind to and downregulate *Dt1.* Soybean has two functional orthologs of *Arabidopsis FT, GmFT5a,* and *GmFT2a,* although when each was constitutively overexpressed in soybean only *GmFt5a* conferred terminal flowering at shoot apical meristems (Takeshima et al., 2019). Main stem growth habit in soybean thus results from the competition between two PEBPs with antagonistic functions, *Dt1* and *GmFT5a,* for binding with *GmFDc1* to regulate floral identity genes in shoot apical meristems.

A second gene, *Dt2,* specifies semideterminate growth in *Dt1/Dt1* backgrounds and at this locus the semideterminate allele *Dt2* is dominant over the indeterminate growth allele *dt2* (Bernard 1972). *dt1* is epistatic to *Dt2* and *dt2,* so in *dt1/dt1* backgrounds the phenotype is determinate regardless of which alleles are present at the *Dt2* locus. *Dt2* was identified by map-based cloning to be a MADS box transcription factor in the APETALA1/SQUAMOSA (AP1/SQUA) subfamily which also contains *GmAP1,* although *Dt2* is not the functional equivalent of *Arabidopsis AP1* (Ping et al. 2014). A dominant gain-of-function mutation results in the functional allele *Dt2*, the protein encoded by which represses the expression of *Dt1* by binding directly to the *Dt1* promoter (Liu et al. 2016). Overexpression of *Dt2* in the indeterminate cultivar Thorne resulted in semideterminate growth, and among transgenic events higher expression of *Dt2* was associated with a higher degree of stem termination and shorter height (Ping et al. 2014). Expression differences resulting from natural variation in the *Dt2* promoter between different soybean varieties carrying distinct versions of the dominant semideterminate *Dt2* allele were also suggested to cause height differences and differing degrees of stem termination (Kou et al. 2021). Chromatin immunoprecipitation sequencing (ChIP-seq) revealed that in addition to repressing *Dt1*, *Dt2* plays a larger role in main stem growth habit by acting as a transcriptional activator of floral activators including *GmSOC1, GmAP1a, GmAP1b, GmFUL, GmSEP1, GmSEP3, GmSPL4a,* *GmSPL4b,* and *GmSPL12* (Zhang et al. 2019). Liu et al. (2016) found that spatiotemporal expression of *Dt2* and *GmSOC1* in the center of the shoot apical meristem was critical for the repression of *Dt1* in the early vegetative growth stages of soybean. Dt2 stimulates the production of GmSOC1, which represses *Dt1* by binding to the regulatory region of *Dt1* and was also found to directly interact with Dt2. Semideterminacy is rare or absent in wild soybeans, suggesting that *Dt2* is a recent mutation which may have occurred post-domestication (Ping et al. 2014). Unlike *Dt1/TFL1*, no equivalent mechanism of stem termination mediated by the spatiotemporal expression of *Dt2* has been described in other plant species. Depending on genetic background and environmental conditions, the terminal growth habit conferred by *dt1* may be hard to distinguish from the terminal growth habit conferred by *Dt2,* and the classification semideterminate is therefore a genotypic class denoting main stem termination not caused by *dt1/dt1* in addition to being a phenotypic class (Bernard 1972).

Plant height

Plant height is determined by internode number and length, and is most important in soybean for its impact on yield and lodging (Niu et al. 2021). Shorter plants are less prone to lodging but often sacrifice pod numbers due to having fewer total nodes. Soybean cultivar heights listed in the germplasm resource information center range from 14 to 334 cm with an average of 87.97 cm (USDA ARS 2022). Height is a complex trait with many genes inolved, particularly genes involved in GA biosynthesis and signaling (Niu et al. 2021).

The past half-decade has seen an outpouring of studies describing manipulations of genes to modify soybean height. Apart from *Dt1* and *Dt2,* several loci affecting soybean height have been reported. Li et al. (2018) mapped an EMS-induced dwarfing mutation conferring reduced plant height and shortened internodes, *GmDW,* to *Glyma.08G165100,* which encodes an ent-kaurene synthase. A single nucleotide polymorphism (SNP) in *GmDW* disrupts GA biosynthesis, and the phenotype can be rescued by the application of GA. CRISPR/Cas9 was used to create quradruple mutants of the four homologs of the MYB TF *LATE ELONGATED HYPOCOTYL* (*LHY*) (*GmLHY1a, GmLHY1b, GmLHY2a, and GmLHY2b*), which resulted in shorter height from reduced GA levels (Cheng et al. 2019). Creating quadruple mutants of the homologs of the flowering time MADS Box TF *GmAP1* increased soybean height, while overexpressing *GmAP1a* reduced plant height (Chen et al. 2020). Yang et al., 2021a, b report that overexpression of the R2R3 MYB TF *GmGAMYB* (*Glyma.13g187500*) increased internode length and made plants taller and more sensitive to GA application. Short Tandem Target Mimic (STTM) mediated knockdown of *GmmiR166* resulted in dwarfing due to down regulation of genes involved in GA biosynthesis including *GmGA1* (*Glyma.09G149200*) and *GmGA2* (*Glyma.20G153400*) and increased expression of *GmGA2ox2* (*Glyma.10G010700*) which contributes to GA catabolysis (Zhao et al. 2022). Overexpression of the RAV TF *GmRav* (*Glyma.10G204400*) reduced soybean height and shortened internodes by binding to two CAACA motifs in the promoter of *GmGA3ox* (*Glyma.13G361700*) to reduce its expression (Xue et al. 2022) An EMS-induced mutation of *GmIAA27* (*Glyma.09G193000*)*,* which encodes an AUX/IAA protein, caused dwarfing, showing a role for auxin in determining plant height in addition to GA (Su et al. 2022).

Several studies have also characterized natural variation in soybean height. Sun et al. (2012) compiled a meta-analysis of seventy-eight soybean height QTL from twelve studies completed in the pre-reference genome era and identified twelve consensus QTL reported across many studies. Another meta-analysis reported 182 QTL for soybean height (Yin et al. 2017). Lee et al. (2015) described six QTLs for plant height using a recombinant inbred line (RIL) population which explained 17 to 18% of the phenotypic variation across 2 years. Li et al. (2019) used QTL mapping and bulked segregant analysis (BSA) to locate six loci associated with plant height and proposed several candidate genes which may underlie them including *Glyma.04G244200* which encodes GA20ox, a key GA biosynthesis enzyme. Xue et al. (2019) mapped QTL for height in a four-way RIL population at a weekly interval and identified a total of thirty-six height QTL across several developmental stages.

Branch number

Branch number is an important trait for determining soybean yield. Branch number is most important for helping to determine the total number of pods per plant, although less branches are desirable in high-density plantings (Shim et al. 2017). Increased branch number can help compensate for yield loss in lower-density soybean plantings, which are preferred in some regions to reduce seed cost (Shim et al. 2017). Lateral branches arise when axillary meristems are initiated around leaf axils and then either remain dormant or continue outgrowth (Wang and Jiao 2018). The components of the gene and hormonal regulatory networks governing the initiation of branches have been extensively studied in other plant species (Wang et al. 2018). In general, auxins and strigalactones inhibit lateral bud outgrowth while cytokinin directly promotes it (Ongaro and Leyser 2008). In *Arabidopsis thaliana,* auxin efflux from the leaf axil allows for elevated expression of *SHOOT MERISTEMLESS (STM)* which is associated with active cell division followed by the expression of *WUSCHEL (WUS)* and *CLAVATA3 (CLV3)* which establish the stem cell organizing center and central zone, respectively (Xin et al. 2017). Several transcription factors have been identified to regulate the initiation of axillary meristems and subsequent shoot branching including *LATERAL SUPPRESSOR (LAS), REVOLUTA (REV)*, *CUP-SHAPED COTYLEDON (CUC),* and *REGULATOR OF AXILLARY MERISTEMS (RAX)* in *Arabidopsis* (Wang and Jiao 2018). An indispensable regulator of shoot branching conserved across many species is *BRANCHED1 (BRC1),* a TCP transcription factor which integrates hormonal and environmental signals and acts as a repressor of bud outgrowth (Wang et al., 2019a, b).

