

Auxin regulation on crop: from mechanisms to opportunities in soybean breeding

Linfang Li (✉ lilinfangqhu@126.com)

Fujian Agriculture and Forestry University <https://orcid.org/0000-0001-8135-0528>

Xu Chen

Fujian Agriculture and Forestry University

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Abstract

Breeding crop varieties with high-yield and ideal plant architecture is a desirable goal of agricultural science. The success of 'Green Revolution' in cereal crops provides opportunities to incorporate phytohormones in crop breeding. Auxin is a critical phytohormone to determinate nearly all the aspects of plant development. Despite the current knowledge regarding auxin biosynthesis, auxin transport and auxin signaling has been well characterized in model Arabidopsis plants, how auxin regulates crop architecture is far from being understood and the introduction of auxin biology in crop breeding stays in the theoretical stage. Here, we give an overview on molecular mechanisms of auxin biology in Arabidopsis, and mainly summarize auxin contributions for crop plant development. Furthermore, we propose potential opportunities to integrate auxin biology in soybean breeding.

Full Text

To meet human demand for food, the 'Green Revolution' in agriculture has saved more than a billion people from starvation in 1960s. The 'Green Revolution' refers to the modification of cereal crop architecture, like rice and wheat, from tall to short and compact plants which are suitable for high-density planting with high-yielding per acre (Peng et al. 1999; Silverstone and Sun 2000; Khush 2001; Boss and Thomas 2002; Sasaki et al. 2002; Spielmeyer et al. 2002; Evenson and Gollin 2003). The semi-dwarf varieties generated from the 'Green Revolution' are lodging resistance which respond to fertilizer inputs properly with an increased yield. Consequently, semi-dwarf plant becomes an ideal shoot architecture during rice and wheat breeding (Hedden 2003). Semi-dwarf plants in 'Green Revolution' are mostly realized by reduced gibberellin (GA) synthesis or signaling (review in (Liu et al. 2021b; Gao and Chu 2020)). DELLA proteins act as negative regulators of GA signaling pathway, and GA-induced DELLA degradation is a central regulatory event for GA-mediated plant development (Sun 2011). Generation of semi-dwarf plant is derived from the reduced GA response caused by DELLA accumulation (Liu et al. 2021b). Apparently, modification of GA pathways becomes an excellent example, providing opportunities to introduce phytohormones in crop breeding.

Among all phytohormones, auxin is the first phytohormone to be discovered, which influences a wide variety of plant developmental processes throughout the plant life span (Benjamins and Scheres 2008). Dynamic regulation of auxin concentration and maintenance of auxin gradient at the level of individual cells determinate cell fate and cell growth plasticity (Leyser 2002). Appropriate auxin gradient is established by coordination of auxin synthesis, auxin transport and auxin signaling. In Arabidopsis, a large number of auxin regulators have been identified, and the molecular mechanisms of auxin regulation on plant development are relatively well characterized among all phytohormones. However, auxin regulation on crop development is far from being understood, and the introduction of auxin pathways in crop breeding stays in the theoretical stage. In this review, we give an overview on recent progress of auxin biology in Arabidopsis, and summarize the current knowledge on auxin regulations in cereal crop development. Meanwhile, we discuss the opportunities to integrate available auxin biology in soybean breeding.

Overview on regulatory mechanisms of auxin in model plant system

Auxin molecules tend to be concentrated in meristems and young plant tissues, which are at the forefront of growth. The optimal auxin distribution within a tissue depends on local auxin biosynthesis and cell-to-cell polar auxin transport. Auxin precisely determinates cell fate, by specifying auxin signal in individual cells and converting auxin perception into a diversity of cell responses on transcriptional, post-transcriptional or post-translational level. In this way, plant cells coordinate their size, division and differentiation based on auxin concentration and auxin gradient. Here, we briefly introduce the recent progress of auxin regulations on biosynthesis, metabolism, transport and signaling level (Fig 1), to provide the basic knowledge for crop development.

Auxin biosynthesis and metabolism

Trp is the precursor of multiple auxin biosynthesis pathways. Currently, the best defined pathway of auxin biosynthesis is the Tryptophan Aminotransferase of Arabidopsis (TAA)/YUCCA route (Won et al. 2011), in which the TAA/Tryptophan Aminotransferase Related (TAR) catalyzes the conversion of Trp to indole-3-pyruvic acid (IPyA) (Stepanova et al. 2008; Tao et al. 2008) and YUCCA flavin-dependent monooxygenases catalyze oxidative decarboxylation of IPyA to be IAA (Zhao et al. 2001; Zhao 2010, 2012)). Through chemical genetic screening, small molecules, L-kynurenine (Kyn) and 5-(4-chlorophenyl)-4H-1,2,4-triazole-3-thiol (yucasin), were successively identified as inhibitors that individually inhibit TAA1/TAR (He et al. 2011) and YUCCA activity (Nishimura et al. 2014). Currently, Kyn or yucasin treatment has been widely used to mimics the deficiency of TAA1/TAR or YUCCA.

Auxin is present in active and inactivate forms. The majority of auxin is amino acid-linked auxins, glycosylated conjugates, and the inactive methyl ester form. Only less than 5% of auxins exist in free form (Percival and Bandurski 1976). Maintenance of appropriate auxin level by auxin homeostasis between inactive (storage) and active (free) form is vital for plant developmental plasticity. IAA inactivation is carried out by IAA conjugation (IAA-sugar conjugates, IAA-amino acid conjugates), IAA oxidation and IAA methylation (review in (Korasick et al. 2013)). GRETCHEN HAGEN 3 (GH3) enzymes encode IAA-amido synthetases, which conjugate excess free IAA to IAA-amino acid conjugates, such as IAA-aspartate (IAA-Asp) and IAA-glutamate (IAA-Glu) (Staswick et al. 2005). Kakeimide (KKI) was identified as specific inhibitor that rapidly (about 10min) suppresses GH3 activity (Fukui et al. 2022). IAA-Asp and IAA-Glu are storage forms of IAA, which can be reverted to IAA by IAA-Leu-Resistant1 (ILR1)/ ILR1-like (ILL) amidohydrolases (Bartel and Fink 1995; Davies et al. 1999). Ester-linked IAA conjugates with glucose (IAA-glc) is another pathway to regulate IAA homeostasis by UDP-glucosyltransferase (UGT) (Jackson et al. 2001; Grubb et al. 2004; Tognetti et al. 2010). Beside of auxin conjugation and glycosylation, IAA can be methylated or oxidized. IAA carboxyl methyltransferase1 (IAMT1) is responsible for converting activate IAA to methyl-IAA ester (MeIAA) (Qin et al. 2005), and Dioxygenase for Auxin Oxidation 1 (DAO1) converts free IAA to inactive auxin form of 2-oxoindole-3-acetic acid (OxIAA) (Porco et al. 2016; Zhao et al. 2013b; Zhang et al. 2016). Interestingly, DAO1 mainly results in the steady-state level changes between OxIAA and IAA conjugates, whereas free IAA level is not

significantly influenced (Zhang et al. 2016; Porco et al. 2016). Hence, auxin homeostasis and catabolism became important features to control endogenous free auxin level.

Auxin transport

Auxin molecules are mainly synthesized in young tissues with high activity of cell division. The natural auxin, IAA is a weak acid ($pK_a = 4.85$), which is not able to cross the PM from the neutral cytoplasm ($pH=7.0$) (Zazimalova et al. 2010). Therefore, cell-to-cell movement of auxin requires an export system. Auxin moves from distal to proximal cells in a polar manner by specific efflux and influx transporters, contributing to the formation of auxin gradient. Local auxin gradient is vital for plant organogenesis and subsequent development (Benková et al. 2003). It has been well studied that polar auxin transport is achieved via the efflux PIN-FORMED (PIN) auxin transporters (Petrasek et al. 2006; Glanc et al. 2018), influx AUXIN-RESISTANT1/LIKE AUX1 (AUX1/LAX) transporters, and some of the B subclass of ATP-BINDING CASSETTE (ABCB) efflux transporters (Geisler et al. 2005; Geisler 2021)).

