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Genetic Regulation of Shoot Architecture

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Abstract

Shoot architecture is determined by the organization and activities of apical, axillary, intercalary, secondary, and inflorescence meristems and by the subsequent development of stems, leaves, shoot branches, and inflorescences. In this review, we discuss the unifying principles of hormonal and genetic control of shoot architecture including advances in our understanding of lateral branch outgrowth; control of stem elongation, thickness, and angle; and regulation of inflorescence development. We focus on recent progress made mainly in *Arabidopsis thaliana*, rice, pea, maize, and tomato, including the identification of new genes and mechanisms controlling shoot architecture. Key advances include elucidation of mechanisms by which strigolactones, auxins, and genes such as *IDEAL PLANT ARCHITECTURE1* and *TEOSINTE BRANCHED1* control shoot architecture. Knowledge now available provides a foundation for rational approaches to crop breeding and the generation of ideotypes with defined architectural features to improve performance and productivity.

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1. FEATURES OF SHOOT ARCHITECTURE

1.1. Diversity in Shoot Architecture

Hundreds of thousands of vascular plant species have distinctive visual appearances and structural features that enable us to recognize, distinguish, and classify them. These differences have evolved to provide each plant type with adaptations suited to a particular environment and strategy for reproduction. Much of the beauty of nature that we see around us is provided by the varied architecture of plants. Although we ultimately hope to understand how such diverse forms have evolved and are formed during plant development, it is beyond the scope of both this review and current knowledge. Instead, we aim to identify unifying principles for the genetic control of shoot architecture. We focus on the few reference and crop species for which we have detailed

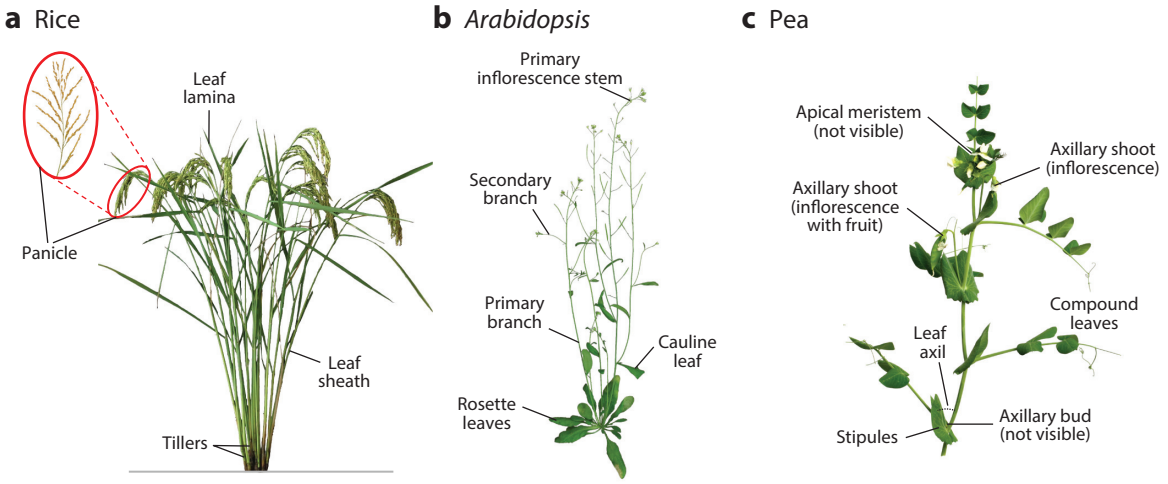

Figure 1

Representation of shoot architectures of (*a*) *Oryza sativa* (rice), (*b*) *Arabidopsis thaliana*, and (*c*) *Pisum sativum* (garden pea). Image in panel *c* from Dreamstime [**https://www.dreamstime.com/**; public domain, Creative Commons Zero (CC0) license].

knowledge, especially *Arabidopsis*, rice, and pea (**Figure 1**), and draw upon specific examples from other species. This review considers only shoot architecture, and we refer the reader to other reviews that consider root architecture (91, 125, 137).

It is imperative to consider crop plants because shoot architecture is fundamentally important to their growth and productivity. Over the last 10,000 years, humans have domesticated and selected a few plants to provide food and materials, and in so doing, selected certain architectural features and phenological characters that lead to greater yield of products, especially seeds and fruits. Further selection and breeding have generated variants with increased yield through improved light interception and photosynthesis and with altered resource allocation. One of the most important advances in plant domestication was the selection of maize (*Zea mays*) from teosinte (*Z. mays* ssp. *parviglumis*), a highly branched grass from Central America. In the selected variants, branching was largely abolished, resulting in a plant comprising a single stem with a terminal male inflorescence (tassel) and usually one lateral female inflorescence (ear or cob). The main gene responsible for this fundamental change that led to decreased branching and an increase in ear size is *TEOSINTE BRANCHED1* (*TB1*) (30, 63), and its orthologs are very important in many species (see Section 4).

A crucial advance in more recent crop genetics was the introduction of semidwarf varieties of wheat and rice. Underpinning the "green revolution," semidwarf genes are involved in metabolism and signaling of gibberellic acids (GAs) (124). Main approaches for increasing crop production include further breeding for plant architectural features, controlling pests, and managing water and nutrients. To meet the challenges of human population growth, urbanization, and environmental change, potential changes in plant architecture may provide solutions and new opportunities for crop production.

Inflorescence: branched structure derived from the stem and bearing multiple flowers

1.2. Plant Architecture as a Product of Development

Plant architecture is plastic; it changes during growth from seedling to mature plant and in response to environmental conditions. This plasticity is brought about by flexible changes in

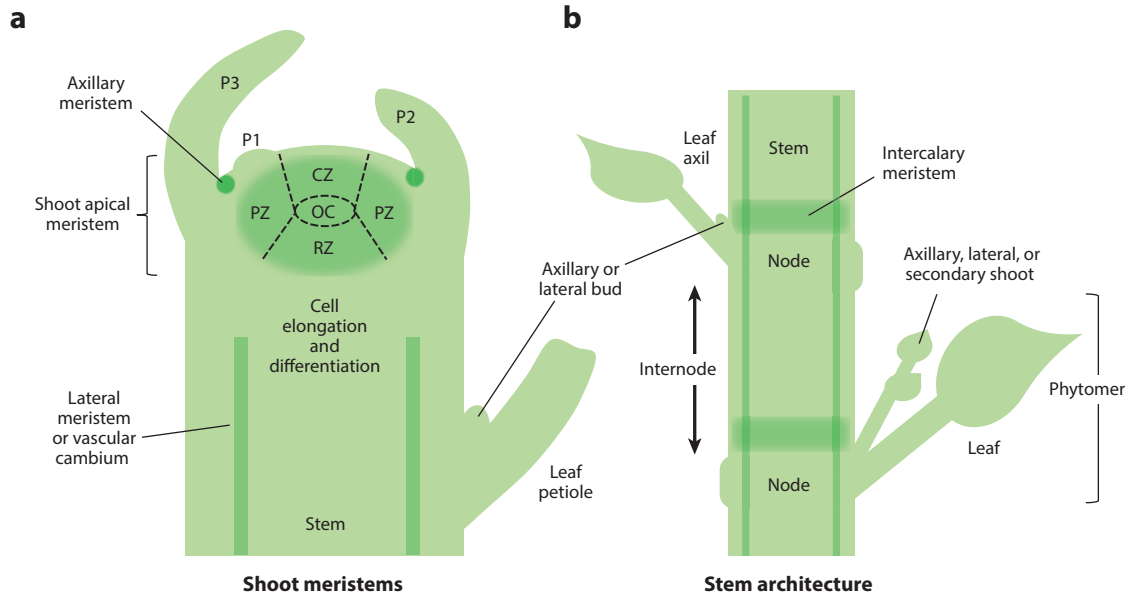

Figure 2

Shoot meristems and architecture. (*a*) Meristems at the shoot apex. P1, P2, and P3 are leaf primordia. (*b*) Stem architecture comprising phytomers and lateral shoots. Images in panels *a* and *b* are not to scale. Abbreviations: CZ, central zone; OC, organizing center; PZ, peripheral zone; RZ, rib zone.

Meristem: a discrete assembly of undifferentiated cells capable of division and subsequent growth to produce new tissues and organs

Shoot apical meristem (SAM): the meristem at shoot apex that gives rise to all other shoot meristems and organs

Intercalary meristem: a meristematic region within the internode of a stem by which the stem can elongate

Axillary meristem (AM): a meristem in the axil of a leaf that gives rise to an axillary bud and axillary shoot

plant development. The body plan is created by meristems that produce new cells and organs (**Figure 2**). The shoot apical meristem (SAM) supports vertical growth. In some plant species, intercalary meristems occur in the stems, which can also give rise to elongation growth. Two types of meristem support lateral growth: axillary meristems (AMs) occur in the axils of leaves and can give rise to lateral or secondary shoots (or branches) and, in some cases, to inflorescences and flowers. By contrast, vascular cambium supports lateral growth in the form of secondary thickening. To avoid potential confusion, we refer to meristems that give rise to secondary shoots as AMs, not as lateral meristems.

Shoot growth and architecture are strictly modular (107). The SAM and resulting AM give rise to the modules known as phytomers (**Figure 2**). A phytomer typically comprises an internode, a node with a leaf, and an AM or bud. Plant growth involves increases in the number and size of phytomers. The SAM adds new phytomers until growth and development stop, such as upon transition to flowering. Morphology is achieved through growth of these modular units and via changes in meristem function, providing flexibility in plant form and function. Phytomers also allow changes in shoot architecture through the outgrowth of lateral buds, producing vegetative and inflorescence branches. The number of branches or tillers is mainly determined by the number of leaves on the primary stem because there is normally only one AM per leaf. However, secondary shoots arising from their leaf axils can produce tertiary shoots.

Plants exhibit polarity and directionality. The SAM and AM represent the main sites for the addition of new cells and organs, and they are carried upward by the growth of the plant. In contrast, the root apical meristem is pushed downward in positive response to gravity. Nutrients and hormones are transported between the meristems and the plant body in defined vascular pathways

to provide resources and to coordinate growth patterns. Thus, there are chemical gradients within the plant that are fundamental to plant development and architecture.