More than 60 QTLs for branch number in soybean have been reported, often in multiple studies (Shim et al. 2017; He et al. 2014; Yang et al., 2021a, b). Branch number in soybean is a complex, quantitative trait controlled by many genes as demonstrated by the fact that in each of these studies the number of branches in the F_2 populations have approximated a normal distribution, ranging from zero to more than fifteen branches on the main stem (Shim et al. 2017; Yang et al., 2021a, b). Chen et al. (2007) reported 12 QTLs specifying branch number in an F_{10} recombinant inbred line (RIL) population containing 154 lines. Shim et al. (2017) performed QTL mapping for branch number in a population of two hundred F_6 RILs. They identified 4 QTLs for branch number, including one on chromosome 6 containing *Glyma06g23410*, a homolog of *A. thaliana BRC1*. Shim et al. (2019) further used GWAS to identify significant regions associated with branch number including the region corresponding to *GmBRC1*. They developed high-branching and low-branching near isogenic lines (NILs) which differed only at the *GmBRC1* locus and found that *Glyma06g23410* was expressed at a significantly lower level in the shoot apices of the high-branching NIL compared to the low-branching NIL, providing further evidence that *Glyma06g23410* is *GmBRC1* and acts as a negative regulator of lateral branch development.

Modifications to soybean branch number have been achieved through the manipulation of the microRNA *GmmiR156b* and the transcription factor gene *GmWRINKLED1B* (*GmWRI1b)* (Guo et al., 2020a; Sun et al., 2019). Overexpression of the microRNA *GmmiR156b* resulted in increased branch number (Sun et al. 2020). *miR156*s have been shown to regulate branching in maize and rice by targeting members of the *SQUAMOSA PROMOTER BINDING PROTEIN-LIKE* (*SPL*) family (Du et al. 2017). Sun et al. (2020) found that *GmmiR156b* functions to promote the initiation and development of SAMs and AMs by negative regulation of several *SPL* homologs including *GmSPL9d.* Overexpression of *GmSPL9d* in *Arabidopsis* reduced branch number and a series of protein-protein interaction assays demonstrated that it could directly interact with the meristem regulatory proteins GmWUSa and GmWUSb (Sun et al., 2019). Additionally, CRISPR/Cas9 induced knockouts of *GmSPL9d* resulted in increased branch number (Bao et al. 2019). Overexpression of *GmWRI1b,* which had been previously characterized for its role in fatty acid biosynthesis, significantly increased branch numbers (Guo et al. 2020a).

Genes related to flowering time and stem growth habit often have pleotropic effects on branch number. Sayama et al. (2010) explored the relationship between flowering time and branch number by carrying out QTL mapping for branch number in a population of 179 RILs grown in two environments both within the whole population and divided among four maturity groups. Among 6 QTLs identified, they found that the two QTLs with the largest effect on branch number mapped to the *E1* and *E3* flowering time loci. Interestingly, the *E1* and *E3* alleles specifying later maturity had opposite effects on branch number, with the former associated with a greater number of branches and the latter associated with fewer. The dominant allele of the growth habit gene *Dt2* which confers semideterminacy has also been implicated as a negative regulator of branch number. Virdi et al. (2021) identified a QTL for branch number in low LD with *Dt2* and posited that this could be a novel QTL distinct from *Dt2* or could be the *Dt2* locus itself. Liang et al. (2022) reported a GWAS which identified *Dt2* as a major gene specifying soybean branch number. Whether this phenotypic change is simply an indirect effect of the change to stem growth habit or a separate pleiotropic function of *Dt2* remains unclear. Additionally, whether the functional *Dt2* allele results in altered branch numbers between the environments where it was favored by selection compared to those environments where it was not favored by selection or simply helps to maintain a more constant branch number across environments also remains to be investigated.

Branch and petiole angles

In soybeans, the layout of the branches and leaves determines the compactness of the overall plant body and contributes to the canopy coverage, the proportion of ground covered by above ground plant organs (Clark et al., 2022; Virdi et al. 2021). Greater canopy coverage and more rapid closure of the crop canopy result in increased interception of light, driving photosynthesis and ultimately, yield. It also aids in the suppression of early-season weeds which compete for resources. Developing more compact crops allows for more plants per unit area, a major component of yield and manipulations of plant architecture facilitating increases in plant populations, has been a key driver of yield gains in wheat, rice, and maize (Liu et al. 2020). In maize, selection for narrower leaf angles enabled greater planting densities, reduced shading, and more efficient capture of sunlight (Lambert and Johnson 1978). Selective breeding for reduced tiller angle in rice has resulted in extremely compact plants that retain efficient light interception under high-density plantings (Zhang et al., 2019). Soybeans display considerable variation in their branch angles and can be classified as wide branch angle (WBA), narrow branch angle (NBA), or intermediate branch angle (IBA) (Fig. 2). Most elite cultivars possess narrower branch angles than those found in landraces and wild soybeans, suggesting that more compact plant architecture is beneficial for increasing yield (Clark et al., 2022; Harder et al. 2007).

The genetic control of leaf and tiller angle in the cereal crops has been studied extensively. Many QTL have been identified which influence tiller angle in rice including (*LAZY1* (*LA1*) (Li et al. 2007), *LOOSE PLANT ARCHITECTURE1* (*LPA1*) (Wu et al. 2013), *TILLER ANGLE CONTROL1* (*TAC1*) (Yu et al. 2007), *TAC3* and *DWARF2* (Dong et al. 2016) and

Fig. 2 Exemplification of three categories of branch angle in soybean: narrow (**a**), intermediate (**b**), and wide (**c**)

leaf angle in maize including *ZmTAC1*, *Upright Plant Architecture1* and *2* (*UPA1* and *UPA2*), *Increased Leaf Inclination1* (*ZmILI1*), and *ZmCLA4* (Tian et al. 2019; Zhang et al. 2014). The genes which underly these loci are mostly involved in the hormonal regulation of either plant responses to gravity or to the establishment and size of the structures connecting the leaf blade and sheath (Cao et al. 2022; Luo et al. 2016; Toyota and Gilroy 2013). For example, in rice and maize the *LAZY* family are regulators of the positioning of PIN auxin transporters in response to gravity (Jiao et al. 2021). Once plants perceive gravity through sedimentation of amyloplasts, they direct shoot growth away from the pull of gravity through asymmetric auxin accumulation leading to differential elongation of cells (Blancaflor 2013). *la1* mutants display no defects in amyloplast sedimentation but fail to establish asymmetrical auxin distributions, leading to wide leaf angles and a spread-out body plan (Li et al. 2007).

Less is known about the genetic regulation of branch angle in soybean. Clark et al. (2022) crossed a WBA RIL (132° angle of nearly opposite branches relative to the main stem) derived from an interspecific cross with *G. soja* with an NBA cultivar (67°). They found that WBA was completely dominant over NBA and identified a single major QTL, *qGmBa1*, underlying soybean branch angle. This QTL was further validated in a subset of the soybean nested association mapping (NAM) population (Song et al. 2017) consisting of 140 RILs derived from a cross between a WBA landrace and an NBA elite cultivar (Clark et al., 2022). These results combined with reports of QTLs in the same region underlying canopy coverage suggest that the gene underlying *qGmBa1* may be responsible for most of the variation observed in soybean branch angles (Xavier et al. 2017; Virdi et al. 2021). Although the inheritance of *qGmBa1* follows a typical qualitative single gene pattern, the quantitative nature of branch angles in natural populations suggests other genes with smaller effects also contribute to this trait.

