

## Review

# Restructuring plant types for developing tailor-made crops

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Received 17 May 2021;

revised 8 July 2021;

accepted 12 July 2021.

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**Keywords:** customized crops, domestication, shoot architecture, meristem fate, branch angle, determinate inflorescence.

## Summary

Plants have adapted to different environmental niches by fine-tuning the developmental factors working together to regulate traits. Variations in the developmental factors result in a wide range of quantitative variations in these traits that helped plants survive better. The major developmental pathways affecting plant architecture are also under the control of such pathways. Most notable are the CLAVATA-WUSCHEL pathway regulating shoot apical meristem fate, GID1-DELLA module influencing plant height and tillering, LAZY1-TAC1 module controlling branch/tiller angle and the TFL1-FT determining the floral fate in plants. Allelic variants of these key regulators selected during domestication shaped the crops the way we know them today. There is immense yield potential in the 'ideal plant architecture' of a crop. With the available genome-editing techniques, possibilities are not restricted to naturally occurring variations. Using a transient reprogramming system, one can screen the effect of several developmental gene expressions in novel ecosystems to identify the best targets. We can use the plant's fine-tuning mechanism for customizing crops to specific environments. The process of crop domestication can be accelerated with a proper understanding of these developmental pathways. It is time to step forward towards the next-generation molecular breeding for restructuring plant types in crops ensuring yield stability.

## Introduction

Life in itself is a dynamic process. The survival of living organisms depends upon their adaptive capability in fluctuating environmental conditions. Our world is continuously changing, and plants being sessile are most affected. However, they are one of the most successful life forms on planet Earth. Their key to survival, as we now slowly understand, is their elaborate gene regulatory network (Castelán-Muñoz *et al.*, 2019; Loreti *et al.*, 2018). These networks are very dynamic and help the plant to respond to even subtle changes in the environment. Alteration in the trait phenotype involves multiple layers of gene regulation. Plants cannot depend on the up/down-regulation of a single gene to perceive the external stimuli. The molecular switches in plants are designed to differentiate between long-term and short-term changes in the environment and act accordingly (Hepworth *et al.*, 2018). The subtle changes in the plant architecture help the plant invade and conquer different ecological niches. Plant architecture is a broad term that includes branching patterns, shapes and organizations of both vegetative and reproductive tissue (Reinhardt and Kuhlemeier, 2002). Certain traits, such as flowering time, are not directly considered a plant architectural trait, but their influence on architecture is so vital that it cannot be left aside while discussing its many aspects (Huyghe, 1998). Similar concepts can be applied to domesticate crops for urban agriculture and novel ecosystems (Kwon *et al.*, 2020). This can be tricky since plant architecture is not entirely under genetic control and

agricultural practices such as irrigation, soil nutrient status play a crucial role in its determination (Durigon *et al.*, 2019; Luo *et al.*, 2020). Nonetheless, the understanding of plant architecture regulating developmental events is crucial for optimizing crops to our requirement.

Plants have developed an intricate system of antagonistically acting regulators that balances their response to such environmental stimuli. These regulators often belong to the same gene family and may even compete for their target site. This system of fine-tuning plant's response to environmental changes helped them to adapt to varied ecological niches. A well-studied effect of this system has been on the plant architecture. The several components of plant architecture, such as branch angle, meristem/floral fate and plant stature, are maintained through varying levels of regulation between such developmental factors. Each of these developmental events has a massive impact on crop domestication and its yield stability. The branch and leaf angle played a significant role in domesticating crops such as rice and maize (Hu *et al.*, 2018; Liu *et al.*, 2019b). The inflorescence meristem determinacy in tomato and legumes like soya bean was a turning point in their domestication event (Pnueli *et al.*, 1998; Tian *et al.*, 2010). With a better understanding of biological networks controlling these events, we can design crops suitable for unconventional ecosystems. This review discusses few such regulatory networks that have tremendous prospects in designing crops with ideal plant architecture. The review also focuses on steps towards utilization of the information acquired for successful crop customization for

adaptation in diverse agro-climatic conditions and accelerating domestication to ensure yield stability.

### CLAVATA-WUSCHEL signalling: maintenance of the shoot apical meristematic cell niche for defining shoot architecture

#### CLAVATA peptides and receptors

The shoot apical meristem (SAM) of a plant is home to the elaborate gene network, which defines its shoot architecture. The axillary and inflorescence meristem, giving rise to leaves, branches and inflorescence, are derived from the SAM (Sharma and Fletcher, 2002; Yang and Jiao, 2016). The role of SAM morphometrics in regulating agronomic yield-contributing traits is also known in crops like chickpea and maize (Basu *et al.*, 2019a; Leiboff *et al.*, 2015; Narnoliya *et al.*, 2019). The population of the meristematic cells is maintained through a feedback loop between the homeodomain transcription factor WUSCHEL (WUS) and its counterpart CLAVATA (CLV) gene family members and newly identified *SQUAMOSA PROMOTER BINDING PROTEIN-LIKE (SPL)* family gene (Fouracre and Poethig, 2019; Somssich *et al.*, 2016). This feedback loop is crucial to determine the fate of meristematic cells and the timing of organ development. The CLV-WUS signalling pathway involves a peptide ligand CLV3, which is perceived by leucine-rich repeat (LRR) receptor complexes (Clark *et al.*, 1995; Figure 1). The CLV3 peptide undergoes post-translational hydroxylation and arabinosylation to be functionally active (Kondo *et al.*, 2006; Ohyama *et al.*, 2009). These post-translational modifications are important for their receptor binding affinity and specificity. The absence of arabinosylation due to the hydroxyproline O-arabinosyltransferase gene mutation resulted in a *clv*-like phenotype in tomato (Xu *et al.*, 2015). However, *Arabidopsis* does not exhibit a similar phenotype (MacAlister *et al.*, 2016). CLV3 is not the only peptide ligand working in the regulation of SAM. There are some other CLAVATA3/EMBRYO SURROUNDING REGION (ESR) CLE peptides, regulating meristem size in rice, maize and soya bean (Hastwell *et al.*, 2015; Je *et al.*, 2016; Suzaki *et al.*, 2008, 2009). The post-translational modification status of these peptides is not fully explored. Thus, much more effort is required to understand the biological significance of such modifications of these peptides. While the *CLV3* is expressed explicitly in *Arabidopsis*' shoot apical region acting as a SAM marker, the soya bean *CLV3* cannot be used as the same (Wong *et al.*, 2013). Several receptors are known to act downstream of CLV3, a well-studied being the LRR receptor-like kinase (RLK) CLV1, which forms a homodimer or heterodimer/tetramer with another RLK, CORNYE (CRN; Bleckmann *et al.*, 2009; Leyser and Furner, 1992). CRN also forms a heterodimer complex with LRR receptor CLV2 to perceive the CLV3 signal (Bleckmann *et al.*, 2009). Some other LRR-RLKs like BARELY ANY MERISTEM (BAM) receptors, RECEPTOR-LIKE PROTEIN KINASE2 (RPK2) and ERECTA are also involved in this pathway (Deyoung and Clark, 2008; Durbak and Tax, 2011; Kinoshita *et al.*, 2010; Nimchuk *et al.*, 2015; Shimizu *et al.*, 2015). These receptor complexes work in coordination with co-receptors CLAVATA3 INSENSITIVE RECEPTOR KINASES (CIKS) to maintain stem cell homeostasis (Hu *et al.*, 2018a).

#### Signalling cascades acting downstream the receptors

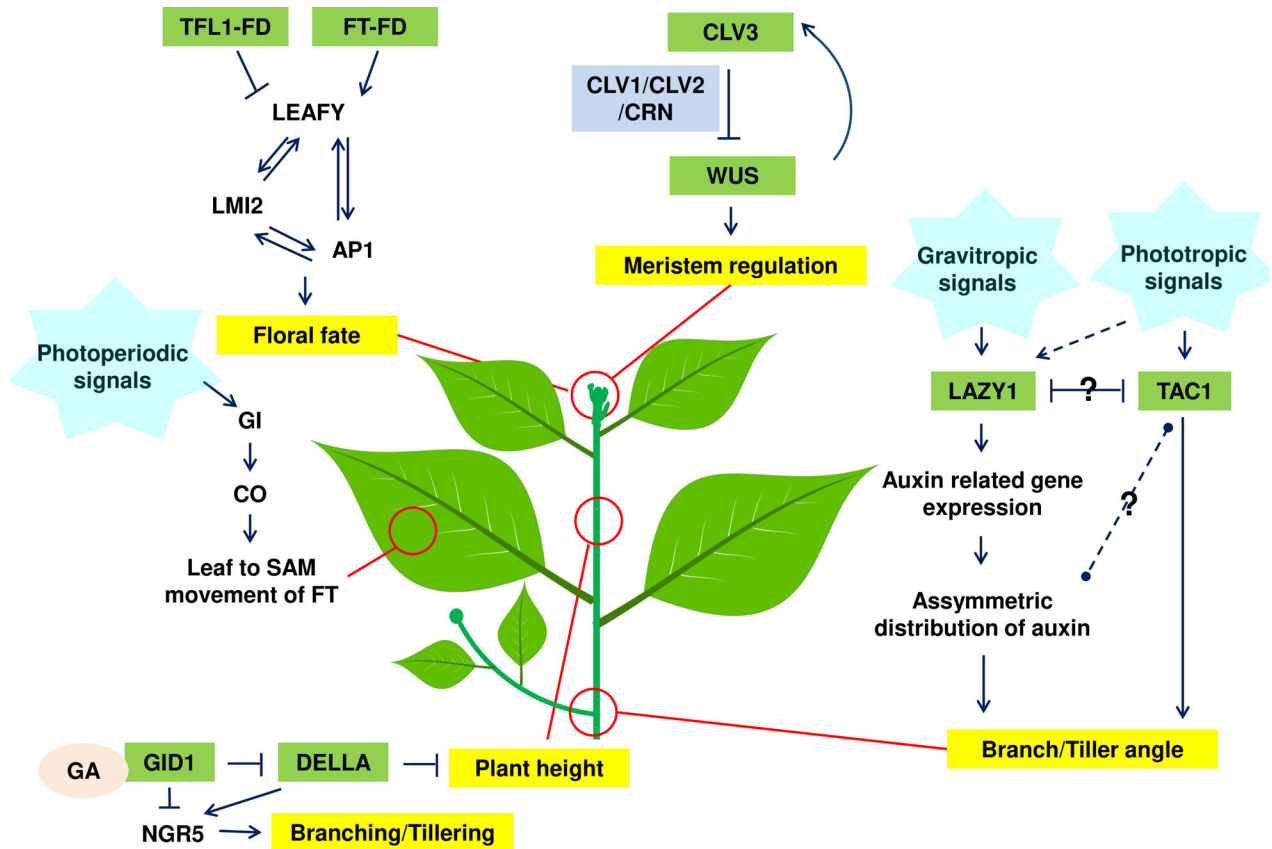
Given the various receptors working in different combinations, a few signalling cascades act downstream of the ligand-receptor

