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CEREAL ARCHITECTURE AND ITS MANIPULATION

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ABSTRACT

Our lives depend on an incredibly small number of cereal species whose grain provides more calories to our diet than any other source. The extraordinary productivity of cultivated cereals reflects millennia of selection, recent directed breeding, and modern agricultural practices. Here, we examine selected architectural and agronomic features of major cereal body parts: leaf, branch, inflorescence, stem and root; and discuss how their manipulation enhanced crop performance. Highlighting synergistic research across laboratory models and field-based systems, we consider how diversified molecular circuitry, novel regulators and conserved components of genetic, hormonal and molecular mechanisms control cereal architecture. Lastly, we emphasise the agricultural importance of developmental decisions during cereal growth and propose future perspectives for robust architectural improvement, made ever more urgent by our accelerating climate crisis.

1 INTRODUCTION

Variation within wild grass species provided fertile ground to domesticate cereals. Ancient farmers selected variants which were easy to grow and harvest and whose grain stored well. Further selection, hybridisation and expansion gradually transformed cereals into predictable food sources for early agrarian societies, and our most productive cereals, maize (*Zea mays* ssp. *mays*), rice (*Oryza sativa*), barley (*Hordeum vulgare* ssp*. vulgare*), wheat (*Triticum aestivum*), and sorghum (*Sorghum bicolor*), still provide most of our calories today (90, 190). Selection for beneficial architectural variation was key to this process, and continues in modern breeding (76, 96, 319, 375). For instance, shorter, stiffer stems protect top-heavy cereals from falling over while apically dominant canopies allow for increased stand density. However, our understanding of the genetic and developmental networks controlling architecture in grasses is patchy. Directly relating well-studied architectural regulatory networks in the dicot model plant Arabidopsis to distantly-related and architecturally distinct grasses is challenging. To address a rising global population and pressures on land use, coupled with our climate crisis, cereal yield must rapidly increase under more variable conditions (113), making it imperative to understand architectural decisions in cereals and how to manipulate them for crop improvement.

1.1 Cereal architecture and phytomeric structure

All plants, including cereals, build their bodies from growing shoot and root tips. Above ground, the shoot tip sequentially adds body units or 'phytomers' (29, 389). The morphological nature of phytomer components varies by species and by developmental phase, the latter broadly moving from vegetative to reproductive, so that plant architecture represents an interplay between species-specific features and coordinated identity shifts over time.

The typical vegetative phytomer has a leaf-bearing node, an axillary bud within the leaf-node axil, and an underlying internode (Figure 1.1). In grasses, vegetative phytomers arrange in alternate, opposite positions along the main stem axis. Cereals leaves have basal sheaths and distal leaf blades separated by a boundary hinge or ligular region. The sheath provides structural support by wrapping around the adjacent internode, while the ligular region allows the leaf blade to bend outward, controlling the adaxial area available for photosynthetic light capture, with the abaxial surfaces of the blade and sheath contributing to gas exchange (302). Since stem internodes do not elongate prior to flowering, the vegetative seedling resembles a compressed nodal stack enshrouded by leaf sheaths. Basal-most axillary buds above the soil at 'crown' level can grow into tillers that reiterate the main shoot developmental pattern. <Figure 1.1 near here>

At the vegetative to reproduction transition, the apex shifts from producing leaves to making a flowering stalk or inflorescence (Figure 1.2). The inflorescence generates reproductive phytomers whose axillary buds can directly form spikelets, the basic reproductive unit of grasses, or undergo rounds of branching before spikelet formation. Variation in inflorescence branching underlies diverse inflorescence architectures in grasses, from the compressed spikes or ears of the Triticaceae to the highly branched panicles of rice. The spikelet itself is a mini inflorescence, flanked by subtending glumes, that generates one or more floret buds (160). Since each fertile floret can generate one grain kernel, the number of fertile florets per inflorescence branch, the number of inflorescence branches, and number of tillers with productive inflorescences all contribute to a plant's the grain-bearing potential. During inflorescence development, vegetative internodes above the basal tiller dramatically elongate while their axillary buds remain dormant, forming an unbranched, elongated stalk. Elongation of the final or 'peduncle' internode pushes the inflorescence out of the final 'flag' leaf sheath, an event called heading. Timing and the extent of stem growth as well as photosynthate accumulation and transport, planting density and resource allocation all influence yield (307). <Figure 1.2 near here>