Leaf petiole angle (LPA) also contributes to soybean canopy structure and light interception. Gamma ray induced mutagenesis of *Increased Leaf Petiole Angle1(GmILPA1)*, which encodes an APC8-like protein, resulted in shorter petioles with larger LPA (Gao et al. 2017). The modification in LPA resulted from the mutant having a smaller pulvinus, a motor organ at the base of the petiole. The pulvinus controls nyctinastic movement in response to changing water levels, which was reduced in the *Gmilp1* mutants. *GmILP1* regulates cell division in the pulvinus, as part of a putative anaphase-promoting complex where it directly interacts with GmAPC13a (Gao et al. 2017). As was observed in rice and maize leaf angles, auxin asymmetry also affects soybean LPA. Zhang et al. (2022) found that CRISPR-Cas9 induced triple and double mutations of *Gmpin1abc* and *Gmpin1bc* resulted in reduced LPA, while double mutation of *Gmpin1de* had the opposite effect. High transcript levels of *GmPIN1a and GmPIN1c* were found in the base of the petiole where auxin concentrations were high, while elevated levels of isoflavones were found in the upper portion of the leaf. Increasing levels of isoflavonoids by multiple methods was also found to disrupt the asymmetric distribution of the GmPIN proteins and resulted in smaller LPAs. Chen et al. (2021) found that overexpressing the TF *GmMYB14* resulted in changes to plant architecture including dwarfing, reduced leaf size, and narrower LPA. These changes were mediated by upregulation of genes involved in the biosynthesis of flavonoids, isoflavonoids, and lignins, as well as genes involved in the auxin and brassinosteriod pathways. In particular, *GmMYB14* binds to the promoter of a *BRASSINOSTEROID-INSENSITIVE 1 ENHANCED 1 (BEN1)* homolog involved in BR catabolism, leading to depleted BR levels and reduced growth. The links between these three studies of LPA need to be further understood but each demonstrates the power of modern genetic tools to alter plant architecture for crop improvement.

Leaf size and shape

In addition to LPA, the dimensions and shapes of leaves can have large effects on plant yield by influencing photosynthetic rates through altered light interception and gas exchange (Mathan et al. 2016). After emergence, the first two soybean nodes after the cotyledons are simple leaves in opposite phyllotaxy (often referred to as the unifoliate leaves), with subsequent leaves normally being compound with three leaflets (referred to as trifoliate) and in alternate phyllotaxy (Yoshikawa et al., 2013). Soybean leaf shapes can be classified based upon the length-to-width ratio of the leaflets; from roundest to most narrow the categories are oval (≤ 2), ovate (2.1–3), lanceolate (3.1–4), linear (4.1–5), and ultra linear (≥ 5.1) (Chen and Nelson 2004) (Fig. 3). Tamang et al. (2022) explored the variation in soybean leaf morphological and anatomical traits and found that the ratio of leaflet length to width ranged from 1.1 to 3.2. They also reported that narrow leaves had greater gas exchange and photosynthetic rates per unit area compared to wider leaves as a result of being thicker with a greater proportion of photosynthesizing mesophyll cells. As with stem growth habit, variation in leaf shape is associated with adaptation to different environments. Narrower leaflets are more common in higher latitudes in both wild and domesticated soybean (Tamang et al. 2022; Yan et al. 2014).

Many of the leaf morphology genes which have been characterized in plants affect cellular division or expansion (Mathan et al. 2016). A single locus, *Ln*, was identified by classical genetic analysis to determine leaf shape, with lines possessing the genotype *Ln/Ln* having broad leaves, *ln/ln* narrow, and heterozygous *Ln/ln* being intermediate (Dinkins et al. 2002). Fine mapping placed *Ln* to be *Glyma.20g116200,* a homolog of *Arabidopsis thaliana JAGGED* (*JAG*), and was thus designated *GmJAG1* (Jeong et al. 2011; Jeong et al. 2012). *AtJAG* encodes a zinc family protein that when mutated results in serrated leaves and narrow floral organs (Ohno et al. 2004). *AtJAG* functions as a direct repressor of *CLAVATA1* and other genes involved in meristem and shoot organ development, as well as genes involved in entry into the S-phase of the cell cycle (Schiessl et al. 2014). Both the broad and narrow leaf alleles of *GmJAG1* display similar expression levels and are expressed most highly in shoot meristems and open flowers (Jeong et al. 2012). In soybean, a single nucleotide substitution within the EAR motif of *GmJAG1* is responsible for the difference between the *Ln* and *ln* phenotypes (Jeong et al. 2012). Both *GmJAG1* and its soybean paralog *GmJAG2* (*Glyma.10g273800*) were able to complement the *jag-3* mutant when overexpressed in *Arabidopsis thaliana*, although the natural function of *GmJAG2 or* whether it plays any role in soybean leaflet shape is unclear (Jeong et al. 2012). Interestingly, the *Ln* gene *GmJAG1* also exerts a pleiotropic effect on seed number per pod (NSPP) number, with the narrow leaf *ln* allele being associated with a greater proportion of four-seeded pods, a relationship that was first observed nearly 90 years ago (Takahashi 1934; Sayama et al. 2017).

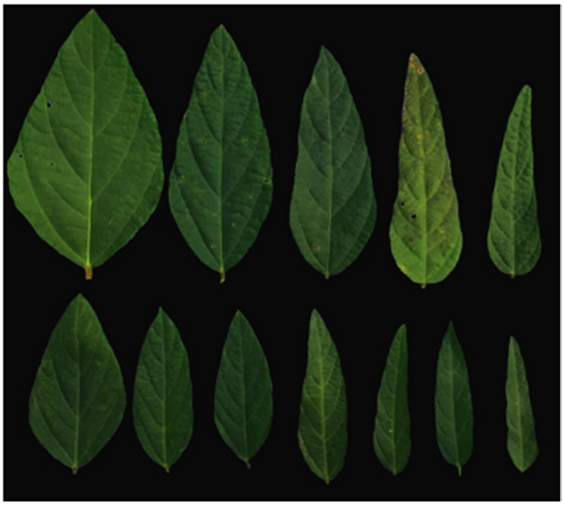

Fig. 3 Variation in leaf shape and size among RILs derived from a cross between cultivated and wild soybeans

In addition to the *Ln* locus, many QTLs for soybean leaf shape have been reported. Mian et al. (1998) identified four significant QTLs associated with leaf area in a population of 120 F_4-derived inbred lines. Orf et al. (1999) developed three RIL populations and reported several significant QTLs for leaf width, leaf length, and leaf area, although none was common to all three populations. Yamanaka et al. (2001) divided leaf shape into principal components and reported seven distinct QTL for components of leaf shape and six for leaf area. The QTL with the largest effect on leaf area in this study overlapped with QTLs for the first and fourth principal components of leaf shape. Kim et al. (2005) reported QTLs in two biparental RIL populations associated with leaf length, width, and the length/width ratio. Unlike most other studies listed here, Kim et al. (2005) distinguished between terminal (the central leaflet of the trifoliate) and lateral leaflet, and surprisingly, found unique loci affecting lateral leaflet dimensions but not terminal leaf dimensions and vice versa. Jun et al., 2014performed QTL mapping for leaf traits in 94 $F_{7:9}$ RILs derived from a biparental cross and reported 10 and 7 significant loci for leaf shape and leaf area, respectively. Wang et al. (2019ab1999; Yamanaka et al. 2001; Kim et al. 2005; Wang et al., 2019ab) explored QTLs for leaf area, leaf length, leaf width, and leaf shape in two biparental populations and identified a total of fourteen significant loci. Several leaf trait QTL are common across these studies including a locus on chromosome nineteen reported by at least four (Orf et al.).

Wild soybean displays a greater range of variation for leaf size and shape than what is found in *G. max* germplasm, with length to width ratios ranging from 1.3 to 6.2 and lengths ranging from 3 to 14 cm (Chen and Nelson 2004). QTL mapping in two biparental RIL populations created by crossing wild soybean with the elite cultivar Williams 82 revealed nineteen total QTLs for leaf size and 9 for leaf shape (Swarm et al. 2019). While most of the wild soybean alleles in this study had negative effects on leaf size, the *G soja* allele of a QTL on chromosome 6 (*qLSZ-6*) detected in both populations had a positive effect (Swarm et al. 2019).