PIN exporters are plant-specific transmembrane proteins, which determinate polar auxin transport in cell-to-cell manner (review in (Bennett 2015; Adamowski and Friml 2015; Feraru and Friml 2008)). Expression pattern associated with cellular polarity of PIN proteins controls the direction of auxin flow during diverse aspects of organ development (Muller et al. 1998; Friml et al. 2002; Benková et al. 2003; Okada et al. 1991; Weijers et al. 2005). Current plant developmental modules support that PIN-dependent auxin transport is required for nearly all the processes of polar organ growth (Han et al. 2021; Adamowski and Friml 2015)). Auxin-induced PLETHORA (PLT) transcription factors display a similar graded distribution as auxin gradient (Aida et al. 2004). The tissue-specific PLT gradients are sufficient to determine stem cell identity, cell expansion and cell differentiation (Galinha et al. 2007). Auxin fine-tunes PLTs expression, meanwhile PLTs regulate PIN functions on transcriptional level (Mahonen et al. 2014; Galinha et al. 2007). Endocytic trafficking and kinase-mediated phosphorylation control cellular PIN distribution and polar targeting. PM-associated PIN proteins are dynamically endocytosed into endosomal compartments, via clathrin-dependent endocytosis (Dhonukshe et al. 2007). Internalized PIN proteins either target to the vacuole for degradation, or be exocytosed to PM, via ADP-RIBOSYLATION FACTOR GUANINE-NUCLEOTIDE EXCHANGE FACTORS (ARF-GEFs) (Kleine-Vehn et al. 2008; Geldner et al. 2003). The endosomal trafficking mainly affects distribution of PIN proteins on PM or within cytosol (review in (Adamowski and Friml 2015)). Recent studies have revealed that phosphorylation and dephosphorylation are essential for PIN activation and polarization (review in (Lanassa Bassukas et al. 2022)). PIN polarity is under the control of phosphorylation events by PINOID AGC kinase (PID), D6 PROTEIN kinase (D6PK), MITOGEN-ACTIVATED PROTEIN kinase cascades (MAPKs) and Ca^{2+} /CALMODULIN-DEPENDENT PROTEIN kinase (CAMK) (review in (Lanassa Bassukas et al. 2022; Barbosa et al. 2018)). PROTEIN PHOSPHATASE 2A (PP2A) acts antagonistically with PINOID on PIN polar targeting, mediating PIN dephosphorylation (Michniewicz et al. 2007). Beside of the canonical PIN proteins, non-canonical PIN proteins with dual localization at both plasma membrane (PM) and endoplasmic reticulum (ER), as well as ER-resident PIN-LIKES (PILS) modulate intracellular auxin transport and auxin homeostasis (Ding et al. 2012; Mravec et al. 2009; Barbez et al. 2012).

Auxin efflux also requires ATP-binding cassette superfamily B (ABCB) proteins, which interact with PIN proteins (Geisler et al. 2005). ABCB19 co-localizes and stabilizes PIN1 in membrane lipid microdomains to enhance PIN1 transport activity (Titapiwatanakun et al. 2009). Computational modelling further supports the synergistic interactions of ABCB and PIN proteins for directional auxin flow (Mellor et al. 2022). Beside of auxin export system, auxin uptake is also an active process which requires proton motive force. AUX1/LAX proteins which encode amino acid/auxin permease (AAP) family of proton symport permeases, serve as auxin influx transporter to establish auxin influx pathway in different organs (review in (Swarup and Peret 2012)).

The coordination of influx and efflux auxin transportation is tightly associated with an appropriate auxin gradient, thereby, plants are able to initiate new organs, display tropisms and rapidly adapt to environmental stresses.

Auxin signaling

Local biosynthesis and polar transport specify auxin concentration and distribution within plant tissues. Upon auxin perception in single cell, the cell surface and nucleus-allocated auxin signaling cascades trigger specific auxin response on transcriptional or post-transcriptional level. Nuclear auxin signaling is comprise of three protein families: the F-box TRANSPORT INHIBITOR RESPONSE 1/AUXIN SIGNALING F-BOX PROTEIN (TIR1/AFB) auxin co-receptors, the Auxin/INDOLE-3-ACETIC ACID (Aux/IAA) transcriptional repressors, and the AUXIN RESPONSE FACTOR (ARF) transcription factors. TIR1/AFB auxin receptors are F-box subunits of SCF E3 ubiquitin ligase complexes, which mediate Aux/IAA degradation via ubiquitination. In the presence of auxin, auxin binds to TIR1/AFB receptors; auxin promotes the interaction between Aux/IAA proteins and SCF TIR1/AFB complex, resulting in the proteasome-mediated Aux/IAA degradation, by SCF E3 ubiquitin ligase (Chapman and Estelle 2009; Leyser 2006)). Aux/IAAs are auxin signaling repressor, forming interactive pairs with ARFs. Degradation of Aux/IAAs releases ARFs, to active transcriptional regulation of ARF-targeted downstream genes (review in (Cance et al. 2022)). Beside of the E3 ligase activity, a recent study identified that adenylate cyclase (AC) activity is an additional function of TIR1/AFB receptors. AC activity of TIR1/AFB is controlled by the C-terminal AC motif, which is enhanced by auxin. TIR1/AFB AC activity is required for rapid auxin response by promotion of cAMP production, independent of E3 ligase-mediated ubiquitination activity (Qi et al. 2022).

Auxin perception and signal transduction not only happen in the nucleus, auxin molecules have to firstly across PM. Hence, another auxin signaling pathway must happen on the cell surface to mediate rapid auxin response. Two decades ago, ABP1 protein was purified from maize coleoptiles by several independent laboratories (Löbler and Klämbt 1985a; Shimomura et al. 1986; Hesse et al. 1989; Tillmann et al. 1989; Lobler and Klambt 1985) and be shown to bind auxin with high affinity in the acidic environment (Löbler and Klämbt 1985b; Jones and Venis 1989; Löbler and Klämbt 1985a). Large number of physiological and developmental studies demonstrated important roles of ABP1 in various auxin-dependent processes (Jones et al. 1998; Chen et al. 2001a; Bauly et al. 2000; Chen et al. 2001b). Despite

of eminent research efforts, CRISPR-CAS9-based ABP1-knockout genetic materials bring debates and puzzling whether ABP1 acts as a dedicated receptor for auxin on cell surface (Gao et al. 2015).

Recent work on PM-localized transmembrane kinase (TMK) defines a novel cell surface-resident auxin perception pathway. TMK1 interacts with ABP1 to stimulate the activity of PM-associated ROPs (Rho-like guanosine triphosphatases GTPase), shaping leaf pavement cell interdigitation (Xu et al. 2014). The interaction between ABP1 and TMK at the cell surface is dependent on ABP1-mediated auxin sensing. Upon auxin perception, TMK1 is also able to interact with and phosphorylate PM-associated H⁺-ATPases, thereby promoting cell-wall acidification and rapid cell expansion (Lin et al. 2021). Meanwhile, small Auxin Up RNA (SAUR) proteins can also stimulate H⁺-ATPase proton pumping activity by inhibiting activity of PP2C.D phosphatases, thereby preventing the dephosphorylation of H⁺-ATPase to stimulate cell expansion (Spartz et al. 2014; Ren et al. 2018; Wong et al. 2021). Strikingly, TMK1 functions not only on the cell surface, but also interacts with nuclear-allocated auxin signaling. Auxin promotes the C-terminal cleavage of TMK1. The cytosolic and nucleus-translocated C terminus of TMK1 specifically interacts with and phosphorylates the nuclear auxin core components, Aux/IAA proteins (IAA32 and IAA34), thereby regulating ARF-dependent nuclear auxin signaling (Cao et al. 2019). Therefore, cell surface-resident auxin signaling collaborates with nuclear auxin signaling via TMK1-Aux/IAA complex, enabling specific auxin response under different concentrations of cellular auxin and leading to complex developmental outcomes (Cao et al. 2019). By comparison of global auxin-triggered phospho-response of *abp1* and *tmk1* loss-of-function mutants, TMK1 and ABP1 indeed mediate large number of overlapping rapid phospho-responses (Friml et al. 2022). Therefore, ABP1 and TMK1 serve as the auxin co-receptors to perceive cell surface auxin signaling, mediating rapid auxin response on the level of protein phosphorylation.

Auxin contribution for crop breeding

The major objective of plant science was to apply our knowledge to increase crop yield. Yield promotion in cereal crops, such as rice is realized through the introduction of semidwarf varieties which reduce GA synthesis and response (review in (Gao and Chu 2020; Liu et al. 2021b)). The resultant semi-dwarf plant not only prevents lodging, but also facilitates fertilizer inputs to improve grain yield. Based on the experience of rice breeding, shaping an ideal shoot architecture in cereal crops is proposed, including semi-dwarf height, being suitable for high-density planting, high-yielding (review in (Gao and Chu 2020)). Beside of ideal shoot architecture, shaping desirable crop plants with an ideal root architecture which has great potential to increase resource-use efficiency is also highlighted in recent years (Panda et al. 2021). Auxin functionality in shoot and root plasticity makes a potential application value of auxin in crop breeding. We here summarize the recent studies of auxin biosynthesis, auxin transport and auxin signaling in crop development (mainly in rice, maize and soybean) (Fig 2) and discuss the possible application of auxin for crop breeding.