system. The mitogen-activated protein kinases MPK3 and MPK6 act downstream of CLV1 and BAM1 receptors in *Arabidopsis* (Betsuyaku *et al.*, 2011; Lee *et al.*, 2019). Cytosolic secondary messenger  $Ca^{2+}$ , mediated through the cGMP-activated  $Ca^{2+}$  channel, also functions downstream CLV3-CLV1 ligand-receptor system in *Arabidopsis* (Chou *et al.*, 2016). In maize, however, the role of the G-protein subunit became evident in signal transduction. An  $\alpha$ -subunit ( $G\alpha$ ) of heterotrimeric GTP binding protein, COMPACT PLANT2 (CT2), interacts with CLV1 homolog, FASCIATED EAR2 (FEA2) in maize (Bommert *et al.*, 2013a). Soon afterwards, the role of the G-protein subunit in CLAVATA signalling unravelled in *Arabidopsis*. The  $G\beta$  subunit of heterotrimeric GTP-binding protein, AGB1, interacts with the RPK2 receptor in *Arabidopsis* to mediate the signal (Ishida *et al.*, 2014, 2016). Similarly, ZmGB1, the  $G\beta$  subunit of heterotrimeric GTP binding protein, works with CT2 downstream of the FEA2 receptor in maize (Wu *et al.*, 2020b). Thus, three different signalling cascades are reported to amplify the signal received from CLV3 to date. Three protein phosphatases, POLTERGEIST (POL), PLL1 and KINASE-ASSOCIATED PROTEIN PHOSPHATASE (KAPP), regulate the CLV1-mediated signalling pathway (Song *et al.*, 2006; Zhao *et al.*, 2011). We have very little understanding of the entities targeted by these signalling cascades. The ultimate target of the CLAVATA signalling pathway is transcriptional regulation of the WUS transcription factor. WUS is the homeobox transcription factor of the WUSCHEL RELATED HOMEBOX (WOX) transcription factor family, which maintains the SAM stem cell population. The CLAVATA signalling pathway represses the transcription of *WUS* to initiate the differentiation of cells, thus maintaining the size of SAM. Interestingly, WUS positively regulates *CLV3* expression by binding to its promoter region through interaction with SHOOT MERISTEMLESS (STM; Su *et al.*, 2020). This feedback loop maintains the stem cell proliferation and differentiation in the apical region.

The meristematic cell population is also regulated by the *SPL* gene, which represses the *WUS* expression via a genetic pathway independent of CLAVATA signalling (Fouracre and Poethig, 2019). Whether it is CLV-WUS or the SPL-WUS pathway, the biological significance of meristematic size regulation is immense. The balance between meristematic cell proliferation and differentiation can be tinkered to achieve the desired effect on crop phenotype. Fine-tuning this regulatory pathway's components holds the key to enhance yield potential through shoot architecture manipulation in crops.

#### Flowering time, floral organ number and fruit size in crops

The CLAVATA signalling pathway involving CLV and WUS primarily determines the fate of meristematic cells in both root and shoot systems. The role of this signalling pathway in root architecture will be a topic for another discussion. Instead, let us focus on the shoot architecture and yield-contributing traits influenced by CLAVATA genes. Natural alleles of the signalling pathway enhance fruit size, tillering and yield in several crops. CLV3 homologs regulate agronomic traits in rice, maize, *Brassica*, tomato, soya bean and chickpea (Basu *et al.*, 2019a; Chu *et al.*, 2006; Fan *et al.*, 2014; Je *et al.*, 2018; Suzaki *et al.*, 2006; Wong *et al.*, 2013; Xu *et al.*, 2015; Figure 2). Similar to the ligand peptide, homologs of CLAVATA signalling receptors have also been identified in crops like rice, maize and tomato (Bommert *et al.*, 2005; Je *et al.*, 2016;



**Figure 1** The regulation of meristem fate, plant height, tillering, branch angle and floral fate in plants. The CLAVATA signalling pathway maintains the meristematic cell population in the shoot apical meristem (SAM) through a feedback loop between CLV3 and WUS. The cell proliferation and differentiation regulation through this module determines the meristem fate in plants. The gibberellin (GA) signalling pathway regulates plant height and tillering through degradation of DELLA and NGR5 through GA-GID1 complex. DELLA competes with NGR5 for GA-GID1 complex binding, thus stabilizing the NGR5 protein. The gravitropic and phototropic stimuli are perceived by LAZY1-TAC1 module to determine the branch/tiller angle in plant. LAZY1 acts in an auxin-dependent pathway to promote narrow branch angle. The mode of action of TAC1 is not yet clear but it promotes wide branch angle. The link integrating LAZY1 and TAC1 pathway can throw some light on the intricacies of branch angle regulation in crops. The floral fate is determined by the tug-of-war between florigen (FT) and antiflorigen (TFL1). Both florigen and antiflorigen are mobile in nature and movement of FT from leaves to SAM in response to photoperiodic signals initiates flowering in plants. TFL1 and FT both form complex with FD to regulate the expression and activity of pioneer transcription factor LEAFY. LEAFY up-regulates the expression of flowering-related genes such as AP1. TFL1 maintains the vegetative state of meristem in its expression domain by inhibiting expression of flowering-related genes. Thus, it plays a key role in maintaining the indeterminate nature of inflorescence. Abbreviations: CLV3—CLAVATA3; WUS—WUSCHEL; TAC1—TILLER ANGLE CONTROL1; GI—GIGANTEA; CO—CONSTANS; FT—FLOWERING LOCUS T; TFL1—TERMINAL FLOWER 1; AP1—APETALA1; LMI2—LATE MERISTEM IDENTITY2; GID1—GIBBERELLIN INSENSITIVE DWARF1; NITROGEN-MEDIATED TILLER GROWTH RESPONSE 5.

Suzaki *et al.*, 2004, 2006; Taguchi-Shiobara *et al.*, 2001; Xu *et al.*, 2015). *Loss-of-function* mutations in *OsWUS* lead to low tillering in rice (Xia *et al.*, 2020). Auxin response is enhanced in this mutant resulting in a more significant apical dominance effect. Interestingly, this gene is not involved in stem cell proliferation and subsequent meristem maintenance in rice (Suzuki *et al.*, 2019a). Instead, it is maintained by the coordinate function of ABERRANT SPIKELET AND PANICLE1 (ASP1) and FLORAL ORGAN NUMBER2 (FON2; Suzuki *et al.*, 2019b). The *CaWUS* gene expression also regulates plant width in chickpea, where larger meristem size correlates with larger plant width (Narnoliya *et al.*, 2019). In tomato, allelic variants of *WUS* and *CLV* homologs control locule number and fruit size (Chu *et al.*, 2019; Muños *et al.*, 2011). Variations in *FEA2* locus increased inflorescence meristem size and kernel row number in maize and thus, have huge potential in yield enhancement

(Bommert *et al.*, 2013b). Similarly, weak alleles of *FASCIATED EAR3 (FEA3)* enhanced yield-related traits in maize (Je *et al.*, 2016). The *THICK TASSEL DWARF1 (TD1)* gene variation has been associated with ear-related trait regulation in maize (Liu *et al.*, 2019a). A *CsCLV3* gene variant regulates carpel number in cucumber (Li *et al.*, 2016). In the *Brassica* family, silique locule number is an important parameter for yield, and mutations in *clv* homologs have multilocular silique phenotype (Xu *et al.*, 2021; Yang *et al.*, 2018). The role of meristem size is also well established in the regulation of flowering time in maize and chickpea (Basu *et al.*, 2019a; Leiboff *et al.*, 2015). The CLV signalling is recently identified as a genetic novelty that helped the land plants to attain three-dimensional organ structures (Whitewoods *et al.*, 2018). The CLV signalling pathway orients the gametophore cell division plane in *Physcomitrella* to regulate its transition from 2D to 3D