Another fundamentally important contributor to shoot architecture is phyllotaxy. The SAM gives rise to leaf primordia in a strictly defined pattern. In *Arabidopsis* and tomato, leaf primordia normally occur with 137.5° intervals between each, generating a spiral arrangement. In rice, other grasses, and peas, the leaf primordia are arranged alternately at 180° to each other, generating a distichous pattern. The arrangement of primordia determines the arrangement of leaves, which in turn determines the arrangement of secondary shoots or branches. Remarkably, the phyllotaxy can change according to developmental programs. In *Arabidopsis*, the cotyledons and the two first vegetative leaves show a decussate (paired and opposite) pattern, before switching to a spiral phyllotaxis for vegetative leaves and inflorescences and finally to a whorled pattern for floral organs (120).

Timing is associated with two very important factors determining shoot architecture. The time interval between production of each leaf primordium is known as the plastochron, whereas the timing of appearance of new leaves is known as the phyllochron (169). For example, if the phyllochron is short, tillers in cereals can be produced within a shorter time period and hence can be much more uniform in size. With a short phyllochron, inflorescences can also develop synchronously. Such factors are very important for yield and uniformity in cereals (106).

Branch: an axillary shoot arising from an axillary bud; also known as a lateral shoot

Phytomer: a repeating module of plant anatomy comprising an internode, a node with a leaf, and an axillary meristem or bud

Tiller: a lateral shoot arising from an axillary bud at basal nodes in cereals and other grasses

Phyllotaxy: radial patterning of leaves around the stem, established by positioning of leaf primordia on the shoot apical meristem

Plastochron: time interval between the formation of each leaf primordium at the shoot apex

Phyllochron: time interval between the appearances of new leaves

1.3. Shoot Architecture and the Environment

Nutrients profoundly impact architecture by changing resource allocation. In nutrient-rich soil, plants invest more in the shoot relative to the root, thus growing taller or larger. Many plants branch more extensively when supplied with nitrate, ammonium, or phosphate. High nitrogen triggers cytokinin (CK) transport from roots to shoots, whereas phosphate represses strigolactone (SL) biosynthesis. These changes in hormone balance control the outgrowth of lateral shoot buds (see Section 4).

Limited water availability in the soil also affects resource allocation, shifting greater investment to roots instead of shoots. Physical forces from gravity and wind are also important in determining architecture (168). Shoots are typically negatively gravitropic. However, lateral shoots often grow at an angle to the main stem, suggesting that they respond differently to gravity. Wind imposes bending strains and thigmomorphogenic responses that can result in shorter and thicker stems (21, 168).

Light intensity and spectral properties affect shoot architecture through the shade response, reflecting competition between plants for light. Low light and increased far-red light inhibit outgrowth of lateral buds while promoting elongation of the main stem. This is very important for how crop plants respond to planting density: To maximize yield per hectare, plants need to be weak competitors (32).

Duration and periodicity of light control the transition from vegetative to reproductive growth, which plays a major role in determining plant architecture. The induction of flowering triggers a switch from the formation of vegetative shoots to the development of inflorescences. Flowering time is vital in crops to ensure that the appropriate vegetative structure has developed to support optimum grain and fruit production. Synchronous flowering is also important in some crops such as rice to ensure uniform panicle and grain at harvest. By contrast, in others such as tomato, it may be desirable for flowering to continue to extend fruit production. Rice is a short-day plant that flowers when day lengths are less than approximately 12 hours (195). *Arabidopsis* is a long-day plant that produces many more leaves (phytomers) when grown in short days. Thus, phenology and the response to day length are vital for optimal development.

2. MERISTEM FUNCTION

2.1. Shoot Apical Meristem

In terms of shoot architecture, the SAM determines plant phyllotaxy and impacts AM formation. Three zones of cells are also recognized in the SAM (**Figure 2**). The central zone (CZ) contains pluripotent stem cells that continuously divide to provide initials for the peripheral zone (PZ), which generates lateral organs at the flanks, and the rib zone (RZ), which forms the stem tissues (170). Below the CZ is the organizing center (OC), which regulates stem cell proliferation in the CZ and differentiation in the PZ and RZ, thus maintaining SAM organization and function (43). The PZ generates both leaf primordia and the AM that later give rise to vegetative branches or to inflorescences.

Maintenance and differentiation of the SAM involve a complex interaction of auxin, CK, and peptides [e.g., CLAVATA3 (CLV3)], which coordinate expression of the *WUSCHEL* (*WUS*) gene. *WUS* is essential for meristem function because mutations lead to a loss of the SAM. *WUS* is expressed in OC cells, and the WUS protein moves from the OC to the overlying CZ and induces expression of *CLV3*. The CLV3 peptide in turn moves to the OC cells to repress expression of *WUS*. This results in a spatially organized feedback loop that helps to maintain cell identity. This WUS-CLV3 pathway is broadly conserved in *Arabidopsis*, rice, maize, tomato, and, presumably, other species. Expression of *WUS* and *CLV3* is further regulated by CK that activates *WUS* and *CLV3* expression but is subject to repression by auxin signaling and WUS in another feedback loop. These spatially separated feedback loops help define and maintain the zones and OC of the SAM (24, 123).

The WUS-CLV loop maintains balance among SAM activities. Yet, other signals must determine the position and timing of primordium formation, hence they determine both phyllotaxy and plastochron duration. Localized concentrations of auxin define the position of the incipient primordia. In *Arabidopsis*, polarized auxin transport by PIN-FORMED1 (PIN1) establishes the localized distribution of auxin and involves a feedback loop between auxin and *PIN1* expression (136). This raises the question as to how the positioning of PIN1 is established. Members of the PLETHORA (PLT) transcription factor family influence the spatial pattern of *PIN1* gene expression (129), which raises a question about the spatial distribution of *PLT* function. Some evidence indicates a feedback loop involving auxin and *PLT* genes as well as mechanostimulation of *PLT* in response to unequal physical forces within the SAM (120, 127).

CK signaling also plays a role in phyllotaxy (11, 169). In rice, the *DECUSSATE* gene acts in CK signaling in the SAM, and mutation results in decussate phyllotaxy instead of distichous (65). Similarly, in maize, the *aberrant phyllotaxy1* (*abphyl1*) mutant initiates leaves into a decussate pattern through changes to CK signaling (46, 83). Subsequent findings revealed that the *abphyl2* mutant, in which the shoot meristems are enlarged and phyllotaxis switches from alternate to decussate, plays a role in glutaredoxin function (193). Thus, numerous molecular components, physical factors, and complex regulatory interactions determine phyllotaxy in plants.

2.2. Axillary Meristems

During leaf development an AM can develop in the axil and subsequently give rise to a secondary shoot in a two-step process. First, the meristem develops into a bud that is initially inhibited (or dormant). Second, the bud can be activated to grow into a secondary shoot that may be vegetative, giving rise to new leaves and axillary buds (new phytomers), as seen during tillering in rice. Alternatively, it can develop immediately into an inflorescence, as seen in *Arabidopsis* and pea (**Figure 1**). The polar auxin transport (PAT) stream, SLs transported from the roots, abscisic

acid (ABA) produced in the bud, and far-red light can inhibit outgrowth of lateral shoots, whereas CKs and sugars activate bud outgrowth. Lateral shoot outgrowth is fundamentally important for controlling shoot architecture (see detailed discussion in Section 4).

Secondary meristem: a meristem such as vascular cambium by which a stem increases in thickness

2.3. Intercalary Meristems

Stems of some plants contain intercalary meristems that support stem growth independently of the shoot apex. Intercalary meristems occur in the internodes of stems usually immediately above a node (**Figure 2**) and are common in grasses. In rice, stem growth from intercalary meristems occurs during submergence under water and so is of agricultural importance both for direct seeding approaches and for flooding tolerance (114). Relatively little is known about the molecular mechanisms controlling growth of intercalary meristems, but this process is triggered by ethylene and promoted by GA. A novel GA-responsive transcription factor (TF) gene, *OsGRF1* (*Oryza sativa GROWTH-REGULATING FACTOR1*), is expressed preferentially in intercalary meristems of rice, and overexpression in *Arabidopsis* leads to inhibition of stem elongation, suggesting a role in stem growth (173). Subsequent RNA-interference experiments in rice revealed that transgenic lines with reduced *OsGRF1* transcript display delayed growth and development, develop small leaves, and have delayed heading, suggesting that this TF is not specific for intercalary meristems (99). In a separate study, *OsCEN1* and *OsCEN2*, which belong to the *TERMINAL FLOWER 1* (*TFL1*)/*CENTRORADIALIS* (*CEN*) gene family in rice, exhibited distinct expression patterns mainly in the secondary meristems. Overexpression of *OsCEN1* and *OsCEN2* in transgenic rice plants results in increased numbers of internodes, shortened length, and altered radial patterns in the elongated internodes; delayed heading; and abnormal panicle architecture, suggesting that these genes regulate the development of basic structures by stimulating the activities of secondary meristems in the uppermost phytomers (211). Thus, the mechanisms that control the activity of intercalary meristems remain unclear because none of these genes appears to be specific.

2.4. Lateral or Secondary Meristems

Lateral or secondary meristems can be viewed as an internal cylinder of meristematic cells within the stem that causes it to grow laterally (i.e., thicken). The main lateral or secondary meristem is the vascular cambium (**Figure 2**), which divides bidirectionally to produce daughter cells for the inner and outer sides. Outer cells differentiate to produce secondary phloem, whereas inner cells produce secondary xylem. This process may continue throughout the life of the plant to achieve stem thickening to support the whole shoot (141). In herbaceous plants, the vascular cambium plays a minor role compared with its function in woody plants. Another lateral meristem is the cork cambium, which gives rise to the periderm and bark in woody plants.

Stem thickening and robustness are very important architectural features in crop plants because the stem supports the weight of the shoot including fruits and seeds. A strong sturdy stem is vital to achieve optimal branch or tiller angle, to resist lodging, and to facilitate machine harvesting (141). Stem thickening is considered in more detail in Section 3.