Shoot height

Semi-dwarf traits have been widely introduced into cereal crops breeding, including reduced plant height, reduced tiller angle and reduced leaf angle. Crop breeding interest in short plant height is mainly derived from their ability of lodging resistance caused by wind. In rice, indole-3-acetic acid glucosyltransferase (*OsIAAGLU*) which catalyzes the conjugation of free IAA with glucose to generate IAA-glucose is involved in the regulation of plant height. Overexpression of *OsIAAGLU* that decreases free auxin level significantly reduces plant height (Yu et al. 2019). On the cellular level, loss of auxin receptors *OsTIR1*, *OsAFB2*, *OsAFB3*, *OsAFB4* and *OsAFB5* in rice, which disrupts auxin perception, also significantly reduces plant height (Guo et al. 2021). Apparently, maintenance of shoot height requires sufficient auxin level. On a tissue level, specific auxin distribution and auxin gradient determine plastic organ formation, which is under the control of auxin transporters. In rice, mutation of the PIN orthologs *OsPIN1b* which disrupts polar auxin transport decreases shoot height (Wang et al. 2022a). Whereas, overexpression of *OsPIN5b* elevates free auxin level but suppresses conjugated auxin level in shoot, thereby resulting in the reduction of plant height (Lu et al. 2015). In maize, two classes of mutants with a dramatic reduction in shoot height, named the dwarf mutants and the brachytic mutants. Among them, *brachytic mutant2* (*br2*) shows compact lower stalk internodes, which is caused by loss of P-glycoprotein (PGP, also named ABCB) function and impaired polar auxin transport (Multani et al. 2003). In Arabidopsis, loss of PGP function is associated with multiple phenotypes in roots (Terasaka et al. 2005; Geisler et al. 2005), whereas the disruption of *ZmPGP1* (*Br2*) in maize has different consequences that causes a specific shortening of lower stalk internodes but not in other tissues. Gene duplication and the specific expression pattern of *ZmPGP1* in elongating internodes provide an opportunity to apply *Zmpgp1* mutant to shape a dwarfish shoot height during maize breeding (Multani et al. 2003; Xing et al. 2015). To explore natural variation and domestication selection of *ZmPGP1* gene, sequence polymorphism of *ZmPGP1* in 349 inbred lines, 68 landraces, and 32 teosintes of maize varieties has identified several SNP variants and indel regions in *ZmPGP1* which have great potential to associate with maize shoot architecture (Li et al. 2019a). Strikingly, overexpression of *ZmPIN1a* in maize displays consistent shoot phenotype as *ZmPGP1* deficiency, resulting in reduced internode length and shorter height (Li et al. 2018a). Although these two types of auxin efflux transporters, PGP and PIN act synergistically to direct polar auxin flow in Arabidopsis (review in (Mravec et al. 2008)), we could not simply imitate the conserved mechanism from Arabidopsis to crop plants. In maize, the reduction of internode is caused by the increased acropetal auxin transport from shoot to root in *ZmPIN1a* overexpressors but decreased auxin basipetal transport from lower to upper internodes in *Zmpgp1* mutant (Li et al. 2018a; Zhang et al. 2018a).

Soybean plants have two growth habits: indeterminate and determinate. Determinate type completes vegetative growth once the plant starts flowering, whereas indeterminate type has continuously vegetative growth during the reproductive phase (Tian et al. 2010). Thus, the different growth pattern of soybean cultivars results in the variation of shoot height and yield. Shoot height is a complex quantitative trait, which is influenced by a variety of phytohormones, including GA, auxin, and cytokinin (Wang et al. 2017). Consistent with the finding in rice, GA plays a vital role in soybean plant height. A number of genes involved in GA biosynthesis or signaling pathways have been reported to regulate soybean height, such as *GmDW1* (*Dwarf Mutant 1*) (Li et al. 2018b), *GmAP1s* (*Apetala1*) (Chen et al. 2020), and *GmLHY* (*Late*

elongated hypocotyl) (Cheng et al. 2019), *ABI3/VP1* gene *GmRAV* (Xue et al. 2022). It is well known that auxin promotes GA biosynthesis (Wolbang and Ross 2001; Ross et al. 2000; Ross et al. 2001). Thus, it is highly possible that auxin interacts with GA to influence shoot height in soybean. Mutant of the *Glycine max long internode 1* (*Gmlin1*), which encodes a homologue of the Arabidopsis long hypocotyl 2 (HY2) gene, exhibits extremely taller and longer internode than soybean wild type plant (Zhang et al. 2022b). Arabidopsis HY2 is involved in phytochrome chromophore synthesis, hence, *Gmlin1* mutant possibly influences the biosynthesis of auxin and GA (Zhang et al. 2022b). As expected, auxin-responsive genes *GmIAA29*, *GmIAA9*, and *GmSAUR* (*Small Auxin Up RNA*) and GA biosynthesis genes *GmGA20ox* and *GmGA3ox* are all upregulated in *Gmlin1* mutant, implying auxin interplays with GA to promote internode elongation (Zhang et al. 2022b). Knock out of auxin transporters *GmPIN1a*, *GmPIN1b* and *GmPIN1c* in soybean displays semi-dwarf phenotype, indicating an involvement of auxin transport in shoot height regulation (Zhang et al. 2022a). Jiang et al. (2018) identified 11 major quantitative trait loci (QTLs) associated with the first pod height from 147 recombinant soybean inbred lines (Jiang et al. 2018). Among this QTL interval, 8 candidate genes including an *auxin response factor 9* (*ARF9*), a *SAUR* family gene, and an *AUX* influx permease are components of auxin signaling or auxin transport (Jiang et al. 2018). A dwarf soybean mutant named *dmbn* was identified from ethyl methanesulfonate (EMS)-mutagenized soybean seeds, and the dwarf phenotype might be associated with an auxin signaling regulator, Aux/IAA protein *GmIAA27* (Su et al. 2022). Furthermore, the *cytokinin response factors 4a* (*GmCRF4a*) promotes cell elongation and shoot height in soybean, as *GmCRF4* is required for *GmYUC* expression which controls auxin biosynthesis (Xu et al. 2022). All these studies imply auxin is associated with soybean plant height (Figure 3).

Despite the studies in crop plants have raised the relationship between auxin and shoot height, the underlying mechanisms are largely unknown. With the help of fundamental research in model plant Arabidopsis, auxin contribution in shoot height can be partially interpreted by the acid growth model. The decades-old auxin-acid growth model has put forward a promotional effect of auxin on cell expansion/elongation through its effect on cell wall acidification (Du et al. 2020). As mentioned above, TMK1-dependent auxin signaling stimulates rapid phosphorylation of PM H⁺-ATPase, and the active of H⁺-ATPase (also named as AHA) causes apoplastic acidification to increase cell wall extensibility (Lin et al. 2021). A type 2C protein phosphatases PP2C.D dephosphorylates AHA to decrease H⁺ pump activity (Spartz et al. 2014; Ren et al. 2018). SAURs inhibit de-phosphorylation activity of PP2C.D, conferring high AHA activity (Spartz et al. 2014; Ren et al. 2018; Wong et al. 2021). Beside of the cell surface auxin signaling, TIR1/AFB-mediated nuclear auxin signaling also mediates auxin acid growth (Fendrych et al. 2018). Therefore, manipulation of TMK1-PP2C.D-SAUR-AHA and TIR1/AFB-AUX/IAA-ARF auxin signaling cascades can be considered as new strategies to optimize crop shoot height.

Leaf and tiller angle

In recent years, improvement of photosynthesis efficiency becomes a major goal for scientists to increase crop yielding, as canopy photosynthesis determines carbohydrate accumulation which is tightly

correlated with biomass growth and crop production (Song et al. 2016). Leaves at the top of a canopy are usually light saturated, while leaves at the bottom layers are light limited. Canopy growth pattern not only influences photosynthesis efficiency, but also determines the planting population in a unit area.