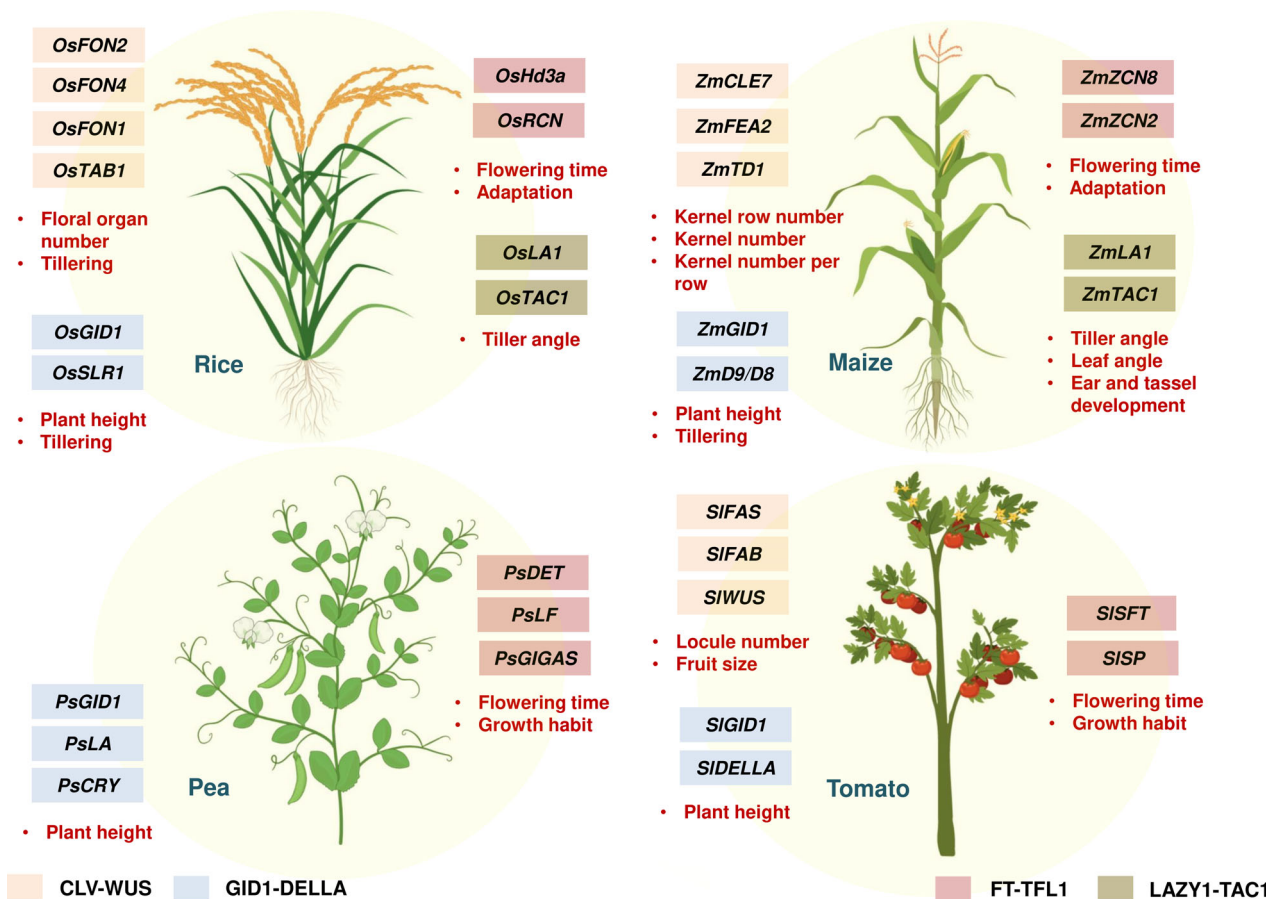
development. Thus, the effect of the CLV-WUS pathway on overall plant architecture is tremendous, so is its potential in agronomic trait regulation.

### GID1-DELLA: the Green revolution impact on plant height and lateral branching

#### The semi-dwarf varieties of the Green revolution resulted from altered GA signalling

The Green revolution resulted in a breakthrough in crop production by introducing high-yielding, semi-dwarf cultivars in rice and wheat in the 1960s and 1970s (Peng *et al.*, 1999; Spielmeier *et al.*, 2002). The semi-dwarf varieties were also resistant to lodging, adding to its yield advantage. The genes responsible for the Green revolution were identified as *Reduced height-1 (Rht-1)* in wheat and *Semi-dwarf1 (SD1)* in rice. The two dwarfing alleles in wheat, *Rht-B1* and *Rht-D1*, are homologs of maize *dwarf-8 (d8)* encoding the *Gibberellin Insensitive (GAI)* gene (Peng *et al.*, 1999; Jobson *et al.*, 2019). The *SD1* locus in rice corresponds to the *GA 20-oxidase gene (Os20ox2)* gene in rice (Spielmeier *et al.*, 2002).

The GA signalling pathway regulates plant height in plants through the GA receptor GIBBERELLIN INSENSITIVE DWARF1 (GID1) and DELLA module. The role of GAs in stem growth was first identified in the study of Banaea (foolish seedling) disease in rice. The fungal pathogen produces GAs that cause excessive elongation of the infected rice plants (Takahashi *et al.*, 1991). GA biosynthesis starts with precursor geranylgeranyl diphosphate (GGDP). Three types of enzymes, terpene synthase (TPS), P450 mono-oxygenases (P450s) and 2-oxoglutarate dependent dioxygenases (2ODDs), catalyse the precursor to bioactive GA (Chen *et al.*, 2014; Fu *et al.*, 2016; Itoh *et al.*, 2004; Spielmeier *et al.*, 2002). The bioactive GA is recognized by GA receptor GID1. In *Arabidopsis*, three orthologs of *GID1*, *AtGID1A*, *AtGID1B* and *AtGID1C*, show partial functional redundancy (Nakajima *et al.*, 2006). Upon GA binding, the GA-GID1 complex initiates degradation of DELLA proteins (RGA, GAI, RGA-LIKE1 (RGL1), RGL2 and RGL3), which are master repressors in plant system (Tyler *et al.*, 2004). DELLA proteins characterized by the presence of a conserved aspartate-glutamate-leucine-leucine-alanine motif belong to the GRAS (GAI, RGA and SCARECROW) family of nuclear proteins with transcriptional regulatory function (Tian



**Figure 2** Developmental regulators characterized in four major crops, two monocots, rice and maize, and two dicots, pea and tomato. Genes belonging to three developmental pathways CLV-WUS, GID1-DELLA, TFL1-FT and LAZY1-TAC1 are highlighted and the agronomic traits they influence are mentioned below the genes. Abbreviations: FLORAL ORGAN NUMBER 4 (FON4), FLORAL ORGAN NUMBER 2 (FON2), FLORAL ORGAN NUMBER 1 (FON1), TILLER ABSENT 1 (TAB1), HEADING DATE 3A (HD3A), RICE CENTRORADIALIS (RCN), GIBBERELLIN INSENSITIVE DWARF1 (GID1), SLENDER RICE1 (SLR1), DWARF8/9 (D8/D9), LAZY1 (LA1), TILLER ANGLE CONTROL 1 (TAC1), FASCIATED EAR (FEA2), THICK TASSEL DWARF1 (TD1), ZEA CENTRORADIALIS (ZCN), DETERMINATE (DET), LATE FLOWERING (LF), FASCIATED (FAS), FASCIATED AND BRANCHED (FAB), WUSCHEL (WUS), SINGLE FLOWER TRUSS (SFT), SELP PRUNNING (SP). The images of the crops are created with Biorender.com.



*et al.*, 2004). Degradation of DELLA proteins occur via a stable complex formation of GA-GID1-DELLA which is recognized by the F-box protein SLEEPY1 (SLY1) in *Arabidopsis*. DELLA is thereafter recruited to the SCF ubiquitin E3 ligase complex for poly-ubiquitination and degraded by the 26S proteasome (Dill *et al.*, 2004). DELLA proteins interact with several transcription regulators to modulate various aspects of plant growth. In rice, the DELLA homolog *Slender rice 1 (SLR1)* is under the regulation of F-box protein GIBBERELLIN INSENSITIVE DWARF2 (GID2) and mutation in any of these genes causes dwarfism (Ikeda *et al.*, 2001; Sasaki *et al.*, 2003). GA signalling repressor such as OsWRKY36 can protect SLR1 from GA-mediated degradation (Lan *et al.*, 2020). Two homologs of *SLR* genes, *SLR1-LIKE (OsSLRL)* genes, are observed in rice genome that lack the DELLA domain and are GA-resistant. The GA-resistant SLR1 protein may be crucial to sustain the growth inhibition during submergence conditions because reduced GA responses increase GA levels and hence promote SLR1 degradation. The GA-dependent plant height regulation involves a crosstalk between several hormonal signalling pathways such as auxin, brassinosteroid (BR), ethylene and strigolactone. GA catabolic genes *GA20ox* and *GA2ox* promote the transcription of several auxin response factor (ARF) and auxin/indole-3-acetic acid (Aux/IAA) family members (Frigerio *et al.*, 2006). DELLA proteins repress BRASSINAZOLE RESISTANT1 (BZR1) binding to the promoters of target BR-responsive genes (Gallego-Bartolomé *et al.*, 2012). Similarly in rice, BR-mediated growth responses are regulated by GA homeostasis; BR promotes expression of GA biosynthetic gene *OsGA3ox* but excess BR promotes GA catabolism (Tong *et al.*, 2014). In rice during prolonged submergence, ethylene-responsive factor family genes down-regulate the expression of GA biosynthetic gene *OsCPS2* and up-regulate GA catabolic gene *OsGA2ox* expression to suppress internode elongation and restrict plant height (Jung *et al.*, 2010; Qi *et al.*, 2011).