2.5. De Novo Meristem Formation and Organogenesis

Plants have a remarkable propensity to replace or repair damaged tissues by forming new stem cell niches that undergo de novo organogenesis to replace lost tissues (135, 149, 190). Dramatically demonstrating this function, detached organs or tissues form pluripotent calli that can regenerate new plant bodies in vitro (13, 35). Controlling the acquisition and maintenance of stem cell

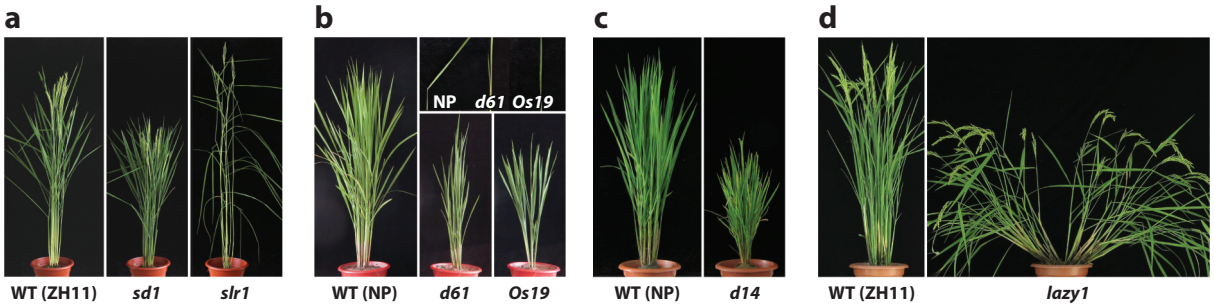

Figure 3

Hormone mutants of rice with altered shoot architecture. (*a*) The *sd1* mutation impairs GA biosynthesis, whereas *slr1* constitutively activates GA response. (*b*) The *d61* and *Os19* mutants are defective in brassinosteroid signaling. Inset shows individual leaves with different leaf angles. (*c*) The *d14* mutant is strigolactone insensitive. (*d*) The *lazy1* mutant shows defective lateral distribution of auxin in stems in response to gravity. Abbreviations: *d14*, *dwarf14*; *d61*, *dwarf61*; GA, gibberellic acid; *Os19*, *OsGRAS19*; NP, Nipponbare; *sd1*, *semidwarf1*; *slr1*, *slender rice1*; WT, wild type; ZH11, Zhonghua11.

activity lies at the core not only of wound responses, but also of diverse developmental programs (40). Auxin, CK, and *WUS* are principle players that mediate somatic pluripotency and de novo regeneration of new stem cell niches. Although not directly relevant to shoot architecture in crops, understanding the mechanisms that control de novo meristem formation is relevant to understanding meristem functioning in general (24).

3. REGULATION OF STEM DEVELOPMENT

3.1. Stem Elongation

Plant height is crucial for adaptation of plants to different environments. Dwarf or semidwarf cereals, which provided the basis for the green revolution, exemplify the importance of stem characters in crops (see also Section 1). Height is determined by several developmental factors such as the number of phytomers and whether a plant exhibits determinate growth or indeterminate growth (see Section 6.5). Here we focus on stem elongation resulting from cell division and expansion from the SAM and intercalary meristems (**Figure 2**).

Stem elongation is controlled by several hormones including GAs, brassinosteroids (BRs), auxin, and SLs (**Figure 3**). It is also controlled by signaling peptides, such as those of the EPIDERMAL PATTERNING FACTOR family, which are recognized by ERECTA-family receptor kinases (160, 171). In SL mutants, a reduction in plant height may be an indirect effect of increased tillering or branching, causing a redirection of resources toward increasing branch number instead of stem elongation (**Figure 3*c***). However, GAs, BRs, and auxin all induce cell expansion.

The cell wall accommodates two apparently conflicting roles: It provides both the elasticity needed for cell expansion and the rigid structural support for tissues and organs. It is composed of a complex network of cellulose, hemicelluloses, pectins, and proteins held together by covalent and noncovalent bonds (153). Cell expansion, therefore, involves cell wall remodeling by breaking some structures and making new ones.

In rice, the GA biosynthesis mutant *sd1* exhibits typical dwarfism while the activation of GA signaling causes higher stature (**Figure 3*a***). A recent study has revealed the genetic link between GA signaling and cellulose synthesis in rice. The DELLA protein SLENDER RICE1 (SLR1)

Determinate growth: shoot growth that is terminated upon loss of apical meristem function such as through terminal differentiation

Indeterminate growth: sustained shoot growth through continued function of the shoot apical meristem

directly interacts with transcription factors NAC29 and NAC31, which activate expression of *MYB61* and *CELLULOSE SYNTHASE* genes. GAs trigger proteasomal degradation of SLR1, release NAC repression, and consequently promote cellulose biosynthesis (58). GA signaling also induces transcription of genes encoding xyloglucan endotransglycosylases and expansins in elongating internodes in rice and *Arabidopsis* (8, 103). These enzymes cleave and regulate xyloglucan polymers and disrupt polysaccharide adhesion, thus increasing cell wall plasticity. In *Arabidopsis* shoot apices, DELLA proteins downregulate expression of several important cell-cycle genes and restrain cell division through direct repression of class I TCP transcription factors, which is important for plant height regulation (28). Thus, GA signaling influences not only cell expansion, but also cell division, in stem elongation.

BRs control cell expansion, as shown clearly in dark-grown seedlings of *Arabidopsis* mutants. For example, BR biosynthesis and receptor mutants have short hypocotyls owing to decreased cell elongation, whereas a dominant constitutive BR signaling mutant has longer hypocotyls (184). In rice and *Arabidopsis* mutants defective in BR biosynthesis or signaling, plant height is dramatically decreased, showing that BRs determine stem elongation in monocotyledonous and dicotyledonous plants (52, 184). BRs are involved in cell wall remodeling and promote cell elongation by stimulating the expression of genes encoding cell wall–loosening enzymes (19, 53, 212). The *brassinosteroid insensitive1* (*bri1*) mutant has reduced expression of *XYLOGLUCAN ENDOTRANSGLYCOSYLASE* genes, and BRs induce synthesis of two receptor-like kinases, HERCULES RECEPTOR KINASE 1 and THESEUS1, which are required for expression of one *XYLOGLUCAN ENDOTRANSGLYCOSYLASE-HYDROLASE* and five *EXPANSIN* (*EXP*) genes (53).

In *Arabidopsis* and rice, two basic helix-loop-helix (bHLH) proteins, ILI1 BINDING bHLH PROTEIN1 (IBH1) and PACLOBUTRAZOL-RESISTANT1 (PRE1), antagonistically regulate cell elongation in response to BRs and GA (85, 210). Recently, a series of bHLH transcription factors including HOMOLOG OF BEE2 INTERACTING WITH IBH1 (HBI1) and ACTIVATOR FOR CELL ELONGATION1-3 (ACE1-3) have been identified as regulators of cell elongation in response to BRs, GA, temperature, light, and developmental stages (6, 64). To promote cell elongation, HBI1 directly binds to the promoters and activates *EXP1* and *EXP8* genes. IBH1 could bind to HBI1 and inhibit HBI1 DNA-binding activity, whereas PRE1 interacts with IBH1 to prevent its inhibition of HBI1 (6). Similarly, ACEs function to activate the expression of cell wall enzymes required for cell elongation. Interaction of IBH1 with ACEs inhibits ACE DNA-binding activities, whereas PRE1 counteracts the ability of IBH1 to affect ACEs (64). Thus, these studies have established a triantagonistic bHLH system that integrates phytohormone signals, environmental changes, and the developmental phase to regulate cell elongation.

Auxin promotes oat coleoptile elongation and phototropic bending (27). As a classical phytohormone regulating plant growth and development, auxin has fundamental roles in rapid stimulation of cell expansion as well as sustained growth over a long time period (145). The mechanisms by which auxin promotes cell expansion and elongation growth are not clear, but they include the control of GA and BR biosynthesis and signaling (186). The role of auxin in tropic responses and, hence, leaf and stem angle is also very important (see Section 3.3).

3.2. Stem Thickness

Stem thickness is important for mechanization of harvesting and for lodging resistance. Evolution and developmental control of lateral meristems have been reviewed in detail (141). Many factors can regulate lateral meristem activity and the secondary thickening of stems. One key player is auxin because removal of the apex reduces lateral meristem activity, but it can be recovered

Inflorescence meristem (IM): a shoot meristem that gives rise to an inflorescence or part of an inflorescence

by apical application of exogenous auxin. Thus, polar auxin transport occurs within the vascular parenchyma, and it also controls vascular cambium activity. SLs are required for controlling stem thickening by auxin, but the mechanism is unknown (3). In *Arabidopsis*, transcriptional regulators SMXL 6, 7, and 8 are required for SL signaling in shoot branching (156, 178), but SMXL3, 4, and 5 are required for phloem development in stems (175). However, in the latter, these proteins act cell autonomously and do not respond to SLs. CKs are essential for cell division in the cambium, and GA and BR signaling influence differentiation of tissues produced by lateral meristems (15). Hormones can also influence stem properties by controlling cell differentiation. For example, mutation in *WALLS ARE THIN1*, which facilitates auxin export from vacuoles in *Arabidopsis*, severely decreases the secondary cell wall thickness of stem fibers without affecting the xylem vessel thickness (133). Development of the vascular tissues is also controlled by signaling peptides, including those of the EPIDERMAL PATTERNING FACTOR family, which regulate the proliferation of procambial cells and their spatial differentiation into xylem and phloem (160, 171).

There are direct links between stem thickening and the induction of flowering. Two MADS-box transcription factor genes, *SUPPRESSOR OF OVEREXPRESSION OF CO1* and *FRUITFULL*, are expressed in the *Arabidopsis* inflorescence meristem (IM) and promote flowering. They also inhibit secondary growth of the stem by affecting the determinacy of cambium (108). In contrast, expression of *CONSTANS* promotes both flowering and secondary thickening in the hypocotyl (151). Mapping and identification of genes that regulate rice architecture including stem height and thickness led to the discovery of *IDEAL PLANT ARCHITECTURE 1* (*IPA1*) (69). Specific *IPA1* alleles result in strong sturdy stems and increased panicle branches (see Section 6). Thus, there is a complex interplay among flowering, inflorescence development, and stem thickening, which deserves further investigation because of its relevance to shoot architecture and crop productivity.

3.3. Stem and Leaf Angle

Stem and leaf angle are vital for optimal light interception and for competition between neighboring plants in natural settings. In arable crops, however, competition between plants is undesirable, so erect forms have been selected. Much progress in understanding the control of stem angle has come from studies of rice where tiller angle is very important for crop productivity. The domestication of wild rice involved selecting for a gene that controls prostrate growth habit. The corresponding *PROSTRATE GROWTH1* gene encodes a C_2-H_2 zinc-finger protein that functions as a nuclear transcription factor. Mutants with this gene disrupted exhibit more erect growth, greater grain number, and higher grain yield, and all cultivated rice varieties carry the same mutation (70, 161).