Canopy architecture is consisted of leaf size and leaf growth angle in dicot, meanwhile includes tiller number and tiller angle in monocot. More upright growing leaves increase light interception across the abaxial and adaxial leaf surface, which has been shown to improve photosynthesis rate (Pendleton et al. 1968). According to the difference in leaf angle, maize plants are divided into three types, namely compact type, intermediate type and flat type (Donald 1968). There is a correlation between leaf angle and canopy photosynthesis, as well as yield: very upright growing leaves is beneficial for the middle leaf to receive light, thereby improving the global photosynthesis efficiency and production (Stewart et al. 2003). Exogenous application of auxin promotes leaf angle in maize (Ji et al. 2022). During leaf angle formation in rice, auxin promotes the elongation of parenchyma cells in leaf lamina joint. Reduction of auxin level by overexpressed IAA-amido Synthetase, Rice *LEAF INCLINATION1 (LC1)* in lamina joint increases flag leaf angle (Zhao et al. 2013a), suggesting auxin level is negatively correlated with leaf angle. Through genetic screening, mutant of *Increased Leaf Angle1 (ILA1)*, a Raf-like mitogen-activated protein kinase kinase kinase (MAPKKK), exhibits a larger leaf angle due to the reduced mechanical strength of lamina joints (Ning et al. 2011). The crucial nuclear auxin signaling components, *OsARF6*, *OsARF17* and *OsARF19* show high abundance in the lamina joint (Zhang et al. 2015; Huang et al. 2021a). *OsARF19* binds to the promoter of *OsGH3-5*, which converts free IAA to IAA conjugates. Overexpression of *OsARF19* or *OsGH3-5* both decreases free IAA level at lamina joints, resulting in an increase of adaxial cell division and an enlarged leaf angle (Zhang et al. 2015). Moreover, *OsARF6* and *OsARF17* directly bind to the *ILA1* promoter and activate *ILA1* expression (Huang et al. 2021a). Consequently, *osarf6 osarf17* double mutant shows an exaggerated enlarged leaf angle (Huang et al. 2021a). The opposite phenotype of *OsARF6*, *OsARF17* and *OsARF19* genetic materials indicates a complicated regulation of auxin signaling for lamina joint development in rice.

Beside of leaf angle, tiller angle is another core constituent of canopy architecture in monocot, to influence light perception and planting density. Significant progress in rice have defined that tiller angle formation is associated with shoot gravitropism (review in (Wang et al. 2022b)). Most knowledge regarding the molecular basis of gravitropism has mainly obtained from the studies in Arabidopsis. Gravitropism is caused by the asymmetric auxin distribution in the upper and lower flanks of root tip or in the abaxial and adaxial cells of shoot upon gravity stimulation (review in (Strohm et al. 2012)). PIN efflux transporters and AUX/LAX influx transporters serve as core regulators to control auxin gradient and asymmetric auxin distribution (review in (Swarup and Peret 2012)). Current understandings on tiller angle regulation are mostly related to auxin. *LAZY1* controls rice tiller angle by negatively regulating polar auxin transport (Zhu et al. 2020; Li et al. 2007). *LAZY2* controls shoot gravitropism and tiller angle by acting upstream of *LAZY1* (Huang et al. 2021b). Downregulation of auxin signaling by disrupting *OsARF12*, *OsARF17* and *OsARF25* promotes tiller angle (Li et al. 2020b), indicating that auxin signaling negatively correlates with tiller angle. PIN-controlled asymmetric auxin distribution happens on PM, whereas, all the core regulators that control tiller angle in rice are mostly nuclear-localized transcriptional factors. It

remains questions whether LAZY1 and other tiller angle-related transcriptional factors directly regulate PM-associated PIN cascade. Interestingly, LAZY1 displays dual localization in both PM and nuclear. LAZY1-interacting protein, named Brevis Radix Like 4 (OsBRXL4) interacts with LAZY1 at the PM, and their interaction determines nuclear localization and functionality of LAZY1 (Li et al. 2019b). PROTEIN KINASE ASSOCIATED WITH BRX (PAX) is able to recruit AtBRX to the PM, in turn inhibits PIN-dependent auxin efflux at lower auxin level in Arabidopsis root (Marhava et al. 2020). A regulatory network of LAZY1-BRX-PIN probably happens for tiller angle formation in rice. To further understand the functional relationship between shoot gravitropism and till angle, Zhang et al. performed a large-scale transcriptome analysis to identify the regulatory network in upper and lower flanks of rice tiller upon gravi-stimulation (Zhang et al. 2018b). Transcriptional factor *HEAT STRESS TRANSCRIPTION FACTOR 2D* (*HSFA2D*) acts as positive regulator upstream of *LAZY1*, and *WUSCHEL RELATED HOMEODOMAIN 6* (*WOX6*) and *WOX11*, are expressed asymmetrically in tiller flanks in response to gravi-stimulation (Zhang et al. 2018b). OsHOX1 and OsHOX28 are further found to restrain lateral auxin transport and then repressing the expression of *WOX6* and *WOX11* in the lower side of shoot (Hu et al. 2020). OsHOX1 and OsHOX28 proteins are also able to bind to the promoter region of *HSFA2D* and suppress the expression of *HSFA2D* and *LAZY1* (Hu et al. 2020).

Compared with the knowledge in rice, soybean study is largely delayed. Soybean is a typical light-sensitive plant, displaying rapid growing of petiole under shade compared with normal light irradiation (Yang et al. 2018). Reduced red-to-farred light intensity ratio promotes the elongation of petiole length, probably caused by the decreased IAA-to-GA content ratio of soybean petiole (Yang et al. 2018). In soybean, an appropriate leaf angle is not simply determined by a general change of auxin content. Auxin displays asymmetric accumulation in leaf petiole base, with more auxin in the lower side than in the upper side, corresponding with the consistent asymmetric pattern of *GmPIN1a/c* abundance. The asymmetric *GmPIN1* expression and auxin accumulation in petiole base result in asymmetric cell expansion to create a desirable petiole curvature in soybean (Zhang et al. 2022a). Accumulating evidences have proved the interactive regulation of phytohormones for leaf angle formation, such as the interaction between brassinosteroid (BR) and auxin (review in (Luo et al. 2016; Li et al. 2020a)). High BR content in the lamina joint promotes leaf petiole angle (Tong and Chu 2018). *GmMYB14* transcriptional factor directly binds to the promoter of *BRASSINOSTEROID-INSENSITIVE 1 ENHANCED 1* (*BEN1*), in turn negatively regulate BR level. The reduction of BR content in overexpressed *GmMYB14* soybean plants causes smaller petiole angle and compacter plant architecture than wild type (Chen et al. 2021). Very limited mechanisms have been studied for soybean petiole angle formation. Currently, the theory of *GmPIN*-dependent asymmetric auxin distribution in leaf petiole base can be a reference to study petiole angle formation and to search for an optimal approach for high-density planting in soybean (Fig 3). With the help of time-series phenotypic data collected by an unmanned aircraft system from 1303 soybean varieties, 35 QTL regions are identified to associate with canopy coverage (Li et al. 2022a), which offers a promising opportunity for soybean breeding with canopy architecture.

Seed quality and yield

During crop breeding, improving yield and seed quality are the most important challenges amongst all breeding issues. Seed number per pod is determined by ovule number which has been well studied in *Arabidopsis* (review in (Cucinotta et al. 2020)). Phytohormones communication, including the crosstalk among auxin, cytokinin, brassinosteroid and gibberellin promotes ovule initiation (Cucinotta et al. 2020). Among them, PIN transporters-driven auxin flow creates an auxin maximum in the founder cells of ovule primordia to direct ovule initiation (Hu et al. 2022; Yu et al. 2020). Hence, it is easy to understand that deficiency of auxin biosynthesis or auxin transport causes defects of ovule initiation and the decrease of seed number. For instance, *Ospin1c Ospin1d* double mutants exhibit severe defects of panicle development (Liu et al. 2022); overexpression of *OsPIN5b* decreases seed setting rate, panicle length and yield per panicle (Lu et al. 2015). However, promotion of seed number is not simply realized by elevation of auxin level. Overexpression of *OsAFB6* in rice greatly elevate spikelet number per panicle and grain yield per plant by increasing cytokinin but decreasing auxin level (He et al. 2018). Therefore, it is not a good idea to improve crop yield directly by increasing auxin transport or auxin biosynthesis. A dominant rice mutant *big grain1 (Bg1-D)* shows obvious bigger seed size. *BG1* gene is specially and rapidly induced by IAA, and overexpression of *BG1* significantly enhances the basipetal IAA transport and IAA level (Liu et al. 2015b). Consequently, *BG1*-overexpressing plants improved biomass and grain yield in rice (Liu et al. 2015b), illuminating a new strategy to apply auxin in crop yielding.