GA signalling pathway mutants have been identified in several crops resulting in dwarf phenotype. Allelic variant of *SIGID1a* gene regulates plant height in tomato. Semi-dominant dwarf allele of *SLR1*, *Slr1-d6*, reduces plant height by 37 per cent and increases yield by 25 per cent (Wu *et al.*, 2018). Semi-dominant dwarf alleles of *OsSLR1* are also created through CRISPR/Cas9 system in rice (Jung *et al.*, 2020). The enzymes working upstream and downstream GID1-DELLA module are also well known for their role in plant height regulation. Maize dwarf mutants, *anther ear1 (an1)* and *dwarf5 (d5)*, have mutations in TPS enzymes involved in GA biosynthesis (Bensen *et al.*, 1995; Fu *et al.*, 2016). Dwarf phenotypes of *dwarf3 (d3)* and *dwarf35 (d35)* mutants attribute to defects in P450 mono-oxygenases (P450s)-mediated steps of GA biosynthesis in maize and rice (Itoh *et al.*, 2004; Winkler and Helentjaris, 1995). Mutations in *GA3ox* genes belonging to the 2ODDs enzyme of GA biosynthesis, maize *Dwarf1 (D1)* from maize, and rice *Dwarf18 (D18)* are also characterized with dwarf phenotype (Chen *et al.*, 2014; Itoh *et al.*, 2001). In maize GA pathway-related genes, *ZmGA3ox2* and *ZmGA2ox* have been identified to regulate plant height through QTL mapping approach (Wang *et al.*, 2016).

### Nitrogen and GA signalling regulates tillering in crops

The Green revolution's semi-dwarf cultivars when subjected to increased nitrogen fertilizer usage led to highly enhanced yield. For quite some time, it was realized that these semi-dwarf varieties were highly dependent on the fertilizer usage for their productivity. The *sd1* mutants are very sensitive to nitrogen and

exhibit increased tillering with increase in nitrogen uptake. The nitrogen-mediated increase in tillering is credited to NITROGEN-MEDIATED TILLER GROWTH RESPONSE 5 (NGR5) transcription factor which recruits polycomb repressive complex 2 (PRC2) to repress branching-inhibitory genes via H3K27me3 modification (Wu *et al.*, 2020a). With increase in fertile tillers, the yield increases. The *ngr5* mutants shows an up-regulation of *D14 (Dwarf14)* and *SPL14*, which are inhibitors of tillering. NGR5 is a target for GA-GID1 complex, which similar to DELLA is targeted for proteasome degradation pathway. DELLA proteins competitively act with NGR5 for the GA-GID1 complex formation. Thus, DELLA stabilizes NGR5 for nitrogen-mediated tillering in rice. A total of five haplotypes have been identified till date in rice, and HAP 2 introgressed NILs showed higher yield even under low nitrogen conditions (Wu *et al.*, 2020a). Thus, it has tremendous potential for decreasing the nitrogen fertilizer dependency of Green revolution varieties for higher yield. The NGR5, earlier known as SMALL ORGAN SIZE1 (SMOS1) and REDUCED LEAF ANGLE1 (RLA1) is known to interact with auxin and BR signalling in rice (Hirano *et al.*, 2017). NGR5 is a positive regulator in the BR signalling pathway and enhance transcriptional activity of BRASSINAZOLE-RESISTANT1 (OsBZR1; Qiao *et al.*, 2017). NGR5 also targets OsPHI-1, which is involved in cell expansion (Aya *et al.*, 2014). Among the genes highly up-regulated in *sd1* mutant was a rice growth regulator *GROWTH REGULATING FACTOR 4 (OsGRF4; Li et al., 2018)*. OsGRF4 positively regulates the expression of various nitrogen-metabolism genes and interacts with repressor of GA signalling pathway. Allelic variation in *OsGRF4* enhances yield and nitrogen use efficiency through coordinating carbon and nitrogen metabolic regulation. Thus, both GRF4 and NGR5 act in GA signalling pathway to mediate nitrogen-dependent tillering and yield enhancement. The rice DELLA protein OsSLR1 also positively regulates tillering by protecting degradation of rice tiller number regulator MONOCULM 1 (MOC1; Liao *et al.*, 2019).

The significance of GID1-DELLA module in regulating several agronomic traits in crops has been reported. This highly conserved module functions in both monocot and dicot alike. The implications of this pathway are in not only restructuring plant but also minimizing the fertilizer usage in crop. This pathway has immense potential in attaining sustainable agriculture, which is the need of the time.

### LAZY1-TAC1: modulating plant branch growth angle, a major plant architectural trait

#### LAZY1 alters local auxin gradient to modify branch angle

Most of the crops today are either erect or semi-erect such as rice, chickpea (Tan *et al.*, 2008; Upadhyaya *et al.*, 2017). It is an improvement over their wild relatives with mostly prostrate or highly branched spreading growth habits (Richards *et al.*, 2019; Singh *et al.*, 2019; Tan *et al.*, 2008). The spreading growth habit will require more space for proper growth and development, which may not benefit the crop's yield per hectare. The growth habit of a plant is the reflection of its branch angle. Plant branch growth angle is both static and plastic. The gravitropic setpoint angle is the predetermined angle a branch makes with respect to gravity independent of any other organ (Roychoudhry and Kepinski, 2015). However, another aspect of the growth angle is that it is flexible and responds to both gravitropic and phototropic stimuli. Members of the IGT/LAZY gene family

mediate the phototropic and gravitropic responses regulating the branch angle. *LZY1* (*LZY1*) and related genes like *LZY2* and *LZY4* perceive the gravitropic signals to alter the local auxin gradient (Hill and Hollender, 2019; Nakamura *et al.*, 2019; Taniguchi *et al.*, 2017). This asymmetric auxin localization induces two WUSCHEL-related homeobox domain genes *WOX6* and *WOX11*, ultimately affecting the branch/tiller angle (Zhang *et al.*, 2018a). Transcriptome data suggest the role of *LZY1* in the regulation of auxin-related gene expressions such as auxin transporter and signalling factors (Zhu *et al.*, 2020b). The maize *ZmLA1* is transcriptionally activated in response to auxin and repressed by light signalling (Dong *et al.*, 2013). *ZmLA1* regulates both ear and tassel development through interaction with a putative kinase and auxin response protein IAA17 in plasma membrane and nucleus, respectively (Dong *et al.*, 2013). Agravitropic *zmla1* mutants, however, do not exhibit any significant variation in leaf angle. Another maize *LZY1* ortholog *ZmCLA4* controls the leaf angle affecting the cell shape and number at the leaf axil (Zhang *et al.*, 2014). Several regulators acting upstream *LZY1* are known to date in rice. The rice HEAT STRESS TRANSCRIPTION FACTOR 2D (*HSFA2D*) positively regulates the expression of *LZY1* (Zhang *et al.*, 2018a). Two Homeobox-leucine zipper transcription factors, *OsHOX28* and *OsHOX1*, bind to the promoter region of *HSFA2D* to repress its expression transcriptionally, thereby regulating branch/tiller angle in rice (Hu *et al.*, 2020). A separate module of microRNA (miRNA) and auxin response factors also act to repress the *LZY1* activity. *OsmiR167a* target three auxin response factors, *ARF12*, *ARF17* and *ARF25*, to induce the asymmetric auxin localization, independent and dependent of the *LZY1* pathway to affect rice tiller angle (Li *et al.*, 2020). Maintaining the concentration of *LZY1* proteins in the nucleus and plasma membrane of the cell is essential for its function. The nuclear localization of *LZY1* in rice is through physical interaction with *Brevis Radix Like 4* (*OsBRXL4*; Li *et al.*, 2019). Excess of *OsBRXL4* disrupts the balance between the *LZY1* plasma membrane: nucleus ratio and results in a wider growth angle (prostrate growth habit). The functional significance of different protein domains of *Arabidopsis* *LZY1* has been deduced. The *Arabidopsis* *LZY1* comprises five short regions of conserved amino acid sequences. A highly conserved CCL domain in the region V of this protein is essential for its function, and mutation in this region severely disrupts its activity. Two amino acids (L92A/I94A) in the conserved region II of *AtLZY1* are crucial, and their alteration completely changed the plant phenotype (Yoshihara and Spalding, 2020). A 'weeping' inflorescence stem phenotype was observed in those mutants instead of a narrow branch angle. Gravitropism and circumnutation are reported to be strongly correlated in rice (Kobayashi *et al.*, 2019). Rice seedlings lose their circumnutation activity in the microgravity environment, and when subjected back to artificial gravity, wild-type seedlings partially gain back their circumnutation ability. However, in *lzy1* mutants, this ability is never restored. These movements are of great agronomic importance to the twining crops such as grapevines and may also be involved in soil root penetration (Minorsky, 2003). Thus, the *LZY1* mediated gravitropic response affects two important agronomic traits, branch angle and circumnutation, in crop plants.