Discussion

Donald (1968) proposed a method and philosophy of crop improvement based around ideal crop forms which he called "ideotypes." A vital component of Donald's approach was a recognition that certain plant architectural phenotypes offer predictable advantages in a particular environment and that the combination of these beneficial traits could constitute a model plant that crop breeders could strive towards. The studies outlined in this review provide a starting point in the goal of developing soybean cultivars with optimized shoot architecture. Rapid advancements in genomic sequencing, genome editing, and other molecular tools offer an unprecedented opportunity for characterizing the genetic control of key architectural traits and translating that knowledge into useful applications for soybean breeders, farmers, and consumers. It has been proposed that targeting multiple genes responsible for architectural traits with the CRISPR/Cas9 endonuclease system could be an effective strategy for developing soybeans with improved architectural traits (Guo et al., 2020a, b). Proof of concept for this approach in other crop species include targeted mutagenesis of *BnaMAX1* homologs in *Brassica napus* resulting in higher-yielding semi-dwarf plants with increased branch number, and the knockout of *TaSPL8* in wheat resulting in higher yields through reduced leaf angle and increased spike number (Liu et al. 2019; Zheng et al. 2020). In soybean, CRISPR/Cas9-mediated knockout of *GmJAG1* in the low-latitude variety *Huachun 6* resulted in the narrow leaf phenotype, increased seed number per pod, and increased yield (Cai et al. 2021).

High-throughput phenotyping offers another emerging suite of tools for exploration of soybean architectural traits. Unmanned aerial vehicle (UAV) based imaging has been employed to phenotype soybean canopy closure, which relates directly to architectural traits like branch and petiole angles (Virdi et al. 2021; Xavier et al. 2017). A multiscale sliding-chord matching approach was used to classify and identify soybean cultivars based on their leaf morphology (Wang et al. 2020), demonstrating the power of imaging to evaluate plant architectural traits. Models of plant growth which incorporate plant architecture can be used to study the effects of different phenotypes on resource partitioning and yield (Fourcaud et al. 2008). The integration of novel genotyping, phenotyping, and computational tools will help eliminate bottlenecks in the study of soybean architectural traits and their genetic basis.

Many of the numerous QTL studies described in this review, particularly for branch number and leaf morphology, suffer from low mapping resolutions as a consequence of small population sizes. Validating these QTLs and pinpointing the genetic variation responsible for them will be required if they are to be useful for soybean improvement. Soybean, as a paleopolyploid crop that has undergone multiple rounds of whole genome duplications, contains multiple copies of nearly three quarters of its genes (Schmutz et al. 2010). The functional divergence of the duplicate paralogs of known shoot architecture genes such as *GmJAG1* and *Dt1* and what their contribution, if any, to shoot architecture is remains to be investigated. New sequencing resources, including the emerging soybean and Glycine pan genomes, provide valuable data for the exploration of genetic differences involved in phenotypic variations in shoot architecture (Liu et al. 2020; Zhuang et al. 2021). Wild soybean and its perennial relatives in the genus Glycine, which display a range of shoot architectural phenotypes far beyond what exists in elite soybean germplasm, remain an important reservoir of novel native genetic variation.

It has been noted that leguminous crops are fundamentally different from the cereals in the way they allocate seed (Liu et al. 2020). As a result, simply mimicking the strategies used to refine shoot architecture in wheat, rice, or maize will be insufficient. Understanding the way phenotypic variation in soybean shoot architecture traits influences yield, stress response, efficiency of resource use, and yield stability in response to increased environmental uncertainty is indispensable for meaningful enhancements of these traits to occur. Just as different main stem growth habits have been essential for adaptation to different environments, so too will the ideal value for the traits discussed in this review change depending on geography, production system, and end market. A "one size fits all approach" for soybean architecture may reduce the potential for achieving optimized traits. It should also be remembered that what is beneficial for yield at the level of a single plant it not always beneficial to yield at the field level. For example, the overexpression of *GmmiR156b* resulted in increased yield per plant because it had more pods on more branches (Sun et al., 2019), but this could potentially be a detrimental trait in high density plantings. A dearth of research comparing the yields of soybean varieties differing in only in a single shoot-architecture locus means that a description of what an ideal soybean will look like in a given environment is largely speculative, however we are optimistic about the potential of yield increases through the development of compact plants with short internode lengths and many pods per node, perhaps through the introgression of the *Dt2* allele conferring semideterminacy, into varieties grown in high-productivity environments. In regions where lower planting densities are preferred, we suspect that introgression of alleles or targeted modifications resulting in higher branch numbers and more spread-out plant architecture (i.e., wider branch angles and increased leaf petiole angles) could provide a productivity boost. A successful strategy of soybean improvement through altered shoot architecture must go hand in hand with agronomic practices in the target population of environments where the improved cultivar will be grown (Table 1).

Table 1 Selected soybean architecture genes and QTLs

Trait	Gene/QTL name	Gene ID	Gene classification	Natural variation affects trait?	References
Stem growth habit	*Dt1*	*Glyma.19g194300*	PEBP	Yes	Liu et al. 2010; Tian et al. 2010
Stem growth habit	*Dt2*	*Glyma.18g273600*	MADs Box TF	Yes	Ping et al. 2014
Stem growth habit	*GmFt5a*	*Glyma.16g044100*	PEBP	Unknown	Takeshima et al., 2019
Plant height	*GmDW*	*Glyma.08G165100*	ent-kaurene synthase	Unknown	Li et al. 2018
Plant height	*GmGAMYB*	*Glyma.13g187500*	R2R3 MYB TF	Unknown	Yang et al., 2021a, b
Plant height	*GmRav*	*Glyma.10G204400*	RAV TF	Unknown	Xue et al., 2022
Plant height	*GmIAA27*	*Glyma.09G193000*	AUX/IAA	Unknown	Su et al. 2022
Plant height	*GmmiR166*	NA	microRNA	Unknown	Zhao et al. 2022
Branch Number	*GmBRC1*	*Glyma06g23410*	TCP TF	Yes	Shim et al. 2019
Branch Number	*GmWRI1b*	*Glyma.15g221600*	Integrase TF	Unknown	Guo et al., 2020a, b
Branch Number	*GmmiR156b*	NA	microRNA	Unknown	Sun et al., 2019
Branch Number	*GmSPL9*	*Glyma.09G113800*	SPL TF	Unknown	Bao et al. 2019
Branch angle	*GmBA1*	Unknown	Unknown	Yes	Clark et al., 2022
Leaf petiole angle	*GmMYB14*	*Glyma.19g164600*	MYB TF	Unknown	Chen et al. 2020
Leaf petiole angle	*GmILP1*	*Glyma.11G026400*	APC8-Like	Unknown	Gao et al. 2017
Leaf petiole angle	*GmPINa*	*Glyma.08G054700*	PIN Auxin Transporter	Unknown	Zhang et al. 2022
Leaf petiole angle	*GmPINc*	*Glyma.09G176300*	PIN Auxin Transporter	Unknown	Zhang et al. 2022
Leaf shape	*GmJAG1/Ln*	*Glyma.20g116200*	C2HC zinc finger	Yes	Jeong et al. 2012

Acknowledgements We would like to thank Dr. Weidong Wang for providing the leaf pictures and critical reading of this manuscript. This work was supported by grants (2018-67013-27425, 2021-67013-33722, and 2022-67013-37037) funded by the Agriculture and Food Research Initiative of the USDA National Institute of Food and Agriculture.

Author contribution Jianxin Ma and Chancelor B. Clark conceived of the content and structure for the article. Chancelor B. Clark performed the literature search, compiled the data, and wrote the manuscript with input from Jianxin Ma.

Funding This work was supported by grants (2018-67013-27425, 2021-67013-33722, and 2022-67013-37037) funded by the Agriculture and Food Research Initiative of the USDA National Institute of Food and Agriculture.

Data availability Not applicable.

Declarations

Ethical approval and consent to participate Not applicable.

Consent for publication Not applicable.

Competing interests The authors declare no competing interests.