Seed filling quality is determined by carbohydrates distribution that derived from leaf photosynthesis. Sucrose is the major carbohydrate, transporting from source to sink to supply for grain filling. Exogenous IAA application enhances the initiation of grain filling by transcriptional upregulation of sucrose transporters and increase of sucrose level (Deng et al. 2021). In maize, overexpression of *YIGE1* enlarges inflorescence meristem size, increases ear length and promotes kernel number, thus enhanced grain yield. *YIGE1*-overexpressors accumulate more IAA but decrease sugar content, implying a feedback regulation between auxin and sugar for seed development (Luo et al. 2022). Sucrose transport is mainly controlled by two types of sucrose transporters: Sugar Will Eventually be Exported Transporters (SWEETs) and sucrose transporters (SUTs/SUCs) (Kuhn and Grof 2010; Baker et al. 2012). Deficiency of sugar transporters blocks sugar transportation, in turn elevating sugar in the source leaves but deprivation of sugar in the sink tissues (seeds) (Julius et al. 2017). Hence, maintenance of appropriate source-to-sink sugar transport is crucial to control seed quality. In barley, mutation of auxin biosynthesis *HvYUCCA4* gene fails to establish carbon metabolism pathway during grain development, thereby affecting starch production for pollen maturation (Amanda et al. 2022). Knockdown of tomato *SIARF4* enhances sugar accumulation in fruit, implying a connection between sugar partitioning and auxin signaling (Sagar et al. 2013). Zhao et al. recently found that rice *dao* mutant, which failed to convert IAA into OxIAA, had defects in sugar partition between source (leaf) to sink (spikelet) tissue (Zhao et al. 2022c). *dao* mutant upregulates auxin signaling component *OsARF18* but downregulates *OsARF2*. *OsARF2* directly binds to the Sugar-Responsive Elements (SuREs) of *OsSUT1* promoter, enable the activation of sugar transport. Strikingly, the cis-element motif of SuREs (GTCTC) shows high sequence similarity with auxin-responsive elements (AuxREs: TGTCTC), implying a synergistic or antagonistic regulation between auxin and sugar on transcriptional level. *OsARF18* acts as a repressor of *OsARF2-OsSUT1* complex, feedback regulates

sugar transport through auxin signaling (Zhao et al. 2022c). Hence, auxin signaling cascade is also involved in carbohydrate partitioning, providing an important implication for raising seed quality.

Improving the ratio of four seeds per pod is a long-term demand for ideal soybean plant breeding (Liu et al. 2020). In the past years, efforts have been made to search for master regulators that control seed number per pod in soybean. So far, *Ln* gene has been cloned as a key factor to control seed set by regulating ovule number per pistil. Accordingly, *ln* mutants display higher percentage of four seeds per pod (Jeong et al. 2011; Jeong et al. 2012). However, limited advance is achieved on seed number control in the recent 10 years. To explore the possible regulatory network, Liu et al. compared the differences of auxin and cytokinin pathways which individually determine ovule initiation and cell division events in soybean and cowpea, trying to understand the underlying mechanism by which cowpea has much more seeds per pod than soybean (Liu et al. 2021a). In Arabidopsis, PIN1-dependent auxin transport determines ovule initiation by establishing auxin maximum in the apex of the ovule primordium (Benková et al. 2003). Interestingly, gene abundance and phosphorylation level of PIN1 in soybean are less than in cowpea, possible leading to the lower efficiency of auxin transport in soybean (Liu et al. 2021a). Thus, elevation of auxin concentration in ovule primordium by blocking auxin efflux becomes a possible idea to raise soybean seed set. Within our expectation, application of auxin efflux inhibitor, methylchlorflurenol (MCF) on soybean foliage during pod initiation elevates pod number by 40% upregulation (Noodén and Noodén 1985). However, the global seed yield per plant did not raise after MCF treatment, because the seeds were smaller in the treated plants than normal (Noodén and Noodén 1985). Consistent with the finding in rice, the carbohydrate source, sucrose flux across seed coat is crucial to fulfill soybean seed filling quality. SWEET transporters GmSWEET10a and GmSWEET10b, responsible for sucrose and hexose transport, serve as master regulators to determine seed size, oil and protein content. GmSWEET10a and GmSWEET10b direct sucrose flow to the developing embryos at the rapid-seed-growth stage, in turn enable a high seed-growth rate, larger seed and higher oil content (Wang et al. 2020). Therefore, improvement of soybean yielding requires integration of multiple signaling instead of sole change of auxin transport. Combination of auxin and sugar transport pathways could be an ideal approach to breed new soybean variety with high quality and high yield.

Root architecture

Root elongation is an important adaptive strategy for crops responding to nitrogen and phosphate deficiency (Sun et al. 2018; Li et al. 2015). Under phosphate deficiency, root hair number and root elongation are essential for phosphate absorption. Root elongation relies on both cell division and cell elongation in the root apical meristem (RAM) and elongation zones, which requires appropriate auxin concentration (Fu et al. 2021; Jiang and Feldman 2003; Di Mambro et al. 2017). Auxin gradient mediated by polar auxin transport has been well known to regulate root elongation. In rice, loss-of-function or gain-of-function of PINs, AUX/LAX and ABAC auxin transporter disrupted auxin gradient in RAM, thereby affecting root elongation. For instance, *Ospin1b* mutant decreases seminal root length (Sun et al. 2018), overexpressed *OsPIN2* inhibits root elongation (Sun et al. 2019), *Osaux1* mutant had longer primary roots but *Osaux3* had shorter primary roots (Yu et al. 2015; Wang et al. 2019a), *ZmPIN1a* overexpressors

increase lateral root density but decrease lateral root elongation (Li et al. 2018a), *Zmpgp1* mutant had shortened roots (Zhang et al. 2018a). Apparently, deficiency of auxin transporters all affects root elongation, owing to the disruption of auxin gradient in root meristem. Distinct with the shorter primary roots of auxin transporter mutants, deficiency of auxin signaling components in *Ostir1 afb2* single and multiple mutants all had longer primary roots than WT (Guo et al. 2021). Compared with the dwarfed roots of *tir1 afbs* multiple mutants in Arabidopsis (Prigge et al. 2020), longer root length in *Ostir1* and *Osafbs* mutants implies a possibility that auxin is overproduced and had an inhibitory effect on root growth in rice (Prigge et al. 2020). Beside of the endogenous auxin regulation, exogenous nutrient supply integrating auxin can reconstruct root architecture. Low nitrate and low phosphate induce root elongation but decrease auxin transport from shoots to roots (Sun et al. 2014). The promotion of root length by nitrate and phosphate starvation was less effective in *Ospin1b* mutant, since *OsPIN1b* transcript is suppressed under low nitrate and low phosphate conditions (Sun et al. 2018). In contrast to the decreased level of *OsPIN1b*, *OsPIN2* expression is enhanced upon phosphate deprivation (Sun et al. 2019). Low phosphate suppresses auxin transport in shoot-to-root direction by OsPIN1b but promotes auxin transport in root-to-shoot direction by OsPIN2 imply that the global auxin concentration should be reduced in RAM during phosphate starvation (Sun et al. 2018; Sun et al. 2019). However, more auxin is deposited in root tip under low phosphate condition (Sun et al. 2019), indicating that not only PIN transporters are involved in low phosphate regulation. OsAUX1 transport the accumulated auxin from the root apex to root differentiation zone, facilitating phosphate acquisition in rice (Giri et al. 2018). Beside of OsAUX1, OsAUX4 also participates in phosphate absorption during root growth (Ye et al. 2021). It has been well known that available phosphate has a significant effect on root hair elongation via auxin regulation. OsAUX1 promotes root hair growth during phosphate starvation, facilitating phosphate absorption via root hairs (Giri et al. 2018).