### TAC1 promotes wider angle in crops and trees

While *LZY1* promotes narrow branch angle in an auxin-dependent manner, another member of IGT family, TILLER ANGLE CONTROL 1 (*TAC1*), promotes wider branch angle in

response to phototropic stimuli (Figure 1). *TAC1* homologs are known in maize, rice, peach and *Miscanthus sinensis* (Dardick *et al.*, 2013; Hollender *et al.*, 2018; Ku *et al.*, 2011; Yu *et al.*, 2007; Zhao *et al.*, 2014). The expression of *TAC1* is influenced by photosynthetic signals and also by light signalling components and receptors. *TAC1* expression is up-regulated under ideal light conditions, possibly through the COP1 signalosome, leading to a wider branch angle for optimal photoreception (Waite and Dardick, 2018). However, during low light or shade conditions, *TAC1* is repressed, and the plant branches are brought closer to the central axis for its upward growth beyond the shade. In peach, the characteristic 'Pillar' or 'Broomy' trait (*br*) phenotype with vertically oriented branches is identified as the result of *loss-of-function* of *TAC1* (Hollender *et al.*, 2018). A sterile alpha motif protein, *WEEP*, highly conserved in vascular plants, causes weeping tree architecture in peach and plum (Hollender *et al.*, 2018). *WEEP* is required for the gravitropic perception and response in these trees. However, the *WEEP* might have adapted to perform a different function in the Brassicaceae family as the *Arabidopsis* *weep* mutant does not exhibit an altered branching phenotype (Hollender *et al.*, 2018). The molecular function and the pathway through which this gene works remain unexplored. The *WEEP* function might be functioning downstream of the *TAC1* pathway to regulate growth responses, as suggested by Hill and Hollender (2019). A direct correlation between auxin signalling and *TAC1* is not yet identified, but studies suggest an integration of both *LZY1* and *TAC1* pathways to maintain the branch angle in an auxin-dependent manner. Light-directed orientation of branch angle through *LZY1* is also reported recently. Both photosynthetic signals and photoreceptors influence the expression of *LZY1* (Waite and Dardick, 2020). The crossover between light and gravitropic signalling is also evident from the modulation of *LZY4* expression in root and hypocotyl of *Arabidopsis* through the accumulation of ELONGATED HYPOCOTYL 5 (*HY5*) and degradation of PHYTOCHROME INTERACTING FACTOR (*PIF*) proteins, respectively (Yang *et al.*, 2020). However, the interaction between the two IGT family genes, *LZY1* and *TAC1*, is not simple, and they are not the direct negative regulator of each other (Hollender *et al.*, 2020). A lot needs to be uncovered about the complexity of this regulation. The thread connecting these two regulators, *LZY1* and *TAC1*, will explain further how the gravitropic and phototropic signals are integrated.

### Branch angle contributing to yield in crops

The branch angle controlled by *LZY1* and *TAC1* affects plant width and thus planting density. Increasing planting density has led to increased yield in several crops such as maize, soya bean and chickpea (Carciochi *et al.*, 2019; Matsuo *et al.*, 2018; Narnoliya *et al.*, 2019). The branch angle is also vital in maintaining tree architecture, where a balance between planting density and shade avoidance needs to be treated with caution. Different groups of plants have different requirements according to their economic use. Farmers will prefer crops with narrow branch angles to accommodate more plants per area, and also, these will be easy to harvest mechanically (Singh *et al.*, 2019). However, too narrow angle could affect the photosynthetic efficiency as well disease susceptibility in crops (Burgess *et al.*, 2017; Wang *et al.*, 2020). One more thing to take into account would be the agricultural practices. Irrigation practices and the application of fertilizers drastically affect the crop architectural parameters. Soil nutrients like nitrogen play a key role in defining

shoot architecture (Luo *et al.*, 2020). While manipulating the branch angle, the stem and branches' mechanical strength should be considered. Wider branch angle and weight of the reproductive organs can lead to instability and breakage during climatic adversity.

The branch angle is one of the crucial traits that need to be explored for modern agriculture. The marginal farmers constitute a major population in developing countries. For them, higher crop yield per hectare, that is productivity, can be achieved by restructuring plant architecture, primarily by increasing plant density (Singh *et al.*, 2019). Achieving higher yield by accommodating more plants per hectare depends on various other aspects that should also be considered.

### TFL1-FT: Floral fate modulation through florigen–antiflorigen determine stem growth habit

#### Floral fate determination through florigen–antiflorigen

Transitioning to the reproductive phase is a crucial decision. The plants need to be sure about investing in reproductive organ development to ensure their progeny's survival. The apical meristem's fate is determined by a complex regulatory network instructing LEAFY (LFY) to initiate flowering. LFY is a key transcription factor that transcriptionally activates a cascade of flowering time and flower development genes (Périlleux *et al.*, 2019). However, two members of the Phosphatidylethanolamine-binding protein (PEBP) family proteins fine-tune the floral fate in plants. The FLOWERING LOCUS T (FT) and the TERMINAL FLOWER1 (TFL1) are the florigen and antiflorigen proteins of the plant kingdom (Lifschitz *et al.*, 2014; Figure 1). Both these proteins exhibit a relatively significant sequence similarity, and substituting a single amino acid (replacing tyrosine at position 85 with histidine) altered the flowering activator function of FT to flowering repressor (Hanzawa *et al.*, 2005). The antagonistic activity here is more apparent as both the florigen and antiflorigen compete with each other for their targets. TFL1 and FT function as mobile transcriptional cofactors in SAM (Goretti *et al.*, 2020). An external loop protruding out of the protein surface defines the florigen and antiflorigen activity of the proteins (Ahn *et al.*, 2006). TFL1 travels within the SAM to form a complex with bZIP transcription factor FD and 14-3-3 proteins to repress flowering-related genes (Zhu *et al.*, 2020c). When the environmental cues favour flowering, the photoperiodic signals are relayed through GIGANTEA and CONSTANS to the FT, which then starts moving from leaf to the SAM (Luccioni *et al.*, 2019). FT is highly expressed in stomata and is involved in the blue light-dependent stomatal opening (Kinoshita *et al.*, 2011). FT activates SOC1 transcription, which in turn activates plasma membrane H<sup>+</sup>-ATPase, AHA5 in guard cells. Similar to TFL1, FT too forms a complex with FD and competes with the TFL1 complex (TFL1-FD-14-3-3) to activate LFY (Figure 1). The importance of LFY in this pathway is now elucidated. LFY is a pioneer transcription factor that can bind to nucleosome allowing its opening and subsequent recruitment of cofactors to facilitate the transcription of downstream flowering genes such as *APETALA1* (*AP1*; Jin *et al.*, 2021). Several direct targets of LFY are identified to date. LFY promotes the expression of *EUI-LIKE P450 A1* (*ELA1*) and *GIBBERELLIN 2-OXIDASE 4* (*GA2ox4*) to inhibit gibberellin accumulation (Yamaguchi *et al.*, 2014). Gibberellin is known to inhibit flower formation. Another target of LFY is a Myb transcription factor LATE MERISTEM IDENTITY2 (LM2), which acts as a cofactor to

LFY during transcriptional activation of flowering genes (Pastore *et al.*, 2011). The ability of LFY to act as a pioneer transcription factor makes its regulation a decisive step towards reproduction phase commitment. In plants with vegetative and reproductive growth cycles, the local level of antiflorigen in vegetative buds suppresses its transition to the flowering stage. The TFL1 and FT genes acquire functional diversity in plants with multiple copies of these genes. Even single-nucleotide alteration in these gene copies can lead to a change in their biological function. Large-scale diversity in terms of allelic variants is observed in crop plants. For example, in sugar beet, two homologs of FT function antagonistically to regulate flowering (Pin *et al.*, 2010). In short-day crops like rice, two different florigens are required for the regulation of flowering. The HEADING DATE 3A (Hd3a) accumulates under short-day conditions, and the other, RICE FLOWERING LOCUS T1 (RFT1), functions under long-day conditions (Komiya *et al.*, 2008). Both these genes form the florigen activating complex with OsFD and 14-3-3 (Brambilla *et al.*, 2017; Taoka *et al.*, 2011). Delayed Heading Date 4 (DHD4), a CONSTANS-like transcription factor, competes with 14-3-3 proteins to interact with OsFD, affecting the complex formation (Cai *et al.*, 2021). Besides, Hd3a also regulates tillering in rice (Tsuji *et al.*, 2015).

The vegetative to reproductive transition and flowering time in crops are important agronomic traits. It drastically affects the crops' ability to cope with stress conditions and maintain yield stability, such as in chickpea (Gaur *et al.*, 2019). Early maturing crops will also be useful in crop rotation as the crops could be harvested on time for the next crop sowing. Thus, understanding the players of the FT-TFL1 module is essential for crop restructuring.

#### Role of florigen–antiflorigen in crop growth habit and adaptation

The florigen and antiflorigen complex involving FT and TFL1 controls the floral fate in crops, affecting their reproductive success. The TFL1 complex targets many other proteins, such as photoperiod signalling components like CCA1 and LHY, and thus play a role in the photoperiod-regulated movement of FT (Goretti *et al.*, 2020). A dominant role of FT over TFL1 is during the reproductive transition, which may be to counterbalance higher levels of TFL1 before flowering. Apart from its role in flowering time, a very interesting phenotype of *tfl1* mutants is the determinate growth habit and clustered flowering. Determinate growth habit is an agriculturally desirable trait selected by breeders for compact plant architecture and higher yield. Identification of a tomato *TFL1* natural gene variant, *self-pruning* (*sp*) mutant, revolutionized its cultivation (Pnueli *et al.*, 1998; Figure 2). Earlier, a short-lived perennial, the modern-day tomato became an annual crop due to the compact and determinate shoot growth habit. Natural variants of TFL1 are favoured not just in tomatoes but also in several crops like soya bean, cotton and strawberries (Koskela *et al.*, 2016; Liu *et al.*, 2010, 2018; Prewitt *et al.*, 2018). One of the first homologs of TFL1 to be characterized is its snapdragon homolog, CENTRORADIALIS (CEN), which, unlike its *Arabidopsis* homolog, does not affect the flowering time (Bradley *et al.*, 1996). It was later assigned as a functional homolog of *Arabidopsis thaliana* CENTRORADIALIS (*ATC*) gene that inhibits floral initiation and is not involved in inflorescence meristem identity regulation (Huang *et al.*, 2012). Among Brassicaceae members, *TFL1* ortholog is characterized in *Brassica napus*, where it negatively regulates flowering time and several other agronomic traits such as branch