References

Bao A, Chen H, Chen L, Chen S, Hao Q, Guo W, Qiu D, Shan Z, Yang Z, Yuan S, Zhang C (2019) CRISPR/Cas9-mediated targeted mutagenesis of *GmSPL9* genes alters plant architecture in soybean. BMC Plant Biol 19(1):1–12. https://doi.org/10.1186/s12870-019-1746-6

Beaver JS, Cooper RL, Martin RJ (1985) Dry matter accumulation and seed yield of determinate and indeterminate soybeans. Agron J 77(5):675–679

Bernard RL (1972) Two genes affecting stem termination in soybeans. Crop Sci 12(2):235–239

Blancaflor EB (2013) Regulation of plant gravity sensing and signaling by the actin cytoskeleton. Am J Bot 100(1):143–152. https://doi.org/10.3732/ajb.1200283

Cai Z, Xian P, Cheng Y, Ma Q, Lian T, Nian H, Ge L (2021) CRISPR/Cas9-mediated gene editing of *GmJAGGED1* increased yield in the low-latitude soybean variety Huachun 6. Plant Biotechnol J 19(10):1898. https://doi.org/10.1111/2Fpbi.13673

Cao Y, Zhong Z, Wang H, Shen R (2022) Leaf angle: a target of genetic improvement in cereal crops tailored for high-density planting. Plant Biotechnol J 20(3):426. https://doi.org/10.1111/2Fpbi.13780

Chang JF, Green DE, Shibles R (1982) Yield and agronomic performance of semi-determinate and indeterminate soybean stem types. Crop Sci 22(1):97–101

Chen Y, Nelson RL (2004) Evaluation and classification of leaflet shape and size in wild soybean. Crop Sci 44(2):671–677. https://doi.org/10.2135/cropsci2004.6710

Chen QS, Zhang ZC, Liu CY, Xin DW, Qiu HM, Shan DP, Shan CY, Hu GH (2007) QTL analysis of major agronomic traits in soybean. Agr Sci China 6(4):399–405. https://doi.org/10.1016/S1671-2927(07)60062-5

Chen L, Nan H, Kong L, Yue L, Yang H, Zhao Q, Fang C, Li H, Cheng Q, Lu S, Kong F Liu B, Dong L (2020) Soybean *AP1* homologs control flowering time and plant height. J Int Plant Biol 62(12):1868-1879. https://doi.org/10.1111/jipb.12988

Chen L, Yang H, Fang Y, Guo W, Chen H, Zhang X, Dai W, Chen S, Hao Q, Yuan S, Zhang C, Huang Y, Shan Z, Yang Z, Qiu D, Liu X, Tran LSP, Zhou X, Cao D (2021) Overexpression of *GmMYB14* improves high-density yield and drought tolerance of soybean through regulating plant architecture mediated by the brassinosteroid pathway. Plant Biotechnol J 19(4):702–716. https://doi.org/10.1111/pbi.13496

Cheng Q, Dong L, Su T, Li T, Gan Z, Nan H, Lu S, Fang C, Kong L, Li H, Hou Z, Kou K, Tang Y, Lin X, Zhao X, Chen L, Liu B, Kong F (2019) CRISPR/Cas9-mediated targeted mutagenesis of *GmLHY* genes alters plant height and internode length in soybean. BMC Plant Biol 19(1):1–11. https://doi.org/10.1186/s12870-019-2145-8

Clark CB, Wang W, Wang Y, Fear GJ, Wen Z, Wang D, Ren B, Ma J (2022) Identification and molecular mapping of a major quantitative trait locus underlying branch angle in soybean. Theor Appl Genet 135(3):777–784. https://doi.org/10.1007/s00122-021-03995-9

Cober ER, Tanner JW (1995) Performance of related indeterminate and tall determinate soybean lines in short-season areas. Crop Sci 35(2):361–364

Cooper RL (1981) Development of short-statured soybean cultivars. Crop Sci 21(1):127–131

Dinkins RD, Keim KR, Farno L, Edwards LH (2002) Expression of the narrow leaflet gene for yield and agronomic traits in soybean. J Hered 93(5):346–351. https://doi.org/10.1093/jhered/93.5.346

Donald CM (1968) The breeding of crop ideotypes. Euphytica 17(3):385–403

Dong H, Zhao H, Xie W, Han Z, Li G, Yao W, Bai X, Hu Y, Guo Z, Lu K, Yang L, Xing Y (2016) A novel tiller angle gene, *TAC3*, together with *TAC1* and *D2* largely determine the natural variation of tiller angle in rice cultivars. PLoS Genetics 12(11):e1006412. https://doi.org/10.1371/journal.pgen.1006412

Du Y, Liu L, Li M, Fang S, Shen X, Chu J, Zhang Z (2017) *UNBRANCHED3* regulates branching by modulating cytokinin biosynthesis and signaling in maize and rice. New Phytol 214(2):721–733. https://doi.org/10.1111/nph.14391

Fehr WR, Caviness CE, Vorst JJ (1977) Response of Indeterminate and Determinate Soybean Cultivars to Defoliation and Half-plant Cut-off. Crop Sci 17(6):913–917

Foley TC, Orf JH, Lambert JW (1986) Performance of related determinate and indeterminate soybean lines. Crop Sci 26(1):5–8

Food and Agricultural Organization of the United Nations (FAO) (2020) Value of agricultural production. https://www.fao.org/faostat/en/#data/QCL. Accessed 10 November 2022.

Foucher F, Morin J, Courtiade J, Cadioux S, Ellis N, Banfield MJ, Rameau C (2003) *DETERMINATE* and *LATE FLOWERING* are two *TERMINAL FLOWER1/CENTRORADIALIS* homologs that control two distinct phases of flowering initiation and development in pea. Plant Cell 15(11):2742–2754. https://doi.org/10.1105/tpc.015701

Fourcaud T, Zhang X, Stokes A, Lambers H, Körner C (2008) Plant growth modelling and applications: the increasing importance of plant architecture in growth models. Ann Bot 101(8):1053–1063. https://doi.org/10.1093/aob/mcn050

Gao J, Yang S, Cheng W, Fu Y, Leng J, Yuan X, Jiang N, Ma J, Feng X (2017) *GmILPA1*, encoding an APC8-like protein, controls leaf petiole angle in soybean. Plant Physiol 174(2):1167–1176. https://doi.org/10.1104/pp.16.00074

Goli A, Weaver DB (1986) Defoliation responses of determinate and indeterminate late-planted soybeans. Crop Sci 26(1):156–159

Guo W, Chen L, Chen H, Yang H, You Q, Bao A, Chen S, Hao Q, Huang Y, Qiu D, Shan Z, Yang Z, Yuan S, Zhang C, Zhang X, Jiao Y, Tran LSP, Zhou X, Cao D (2020a) Overexpression of GmWRI1b in soybean stably improves plant architecture and associated yield parameters, and increases total seed oil production under field conditions. Plant Biotechnol J 18(8):1639–1641. https://doi.org/10.1111/pbi.13324

Guo W, Chen L, Herrera-Estrella L, Cao D, Tran LSP (2020b) Altering plant architecture to improve performance and resistance. Trends Plant Sci 25(11):1154–1170. https://doi.org/10.1016/j.tplants.2020.05.009

Harder D, Sprague C, Renner K (2007) Effect of soybean row width and population on weeds, crop yield, and economic return. Weed Technol 21:744–752

He Q, Yang H, Xiang S, Wang W, Xing G, Zhao T, Gai J (2014) QTL mapping for the number of branches and pods using wild chromosome segment substitution lines in soybean [*Glycine max* (L.) Merr.]. Plant. Genet Res 12(S1):172–S177. https://doi.org/10.1017/S1479262114000495

Heatherly LG, Smith JR (2004) Effect of soybean stem growth habit on height and node number after beginning bloom in the midsouthern USA. Crop Sci 44(5):1855–1858. https://doi.org/10.2135/cropsci2004.1855

Hedden P (2003) The genes of the green revolution. Trends Genet 19(1):5–9. https://doi.org/10.1016/S0168-9525(02)00009-4

Hicks DR, Pendleton JW, Bernard RL, Johnston TL (1969) Response of soybean plant types to planting patterns. Agron J 61(2):290–293

Jeong N, Moon JK, Kim HS, Kim CG, Jeong SC (2011) Fine genetic mapping of the genomic region controlling leaflet shape and number of seeds per pod in the soybean. Theor Appl Genet 122(5):865–874. https://doi.org/10.1007/s00122-010-1492-5

Jeong N, Suh SJ, Kim MH, Lee S, Moon JK, Kim HS, Jeong SC (2012) Ln is a key regulator of leaflet shape and number of seeds per pod in soybean. Plant Cell 24(12):4807–4818. https://doi.org/10.1105/tpc.112.104968

Jia Y, Li K, Liu H, Zan L, Du D (2019) Characterization of the *bna10. TFL1* gene controls determinate inflorescence trait in Brassica napus L. Agron 9(11):722. https://doi.org/10.3390/agronomy9110722