Lateral and adventitious roots increase the volume of soil reached by the root, whose number and distribution are major determinants of root architecture. In rice, crown root plays a vital role in generating lateral root. Auxin signaling is required for crown and lateral root development, as the deficiency of auxin signaling components such as *Ostir1*, *Osaafb2*, *Osiiaa23*, *Osiiaa13* mutants all suppress crown and lateral root growth (Guo et al. 2021; Yamauchi et al. 2019; Kitomi et al. 2012), and gain-of-function of *OsIAA11* blocks lateral root initiation (Zhu et al. 2012; Kitomi et al. 2012). Particularly in *Osiiaa23* mutant, lateral and crown root primordium are absent and the quiescent center (QC) identity is lost in root meristem, indicating a central role of OsIAA23 in specifying crown and lateral root initiation (Jun et al. 2011). *OsIAA23* is specifically expressed in the root QC, therefore, OsIAA23-mediated auxin signaling determines the maintenance of postembryonic root stem cells (Jun et al. 2011). Through mutant screening, the rice *crown rootless1 (crl1)* mutant is identified which is incapable to produce any crown root primordia and *crl5* mutant has very few crown roots (Inukai et al. 2005; Kitomi et al. 2011). Auxin activates *Crl1* and *Crl5* expression, and OsARF1 binds to the promoter region of these two genes to initiate crown roots (Inukai et al. 2005; Kitomi et al. 2011). Thus, *Crl1* and *Crl5* function as mediators to connect auxin signaling with crown and lateral root development. Few crown roots of *crl4* mutants are caused by the mutation of a *guanine nucleotide exchange factor for ADP-ribosylation factor (OsGNOM1)* gene, which is

responsible for vesicle trafficking of PIN transporters (Liu et al. 2009). Correspondingly, overexpressed *OsPIN2* disrupts basipetal auxin transport in root epidermis and reduces lateral root density (Sun et al. 2019). Beside of auxin signaling and transport, auxin synthesis by the TAA/YUC pathway is sufficient for crown root initiation. In rice, *Ostaa1* mutant has few crown roots and a lack of lateral roots (Yoshikawa et al. 2014). Interestingly, the crown rootless phenotype of *Ostaa1* mutant was partially rescued by overexpression of *WUSCHEL RELATED HOMEBOX11 (OsWOX11)*, which expresses in emerging crown roots and in cell division regions of the root meristem (Zhao et al. 2009). *OsWOX11* abundance is stimulated by *OsYUC* overexpressors but repressed in *Ostaa1* mutants (Zhang et al. 2018c). Accordingly, overexpression of *OsYUCs* induces ectopic adventitious root and shortened seminal roots (Zhang et al. 2018c). Apparently, *OsYUC*, auxin and *OsWOX11* establish a fine-tuning module for crown root development (Zhang et al. 2018c). Altogether, despite crown root behaves as a new root organ in rice, auxin regulation for root development is generally conserved in dicot Arabidopsis and monocot rice plants.

Crop plant growth in field is comprehensively affected by a general root architecture, thus it is not possible to consider root growth by a single factor of primary root or lateral root. The root system architecture (RAS) becomes a new criterion in crop planting, since RAS is responsible for nutrient and water absorption which interacts with soil microbial communities. Optimal RAS determines the utilization efficiency of nutrient fertilizer and water, to determine crop adaptation, yield and biomass. RAS has been proposed as the key to second 'Green revolution' (Bender et al. 2016). However, there is no explicit quality index of RAS ideotype for crop breeding due to complex soil environment (Uga 2021; Lynch 2019). Evidences from a certain amount of studies highlight the central role of auxin in orchestrating RAS, thus, design-oriented root breeding can be improved by genetic manipulation of auxin pathways. Actually, to adapt to different abiotic stress conditions, such as drought, hypoxic, nitrogen deficiency or phosphorus deficiency, roots display very different structure which are reflected by the depth of primary roots and the angle and direction of lateral roots (Uga 2021). The steeper root growth angle (RGA), which were formed in response to gravity, enhances rice resistance to drought condition by accessing to deep-soil water (Uga et al. 2015). As the same time, a deeper root system was beneficial for acquisition of nitrate and other nutrients that are more abundant in deeper soil layers (Wasson et al. 2012). In rice, *DEEPER ROOTING 1 (DRO1)* is a major QTL, which controls root growth angle and improves rice grains under drought condition (Uga et al. 2013). *DRO1* is involved in cell elongation in the root tip that causes asymmetric root growth and downward bending of root tip in response to gravity. *DRO1* is negatively regulated by auxin signaling regulator OsARF1/OsARF23, which binds to the promoter of *DRO1*. Therefore, overexpression of *DRO1* confers greater gravitropic curvature to grow roots to deeper soil (Uga et al. 2013). In contrast, in response to hypoxic stress, rice develops soil-surface root (shallow roots) to access oxygen from air by reducing gravity response (Kitomi et al. 2020; Uga 2021). QTL for *SOIL SURFACE ROOTING1 (qSOR1)*, a homolog of *DRO1*, regulates rice yields in high salt condition. Roots of *qsor1* mutant develop particular structure on the soil surface, which enable plants to avoid hypoxic stress. The expression of *qSOR1* is negatively regulated by auxin signaling, which may be caused by the presence of auxin response element in *qSOR1* promoter (Kitomi et al. 2020). *DULL NITROGEN RESPONSE1 (DNR1)* is a major QTL associated

with nitrogen uptake, which encodes an aminotransferase that catalyzes the conversion of indole-3-pyruvate to L-Trp, thus antagonizing auxin biosynthesis. A 520-bp segment in the promoter of *DNR1* is absent in *indica* varieties but present in *japonica* varieties, which coincides with the generally lower *DNR1* abundance in *indica* than in *japonica*. In *indica*, lower protein abundances of DNR1 promotes auxin biosynthesis, consequently stimulates OsARF-mediated activation of nitrate metabolic pathway. As a result, *DNR1*^{*indica*} allele improves rice yielding with reduced nitrate requirement (Zhang et al. 2021). Apparently, auxin biology has been incorporated in optimizing crop root architecture and has great potential for second 'Green Revolution'.

Root symbiosis

In recent years, the goal of crop breeding has gradually moved from high yield demand to sustainable crop developing with high quality and safety. To solve the pollution problem from high amount of fertilizer in soil, utilization of plant growth-promoting microbes could be a wise choice. The beneficial microbes associated with roots facilitate plant growth by providing them with resources like nitrogen or phosphorus (Perez-Montano et al. 2014). Thanks to the development of "omics" approaches, the molecular mechanisms of plant-microbe interaction are gradually uncovered. The promotional effect of beneficial microbes for plant growth can be partially interpreted by auxin production from microbes.

Arbuscular mycorrhiza (AM) is a major root symbiosis manner in rice to provide phosphate and other nutrients (review in (Huang et al. 2022)). AM colonization promotes auxin accumulation in soybean, maize, medicago and tomato (Shaul-Keinan et al. 2002; Kaldorf and Ludwig-Müller 2000; Meixner et al. 2005). In tomato, exogenous auxin treatment or auxin overproduction by loss-of *SIGH3.4* function increases arbuscule abundance, and the elevated auxin response was mainly present within arbuscule-containing cells (Chen et al. 2022). AM colonization stimulates auxin response and auxin level in host roots, meanwhile the over-accumulated auxin level feed-back constrains auxin biosynthesis in host plant (Chen et al. 2022). Inhibition of auxin transport by NPA inhibitor greatly suppresses mycorrhization level (Chen et al. 2022). Hence, auxin is positively correlated with AM colonization, as shown by high auxin level/signaling promotes but auxin deficiency suppresses AM symbiosis (Hanlon and Coenen 2011; Etemadi et al. 2014; Guillotin et al. 2017; Chen et al. 2022). Despite a certain amount of genetic evidences have proved auxin is required for AM colonization, the underlying mechanisms remain to be explored.

Legumes plants can form symbiosis not only with AM, but also with soil bacteria (rhizobia) to generate nodule. Nodule converts atmospheric nitrogen into ammonia to overcome nitrogen shortage in the host plant. Nodule is mainly divided to two type, determinate and indeterminate nodule, relied on the maintenance duration of nodule meristem (Sprent and James 2007). Soybean and lotus produce determinate nodules whose meristem losses soon after nodule formation, but medicago nodule is indeterminate type which possess a persistent apical meristem (Popp and Ott 2011). Auxin response in root hair occurs rapidly in response to rhizobia infection (Breakspear et al. 2014; Nadzieja et al. 2018). An auxin maximum is established by collaborating local auxin biosynthesis, auxin transport and auxin signaling pathways during nodule organogenesis. Local auxin biosynthesis is activated below the site of

rhizobia inoculation in indeterminate nodule (Schiessl et al. 2019). In soybean, the expression of auxin biosynthesis gene *GmYUC2a* reaches peak at the very early stage before the emergence of nodule primordium (Wang et al. 2019b). Beside of local auxin biosynthesis, auxin methyl ester form (MeIAA) is elevated at the early stage of nodule initiation. Silence of *IAA carboxyl methyltransferase 1(IAMT1)*, which converts free IAA into MeIAA, inhibits nodule development in root cortex layer (Goto et al. 2022). PIN-dependent auxin transport is a determinant to establish auxin maximum for organ initiation, including nodule initiation. Loss of *GmPIN1* function in *Gmpin1abc* triple mutant generates clusters of abnormal dividing cells and defective nodule primordia, and thus reducing nodule number (Gao et al. 2021). Once auxin response is defected, nodule initiation and development is also severely influenced, as seen by the decreased nodule number in deficiency of auxin signaling components in *GmTIR1/AFB3*-knockdown lines (Cai et al. 2017) and *GmARF8a*-overexpression lines (Wang et al. 2015).