Breeders match suites of beneficial variants in reproductive and vegetative architectural features (ideotypes) to growing conditions and downstream end use (78). Breeding for single genes and/or traits is challenging since individual factors often have both direct and indirect impacts on grain size, number and quality, which can interact, sometimes antagonistically (32, 325, 326, 385, 392, 402). Defining the regulatory modules and interacting pathways that control architecture over time can help dissect these pleiotropic effects.

2. Leaves

Selecting beneficial variation in cereal leaf architecture can improve crop performance (124, 198, 240). For instance, larger, erect leaves more efficiently collect light and increase yield in dense plantings (329, 388) while increasing photosynthetic capacity may help sustainably meet projected yield demands (97, 222, 276, 295, 434). Here, we focus on the development and manipulation of gross leaf architecture traits such as sheath to blade ratio, width, length and angle (219); readers are directly elsewhere for discussions of leaf anatomy, metabolism, senescence and vascular patterning (97, 327, 434).

Leaves develop through cell division, expansion and differentiation along proximodistal (tip to base), mediolateral (middle-to-edge), and adaxial–abaxial (top-bottom) axes (310). Normally Class I *KNOTTED-LIKE HOMEOBOX* (*KNOX*) meristem identity genes, such as *knotted1* (*kn1*) of maize or *ORYZA SATIVA HOMEOBOX 1* (*OSH1*) of rice (142, 241, 271) promote proliferation in the meristem by

enhancing cytokinin and restricting gibberellin biosynthesis (117, 145, 411) and through antagonising expression of differentiation-associated genes (34). Leaf primordia are marked by encircling straps of peripheral cell initials whose high auxin levels downregulate *KNOX* genes. Each primordium's initials bulge off to form an early leaf blade that grows over the shoot apex as proliferation in the basal primordium displaces expanding cells upward (266, 321). The lower part of the primordium strap is made up of an upper region that forms the leaf sheath, and a lower region forming the node, the subjacent internode and the axillary bud of the underlying leaf (152, 160, 310). *KNOX* genes also act as proximal identity factors (94, 95, 330) which are restricted in growing leaf blades by leaf MYB and LATERAL ORGAN BOUNDARY (LOB) transcription factors, an event facilitated by auxin and chromatin modifications (24, 111, 205, 211, 226, 282, 314, 315, 318, 351, 357, 367). Boundary, *KNOX* and *KNOX* co-factor genes are redeployed at the sheath-blade boundary to specify the ligular region (153) which develops a prominent midrib (central vein) and two boundary organs: an adaxial epidermal flap called the ligule and thickened boundary wedges called auricles (160). The leaf blade differentiates first, followed by the sheath and internode whose later elongation elevates the blade into the canopy as the blade unfurls to tilt outward (Figure 1.1, 1.2). Cereal leaf architecture appears controlled by mostly small effect genetic variants while mutant studies indicate a complex interplay of genetics and hormonal signalling regulate multiple features such as leaf angle, discussed below.

2.1 Leaf angle

The leaf angle (LA) between the leaf midrib and the stem (Figure 1.1) determine whether cereal canopy architecture is wide and open or dense and narrow, thereby influencing light penetration, capture and saturation as well as neighbour competition. More upright leaves improve vertical distribution of light through the canopy, increasing both photosynthetic efficiency and possible planting density, leading to strong selection for variants with smaller LA, especially in high-yielding maize and rice (11, 85, 87, 233, 253, 303, 329).