Jiao Z, Du H, Chen S, Huang W, Ge L (2021) *LAZY* gene family in plant gravitropism. Front Plant Sci 11:606241. https://doi.org/10.3389/fpls.2020.606241

Jun TH, Freewalt K, Michel AP, Mian R (2014) Identification of novel QTL for leaf traits in soybean. Plant Breed 133(1):61–66. https://doi.org/10.1111/pbr.12107

Khush GS (2001) Green revolution: the way forward. Nat Rev Genet 2(10):815–822. https://doi.org/10.1038/35093585

Kim HK, Kang ST, Suh DY (2005) Analysis of quantitative trait loci associated with leaflet types in two recombinant inbred lines of soybean. Plant Breed 124(6):582–589. https://doi.org/10.1111/j.1439-0523.2005.01152.x

Kou K, Su T, Wang Y, Yang H, Du H, He M, Li T, Ma L, Liao C, Yang C, Shi W, Chen L, Li Y, Yang B, Kong L, Li S, Wang L, Zhao X, Lu S et al (2021) Natural variation of the *Dt2* promoter controls plant height and node number in semi-determinant soybean. Mol Breed 41(40):1–12. https://doi.org/10.1007/s11032-021-01235-y

Kuroda T, Saitoh K, Mahmood T, Yanagawa K (1998) Differences in flowering habit between determinate and indeterminate types of soybean. Plant Prod Sci 1(1):18–24

Lambert RJ, Johnson RR (1978) Leaf angle, tassel morphology, and the performance of maize hybrids. Crop Sci 18(3):499–502

Lee S, Jun TH, Michel AP, Mian R (2015) SNP markers linked to QTL conditioning plant height, lodging, and maturity in soybean. Euphytica 203(3):521–532. https://doi.org/10.1007/s10681-014-1252-8

Li P, Wang Y, Qian Q, Fu Z, Wang M, Zeng D, Li B, Wang X, Li J (2007) *LAZY1* controls rice shoot gravitropism through regulating polar auxin transport. Cell Res 17(5):402–410. https://doi.org/10.1038/cr.2007.38

Li ZF, Guo Y, Ou L, Hong H, Wang J, Liu ZX, Guo B, Zhang L, Qiu L (2018) Identification of the dwarf gene *GmDW1* in soybean (*Glycine max* L.) by combining mapping-by-sequencing and linkage analysis. Theoret Appl Genet 131(5):1001–1016. https://doi.org/10.1007/s00122-017-3044-8

Li R, Jiang H, Zhang Z, Zhao Y, Xie J, Wang Q, Zheng H, Hou L, Xiong X, Xin D, Hu Z (2019) Combined linkage mapping and BSA to identify QTL and candidate genes for plant height and the number of nodes on the main stem in soybean. Int J Mol Sci 21(1):42. https://doi.org/10.3390/ijms21010042

Liang Q, Chen L, Yang X, Yang H, Liu S, Kou K, Fan L, Zhang Z, Duan Z, Yuan Y, Liang S, Liu Y, Lu X, Zhou G, Zhang M, Kong F, Tian Z (2022) Natural variation of Dt2 determines branching in soybean. Nat Commun 13(1):6429. https://doi.org/10.1038/s41467-022-34153-4

Liu X, Jin J, Wang G, Herbert SJ (2008) Soybean yield physiology and development of high-yielding practices in Northeast China. Field Crops Res 105(3):157–171. https://doi.org/10.1016/j.fcr.2007.09.003

Liu B, Watanabe S, Uchiyama T, Kong F, Kanazawa A, Xia Z, Nagamatsu A, Arai M, Yamada T, Kitamura K, Masuta

C, Harada K, Abe J (2010) The soybean stem growth habit gene Dt1 is an ortholog of Arabidopsis *TERMINAL FLOWER1*. Plant Physiol 153:198–210. https://doi.org/10.1104/pp.109.150607

Liu Y, Zhang D, Ping J, Li S, Chen Z, Ma J (2016) Innovation of a regulatory mechanism modulating semideterminate stem growth through artificial selection in soybean. PLoS Genet 12:1005818. https://doi.org/10.1371/journal.pgen.1005818

Liu K, Cao J, Yu K, Liu X, Gao Y, Chen Q, Zhang W, Peng H, Du J, Xin M, Hu Z, Guo W, Rossi V, Ni Z, Sun Q, Yao Y (2019) Wheat *TaSPL8* modulates leaf angle through auxin and brassinosteroid signaling. Plant Physiol 181(1):179–194. https://doi.org/10.1104/pp.19.00248

Liu Y, Du H, Li P, Shen Y, Peng H, Liu S, Zhou GA, Zhang H, Liu Z, Shi M, Huang X, Li Y, Zhang M, Wang Z, Zhu B, Han B, Liang C, Tian Z (2020) Pan-genome of wild and cultivated soybeans. Cell 182(1):162–176. https://doi.org/10.1016/j.cell.2020.05.023

Liu X, Chen J, Zhang X (2021) Genetic regulation of shoot architecture in cucumber. Hortic Res 8:143. https://doi.org/10.1038/s41438-021-00577-0

Luo X, Zheng J, Huang R, Huang Y, Wang H, Jiang L, Fang X (2016) Phytohormones signaling and crosstalk regulating leaf angle in rice. Plant Cell Rep 35(12):2423–2433. https://doi.org/10.1007/s00299-016-2052-5

Marth PC, Audia WV, Mitchell JW (1956) Effects of gibberellic acid on growth and development of plants of various genera and species. Bot Gaz 118(2):106–111

Mathan J, Bhattacharya J, Ranjan A (2016) Enhancing crop yield by optimizing plant developmental features. Development 143(18):3283–3294. https://doi.org/10.1242/dev.134072

Maw SL, Nelson RL (1988) Effect of plant height and flowering date on seed yield of determinate soybean. Crop Sci 28(2):218–222

McGarry RC, Ayre BG (2012) Manipulating plant architecture with members of the *CETS* gene family. Plant Sci 188:71–81. https://doi.org/10.1016/j.plantsci.2012.03.002

McWilliams DA, Berglund DR, Endres GJ (1999) Soybean growth and management quick guide. North Dakota State University Extension Service

Mian MAR, Wells R, Carter TE Jr, Ashley DA, Boerma HR (1998) RFLP tagging of QTLs conditioning specific leaf weight and leaf size in soybean. Theor Appl Genet 96:354–360

Neyshabouri MR, Hatfield JL (1986) Soil water deficit effects on semideterminate and indeterminate soybean growth and yield. Field Crop Res 15(1):73–84

Niu Y, Chen T, Zhao C, Zhou M (2021) Improving crop lodging resistance by adjusting plant height and stem strength. Agronomy 11(12):2421. https://doi.org/10.3390/agronomy11122421

Njogu MK, Yang F, Li J, Wang X, Ogweno JO, Chen J (2020) A novel mutation in TFL1 homolog sustaining determinate growth in cucumber (Cucumis sativus L.). Theor Appl Genet 133(12):3323–3332. https://doi.org/10.1007/s00122-020-03671-4

Ohno CK, Reddy GV, Heisler MG, Meyerowitz EM (2004) The Arabidopsis *JAGGED* gene encodes a zinc finger protein that promotes leaf tissue development. Development 131(5):1111–1122. https://doi.org/10.1242/dev.00991

Ongaro V, Leyser O (2008) Hormonal control of shoot branching. J Exp Bot 59(1):67-74. https://doi.org/https://doi.org/10.1093/jxb/erm134

Orf JH, Chase K, Jarvik T, Mansur LM, Cregan PB, Adler FR, Lark KG (1999) Genetics of soybean agronomic traits: I comparison of three related recombinant inbred populations. Crop Sci 39:1642–1651

Ping J, Liu Y, Sun L, Zhao M, Li Y, She M, Sui Y, Lin F, Liu X, Tang Z, Nguyen H, Tian Z, Qiu L, Nelson RL, Clemente TE, Specht JE, Ma J (2014) *Dt2* is a gain-of-function MADS-domain factor gene that specifies semideterminacy in soybean. Plant Cell 26(7):2831–2842. https://doi.org/10.1105/tpc.114.126938