Tillers or branches exhibit negative gravitropism, which is sensed as mechanostimulation and mediated by the redistribution of auxin in the stem. Sensing mechanical stresses in the responsive cells may include forces generated by the sedimentation of starch granules in gravity-sensing cells called statocytes (55). Thus, in rice, starch-deficient mutants lacking subunits of the key starch biosynthetic enzyme ADP-glucose pyrophosphorylase exhibit reduced gravitropic response, increased tiller angle, and reduced grain yield (118). Consistent with this observation, *Arabidopsis* starchless mutants lacking phosphoglucomutase exhibit reduced gravitropic response (76).

Studies of the rice *lazy1* (*la1*) mutant, which shows weakened gravitropism (**Figure 3*d***), have revealed that *LA1* acts on the polar auxin transport stream to redistribute auxin preferentially to the lower side of the shoot after gravistimulation (87, 201). This results in more extensive growth on the lower side and upward curvature of the stem. The LA1 protein has transmembrane and nuclear localization domains, suggesting that it may shuttle between the plasma membrane and

the nucleus. The *la1* mutant affects both tiller and leaf angle, suggesting a common gravitropic mechanism for stems and leaves (87). Whereas auxin transport–defective mutants generally exhibit severe phenotypes, *la1* mutants exhibit a relatively specific effect that could be due to the particular site of *LA1* expression. However, overexpression of *OsPIN2* increases tiller angle and represses *LA1* expression (23). Recent studies have characterized *LA1* orthologs in *Arabidopsis* (202) and maize (34) as well as the *LAZY1-LIKE* gene family in *Arabidopsis* and *Medicago truncatula* (45, 166). The *ZmLA1* gene regulates shoot gravitropism and inflorescence development and is responsive to auxin and light (34). In *Arabidopsis*, *AtLAZY1* controls the gravitropic response and branch angle of inflorescence stems (202). The *LAZY1-LIKE* genes are expressed in statocytes, and they control shoot and root gravitropism by regulating polar auxin transport in response to gravity stimulation (166). Loss of the *NEGATIVE GRAVITROPIC RESPONSE OF ROOTS* gene, which belongs to the *LAZY* family, results in negative root gravitropism and upward-growing roots in *M. truncatula* and *Arabidopsis* (45). Further evidence for auxin transport comes from a mutant lacking α-1,3-fucosyltransferase (the *fuct1* mutant) with defective PAT and a weak gravitropic response (54).

Evidence for SLs in shoot gravitropism came from the isolation of mutants that suppress the *la1* phenotype. This led to the identification of several *SUPPRESSOR OF LAZY1* genes, some of which encode SL biosynthesis or response proteins. However, a further study showed that SL acts indirectly by suppressing auxin biosynthesis (142).

BRs are also involved in the regulation of tiller and leaf angle. The rice *dwarf61* (*d61*) mutant indicates a role for BR signaling: *d61* exhibits erect leaves owing to impaired development of the lamina joint (**Figure 3*b***) (192). Leaf angle phenotype, designated by the degree of leaf blade bend away from the vertical axis of the leaf sheath, is a typical character of BR biosynthesis and signaling mutants such as *d2*, *Osdwarf4–1*, *d1*, *dwarf and low-tillering*, *m107* (a gain-of-function mutant in BR biosynthetic gene *D11*), *OsGRAS19* RNA-interference plants and knockout mutants generated by CRISPR-CAS9 (**Figure 3*b***), and the *taihu dwarf1* mutant (22, 56, 57, 139, 162, 167, 180). The *D2* gene encodes an enzyme of BR biosynthesis and is important in many rice cultivars (33). Furthermore, rice *LEAF AND TILLER ANGLE INCREASED CONTROLLER* gene encodes a CCCH-type zinc-finger protein and regulates BR signaling. Its mutation results in increased tiller and leaf angle (179). As exemplified by the rice BR-deficient mutant *Osdwarf4–1*, grain yields can be improved under dense planting, even without extra fertilizer (139). Thus, modulating tiller and leaf angles may greatly improve crops.

Another important gene, *LOOSE PLANT ARCHITECTURE1*, is required for the gravitropic response and regulates both tiller and leaf angle (187). In the rice mutant *Ostil1*, *OsNAC2* over-accumulation causes pleiotropic effects in shoot architecture including increased tiller number, reduced plant height, and greater tiller angle (102). *TILLER ANGLE CONTROL1* (*TAC1*) and *TAC3* are particularly important for tiller angle control in rice cultivars, but the molecular mechanism remains unclear (33, 203). The *TAC1* ortholog in maize might control leaf angle and has been utilized in crop breeding to improve shoot architecture (81).

4. MOLECULAR MECHANISMS REGULATING SHOOT BRANCHING

4.1. Initiation of Axillary Meristems and Buds

Shoot branching may be controlled during bud formation and during bud outgrowth. Understanding the control mechanisms and finding genes potentially useful in breeding have benefitted greatly from studies of mutants with altered numbers of lateral shoots or tillers. Some of these mutants fail to produce viable lateral meristems or buds. Most important among the

genes identified, *LATERAL SUPPRESSOR* in tomato, its *Arabidopsis* ortholog *LAS*, and the rice ortholog *MONOCULM1* (*MOC1*) encode a GRAS family nuclear protein (51, 90, 147). The tomato *lateral suppressor* mutant fails to produce lateral meristems during the vegetative phase, but on transition to the reproductive phase, lateral meristems arise in the leaf axils and may induce lateral branches and inflorescences. However, few flowers are produced, and they have defective floral organs compared with wild-type plants (147). The *Arabidopsis las* mutant cannot form lateral shoots during vegetative development but forms lateral buds during the reproductive phase. During vegetative growth, AMs initiate at a distance from the SAM and require LAS function; in the reproductive phase, they initiate close to the SAM and do not require LAS (51).

The rice *moc1* mutant has only a single primary stem (culm) with no tiller, and the panicles produce fewer rachis branches and spikelets than do wild-type plants (90). Failure to produce axillary buds causes this phenotype. Expression of *MOC1* is initially restricted to a few epidermal or subepidermal cells in the leaf axils. It is then expressed in the AM and subsequently the entire tiller bud including axillary leaf primordia and young leaves. In contrast, *MOC1* expression is not detected in the SAM. In wheat, the *TaMOC1* gene is primarily involved in spikelet development (207). These observations indicate that gene function is broadly conserved between species, but detailed phenotypic and developmental effects are species specific.

Expression of *ORYZA SATIVA HOMEOBOX 1* (*OSH1*) and *TB1*, which are required for meristem function and bud activity, is not detected in *moc1*, suggesting that *MOC1* is a key regulator of AM formation (90, 143). Another rice mutant, *tillering and dwarf 1* (*tad1*), has increased tiller number. The *TAD1* gene encodes a coactivator of the ANAPHASE-PROMOTING COMPLEX (APC/C), a multisubunit E3 ligase that helps control the cell cycle. TAD1 interacts with MOC1 and OsAPC10, targeting MOC1 for degradation in a cell-cycle-dependent manner (93, 189). Therefore, the high-tillering phenotype of *tad1* effectively results from elevated levels of functional MOC1.

Another rice mutant exhibits similar phenotypes to *moc1* but is less severe. Although the *moc3* mutant forms lateral buds, they are disrupted and do not form tillers. The *MOC3* gene is the rice ortholog of *WUS* (*OsWUS*). A point mutation in coding sequence causes premature termination of the OsWUS protein and results in the *moc3* phenotype. CKs induce *OsWUS*, and several two-component CK response regulators are downregulated in *moc3* (97). The rice *TILLERS ABSENT1* locus was also identified as *OsWUS*. It induces expression of *OSH1* and plays important roles in maintaining the premeristem zone and in promoting AM formation (164). In addition, a deletion of seven amino acids in the homeobox domain of OsWUS causes the developmental defects of the *sterile and reduced tillering 1* mutant (112). These results show that the WUS regulatory system is essential for AM function in rice.

Other genes required for AM formation in rice are *LAX PANICLE1* (*LAX1*) and *LAX2* (117, 158). The *lax1* and *lax2* mutants are similar: They have fewer AMs at the vegetative stage and lack an AM in most of the lateral branches of the panicle. Although both LAX1 and LAX2 are nuclear proteins and physically interact with each other, only LAX2 contains a plant-specific conserved domain. Yet, LAX1 and LAX2 may act together or in conjunction with other proteins such as MOC1 to regulate AM formation. In dicot plants, a MYB transcription factor gene known as *BLIND* in tomato (146) and its ortholog *REGULATORS OF AXILLARY MERISTEMS* in *Arabidopsis* (113) also regulate AM initiation.

Some aspects of AM development involve the same proteins as in SAM development, whereas other aspects involve proteins that also regulate inflorescence development (183). A future challenge is to understand the mechanisms by which these different meristems are produced. The formation of inflorescence architecture is discussed below (see Section 5).

4.2. Control of Branching by the *TB1* Gene

Discovered in maize, *TB1* is a key gene in the control of branching. A dominant overexpressed variant of *TB1* suppressed lateral shoots during the domestication of teosinte (63). Whereas teosinte is highly branched, commercial maize has a single culm bearing an apical male tassel and a lateral female ear. High expression of *TB1* increased the repression of branching in maize. Causing this increase, the transposable element Hopscotch became inserted ~60 kb upstream of *TB1* ~10,000 years before the domestication of maize. As such, subsequent selection acted on this existing variant rather than on a new mutation (157).

Apical dominance: growth inhibition of axillary or lateral buds by the growing shoot apex

The *TB1* ortholog is known as *OsTB1* or *FINECULM1* in rice and as *BRANCHED1* (*BRC1*) in *Arabidopsis*, pea, and tomato (2, 17, 104, 110). The *TB1/BRC1* gene encodes a TCP transcription factor and is specifically expressed in axillary buds. Consistent with maize, overexpression of these genes suppresses branching, whereas loss-of-function mutations result in increased branching (49). Consequently, researchers hypothesized that *TB1/BRC1* is required to inhibit bud outgrowth and suppress branching. However, more recent studies show that branching can be suppressed even in the absence of *BRC1* and activated in its presence (148). Therefore, *BRC1* may determine bud activation potential and, thus, modulates branching (49, 148).

4.3. Apical Dominance and Outgrowth of Axillary Buds

Outgrowth of dormant or inhibited axillary buds can be triggered by several factors including light quality (far red), nutrients (e.g., nitrate), and damage to the shoot apex. The classical experimental demonstration is to decapitate a plant. Lateral buds then grow out into secondary shoots, demonstrating the shoot apex inhibits bud outgrowth, which is referred to as apical dominance. Because applying auxin to the decapitated shoot often inhibits outgrowth of lateral shoots, researchers hypothesized that auxin provides the primary signal to impose apical dominance (29, 31).