Not only the sole auxin regulation, auxin also interacts with cytokinin and flavonoid to coordinate nodule initiation. In medicago, cytokinin perception mutant *cytokinin response1 (cre1)* fails to initiate nodule. Meanwhile, polar auxin transport, auxin biosynthesis and auxin signaling pathways are all defective in *cre1* mutant. Surprisingly, nodulation defects of *cre1* mutant can be rescued by application of auxin transport inhibitor (Ng et al. 2015). Deficiency of flavonoid production by silence of *chalcone synthase (CHS)* promotes auxin transport but fails to initiate nodule (Wasson et al. 2006). In *L. japonicus*, the dominant *snf2* mutation, which constitutively activates cytokinin signaling pathway, causes spontaneous nodule formation in the absence of rhizobia. Auxin is over-accumulated in *snf2* nodules, indicating that cytokinin positively regulate auxin accumulation during nodule development (Suzaki et al. 2012). Apparently, an unknown causal relationship exists among auxin, cytokinin and flavonoid for nodule initiation. During soybean nodule primordium formation, flavonoids induce lateral distribution of *GmPIN1* and cytokinin re-orientates GmPIN1 cellular localization (Gao et al. 2021). The coordination of flavonoids and cytokinin on GmPIN1 establish an appropriate auxin gradient at nodule primordium (Gao et al. 2021). Interestingly, nodule and lateral root, as lateral root organs, share overlapping developmental program at their initiation stage, which are both dependent on a local auxin biosynthesis and cytokinin. The core regulator *NODULE INCEPTION (NIN)* stimulates *LOB-DOMAIN PROTEIN 16 (LBD16)*, in turn activates YUC-dependent auxin biosynthesis for nodule initiation in medicago (Schiessl et al. 2019). Therefore, cytokinin signaling positively regulates auxin accumulation for nodulation, but whether flavonoids have a general inhibitory effect on auxin transport during nodule organogenesis is still unknown. Recent studies on Cryptochrome 1(CRY1)-dependent light signaling highlights the promotional effect of light signaling in shoot for soybean root nodulation. The mobile transcriptional factors TGACG-motif binding factor 3/4 (GmSTF3/4) and FLOWERING LOCUS T (GmFTs), which move from shoots to roots, activate nodulation events including upregulation of *GmNIN*, *nuclear factor Y (GmNF-YA1 and NF-YB1)* and *GmENOD40* transcripts(Wang et al. 2021; Li et al. 2022b). Soybean *GmSTFs* are orthologs of Arabidopsis *HY5*, which has been well characterized as a central regulator of light signaling, directly or indirectly controls auxin transport and auxin signaling on transcriptional level (Cluis et al. 2004; Sibout et al. 2006; van Gelderen et al. 2018). Thus, auxin regulation possibly also contributes to GmSTF-dependent soybean nodulation. Taken together, auxin plays a critical role for determinate and indeterminate nodule development (Figure

3). How can we apply the current molecular mechanisms in legume plants breeding, and how can we integrate the belowground root symbiosis with aboveground yield are deserved our further investigation.

Perspective and opportunities in soybean breeding

The studies in *Arabidopsis* are important for understanding the molecular mechanisms of auxin regulations on organ development, and the added information from other crop systems is indispensable to learn the possible applications of auxin in agricultural system. More and more QTLs associated with important traits are related to auxin (Zhao et al. 2021; Bettembourg et al. 2017; Guo et al. 2022; Zhao et al. 2022b; Liu et al. 2015a; Wang et al. 2016; Zhao et al. 2022a; Ping et al. 2022), implying auxin engineering has tremendous potential for manipulation of crop architecture during molecular breeding. According to the 'Green Revolution' concept in rice, Liu et al proposed a potential strategy to achieve ideal soybean plant, with desirable soybean traits of appropriate plant height, more internodes but short internode length, few branches, high podding rate, high ratio of four seed per pod, and small leaf petiole angle (Liu et al. 2020). However, it is impossible to simply transform the experience from rice and maize in soybean breeding. Firstly, compared with the compact shoot architecture for high-density planting in rice and maize, it is hard to quantitatively define the ideal soybean shoot architecture. Since the soybean traits, such as leaf angle, leaf size, podding rate, internode length, branch number show intensively feedback regulation on each other. Secondly, soybean nodule system has been considered in most cropping systems, thus the ideal root architecture and nodule-nitrogen fixation ability should be included in the ideal soybean model. Apparently, soybean breeding requires a global consideration of above- and underground tissues with energy consumption and partitioning (Figure 3). Compared with model *Arabidopsis* plant, two whole-genome duplication results in high redundancy of gene function in soybean. From another perspective, gene redundancy offers a good opportunity to manipulate auxin pathways by generating mild auxin-related aberrant soybean plants, making a possibility to reshape an ideal soybean architecture.

Statements And Declarations

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The authors declare no conflict of interest

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Author Contributions

Linfang Li and Xu Chen carried out the literature review, designed the figures and wrote the manuscript. All authors read and approved the final manuscript.

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Figures

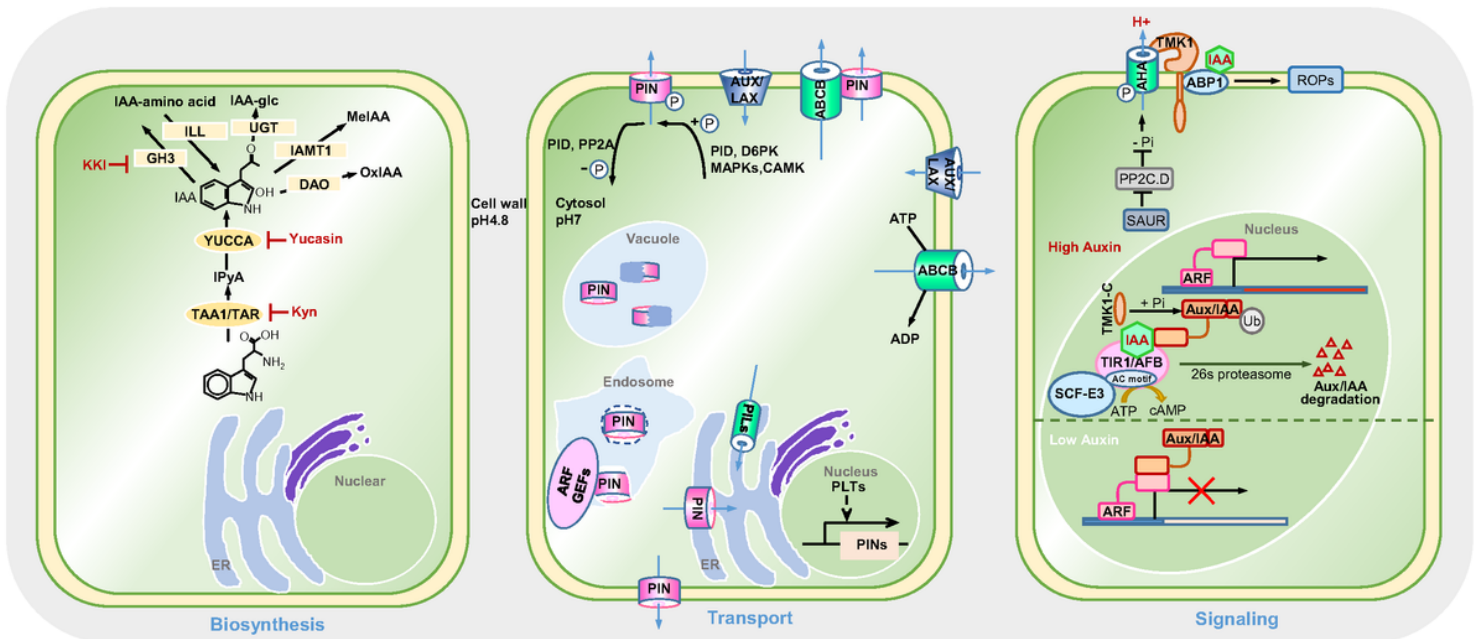


Figure 1

Overview of molecular mechanisms of auxin biosynthesis, auxin transport and auxin biosynthesis in Arabidopsis plants.