number, silique number and plant height (Sriboon *et al.*, 2020). Though paralogs of *FT* and *TFL1* are reported in *B. napus*, they are not functionally redundant (Guo *et al.*, 2014). The *CsTFL1* gene in cucumber regulates flowering time and determinacy through interaction with *CsNOT2a* (Njogu *et al.*, 2020; Wen *et al.*, 2019). Among the legumes, *TFL1* has been reported to control the stem growth habit in pea, soya bean, common bean, mung bean, pigeon pea and cowpea (Dhanasekar and Reddy, 2015; Foucher *et al.*, 2003; Li *et al.*, 2018a; Liu *et al.*, 2010; Repinski *et al.*, 2012; Saxena *et al.*, 2017). The regulation of stem growth habits in legumes is complex due to the involvement of primary and secondary inflorescence meristem. In pea, three homologs of *TFL1* are reported, *PsTFL1a*, *PsTFL1b* and *PsTFL1c*, among these pea *DETERMINATE* (*PsTFL1a*) is the functional homolog of *Arabidopsis TFL1* (Figure 2). It specifies the primary inflorescence meristem identity but does not affect flowering time. The *LATE FLOWERING* (*PsTFL1c*) gene is involved in flowering time regulation. Both these genes work together to regulate stem growth habit in pea (Foucher *et al.*, 2003). Similarly, in soya bean, *GmDt1* and *GmDt2* are involved in meristem determinacy regulation (Liu *et al.*, 2010; Ping *et al.*, 2014). While *GmDt1* is the ortholog of *Arabidopsis TFL1*, *GmDt2* encodes for a MADS-box transcription factor. In barley, the *loss-of-function* of *mat-c* locus (*HvTFL1*) resulted in an early flowering phenotype (Matyszczyk *et al.*, 2020). The cotton *CEN* regulates the determinacy of inflorescence meristem resulting in clustered fruiting and early maturing genotypes (Liu *et al.*, 2018). The *FT* gene in cotton is also characterized. Overexpression of *GhFT* in tobacco alters the flowering time along with several plant architecture parameters (Li *et al.*, 2015). Similar is the case in sesame (Zhang *et al.*, 2018b). Four homologs of *TFL1* have been reported in apple, *MdTFL1-1* (*MdTFL1*), *MdTFL1-2* (*MdTFL1a*), *MdCENa* and *MdCENb* (Mimida *et al.*, 2009). The *TFL1* genes also play an important role in the heat stress response of apples (Weigl *et al.*, 2015). Four *14-3-3* gene family proteins are identified, which regulate vegetative to reproductive transition through interaction with *MdTFL1* and *MdFT* in apple (Zuo *et al.*, 2021). *EjTFL1* genes (*EjTFL1-1* and *EjTFL1-2*) promote growth but inhibit flower bud differentiation in loquat by integrating photoperiod signals (Jiang *et al.*, 2020). Repression of *TFL1* and induction of *FT* mediates floral induction in pear (Bai *et al.*, 2017). The role of this pathway in the regulation of inflorescence architecture and flowering time is thus well established across vascular plants.

Natural genetic variations in these pathway components also help plants adapt to different climatic conditions. The successful adaptation of flax to northern latitudes is partly due to natural variations in *LuTFL1* gene (Gutaker *et al.*, 2019). Similarly, natural variations of *GmFT2b*, an ortholog of *FT* are associated with adaptation to high-latitude regions in soya bean. *Hap3*, a major *GmFT2b* haplotype, is associated with significantly earlier flowering at higher latitudes (Chen *et al.*, 2020). The florigens in rice act downstream the *CONSTANS* homolog, *Heading date 1* (*Hd1*). *Hd1* interacts with a CCT transcription factor *Grain number, plant height, and heading date 7* (*OsGhd7*) gene to suppress florigen gene expression (Nemoto *et al.*, 2016; Zhang *et al.*, 2017). The natural alleles of *Hd1* are associated with the adaptation of temperate *japonica* rice plants to the tropical region (Kim *et al.*, 2018). Homologs of rice *OsGhd7* in maize are *ZmCCT9* and *ZmCCT10*. Harbinger-like transposon acts as a *cis*-regulatory element to repress *ZmCCT9* expression in higher latitudes (long-day condition) to promote flowering. These transposon-derived variations helped maize conquer a more comprehensive latitude

range by manipulating florigens (Huang *et al.*, 2017). Thus, regulators acting upstream the florigen signalling also show great potential from a breeding perspective. The allelic variant of *LuTFL1* prevalent in northern latitude resulted in better fibre production over oil, longer stems, smaller seeds and fewer axillary branches. Interestingly, the alteration in *FT* genes in common ragweed is credited to its successful invasion in North European region due to early flowering and maturing phenotype (Kralemann *et al.*, 2018). The *TFL1* is also reported to be involved in the regulation of tuber formation in potato, maintaining juvenility in citrus and determining axillary meristem identity in ryegrass (Guo *et al.*, 2010; Jensen *et al.*, 2001; Pillitteri *et al.*, 2004). The vernalization gene *VRN3* is also a homolog of the *FT* gene in wheat and barley (Yan *et al.*, 2006). Insertion of a retrotransposon in wheat *FT* gene promoter led to the early flowering phenotype in wheat. Thus, the *TFL1-FT* pathway is involved in varied aspects of plant growth and development.

The determinate growth type is full of potential in terms of yield due to restricted vegetative growth (Hegde, 2011). The photosynthates could now be devoted to the crops' reproductive growth and, thus, enhanced yield. The restricted vegetative growth also helped the crop with lodging problems. The *loss-of-function* alleles of *TFL1* can lead to early-flowering and maturing genotypes with restricted vegetative growth and higher yield. Hybrid varieties of tomato with alteration in florigen-antiflorigen levels have dramatically increased yield due to optimization of plant architecture (Jiang *et al.*, 2013). These features make this gene and its regulatory network a gold mine for shoot architecture alteration and adaptation to different ecological niches without compromising yield.

## Developmental regulators: Steps towards the 'ideal' plant architecture

### Step 1: Delineation of superior allelic variants for key developmental genes regulating plant architectural traits

The role of plant architecture in domestication and yield enhancement of crops is well recognized. The term ideal plant architecture will have a different meaning for different plant groups. For the green leafy vegetables, seed size is not a concern; instead, it is the vegetative foliage that's of economic use. The determinate plant types with restricted vegetative growth will not be desirable there. Alteration in plant architecture has shaped the major crops as we know them today. In cereals such as rice, wheat and maize, the tillering as well as leaf and tiller angle play a vital role in optimizing their yield. Erect shoot architecture enhances yield in these crops by influencing light perception and CO<sub>2</sub> uptake into the canopy (Burgess *et al.*, 2017; Richards *et al.*, 2019; Song *et al.*, 2013). Too wide or too narrow angle affects the photosynthesis efficiency, disease susceptibility and yield in these crops (Abichou *et al.*, 2019; Ku *et al.*, 2010; Wang *et al.*, 2020). Determinate inflorescence in cucumber and legumes has helped us to cope with excess vegetative growth and facilitate mechanical harvesting (Hegde, 2011; Wen *et al.*, 2019). Whatever be the ideal parameters, it is time to speed up the breeding process. The pathways affecting these architecture contributing traits are slowly unravelling. The natural variants of the developmental pathway genes are unfortunately not yet fully explored. The meristem fate, plant height, branching, branch angle and floral fate in crops are crucial in determining its shoot architecture. The *CLV-WUS*, *GID1-DELLA LAZY1-TAC1* and *TFL1-*



FT modules play key roles in the regulation of these traits. Transient gene expression changes can be used to study these genes' effects in different ecosystems through viral transfection technology. Developmental events can be altered to regulate flowering time, vernalization requirement or plant height as per real-time weather monitoring in monocots and dicots transiently (Torti *et al.*, 2021). If the system works for a particular climatic condition, efforts to incorporate the changes in the genome will be more fruitful. For example, altering FT expression in *Arabidopsis*, tomato, wheat and tobacco altered the flowering time; however, genes acting upstream or downstream of this cascade did not have the same effect (Torti *et al.*, 2021). Thus, this cost-effective large-scale screening system could help us target the best candidate for trait regulation. Large-scale mining of these candidates' allelic variants across crop germplasm can shed some light on their role diversification.