More recently, bud outgrowth has been investigated genetically in several species. Researchers isolated and characterized highly branched mutants including *more axillary growth* mutants in *A. thaliana*, *high tillering dwarf* mutants in rice (*O. sativa*), *ramosus* mutants in pea (*P. sativum*), and *decreased apical dominance* mutants in petunia (*Petunia hybrida*). Several of these genes are required for SL biosynthesis or SL perception, indicating that SLs are new phytohormones that inhibit bud outgrowth to regulate shoot branching (4, 47, 172, 185).

The natural auxin indole-3-acetic acid (IAA) stimulates SL biosynthesis (31, 185), providing a potential mechanism for inhibiting bud outgrowth (**Figure 4**). In contrast, CKs transported from roots to shoot promote bud growth (31, 39). Stimulating CK production via soil nitrate may promote outgrowth of axillary buds. However, auxin may downregulate expression of *ADENYLATE ISOPENTENYLTRANSFERASE* family members and repress CK biosynthesis to antagonize the nitrate effect (115, 163). A key target for hormone signaling is likely the *TB1/BRC1* gene: SL promotes but CK inhibits its expression (36). A role for ABA has also recently come into focus with the demonstration that *BRC1* stimulates ABA biosynthesis through activation of transcription factors involved in the regulation of the ABA biosynthesis pathway (48, 196). Furthermore, GA and BR, respectively, may inhibit and promote bud outgrowth (132). More recently, researchers have proposed that sugars produced in source leaves trigger bud growth when demand from the apex is reduced or lost such as through decapitation. Exogenously supplied sucrose can also promote bud release and repress the expression of *BRC1* (105). Thus, several hormonal, nutritional, and environmental factors act collectively to control bud outgrowth, with *TB1/BRC1* as the focal point determining bud activation potential (**Figure 4**) (148).

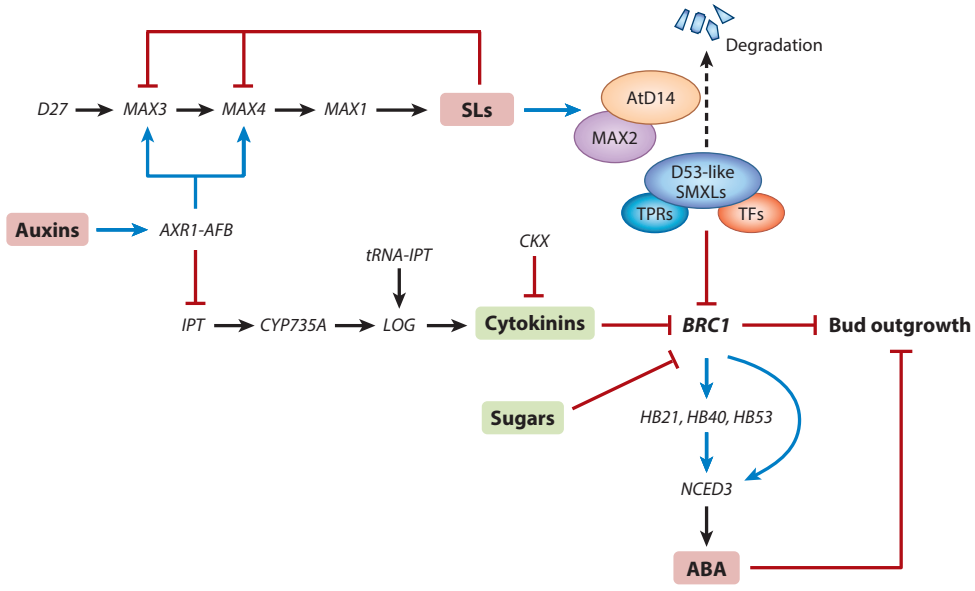

Figure 4

Genetic interactions of major regulatory genes that control shoot branching in *Arabidopsis* and pea. Blue arrows indicate positive regulation, red lines indicate inhibition, and black arrows indicate genetic pathways. In this model, *BRC1* functions as a signal integrator to repress bud outgrowth. SLs activate *BRC1* expression by stimulating degradation of the D53-like SMXL repressor proteins, while repressing their own biosynthesis by downregulating expression of *MAX3* and *MAX4*. Cytokinins and sugars repress *BRC1* expression. Auxins upregulate expression of *MAX3* and *MAX4* but downregulate *IPT* gene family members through the AXR1-AFB-mediated signaling pathway, leading to promotion of SL biosynthesis and repression of cytokinin biosynthesis. In addition, *BRC1* promotes ABA accumulation through transcriptional activation of *HB21*, *HB40*, *HB53*, and *NCED3*, thus triggering suppression of bud development under light-limiting conditions. Abbreviations: ABA, abscisic acid; AtD14, *Arabidopsis* DWARF14; *AXR1-AFB*, *AUXIN RESISTANCE PROTEIN 1-AUXIN SIGNALING F-BOX PROTEIN*; *BRC1*, *BRANCHED 1*; *CKX*, *cytokinin oxidase/dehydrogenase*; *CYP735A*, *cytochrome P450 monooxygenase 735A*; *D27*, *DWARF 27*; D53-like SMXLs, DWARF53-LIKE SMAX1-LIKEs; *HB21*, *HB40*, and *HB53*, *HOMEOBOX PROTEIN 21*, *40*, and *53*; *IPT*, *ADENYLATE ISOPENTENYLTRANSFERASE*; *LOG*, *LONELY GUY*; *MAX1*, *MAX2*, *MAX3*, and *MAX4*, *MORE AXILLARY GROWTH 1*, 2, *3*, and *4*; *NCED3*, *9-CIS-EPOXYCAROTENOID DIOXYGENASE 3*; SLs, strigolactones; TFs, transcription factors; TPRs, TOPLESS-related proteins; *tRNA-IPT*, *transfer RNA isopentenyltransferase*.

4.4. Molecular Model of Lateral Bud Outgrowth

Outgrowth of lateral buds is best explained as a two-phase process, involving first rapid activation and expansion of the bud and then sustained branch growth (**Figure 5**). The first phase of outgrowth is consistent with the "nutritive hypothesis," which is explained in terms of competition for resources (126). In addition to being the source of IAA for the PAT stream, the shoot apex comprising the SAM and expanding leaves is a strong sink for assimilates produced by source leaves. The SAM is prioritized over or competes with axillary buds for resources, the most important of which is likely to be sugar. Upon damage or removal of the apex, resources become available for transport to the lateral buds. Such buds should not be considered dormant because they are fully hydrated and metabolically active, but *BRC1*, the actions of SL and ABA, and limited resources inhibit their outgrowth. The buds may best be considered to be in an "idling" mode

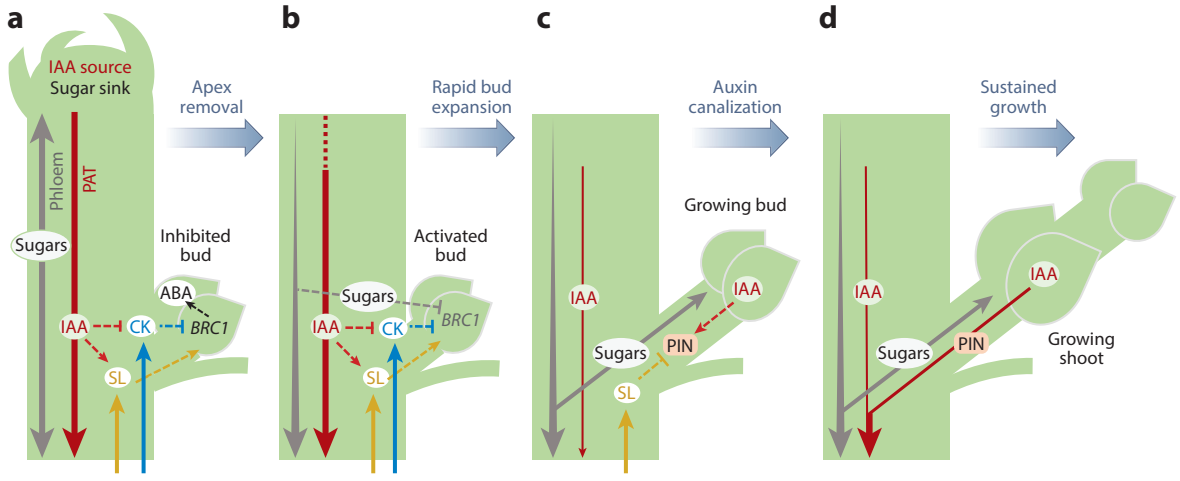

Figure 5

Outgrowth of lateral buds. Dashed arrows indicate positive regulation, and dashed lines indicate inhibition. This unifying model is based mainly on research conducted on *Arabidopsis* and pea plants to explain hormonal and nutritional control of bud outgrowth triggered by removal of the shoot apex. (*a*) A central role for *BRC1* in the inhibition of bud growth is assumed, integrating information from SLs and CK while activating ABA biosynthesis. SLs (*solid yellow arrows*) and CK (*solid blue arrows*) are transported from the roots. IAA activates SL action, which enhances *BRC1* expression, but represses CK action, which represses *BRC1* expression. As a result, *BRC1* expression is activated by IAA. (*b*) Upon removal of the apex (the main sink of sugar), a very rapid redistribution of nutrients occurs through the phloem (*solid gray arrow*). The uptake of sugar by the buds triggers repression of *BRC1* expression, activating metabolism, and uptake of water, leading to expansion growth of the bud. (*c*) Decline in the PAT stream (*solid red arrow*) leads to passive efflux of IAA from the bud, which promotes polarization of PIN proteins for polar export of IAA while SL antagonizes PIN polarization. (*d*) PIN proteins and cellular differentiation in the stem of the axillary shoot establish auxin canalization, leading to vascular connectivity and sustained outgrowth of the axillary shoot. Abbreviations: ABA, abscisic acid; *BRC1*, *BRANCHED1*; CK, cytokinin; IAA, indole-3-acetic acid; PAT, polar auxin transport; PIN, PIN-FORMED; SL, strigolactone.

that the appropriate combination of signals including metabolites, hormones, and light can switch into a growth phase.