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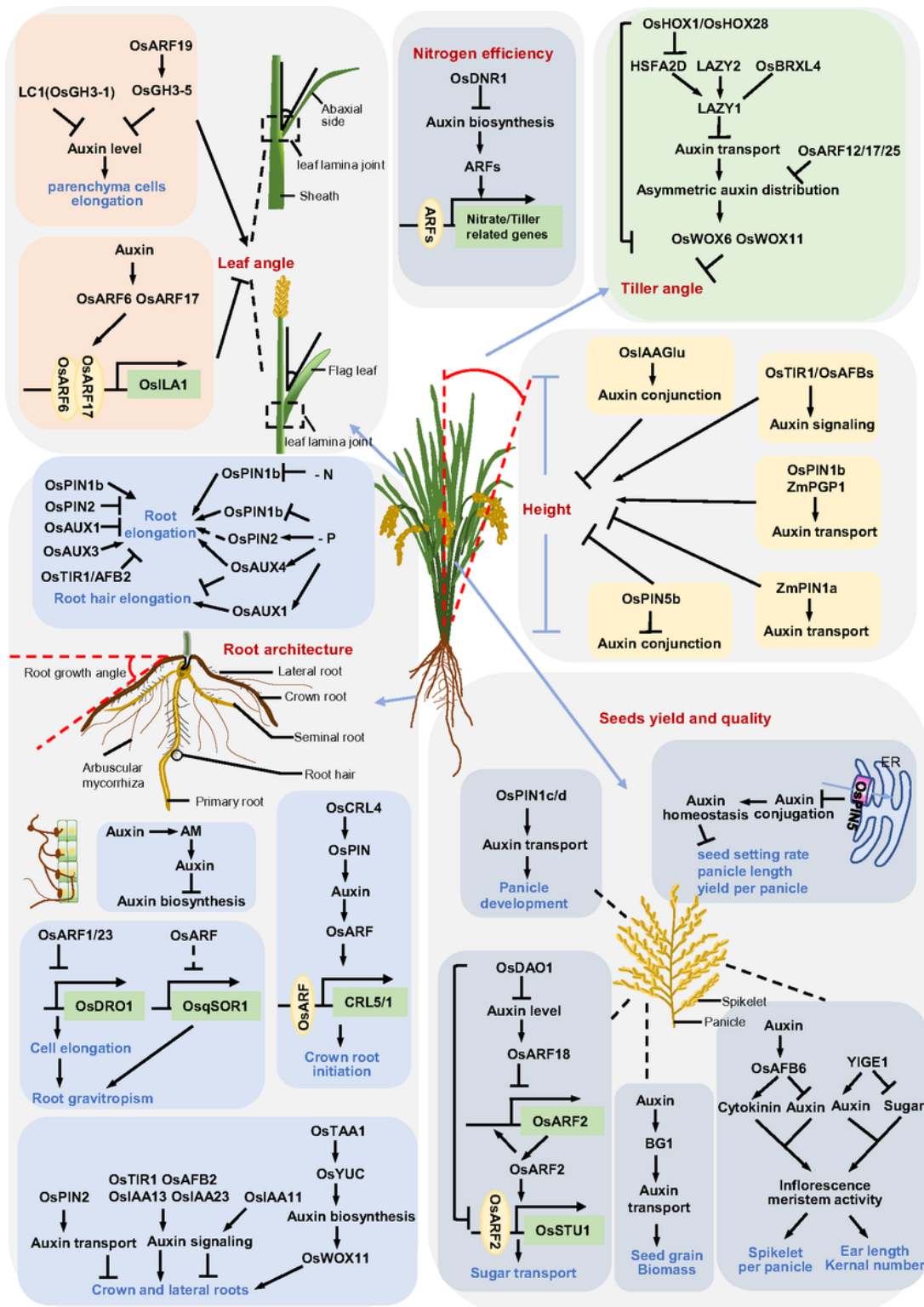


Figure 2

Regulatory network of auxin biology for rice plant development, regarding auxin contributions to shoot height, leaf petiole angle, tiller angle, seed development, root architecture and nutrient absorption.

Arrows indicate promotion or activation; truncated connectors indicate repression or negative effects; dashed arrows indicate the regulatory mechanisms remain unclear. Created with PowerPoint2019.

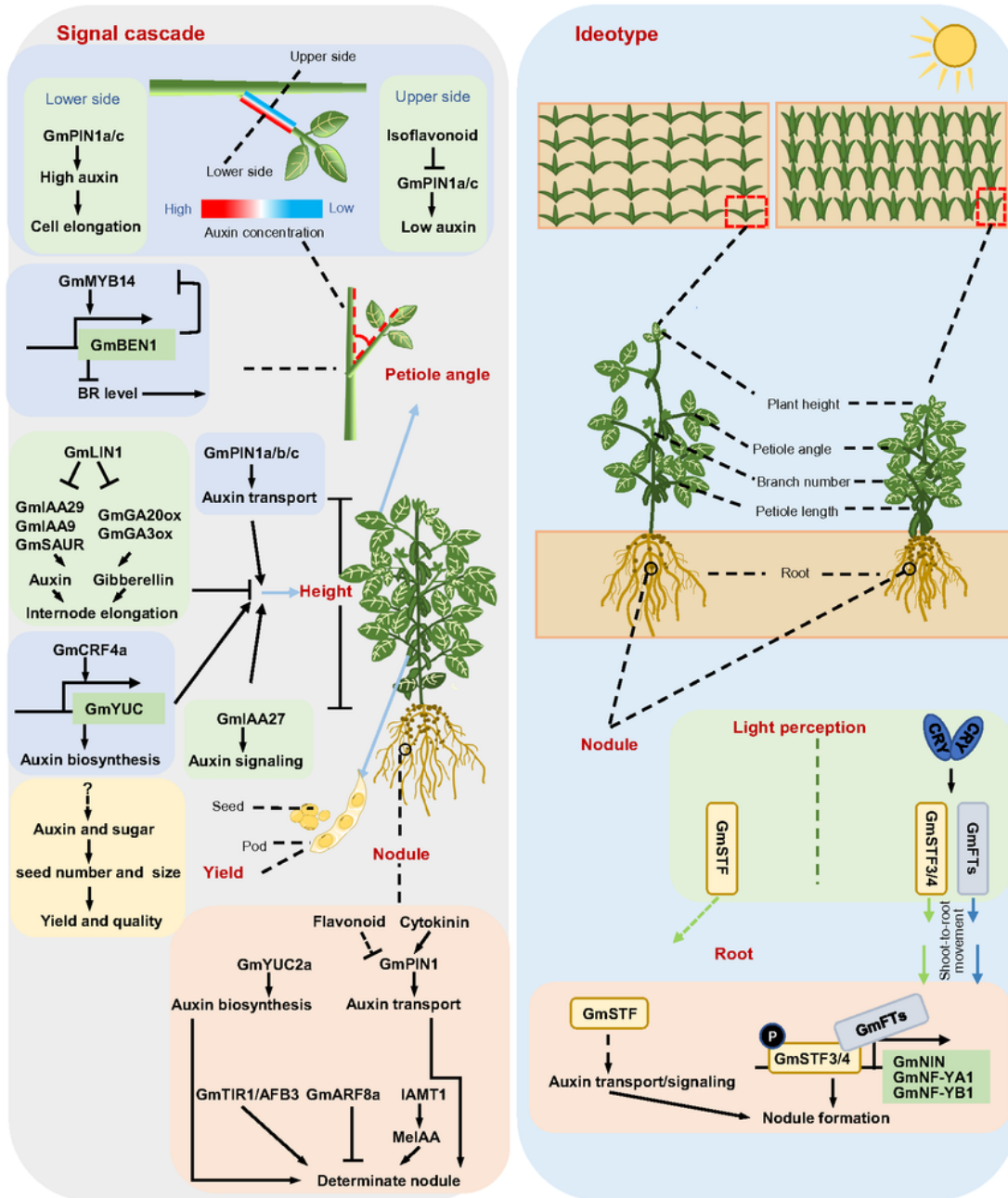


Figure 3

Recent progress of auxin biology for soybean plant development, regarding auxin contributions to shoot height, leaf petiole angle and nodule development. The ideal soybean model with compact shoot architecture, high photosynthesis efficiency and high nitrogen-fixation ability is proposed in the right panel.

Arrows indicate promotion or activation; truncated connectors indicate repression or negative effects; dashed arrow indicate the regulatory mechanisms remain unclear. Created with PowerPoint2019.