Pingali PL (2012) Green revolution: impacts, limits, and the path ahead. Proc Natl Acad Sci Unit States Am 109(31):12302–12308. https://doi.org/10.1073/pnas.0912953109

Pnueli L, Carmel-Goren L, Hareven D, Gutfinger T, Alvarez J, Ganal M, Zamir D, Lifschitz E (1998) The *SELF-PRUNING* gene of tomato regulates vegetative to reproductive switching of sympodial meristems and is the ortholog of CEN and TFL1. Development 125(11):1979–1989

Reinhardt D, Kuhlemeier C (2002) Plant architecture. EMBO Rep 3:846–851. https://doi.org/10.1093/embo-reports/kvf177

Sayama T, Hwang TY, Yamazaki H, Yamaguchi N, Komatsu K, Takahashi M, Suzuki C, Miyoshi T, Tanaka Y, Xia Z, Tsubokura Y, Watanabe S, Harada K, Funatsuki H, Ishimoto M (2010) Mapping and comparison of quantitative trait loci for soybean branching phenotype in two locations. Breed Sci 60(4):380–389. https://doi.org/10.1270/jsbbs.60.380

Sayama T, Tanabata T, Saruta M, Yamada T, Anai T, Kaga A, Ishimoto M (2017) Confirmation of the pleiotropic control of leaflet shape and number of seeds per pod by the *Ln* gene in induced soybean mutants. Breed Sci 67(4):363–369. https://doi.org/10.1270/jsbbs.16201

Schiessl K, Muiño JM, Sablowski R (2014) Arabidopsis JAGGED links floral organ patterning to tissue growth by repressing Kip-related cell cycle inhibitors. Proc Natl Acad Sci USA 111(7):2830–2835. https://doi.org/10.1073/pnas.1320457111

Schmutz J, Cannon SB, Schlueter J, Ma J, Mitros T, Nelson W, Hyten DL, Song Q, Thelen JJ, Cheng J, Xu D et al (2010) Genome sequence of the palaeopolyploid soybean. Nature 463(7278):178–183. https://doi.org/10.1038/nature08670

Schug H, Reisig D, Huseth A, Thrash B, Vann R (2022) *Helicoverpa zea* (Lepidoptera: Noctuidae) thresholds and yield compensation between soybeans with determinate and indeterminate growth habits. J Econ Entomol 115(5):1564–1570. https://doi.org/10.1093/jee/toac119

Sedivy EJ, Wu F, Hanzawa Y (2017) Soybean domestication: the origin, genetic architecture, and molecular bases. New Phytol 214(2):539–553. https://doi.org/10.1111/nph.14418

Shim S, Ha J, Kim MY, Choi MS, Kang ST, Jeong SC, Moon JK, Lee SH (2019) GmBRC1 is a candidate gene for branching in soybean (*Glycine max* (L.) Merrill). Int J Mol Sci 20(1):135. https://doi.org/10.3390/ijms20010135

Shim S, Kim MY, Ha J, Lee YH, Lee SH (2017) Identification of QTLs for branching in soybean (*Glycine max* (L.) Merrill). Euphytica 213(9):1–9. https://doi.org/10.1007/s10681-017-2016-z

Song Q, Yan L, Quigley C, Jordan BD, Fickus E, Schroeder S, Song BH, Charles An YQ, Hyten D, Nelson R, Rainey K, Beavis WD, Specht J, Diers B, Cregan P (2017) Genetic characterization of the soybean nested association mapping population. Plant. Genome 10(2):2016-10plantgenome2016.10.0109. https://doi.org/10.3835/plantgenome2016.10.0109

Specht JE, Diers BW, Nelson RL, de Toledo JFF, Torrion JA, Grassini P (2014) Soybean. In: Smith S, Diers B, Specht J, Carver B (eds) Yield gains in major U.S. field crops, volume 33, Wiley, New York, pp 311–355. https://doi.org/10.2135/cssaspecpub33.c12

Su B, Wu H, Guo Y, Gao H, Wei Z, Zhao Y, Qiu L (2022) *GmIAA27* encodes an AUX/IAA protein involved in dwarfing and multi-branching in soybean. Int J Mol Sci 23(15):8643. https://doi.org/10.3390/ijms23158643

Sun Y, Luan H, Qi Z, Shan D, Liu C, Hu G, Chen Q (2012) Mapping and meta-analysis of height QTLs in soybean. Legume Genomics Genet 3(1):1–7. https://doi.org/10.5376/lgg.2012.03.0001

Sun Z, Su C, Yun J, Jiang Q, Wang L, Wang Y, Cao D, Zhao F, Zhao Q, Zhang M, Zhou B, Zhang L, Kong F, Liu B, Tong Y, Li X (2019) Genetic improvement of the shoot architecture and yield in soya bean plants via the manipulation of GmmiR156b. Plant Biotechnol J 17(1):50–62. https://doi.org/10.1111/pbi.12946

Sussex IM, Kerk NM (2001) The evolution of plant architecture. Curr Opin Plant Biol 4(1):33–37. https://doi.org/10.1016/S1369-5266(00)00132-1

Swarm SA, Sun L, Wang X, Wang W, Brown PJ, Ma J, Nelson RL (2019) Genetic dissection of domestication-related traits in soybean through genotyping-by-sequencing of two interspecific mapping populations. Theor Appl Genet 132(4):1195–1209. https://doi.org/10.1007/s00122-018-3272-6

Takahashi N (1934) Linkage relation between the genes for the form of leaves and the number of seeds per pod of soybeans. Jpn J Genet 9:208–225

Takeshima R, Nan H, Harigai K, Dong L, Zhu J, Lu S, Xu M, Yamagishi N, Yoshikawa N, Liu B, Yamada T, Yoshikawa N, Liu B, Yamada T, Kong F, Abe J (2019) Functional divergence between soybean *FLOWERING LOCUS T* orthologues *FT2a* and *FT5a* in post-flowering stem growth. J Exp Bot 70(15):3941–3953. https://doi.org/10.1093/jxb/erz199

Tamang BG, Zhang Y, Zambrano MA, Ainsworth EA (2022) Anatomical determinants of gas exchange and hydraulics vary with leaf shape in soybean. Ann Bot mcac118. https://doi.org/10.1093/aob/mcac118

Teichmann T, Muhr M (2015) Shaping plant architecture. Front. Plant Sci 6:233. https://doi.org/10.3389/fpls.2015.00233

Thompson JA, Bernard RL, Nelson RL (1997) A third allele at the soybean dt1 locus. Crop Sci 37(3):757–762

Tian J, Wang C, Xia J, Wu L, Xu G, Wu W, Li D, Qin W, Han X, Chen Q, Jin W, Tian F (2019) Teosinte ligule allele narrows plant architecture and enhances high-density maize yields. Science 365(6454):658–664. https://doi.org/10.1126/science.aax5482

Tian Z, Wang X, Lee R, Li Y, Specht JE, Nelson RL, McClean PR, Qiu L, Ma J (2010) Artificial selection for determinate growth habit in soybean. Proc Natl Acad Sci Unit States Am 107(19):8563–8568. https://doi.org/10.1073/pnas.1000088107

Toyota M, Gilroy S (2013) Gravitropism and mechanical signaling in plants. Am J Bot 100(1):111–125. https://doi.org/10.3732/ajb.1200408

United States Department of Agriculture: Agricultural Research Service (USDA ARS) (2022) US National Plant Germplasm System, GRIN Global. https://npgsweb.ars-grin.gov/gringlobal/search. Accessed 10 November 2022.