Identification of allelic variants of a gene of interest involves large-scale genotyping of germplasm resources. Modern age genomics-assisted breeding strategies are slowly and steadily replacing traditional breeding approaches. The cost of genotyping natural accessions and mapping/mapping populations through sequencing gets halved every 5 years. The availability of the sequenced genome has revolutionized the way we think about crop improvement. This is the era of pan-genomes where novel genomic sequences in wild and cultivated gene pools of a crop can be decoded (Hirsch *et al.*, 2014; Liu *et al.*, 2020b; Zhao *et al.*, 2018; Zhou *et al.*, 2020). With advances in technologies platinum quality genome assemblies are now available for number of crops (Mussurova *et al.*, 2020). Multiple reference genomes and platinum standard pan-genomes are the solutions for the cultivar-specific variations, either acquired or discarded during evolution (Zhou *et al.*, 2020). This sequence information can be efficiently utilized for association mapping and identifying regions of selective sweep in major crops with complex trait phenotype. The quantitative trait loci (QTL) mapping approaches using mapping/mutant population have been stretched to other arenas evolving expression QTL (eQTL), protein QTL (pQTL), metabolome QTL (mQTL) and MutMap strategies (Peng *et al.*, 2019; Suhre *et al.*, 2020; Szymański *et al.*, 2020). Thus, providing a holistic viewpoint to the marker's yield potential. The declining sequencing cost and ease of handling big data have enabled researchers to delineate trait-linked molecular tags at a genome-wide level in number of crops (Basu *et al.*, 2019a, 2019b; Jia *et al.*, 2020; Lu *et al.*, 2020; Narnoliya *et al.*, 2019; Shin *et al.*, 2020; Zhang *et al.*, 2019; Zhao *et al.*, 2019b). The sequence information can be utilized to map the variations in key regulators of crucial developmental pathways. Genomic resources in form of transcriptome data, metabolomics data and proteomics data can also help in identifying gene regulatory hubs and major players involved in trait regulation. The best approach for scanning large germplasm set would be constructing a core/minicore collection representing the phenotypic and genotypic diversity within the germplasm resource. A smaller set of core/minicore collection accessions will be easy to phenotype and genotype (Kumar *et al.*, 2020; Upadhyaya *et al.*, 2019). Mining out novel genetic variants in the wild germplasm and landraces has been an excellent strategy for identifying development and architecture-related allelic variants that generally get lost during domestication (Imam *et al.*, 2016; Mishra *et al.*, 2016). Precise phenotyping in control and field conditions and rapid, cost-effective genotyping using fluorescence-, array- and sequencing-based techniques are key to delineate trait-regulating allelic variants. Phenotyping large-scale

crops in the field have been the limiting point for many years. However, things are changing with advances in artificial intelligence. Phenotyping using robotics platforms and drone-based imagery minimizes the effort required to phenotype plant architectural parameters in large-scale populations (Zhao *et al.*, 2019a). The availability of low-cost, unmanned aerial vehicles (UAV) has accelerated canopy phenotyping in the number of crops and trees (De Swaef *et al.*, 2021; Gómez-Gálvez *et al.*, 2021). High-throughput phenotyping of a training population can help predict phenotype of test population through prediction models (Akdemir and Isidro-Sánchez, 2019; Eeuwijk *et al.*, 2019). Algorithms extract key features from the training population to create a suitable model based on which phenotype of test populations can be predicted. The genetic landscape of developmental regulators within germplasm when integrated with precise phenotyping data helps us delineate the superior allelic variant of that gene. Approaches such as the association mapping and quantitative trait locus (QTL) mapping can be efficiently utilized to check the potential of mined allelic variants in regulating agronomic traits such as branch angle, flowering time, stem growth habit, fruit size and so on, thus, providing a holistic viewpoint of the variant's yield potential.

## Step 2: Translational genomics approaches for crop customization

The superior allelic variants of genes (CLV1-WUS, GID1-DELLA, LAZY1-TAC1 and FT-TFL1) modulating traits like meristem fate, plant height, branching, branch angle and floral fate, screened from the crop germplasm can improve the commercially popular cultivars of crop plants. Once the superior allele is identified, there are two basic approaches for improving crop architecture. In this regard, the widely accepted approach is genomics-assisted breeding to introduce traits of interest from a donor to commercial cultivars. The popularity of marker-assisted selection, genomics-assisted breeding is shooting up, and gene pyramiding to introduce multiple beneficial traits has facilitated crop improvement programmes (Fuchs, 2017; Liu *et al.*, 2020a). Our goal should be selecting gene variants with negligible pleiotropic/epistatic effects but improving overall agronomic performance. Till date, the genomics-assisted breeding approach has been majorly utilized in biotic and abiotic stress tolerance enhancement in cereals, legumes such as rice, wheat, barley, soya bean, chickpea and groundnuts (<https://www.icrisat.org/genomics-assisted-breeding-2-0-for-sustainable-agriculture/>). Genomics-assisted breeding efforts in chickpea have resulted in drought-resistant and fusarium wilt resistance cultivars (Roorkiwal *et al.*, 2020). Several other success stories of improved cereals and legumes have been summarized by Varshney *et al.* (2021). Gene pyramiding in rice has developed superior rice cultivars resistant to bacterial blight, blast and sheath blight diseases (Jamaluddin *et al.*, 2020; Ramalingam *et al.*, 2020). Similar efforts are required for the optimization of plant architecture in crops. The concept of genomic selection has also been proven beneficial in enhancing genetic gains from complex traits using alleles with both major and minor effects on trait phenotype (dos Santos *et al.*, 2016; Spindel *et al.*, 2015). Thus, the same approach can be utilized for maintaining yield stability through plant architectural trait manipulation. Digitization of agriculture is essential for designing crops suitable to different niches.

Another potential approach for crop improvement is the genome-editing strategy. Among the different genome-editing approaches, the CRISPR/Cas system gained high popularity and

acceptance due to the ease of targeting the genome and various applications in plant breeding (Zhu *et al.*, 2020a). Genome-editing strategies reduce the timespan to generate an elite cultivar from 8–12 years to just 4–6 years (Chen *et al.*, 2019). The amalgamation of genome-editing technology with genomics and molecular genetics and breeding approaches can efficiently target the regulatory modules affecting plant architecture. A beautiful example of the same is the development of compact high-yielding tomato cultivar suitable for urban agriculture (Kwon *et al.*, 2020). The stacking of three gene variants, *ERECTA* for stem length, *SP5G* for rapid flowering, and *SP (TFL1)* for determinacy and growth termination, have customized tomato cultivar through CRISPR/Cas technology. The developed tomato cultivar has the ideal architecture for crop systems in a low land resource urban arena. Thus, gene pyramiding has been a strategy used in both breeding and genome editing for crop improvement. The use of CRISPR-based targeted editing of multiple genes, including *SP*, *CLV3* in Solanaceae, has resulted in *de novo* domestication and improved yield in wild tomato *Solanum pimpinellifolium* and orphan crop groundcherry (*Physalis pruinosa*; Lemmon *et al.*, 2018; Li *et al.*, 2018c).

Minimizing the time to develop a new and improved restructured plant type is important in any crop improvement programme. The CRISPR/Cas system, when integrated into haploid-induced population, results in commercially ready elite cultivars in sweetcorn and maize (Kelliher *et al.*, 2019). This technology, termed as the HI Edit system, can produce edited haploid plants that lack editing machinery and parental DNA (Kelliher *et al.*, 2019). The haploid induction eliminates the six generations of self-pollination to produce inbred lines. Another strategy to minimize the advancement of generation timespan in both the translation approaches is the speed breeding (Jähne *et al.*, 2020; Watson *et al.*, 2018). Five generations of crops can be advanced in a single year through speed breeding, which is beneficial for both agriculture and research purposes. Developing elite cultivars suitable for a specific ecological niche is the way forward towards ensuring food and nutritional security to the ever-increasing global population (Figure 3). We have the technologies for tailor-made customized crops; we need to identify targets to fine-tune the trait phenotype.

One must understand that while discussing crops, the yield is also dependent on the agricultural practices. Soil nutrient profile, water content and the utilization of fertilizers and pesticides drastically affect crop yield. Along with restructuring the crop architecture, good agricultural practices are crucial. Modernization of agricultural practices through advanced satellite imagery and remote sensing-based information on environmental conditions such as soil moisture and nutrient properties, temperature variations during flowering and seed filling stages, and rainfall and storm updates can minimize yield loss in major crops globally (Adams *et al.*, 2021; De Swaef *et al.*, 2021; Pineda *et al.*, 2021). Artificial intelligence could be efficiently utilized to predict yield in crops and even minimize use of fertilizers according to soil nutrient profile.

The plants have evolved intricately acting protein systems to bring about phenotype changes in quantitative terms instead of an on and off switch (Figure 1). This tried-and-tested protein network holds the solution to our 'ideal plant architecture' problem. Altering the upstream and downstream regulatory elements of these key regulator genes can introduce novel allelic variants and haplotypes in a cropping system. The genetic profile of the available natural germplasm and gene-edited lines needs to