While mechanical strength of the blade and ligular tissues can impact LA (270), morphological variation of the auricle and ligule primarily controls LA (177, 239, 296). The boundary promotes bending since loss of ligules and auricles, such as in the maize *liguleless1* (*lg1*) mutants, lead to upright leaves and more grain (278). *LG1* encodes a SQUAMOSA PROMOTER-BINDING-LIKE (SPL) transcription factor whose orthologs specify and position the boundary in maize, wheat and rice by influencing auxin distribution and *KNOX* gene expression (18, 153, 185, 188, 216, 255–257, 421). Increased adaxial versus abaxial cell elongation in the ligule determines the extent of leaf bending, an event promoted by BRASSINAZOLE RESISTANT1 (BZR1), BRASSINOSTEROID-RESPONSIVE LEAF ANGLE REGULATOR 1 (BLR1) and other factors downstream of brassinosteroid (BR) (15, 37, 38, 48, 73, 143, 303, 346, 410,

422). Other hormones, such as GA and auxin, also regulate LA, often by cross talk with BR (203, 227, 239), while other regulatory genes control LA via this hormonal network. For example, moderate overexpression of the indeterminate domain protein LOOSE PLANT ARCHITECTURE 1 (LPA1) reduces tiller and leaf angle by suppressing auxin-BR cross talk (215, 397) which allows increased planting density without decreasing tiller number or seed weight (343). Quantitative trait loci (QTL) in maize, rice, wheat and sorghum demonstrate the importance of ligular developmental regulators to LA in the field (139, 192, 217, 245, 340, 355, 364). The maize x teosinte *Upright Plant Architecture2* (*UPA2*) QTL is a teosinte-derived regulatory SNP which reduces LG1 activation of *ZmRAVL1*, a gene promoting BR biosynthesis, thus reducing BR content and leaf angle in teosinte (356). This teosinte *UPA2* allele was lost during domestication, but increased yield under dense planting when re-introduced into elite hybrid maize (356), showcasing that wild alleles, potentially deleterious during initial cultivation, can be advantageous under modern agricultural practices. Interestingly, strigalactones (SL), a root-derived hormone, reduce LA in rice under nutrient deficiency (324), potentially explaining nitrogen-dependent increases in LA (229). These examples suggest that targeting hormonal cross-talk and appreciating the interaction between LA and agronomic practices may help manipulate LA for crop improvement.

2.2 Leaf blade to sheath ratio

Erect leaves may be most beneficial higher up (222, 239, 434), leading to the concept of 'smart canopies' which spatially optimise metabolism and architecture (276). Since the shoot meristem generates leaves in sequence, understanding how leaf maturation changes in successive phytomers may help tailor canopy architecture. For instance, the sheath to blade ratio in rice declines over time, thus influencing the blade area available for light capture, a trend recently shown to reflect the progressive reduction in expression of three *BLADE-ON-PETIOLE* (*BOP*) genes (360) which encode BTB-POZ-ANKYRIN transcription factors regulating proximal and boundary tissues in monocot and dicot leaves (120, 235, 244, 349, 361). Spatiotemporal regulation of *OsBOP*s in the rice leaf act downstream of the deeply-conserved phase change pathway mediated by miR156 antagonism of SPL transcription factors (132, 361, 379), emphasising how heterochronic shifts in developmental events influence agronomic traits, a consistent theme in agronomic improvement (379).

2.3 Leaf size

Larger leaves were selected during domestication (249, 289). Many genes link leaf biomass and grain size, but microRNA miR396, GROWTH REGULATING FACTORS (GRFs) and GRF-INTERACTING FACTORS (GIFs) stand out as a central circuit regulating cell cycle and differentiation potential during organogenesis (165, 208). Loss of function *grf* or *gif* mutants have more narrow and smaller leaves,

stems and grain while gain of function mutants show enlarged organs and grain (118, 201, 223, 323, 419). Major alterations to this circuit have limited agronomic potential, but small modulations of the interaction between miR1396 and GRF transcripts appear beneficial and were selected during maize and rice cultivation (208). For instance, a dominant rice QTL for grain size, *GRAIN SIZE of CHROMOSOME2* (*GS2*), resulting from variation within *OsGRF4* that disrupts miR396-mediated degradation, increases seed size and weight, enlarges leaves and accelerates germination without major changes to plant height or inflorescence structure (43, 84). Importantly, *GS2* is a rare allele with potential in current germplasm, as demonstrated for another *OsGRF4* allele with altered miR396 regulation (126).