Upon removal of the apex, sugars immediately become redistributed in the plant and become available to the buds. Growth of the pea bud is observable 2 h after decapitation. This correlates with the rate of [^{13}C]sucrose transport from the tip to the bud. Furthermore, addition of sucrose to inhibited buds can rapidly activate their growth (105). Studies on shoot branching in barley, sorghum, and wheat have also indicated a strong association between sucrose supply and axillary bud growth (38, 71–73). Furthermore, the rice *moc2* mutant has reduced sucrose supply to buds owing to a disruption of fructose-1,6-bisphosphatase activity. It also exhibits significantly reduced tiller numbers owing to a deficiency in tiller bud outgrowth (79). In contrast to the rapid redistribution of sucrose, depletion of IAA in the PAT stream as a result of decapitation is much slower (7, 18, 105) (**Figure 5**).

The auxin transport canalization hypothesis can explain the second phase of bud outgrowth (138). Depletion of IAA in the PAT facilitates passive flux of auxin out of the bud. This efflux, in turn, results in the upregulation and polarization of PIN proteins in the direction of the flux. PIN proteins are then upregulated and polarized in the direction of the flux. This leads to the establishment of a "canal" exporting the auxin from the bud to the stem (26, 86, 130, 150). Such export of auxin is considered essential for bud growth (31). One important function of SL signaling deduced from studies in *Arabidopsis* is to induce clathrin-mediated endocytosis of PIN1 to deplete

the PIN1 auxin efflux protein from the plasma membrane of cells in the stem (26, 150). This impairs establishment of canalized auxin export from the bud into the stem and inhibits growth of the bud into a lateral shoot (31). Sustained IAA export leads to vascularization, which is necessary to support sustained outgrowth (**Figure 5**). However, outgrowth is not necessarily maintained if the plant environment changes such that lateral shoot outgrowth is slowed or arrested. Thus, the outgrowth of lateral shoots and architecture of the shoot are highly responsive to environmental conditions.

5. INFLORESCENCE DEVELOPMENT

5.1. Types of Inflorescence

Higher plants display a variety of inflorescence architectures progressing in complexity from a solitary flower to structures that contain multiple branches and flowers. The genetic basis of inflorescence initiation and development has been extensively studied in *Arabidopsis* and crops such as tomato (*Solanum lycopersicum*), rice (*O. sativa*), and maize (*Z. mays*) (182). *Arabidopsis* exhibits indeterminate growth, and upon floral induction, its secondary inflorescence branches are initiated from the main stem in a basipetal direction (**Figure 6*a***). Tomato is a model for "sympodial" plants including many trees and numerous other perennial species, and its lateral inflorescence branches develop new branches on the flanks of older branches that have terminated in flowers to give rise to compound inflorescences that undergo multiple flowering transitions throughout their life (**Figure 6*b***) (9). In contrast, rice tillers transition from vegetative to reproductive SAMs to produce panicles that give rise to primary and secondary rachis meristems and further generate spikelet and floral meristems (SM and FM, respectively) in a determinate pattern (**Figure 6*c***). More complicated, maize inflorescence architecture contains two distinct inflorescences, tassel and ear, bearing male and female flowers, respectively. The tassel is derived from the SAM and

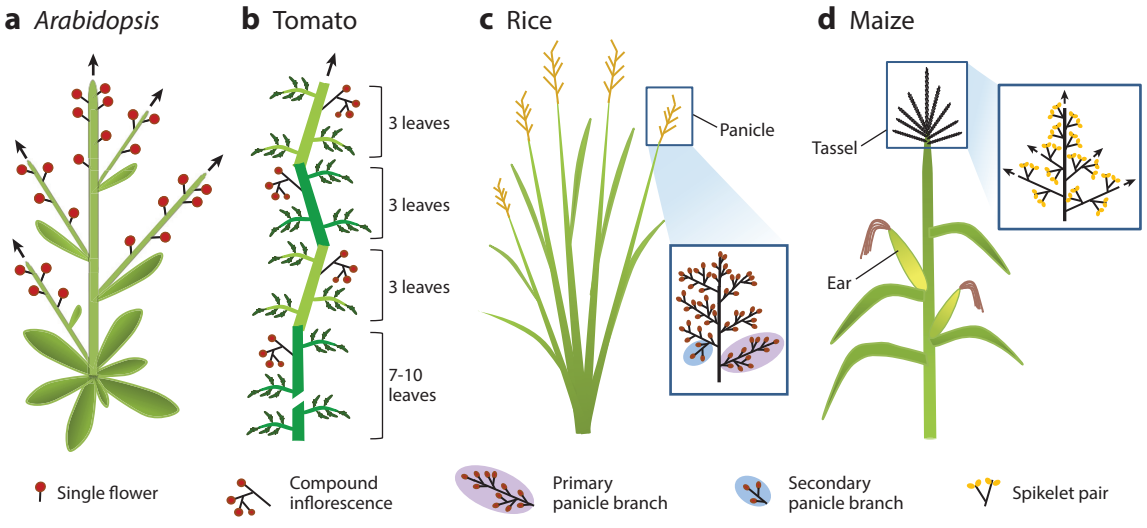

Figure 6

Inflorescence architecture of *Arabidopsis*, tomato, rice, and maize. Black arrows indicate indeterminate inflorescences. (*a*) *Arabidopsis* inflorescence displaying indeterminate growth. (*b*) Tomato produces three leaves before terminating with a compound inflorescence that consists of sequentially formed short branches each terminated with a single flower. (*c*) Rice panicle contains a series of primary and secondary branches. (*d*) Maize tassel and ear are composed of elaborately arranged spikelet pairs.

consists of long, indeterminate branches at its base and a central spike with shorter branches containing spikelet pairs, whereas the ears are positioned laterally in the axils of leaves and contain only short branches (**Figure 6*d***). However, the inflorescence architectures of tassel and ear have a common structure in which an apical indeterminate IM gives rise to a series of determinate spikelet-pair meristems that initiate two SMs, each of which initiates two FMs (37).

Sympodial: refers to growth of determinate plants in which uppermost axillary meristems sequentially adopt the roles of apical meristem

Monopodial: refers to growth of plants upward from the apical meristem only

5.2. Meristem Activities and Inflorescence Branching

The developmental fate of AMs controls inflorescence branching. During phase transition, a vegetative SAM is first converted into an IM, which produces AMs that either transition into flower-bearing shoots or differentiate into flowers (182). In the inflorescence of *Arabidopsis* and maize ear, FMs are directly generated from the IMs. In rice panicle and maize tassel, IMs produce several primary and secondary branch meristems, i.e., rachis-branch meristems, and further develop into SMs. In tomato, a sympodial IM arises and subsequently produces a new IM on its flank before differentiating into an FM. The number and organization of branches initiating SMs and FMs determine variation in inflorescence architecture.

Advances in genetic regulation of IM activity have been comprehensively reviewed (10, 123, 165, 208). Balance between activation and termination of IMs, SMs, and FMs in monopodial plants and variations in sequential meristem termination and reactivation in sympodial plants determine the diversity of inflorescence branching and number of flowers. Here, we provide a brief summary of the critical genes controlling meristem maturation and thus modulating the architecture of multiflowered inflorescence.

5.3. Genetic Regulation of Inflorescence Development

In *Arabidopsis*, the WUS-CLV feedback regulatory loop defines the IMs (see Section 2). Mutation in *CLV1*, *CLV2*, or *CLV3* causes overproliferation of stem cells, leading to enlarged IMs and FMs and increased numbers of flowers and floral organs (25, 41, 67). Several floral identity genes further determine inflorescence morphology. These include *LEAFY* (*LFY*), *APETALA1* (*AP1*), and *CAULIFLOWER*, which determine IM identity, as well as *AP3* and *PISTILLATA*, which regulate the morphology of floral organs (182, 208). The transcription factor LFY is important for activating the expression of multiple floral homeotic genes, and LFY-dependent activation of *AP3* requires the activity of *UNUSUAL FLORAL ORGANS* (*UFO*) (84). UFO is an F-box protein that interacts with LFY to form a flower-specification complex and that triggers degradation of LFY (20, 155). In petunia, *EVERGREEN* encodes the WOX homeodomain protein, which is exclusively expressed in incipient lateral IMs and is required for the activation of *DOUBLE TOP*, the homolog of *UFO* (134).

In tomato, the inflorescence branching mutants *fasciated and branched* (*fab*) and *fasciated inflorescence* (*fin*) exhibit extra flowers and fruit organs owing to enlarged meristems (188). The *FAB* gene encodes the tomato ortholog of CLV1, and *FIN* encodes an arabinosyltransferase that is localized in the Golgi apparatus. The exogenous triarabinosylated tomato CLV3 peptide could rescue the meristem enlargement phenotypes of *fin* but has no effect on the *fab* mutants, suggesting that arabinosylation of CLV3 and related CLE peptides is required to fully activate the conserved CLV-WUS circuit. The triarabinosylation of CLV3 peptide has been demonstrated biochemically in *Arabidopsis* (116).

In contrast, the rate of meristem maturation has a profound influence on tomato inflorescence architecture (121). The tomato *COMPOUND INFLORESCENCE* and *ANANTHA* (*AN*) genes, which encode homologs of WUS-RELATED HOMEOBOX 9 and UFO, respectively, are sequentially expressed during the gradual phase transition of IMs to FMs. They also control

inflorescence architecture by promoting the transition from IMs to flowers. Independent alleles of *COMPOUND INFLORESCENCE* are responsible for most inflorescence variation among domesticated tomatoes, whereas the mutation *an* stimulates branching in pepper plants that normally have solitary flowers, suggesting that temporal changes in the acquisition of floral fate is important for sympodial inflorescences in Solanaceae (94). The tomato mutant *terminating flower* (*tmf*) flowers early and converts multiflowered inflorescence into a solitary flower owing to precocious activation of the conserved floral specification complex encoded by *AN* and *FALSIFLORA*. Thus, TMF regulates the time of *AN* activation to synchronize flowering transition (101).

5.4. Regulation of Inflorescence Architecture in Cereals

The rice *TAWAWA1* gene encodes a homolog of tomato *TMF*. It also suppresses rapid transition of IMs into SMs to regulate panicle architecture. A gain-of-function allele of this gene extends inflorescence branching before spikelet formation and increases both spikelet number and grain number per plant (200).