Villalobos-Rodriquez E, Shibles R (1985) Response of determinate and indeterminate tropical soybean cultivars to water stress. Field Crops Res 10:269–281

Virdi KS, Sreekanta S, Dobbels A, Haaning A, Jarquin D, Stupar RM, Lorenz AJ, Muehlbauer GJ (2021) Branch angle and leaflet shape are associated with canopy coverage in soybean. Sci Rep. https://doi.org/10.21203/rs.3.rs-806530/v1

Wang Z, Zhou Z, Liu Y, Liu T, Li Q, Ji Y, Li C, Fang C, Wang M, Wu M, Shen Y, Tang T, Ma J, Tian Z (2015) Functional evolution of phosphatidylethanolamine binding proteins in soybean and Arabidopsis. Plant Cell 27(2):323–336. https://doi.org/10.1105/tpc.114.135103

Wang B, Gao Y, Yuan X, Xiong S, Feng X (2020) From species to cultivar: Soybean cultivar recognition using joint leaf image patterns by multiscale sliding chord matching. Biosyst Eng 194:99–111. https://doi.org/10.1016/j.biosystemseng.2020.03.019

Wang B, Smith SM, Li J (2018) Genetic regulation of shoot architecture. Annu Rev Plant Biol 69:437–468

Wang Y, Jiao Y (2018) Axillary meristem initiation – a way to branch out. Curr Opin Plant Biol 41:61–66. https://doi.org/10.1016/j.pbi.2017.09.001

Wang M, Le Moigne MA, Bertheloot J, Crespel L, Perez-Garcia MD, Ogé L, Demotes-Mainard S, Hamama L, Davière JM, Sakr S (2019b) *BRANCHED1*: a key hub of shoot branching. Front Plant Sci 10:76. https://doi.org/10.3389/fpls.2019.00076

Wang L, Cheng Y, Ma Q, Mu Y, Huang Z, Xia Q, Zhang G, Nian H (2019a) QTL fine-mapping of soybean (*Glycine max* L.) leaf type associated traits in two RILs populations. BMC Genom 20(260):1–15. https://doi.org/10.1186/s12864-019-5610-8

Wilcox JR, Sediyama T (1981) Interrelationships among height, lodging and yield in determinate and indeterminate soybeans. Euphytica 30(2):323–326

Woodworth CM (1932) Genetics and breeding in the improvement of the soybean. Bull Univ Ill Agric Exp Stn Champaign 384

Wu X, Tang D, Li M, Wang K, Cheng Z (2013) Loose Plant Architecture1, an INDETERMINATE DOMAIN protein involved in shoot gravitropism, regulates plant architecture in rice. Plant Physiol 161(1):317–329. https://doi.org/10.1104/pp.112.208496

Xavier A, Hall B, Hearst AA, Cherkauer KA, Rainey KM (2017) Genetic architecture of phenomic-enabled canopy coverage in Glycine max. Genetics 206:1081–1089. https://doi.org/10.1534/genetics.116.198713

Xin W, Wang Z, Liang Y, Wang Y, Hu Y (2017) Dynamic expression reveals a two-step patterning of *WUS* and *CLV3* during axillary shoot meristem formation in Arabidopsis. J Plant Physiol 214:1–6. https://doi.org/10.1016/j.jplph.2017.03.017

Xue H, Tian X, Zhang K, Li W, Qi Z, Fang Y, Li X, Wang Y, Song J, Li WX, Ning H (2019) Mapping developmental QTL for plant height in soybean [*Glycine max* (L.) Merr.] using a four-way recombinant inbred line population. PloS One 14(11):e0224897. https://doi.org/10.1371/journal.pone.0224897

Xue Y, Zhang Y, Shan J, Ji Y, Zhang X, Li W, Li D, Zhao L (2022) Growth repressor GmRAV binds to the *GmGA3ox* promoter to negatively regulate plant height development in soybean. Int J Mol Sci 23(3):1721. https://doi.org/10.3390/ijms23031721

Yan X, Zhao H, Liu X, Li Q, Wang Y, Yuan C, Dong Y (2014) Phenotypic traits and diversity of different leaf shape accessions of the wild soybean (Glycine soja Sieb. et Zucc.) in China. Can J Plant Sci 94(2):397–404

Yang Y, Lei Y, Bai Z, Wei B, Zhang H, Zhang R (2021a) Physical mapping and candidate gene prediction of branch number on the main stem in soybean [*Glycine max* (L.) Merr.]. Genet Resour Crop Evol 68(7):2907–2921. https://doi.org/10.1007/s10722-021-01163-y

Yang X, Li X, Shan J, Li Y, Zhang Y, Wang Y, Li W, Zhao L (2021b) Overexpression of *GmGAMYB* accelerates the transition to flowering and increases plant height in soybean. Front Plant Sci 12:667242. https://doi.org/10.3389/fpls.2021.667242

Yamanaka N, Ninomiya S, Hoshi M, Tsubokura Y, Yano M, Nagamura Y, Sasaki T, Harada K (2001) An informative linkage map of soybean reveals QTLs for flowering time, leaflet morphology and regions of segregation distortion. DNA Res 8:61–72

Yin Z, Qi H, Chen Q, Zhang Z, Jiang H, Zhu R, Hu Z, Wu X, Li C, Zhang Y, Liu C, Hu G, Xin D, Qi Z (2017) Soybean plant height QTL mapping and meta-analysis for mining candidate genes. Plant Breed 136(5):688–698. https://doi.org/10.1111/pbr.12500

Yoshida K, Nomura F, Gotoh K (1983) Significance of intraplant flowering date in soybean seed production: 2. number of flowers, podding efficiency, nodal distribution of pods and yield components among different flowering dates. Jpn J Crop Sci 52(4):567–573

Yoshikawa T, Ozawa S, Sentoku N, Itoh JI, Nagato Y, Yokoi S (2013) Change of shoot architecture during juvenile-to-adult phase transition in soybean. Planta 238(1):229–237. https://doi.org/10.1007/s00425-013-1895-z

Yu B, Lin Z, Li H, Li X, Li J, Wang Y, Zhang X, Zhu Z, Zhai W, Wang X, Xie D, Sun D (2007) *TAC1*, a major quantitative trait locus controlling tiller angle in rice. Plant J 52(5):891–898. https://doi.org/10.1111/j.1365-313X.2007.03284.x

Yue L, Li X, Fang C, Chen L, Yang H, Yang J, Chen Z, Nan H, Chen L, Zhang Y, Li H, Hou X, Dong Z, Weller JL, Abe J, Liu B, Kong F (2021) FT5a interferes with the *Dt1-AP1* feedback loop to control flowering time and shoot determinacy in soybean. J Integr Plant Biol 63(6):1004–1020. https://doi.org/10.1111/jipb.13070

Zhang J, Ku LX, Han ZP, Guo SL, Liu HJ, Zhang ZZ, Cao LR, Cui XJ, Chen YH (2014) The *ZmCLA4* gene in the *qLA4-1* QTL controls leaf angle in maize (Zea mays L.). J Exp Bot 65(17):5063–5076. https://doi.org/10.1093/jxb/eru271

Zhang D, Wang X, Li S, Wang C, Gosney MJ, Mickelbart MV, Ma J (2019) A post-domestication mutation, Dt2, triggers systemic modification of divergent and convergent pathways modulating multiple agronomic traits in soybean. Mol Plant 12(10):1366–1382. https://doi.org/10.1016/j.molp.2019.05.010

Zhang Z, Gao L, Ke M, Gao Z, Tu T, Huang L, Chen J, Guan Y, Huang X, Chen X (2022) GmPIN1-mediated auxin asymmetry regulates leaf petiole angle and plant architecture in soybean. J Integr Plant Biol 64(7):1325–1338. https://doi.org/10.1111/jipb.13269

Zhao C, Ma J, Zhang Y, Yang S, Feng X, Yan J (2022) The miR166 mediated regulatory module controls plant height by regulating gibberellic acid biosynthesis and catabolism in soybean. J Integr Plant Biol 64:995–1006. https://doi.org/10.1111/jipb.13253

Zheng M, Zhang L, Tang M, Liu J, Liu H, Yang H, Fan S, Terzaghi W, Wang H, Hua W (2020) Knockout of two *Bna MAX 1* homologs by CRISPR/Cas9-targeted mutagenesis improves plant architecture and increases yield in rapeseed (*Brassica napus L.*). Plant Biotechnol J 18(3):644–654. https://doi.org/10.1111/pbi.13228

Zhuang Y, Wang X, Li X, Hu J, Fan L, Jackson S, Doyle J, Zhang XS, Zhang D, Ma J (2021) A super-pangenome framework of the genus Glycine unveils polyploid evolution and life-strategy transition. Research Square. https://doi.org/10.21203/rs.3.rs-548382/v1