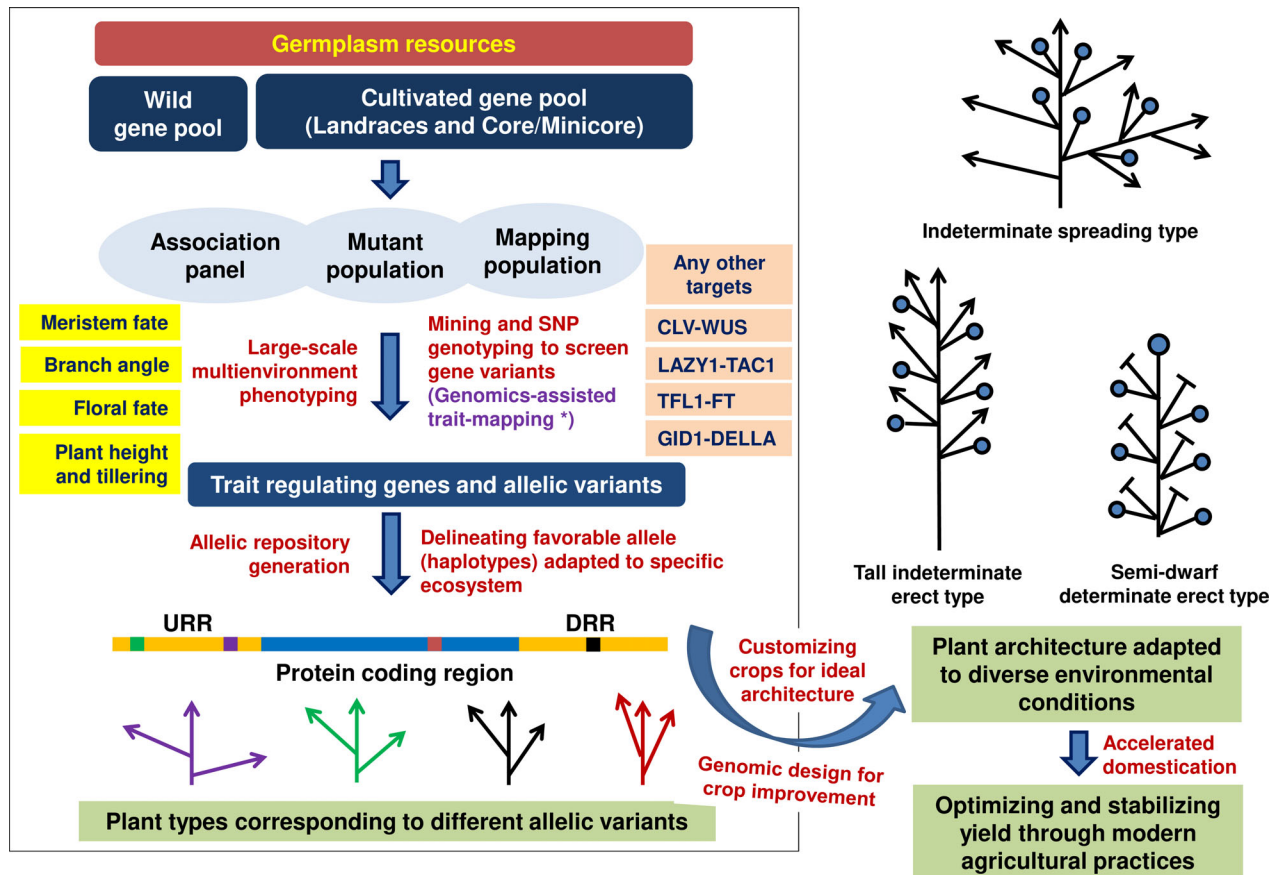
be available for the breeders and researchers involved in crop improvement programmes. A complete resource of genetic markers including the ones altering gene phenotype and the ones defining the genetic background of high-yielding commercial lines can be efficiently used for gene pyramiding. These efforts should be at national and international levels for each of the commercially important crops. This allele repository will help define the plant architecture suitable for a specific environment. A very good example in this regard has been in case of the Green Super Rice (GSR) varieties in Africa and Asia (Yu *et al.*, 2020). Multiple steps of gene regulation in plants hold the key to precise trait manipulation.

## Concluding remarks

Breeders worldwide have tried to identify genetic variants providing the desired phenotype in every genetic background and every environmental niche. The quantitative nature of trait regulation and multiple functions of candidate genes make this effort relatively futile. There are quite a few successes in resistance breeding imparting stress tolerance to crop plants; however, such efforts in restructuring plant architecture are scarce (Basu *et al.*, 2019a; Narnoliya *et al.*, 2019; Wu *et al.*, 2020a; Zhang *et al.*, 2018b; Zhu *et al.*, 2019). Ever-changing climatic conditions and the adversities the plant faces can be minimized if the domestication and architectural traits are focused. The Green revolution gene-introgressed rice and wheat cultivars are highly dependent on nitrogen-based fertilizers for optimum yield. Nitrogen affects plant architecture through the modulation of hormonal signalling (Luo *et al.*, 2020). Nitrogen influences the floral fate as it alters the timing of vegetative to reproductive stage transition in crops. The influence on floral fate affects cereal crop architecture, panicle structure and grain yield. Nitrogen is also known to impact the shoot branching in crops. However, restricted use of fertilizers is necessary for agriculture sustainability. Increasing the nitrogen-use efficiency in crops is one of the ways to tackle this problem. Soil nutrient and moisture are among the major contributors to plant architecture variation within a crop. They influence meristem fate and branching through the modulation of plant signalling pathways. Thus, while trying to optimize the crop canopy, one must always consider these factors.

The plant architecture should be optimized not just for higher yield but also for yield stability. Winter crops often face rising temperatures during their reproductive stages leading to yield loss in tropical countries. Manipulating the floral fate will help in developing early maturing cultivars in those crops. Another potential yield loss segment is during harvesting. Mechanical harvesting is always preferred in crops like chickpea to reduce harvest costs and accelerate harvesting (Roorkiwal *et al.*, 2020). Erect plant types are amenable to mechanical harvesting and thus are preferred among the crops. Erect plant types can also be accommodated in more numbers than spreading plant types. Thus, there is an added advantage of branch angle manipulation in ensuring yield stability.

Plants have adapted to different environments by fine-tuning their response to external cues in a highly regulated manner. The SAM being the repository of stem cells determines the architecture of the shoot system. Both the vegetative tissues such as leaves and branches and reproductive inflorescence arise from this meristem repository. Thus, the 'CLV-WUS' pathway, which determines the fate of these cells, plays a crucial role in specifying



**Figure 3** Diagrammatic representation of developing repository of allelic variants in germplasm and utilizing those resources to accelerate domestication and stabilizing yield in crops. The germplasm resources need to be explored for identification of allelic variants of key developmental regulators modulating plant architectural traits. A high-throughput genotyping and precise phenotyping is essential to evaluate trait-influencing potential of screened genetic/allelic variations in germplasm. Depending upon the adaptive advantage of the allele phenotype, a superior allele needs to be selected for specific ecosystems. The upstream/downstream regulatory regions (URR/DRR) of these gene modules such as *CLV-WUS*, *GID1-DELLA*, *LAZY1-TAC1* and *TFL1-FT* are the hotspot for quantitative trait variations. As an example, different plant growth type phenotype corresponding to allelic variants of a regulatory gene is illustrated in the Figure. The developed germplasm allelic repository can be now utilized for customizing crops adapted to specific environments through various genomic crop improvement approaches such as genomics-assisted breeding, genomic selection and genome-editing strategies. Depending upon the environmental requirement, we can alter the meristem fate, branch angle and floral fate in crops for successful colonization and yield stability. Fine-tuning agricultural practices such as irrigation and fertilizer application with developmental events will help us achieve yield stability in crops. \* Most popular genomics-assisted trait mapping approaches available are QTL mapping, Fine-mapping, QTLseq, Association mapping and Genomic selection.

plant architecture. The four main plant architectural traits, plant height, branching, branch angle and floral fate, are under the control of the '*GID1-DELLA*' module, '*LAZY1-TAC1*' module and '*TFL1-FT*' module, respectively. These regulatory networks played a significant role in crop domestication, and it is time to explore and exploit them to customize crops further.

First and foremost, we need to understand the targets and mechanisms through which these pathways function. There is no information linking the *LAZY1* and *TAC1* mode of action yet. Also, the abovementioned pathways are not exclusive in the regulation of these traits. The genetic network involving *STM* is well established for its role in *SAM* maintenance (Long *et al.*, 1996). Similarly, pathways are working parallelly to regulate branch angle and plant growth habit. Few genes explored in this direction are *PROSTRATE GROWTH1 (PROG1)*, *IDDISHOOT GRAVITROPISM* genes (*SGRs*), *TILLER ANGLE INCREASED CONTROLLER (OsLIC)* and *PHOSPHOGLUCOMUTASE* genes (Kim *et al.*,

2016; Kolesnikov *et al.*, 2016; Tan *et al.*, 2008; Wang *et al.*, 2008). We also need to understand the significance of the presence of highly similar copies of these genes in plant genomes. For example, there are two homologs of *TFL1* in pea, the *DETERMINATE* and *LATE FLOWERING*, which performs distinct function during inflorescence development (Foucher *et al.*, 2003). Identifying the key players will provide us with a broader perspective on how the trait phenotype can be manipulated. The next course of action should be exploring the available germplasm resources and developed populations for allelic variants on these genes and their effect on the phenotype. Learning from the natural variants, we can introduce a range of precise mutations within the genes to develop a repository of alleles giving a wide range of phenotypes. Evaluation of these alleles under different environmental conditions will delineate alleles performing better under certain conditions. The availability of information on allelic variants can help the researchers and

breeders to mix and match as per the requirement. While the present review targets few regulatory networks for restructuring plants, one must understand that plant architecture is a vast arena and involves several such regulatory networks. All these factors are equally important for enhancing and stabilizing yield components. The positive and negative regulators of GA signalling can be an excellent target for fine-tuning yield-contributing traits in crops. The regulation of gibberellin in rice for internode length determination through *ACCELERATOR OF INTERNODE ELONGATION 1 (ACE1)* and *DECELERATOR OF INTERNODE ELONGATION 1 (DEC1)* is one such example (Nagai *et al.*, 2020). The FT-TFL1 module may also influence plant height as the determinate genotypes exhibit a dwarf phenotype. SAM morphometrics is reported to influence plant height in chickpea (Narnoliya *et al.*, 2019). A thorough study may shed some light into how meristem fate regulates plant height in crops.

Similarly, lateral branching is under the regulation of axillary meristem. The shoot branching is mainly under the control of hormonal signalling, especially auxin, brassinosteroids and strigolactones (Barbier *et al.*, 2019). Interestingly the lateral branching in the root system is regulated by the *CLAVATA* signalling pathway (Araya *et al.*, 2014; Dong *et al.*, 2019). It will be interesting to explore its role in shoot branching as well. Technological advances in crop improvement need to be utilized up to their full potential. Using our understanding of the key plant architecture regulating developmental pathways, we can accelerate domestication of crop to achieve yield stability. Innovations in crop genomics and next-generation molecular breeding will provide us with the stability to tackle food shortages under depleting land resources.

## Acknowledgements

The financial support provided by the Department of Biotechnology (DBT), Ministry of Science and Technology, Government of India is acknowledged. UB acknowledges the UGC (University Grant Commission) for the Senior Research Fellowship award.

## Conflict of interest

The authors declare no conflict of interest.

## Author's contribution

UB and SKP designed and drafted the manuscript. Both authors gave the final approval of the version to be published.

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