CKs promote cell division and play a conserved role in regulating reproductive meristem size. The rice QTL *Grain number 1a* (*Gn1a*) encodes a CK oxidase/dehydrogenase OsCKX2 that catalyzes degradation of CK and is preferentially expressed in IMs and flowers (5). *DROUGHT AND SALT TOLERANCE* encodes a zinc-finger transcription factor that directly activates expression of *Gn1a/OsCKX2* (88). Mutations in *Gn1a/OsCKX2*, *DROUGHT AND SALT TOLERANCE*, or *LONELY GUY* (which encodes a CK-activation enzyme) could lead to altered CK distribution in IMs and consequently change the IM and rachis-branch meristem activities (5, 82, 88).

Furthermore, rice *moc1*, *lax1*, and *lax2* mutants display serious defects in the initiation and maintenance of the AM during the vegetative phase and of rachis-branch meristems during the reproductive phase. These defects lead to fewer tillers and compromised panicle development (77, 90, 117, 158), suggesting that different meristems may share similar regulatory mechanisms. The rice *FRIZZY PANICLE* gene and its maize ortholog *BRANCHED SILKLESS1* are required to establish FMs from SMs and prevent AM formation within SMs (78).

In maize, the classical *ramose* mutants *ra1*, *ra2*, and *ra3* display highly branched inflorescence phenotypes. *RA1* encodes a C_2H_2-type zinc-finger transcription factor that directs meristem identity from indeterminate to determinate and is expressed at the primordia of the spikelet-pair meristem in short branches of the tassel (174). RA2 is a LATERAL ORGAN BOUNDARY domain-containing transcription factor that is expressed in the primordia of the spikelet-pair meristem, SM, and branch meristems. RA2 may promote *RA1* expression in the developing inflorescence to limit meristem growth (14). RA3 is a trehalose-6-phosphate phosphatase that may modulate sugar signals through production of trehalose to regulate inflorescence development (144). Moreover, RAMOSA ENHANCER LOCUS 2 (REL2) is a maize homolog of transcriptional corepressor TOPLESS (TPL) and is involved in auxin-related inflorescence development. The *rel2* mutant dramatically enhances *ra1* and *ra2* phenotypes, suggesting that REL2 represses RA1 function through formation of a transcriptional complex (44).

Taken together, meristem identity, meristem size, and the rate of meristem maturation make major contributions to inflorescence architecture, which determines flower number, floral organ size, and, consequently, reproductive success and crop yield. Comparative analysis of key regulatory genes and signaling pathways in inflorescence development in eudicots and grasses is revealing the conserved and divergent aspects of the genetic basis of inflorescence architecture. Further elucidation of the molecular features and evolutionary adaption of critical genes controlling inflorescence morphogenesis will greatly facilitate breeding crop varieties with increased grain yields.

6. PLANT ARCHITECTURE AND CROP BREEDING

6.1. Challenges and Goals

Heterosis: increased vigor and productivity of hybrid offspring relative to the parents; also known as hybrid vigor

Ideotype: a proposed plant type with characteristics suited to a particular purpose or outcome

One of the most important scientific challenges is how an increasing world population will feed itself on a finite amount of arable land (12). Main food crops include cereals such as rice, wheat, and maize as well as potato, cassava, and soybean. Because they are so important, cereals have been the subject of much progress particularly in relation to plant architecture and yield.

Plant architecture is the primary factor underlying "unit area yield" and is important for agricultural practices such as mechanization. Over recent decades, breeding practices have greatly increased cereal grain yield mainly owing to the adoption of semidwarf alleles and the development of hybrids. Characterization and application of semidwarf gene *sd1* has greatly improved the lodging resistance and grain yield of cereals, leading to the green revolution. The application of semidwarf varieties together with associated improvements in crop production almost doubled rice production in Asia between 1960 and 1998 (75). Exploitation of heterosis in maize and rice has been another important application of genetics in agriculture that led to tremendous increases in yield. Discovery of male sterile wild rice *Oryza rufipogon* introduced the possibility of hybrid rice production (204, 205). Further identification of cytoplasmic and environmentally sensitive male sterile mutants greatly facilitated rice breeding and benefitted productivity worldwide (89, 100). New developments in molecular biology, genomics, and genome editing have increased the number of methods and resources used to enhance breeding effectiveness and efficiency.

6.2. Ideal Plant Architecture in Rice

Donald (32) proposed the concept of designing an optimal plant architecture or ideotype for wheat. Subsequently, the International Rice Research Institute proposed a "new plant type" or "ideal plant architecture" featuring few unproductive tillers, more grains per panicle, and thick stems (74). These complex agronomic traits are regulated by multiple QTLs, including *IPA1/WFP*, *Gn1a*, *Ghd7*, *DENSE AND ERECT PANICLE1*, *STRONG CULM2*, and *SPIKELET NUMBER* (5, 42, 60, 69, 111, 119, 159, 191). Among these genes, *IPA1/WFP* has profound effects on rice plant architecture and substantially influences rice grain yield (69, 111, 209); therefore, it deserves particular attention (**Figure 7**).

The *IPA1* gene encodes OsSPL14, a *SQUAMOSA* promoter binding protein–domain transcription factor, and is regulated by OsmiR156 and OsmiR529 (69, 111, 206). A point mutation in the OsmiR156 recognition site relieves OsmiR156-mediated repression on *IPA1*, leading to an "ideal" rice plant with fewer tillers, increased plant height, lodging resistance, and enhanced grain yield (69, 98, 111). Furthermore, characterization of the QTL *qWS8/ipa1-2D* revealed a different mechanism to elevate *IPA1* expression. In the super rice Yongyou12 and related varieties, a natural tandem array in the *IPA1* promoter elevates *IPA1* expression by promoting an open chromatin structure and attenuating the epigenetic repression of *IPA1*. Consequently, enlarged IMs, more primary branch primordia, and increased numbers of primary panicle branches result in superior rice yield (209). Systematic analysis of *IPA1* expression levels and yield-related traits indicate that *IPA1* has opposite effects on tiller number and panicle branches in a dosage-dependent manner. Thus, fine-tuning *IPA1* expression may produce the optimal high-yield plant architecture (209).

Intriguingly, different microRNAs and ubiquitination modifications could regulate IPA1 function at post-transcriptional and protein levels in a tissue-specific manner (**Figure 7**). The *IPA1* transxxcript is targeted mainly by OsmiR156 in the shoot apex but mainly by OsmiR529 in the young panicle (66, 69). In addition, the RING-finger E3 ligase IPA1 INTERACTING PROTEIN1 stabilizes IPA1 in shoot apexes through K63-linked polyubiquitination, but it

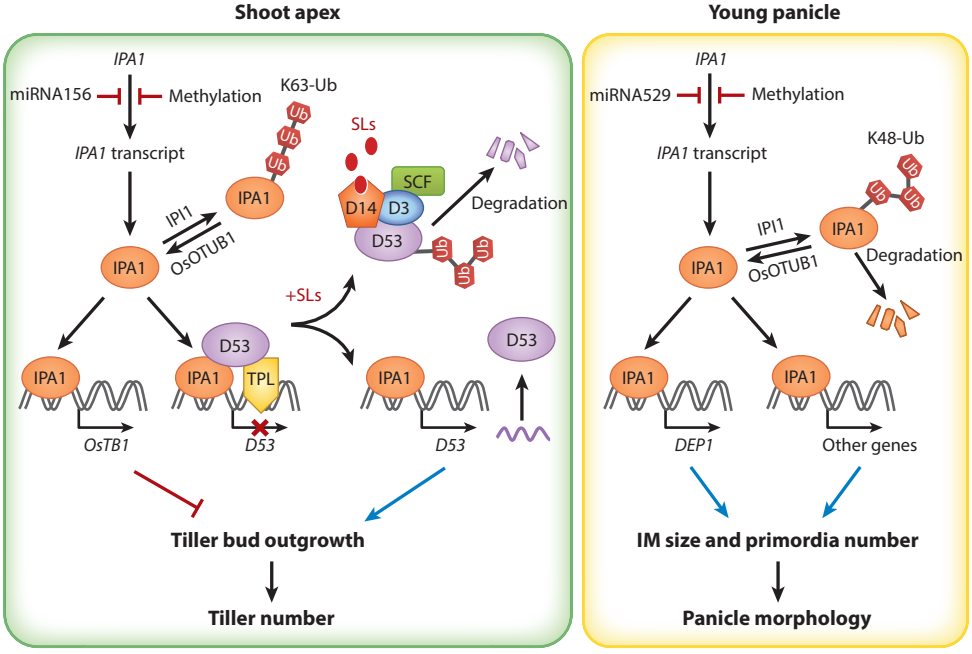

Figure 7

IPA1 gene function in rice. Blue arrows indicate positive regulation, red lines indicate inhibition, and black arrows indicate mechanistic steps. Function is somewhat different in shoot apex (*left*) compared with young panicles (*right*). In shoots, *IPA1* is subject to repression by miRNA156 and DNA methylation. The IPA1 protein promotes expression of target genes including *OsTB1* and *D53*, which inhibit and promote bud outgrowth, respectively. However, D53 is degraded in response to SLs, and D53 protein represses expression of *D53* in a feedback loop. Thus, IPA1 participates in the fine control of tillering, in concert with SLs and potentially other signals. Furthermore, IPA1 is polyubiquitinated at K63, which potentially modulates its activity. In panicles, *IPA1* is subject to repression by miRNA529. The IPA1 protein increases IM size and primordia number through activating expression of numerous genes including *DEP1*. However, IPA1 is subject to polyubiquitination at K48 and degradation, thereby providing further control of panicle development. A RING-finger E3 ligase IPI1 is responsible for ubiquitination of IPA1 at K63 and K48, while OsOTUB1 mediates deubiquitination of K63- and K48-linked Ub and regulates the stability of IPA1. Thus, fine control of IPA1 function in different organs has profound effects on plant architecture and, hence, on yield. Abbreviations: D3, D14, and D53, DWARF3, DWARF14, and DWARF53; *DEP1*, *DENSE AND ERECT PANICLE1*; IM, inflorescence meristem; *IPA1*, *IDEAL PLANT ARCHITECTURE 1*; IPI1, IPA1-INTERACTING PROTEIN1; K48 and K63, lysine 48 and lysine 63; miRNA156 and miRNA529, microRNA 156 and microRNA 529; OsOTUB1, *Oryza sativa* ovarian tumor domain-containing ubiquitin aldehyde-binding protein 1; *OsTB1*, *Oryza sativa Teosinte Branched1*; TPL, TOPLESS; SCF, SKP-CULLIN-F-BOX complex; SLs, strigolactones; Ub, Ubiquitin.

promotes the degradation of IPA1 in panicles through K48-linked polyubiquitination (177). The rice ortholog of human OTUB1 (ovarian tumor domain-containing ubiquitin aldehyde-binding protein 1) has recently been shown to regulate the stability of IPA1/OsSPL14 through cleavage of K48- and K63-linked ubiquitin chains of IPA1 (181). The IPA1 protein functions as a transcription factor that directly binds to GTAC motifs to activate expression of *OsTB1* and *DENSE AND ERECT PANICLE1*. IPA1 also binds to TGGGCC/T motifs through its interaction with PROLIFERATING CELL FACTOR 1 or 2 (98). IPA1 also activates expression of *D53*, which encodes a key target of the SL signaling pathway. Surprisingly, through their physical interaction,

D53 inhibits the transcriptional activator function of IPA1. This indicates that IPA1 functions as one of the long-speculated transcription factors involved in SL signaling (152) and plays a critical role in the feedback regulation of SL-induced *D53* expression (154, 197). These discoveries reveal context-dependent mechanisms and regulatory networks of IPA1 that could provide genetic resources and approaches for breeding high-yield rice varieties.

6.3. Contribution of Heterosis to Rice Plant Architecture

Another way to achieve maximum benefit from the rational design approach is to exploit heterosis or hybrid vigor in crops, as has been achieved with great success in crops such as maize and rice. Heterosis has provided significant yield benefits in hybrids within the *indica* subspecies, which is dominant in Southern Asia including China, India, Vietnam, and Indonesia. More recently, this approach has been extended to include hybrids between *indica* and *japonica* subspecies through identification and application of wide-compatibility alleles (131, 194). Large-scale sequencing and phenotyping of hybrid rice varieties have been used to elucidate genetic and molecular parameters of heterosis (61, 62). Several critical loci contributing to yield traits were identified, and their effects on heterotic advantage were evaluated systematically. In particular, in the *indica-japonica* hybrid, *IPA1* is a critical gene regulating plant architecture. The rare allele *ipa1-1D* significantly enhances grain number per panicle, whereas the wild-type allele *IPA1* promotes panicle number and seed set. The heterozygote *IPA1/ipa1-1D* shows strong overdominance for yield per plant and could explain nearly half of the heterosis advantage in this intersubspecific hybrid cross (62, 209). In the *indica-indica* crosses of a three-line system, the grain yield and flowering time of plants heterozygous for *Heading date 3a*, a rice ortholog of the *Arabidopsis FLOWERING LOCUS T* (*FT*) and tomato *SINGLE FLOWER TRUSS* (*SFT*) genes, were better than for either of the two homozygous parental genotypes. Furthermore, in the *indica-indica* crosses of a two-line system, the QTL *Ghd8* and thermosensitive genic male sterile gene *tms5* had large beneficial effects on grain yield, whereas *LAX1* and *GW3q6* QTL contributed to grain weight and *OsMADS51* regulated heading date (62). These observations open up new opportunities to enhance plant architecture through the use of heterosis.

6.4. Improving Rice Architecture Through Rational Design

Breeding for high yield, superior quality, and multiple-stress tolerance has always been an ultimate goal for crop breeders (176). However, rice yields per hectare have plateaued in China, Indonesia, Japan, and Korea, and although rising in India and Vietnam, the rates of increase are too slow to fulfill the demands (50). Although great advances have been made in developing superior varieties over past decades, improving yield, quality, and resistance traits by traditional breeding approaches is increasingly challenging, owing to the complexity of these agronomic traits and lack of knowledge of how these traits are determined. Therefore, it is important to dissect the genetic networks regulating important agronomic traits and make full use of germplasm resources to develop new and effective breeding systems.

Tremendous progress has been made in understanding the molecular basis of plant architecture and heterosis in cereals as well as in developing thousands of molecular markers for precise marker-assisted breeding (131). Because *IPA1* functions as a central component of a regulatory network shaping the ideal plant architecture in rice (69, 98, 111, 177, 209), beneficial *ipa1-1D* alleles have been introduced into *indica* or *japonica* cultivars by molecular marker-assisted selection. A series of new elite varieties such as "Jiayou Zhongke" have also been cultivated. These varieties show obvious characteristics of ideal plant architecture including moderate plant height, few

nonproductive tillers, strong culms, vigorous roots, and large panicles. They exhibit significantly higher yield as well as improved lodging tolerance and are fit for direct sowing and mechanized cultivation (69, 209; J. Li, unpublished data). Reasonably dense planting can also enhance crop production per unit area without sacrificing quality. The rare alleles *ipa1-1D* and *ipa1-2D* could significantly reduce tiller number while increasing grain yield, allowing further improvement in plot yield through increasing plant density (69, 209). Rice tiller angle is important for efficiency of light capture, disease resistance, and planting density, and genes such as *TAC1*, *TAC3*, and *D2* can help achieve it (33, 203). A beneficial *tac1* allele generates compact plant architecture and has been extensively utilized in densely planted rice varieties grown in high-latitude temperate areas (203). Thus, beneficial alleles of key genes that control rice plant architecture can facilitate the breeding of new elite rice varieties with high yield and fit for agriculture (131).

6.5. Genetic Control of Inflorescence Architecture, Flowering, and Yield in Tomato

Determinate growth and indeterminate growth habits have profound effects on inflorescence branching and compactness, which enable plants to be grown at higher density and simultaneously to increase yield and facilitate large-scale harvesting. In *Arabidopsis*, *FT* is a key flower-promoting gene, whereas *TFL1* is required for a flower-repressing signal (16, 140). Homologs of *FT* and *TFL1* have been targeted for agricultural adaptations in many crops including rice, soybean, tomato, barley, beans, beets, and sunflower (68, 122). The tomato *self-pruning* (*sp*) mutant discovered 90 years ago has facilitated the transformation of indeterminate plants into new determinate forms and radically changed shoot architecture (198). Tomato *SP* is an ortholog of *Antirrhinum majus CEN* and *A. thaliana TFL1* genes and encodes a repressor of flowering in the CETS protein family (92, 128). Tomato *SFT* is an *FT* ortholog and triggers graft-transmissible signals that complement late flowering and highly vegetative phenotypes of *sft* plants (68, 80). Mutations in *SFT* can increase yield in determinate plants (80), and the heterozygous *sft* mutations result in a partial and dose-dependent regulation of flower-promoting activity that weakly suppresses *sp*, leading to more sympodial shoots and inflorescences (68). Furthermore, through screening for suppressors of the *sp* mutant, a weak allele of *SFT* and two mutations in *SUPPRESSOR OF SP* (*SSP*) have been identified to suppress the bushy and determinate growth habit of field tomatoes. *SSP* encodes a bZIP transcription factor that is a homolog of *Arabidopsis* FLOWERING LOCUS D and could form a complex with a 14-3-3 protein, SP, and SFT (1, 122). More importantly, the optimal combination of heterozygous mutations in *ssp* and weak alleles of *sft* could set up a novel partially determinate architecture and further promote increased yields, demonstrating that exploiting combinations of selected mutations in multiple components required for flowering control could optimize tomato productivity. These discoveries offer a new strategy to boost crop productivity in tomato (122).

6.6. Applying Lessons from Rice and Tomato to Other Crops

Genome editing that enables targeted genome modification in various organisms has recently been revolutionizing basic and applied biology, including plant genome engineering and crop breeding. Favorable traits may be created through direct insertion, replacement, or removal of target DNA sequences from a genome using sequence-specific nucleases. This "genome surgery" based on knowledge of critical genes and alleles that control agronomic traits is precise and predictable and allows for simultaneous modification of multiple genetic loci to produce elite varieties, which will greatly facilitate crop breeding (59).

Genome editing based on the CRISPR-Cas9 system has been used to improve critical agronomic traits including crop yield, stress tolerance, nutritional value, and resistance to herbicides and pests (199). Recently, a large-scale CRISPR-Cas9-mediated mutagenesis was applied to generate a mutant library in rice that contains more than 90,000 targeted loss-of-function mutants, providing a useful resource for functional research and rice breeding (96, 109). Furthermore, overexpression of the maize genes *BABY BOOM* and *WUS2* increases the transformation frequencies in maize and other crops including sorghum, sugarcane, and *indica* rice (95), suggesting the transformation efficiency in recalcitrant crop species may be improved through overexpressing more such genes.

Humans have been manipulating crop genomes for more than 10,000 years, albeit in a random and nontargeted manner and most often using only simple trial-and-error approaches (59). Today, the rational design concept, exploitation of heterosis, and genome-editing systems are being simultaneously developed to create new rice ideotypes designed and produced for specific purposes. In the near future, new breeding systems based on integrated information from genetic resources, genome sequences, and gene functions as well as new technologies based on genome editing and effective crop transformation will accelerate improvements in crop plant architecture and drive major advances in crop production.

SUMMARY POINTS

1. Shoot architecture is highly divergent between different plant taxa but is determined by common developmental processes and principles based on meristems and phytomers.
2. The SAM and intercalary meristem support vertical growth; secondary meristems determine lateral growth; AMs produce lateral organs; and IMs give rise to panicles, spikelets, and flowers.
3. GA, BR, auxin, and SLs control plant height through regulating cell elongation and cell division.
4. Gravistimulation, auxin distribution, asymmetric gene expression, and BR responses regulate stem and leaf angle.
5. Shoot branching involves bud initiation, activation, and expansion as well as sustained branch growth, which is regulated by a complex network involving phytohormones, sugars, environmental signals, and gene expression.
6. The *TB1/BRC1* gene serves a central coordinating role in the control of lateral branch outgrowth but does not alone determine it.
7. IM identity, size, and maturation rate collectively determine flower number, floral organ size, and, consequently, reproductive outcome and yield in fruit and grain crops.
8. The *IPA1* gene functions as a central regulator in the formation of plant architecture and has enormous potential for improving grain yield.

FUTURE ISSUES

1. New genes to provide optimal light interception, resource allocation, planting density, robustness, and ease of harvesting in a range of crops should be characterized at the molecular level.

2. Future research should be directed toward understanding the regulation and mode of action of key genes influencing architecture, such as the transcriptional regulator IPA1 in rice, which controls shoot branching, stem thickness, plant height, panicle morphology, and, hence, grain yield.
3. Powerful breeding systems based both on integrated information from functional genomics, genetic resources, and molecular markers and on knowledge of valuable architectural traits will facilitate breeding of defined ideotypes in more crops.
4. Innovations in exploiting heterosis and genome-editing systems of appropriate crops will further accelerate crop development.

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Errata

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