Leaf size incorporates different variables including leaf length, width and area. Kinematic analyses in maize revealed that leaf basal division zone size increases leaf elongation rate and duration, and thus final leaf length (266, 267). Spatial regulation of GA metabolism plays a central role in regulating division zone size, as well as transcriptional circuits, including miR319-GRF-GIFs, hormonal cross-talk and light interception (59, 265, 323, 348). In addition, the *PLASTOCHRON1* (*ZmPLA1*) gene functions to lengthen the proliferative and elongation phases of leaf growth which correlates with seedling vigour, biomass and grain yield (345), another example of heterochronic control of agronomic traits.

Lateral cells recruited early in leaf development by WUSCHEL HOMEOBOXs (WOXs) proliferate and expand to widen the leaf blade and sheath in multiple grasses (46, 138, 263, 264, 312, 313, 416). WOXs also likely repress *YABBY* (*YAB*) genes important for boundary and mid-rib formation (56, 260, 409), and underlie QTL controlling LA and internode length as well as leaf width in maize (340). Regulatory pathways within the primordium also regulate growth along the lateral axis, such as BROAD LEAF1 (BL1) which controls lateral proliferation of cell files to influence final leaf width in barley (155).

2.4 Leaf surfaces

Opposing adaxial and abaxial leaf identities drive the marginal proliferation necessary to form the smooth, flat leaf lamina (189, 373). HD-ZIP transcription factors conferring adaxial identity and KANADI transcription factors conferring abaxial identity also regulate leaf blade rolling (140, 420) which occurs in grasses due to shrinkage of ‘bulliform’ cells on the adaxial blade epidermis. Other factors, including BR and auxin, control the extent of leaf rolling by regulating bulliform specialisation, polar distribution and size as well as leaf thickness (88, 141, 144, 164, 399, 406, 420). Moderate leaf rolling in rice supports high yields by enhancing photosynthesis and upright posture (396), although variation in drought-induced leaf rolling may not always be related to bulliform size or number (35). Leaf rolling

in wheat may improve water use under drought (331), with suggestions of genetic conservation with rice (371).

2.5 Leaf perspectives

As primary producers, leaves are key to crop productivity. Forward, reverse and association genetic approaches will continue to reveal additional genes and signalling pathways involved in leaf architecture which may be mobilised to improve crop performance. Single cell RNA sequencing provides a highly resolved view of the cell identities and developmental trajectories of complex tissues. Applied to the leaf, this approach is complimentary to genetic approaches and may point to additional regulatory functions important for leaf development and emergence, as recently shown for maize (311).

3 Tillers

Domestication and breeding of barley, wheat and rice produced low and synchronous tillering cultivars, aiding grain harvest. However, the semi-dwarf plants of the Green Revolution show increased tiller number (119, 128, 207, 280) while fertilizers such as Nitrogen (N) and Phosphorus (P) can also increase tillering (17, 44, 297, 387). Fertilisers come with negative environmental impacts, including water contamination (4, 247, 425) and global P shortages may limit P-fertilizer use in the future (4). As such, understanding how endogenous molecular and genetic pathways control resource allocation, tillering and plant architecture will help to sustainably optimize cereal yield.

3.1 Tiller Angle

Tiller angle, defined as the angle between the main stem (culm) and tillers (Figure 1.2), has significant agronomic implications. Crops with excessively wide tiller angle occupy too much space, easily lodge and shade themselves and each other, yet overly compact plants inefficiently capture light. So, optimal tiller number and angle maximizes photosynthetic efficiency and yield. In rice, mutations in the *PROSTRATE GROWTH1*, encoding a C2-H2 zinc-finger transcription factor, were selected during domestication and lead to more erect growth and increased yield (127, 398) as was reduced expression of the TCP transcription factor *TILLER INCLINED GROWTH 1* (*TIG1*) gene (424). While erect growth is a common outcome from selective breeding, compact forms can also increase susceptibility to humidity-related diseases, suggesting that other factors must be considered when breeding for an ideal tiller angle. For example, pyramiding QTLs for disease resistance and wider tiller angle can enhance sheath blight (SB) resistance in rice (438). Dynamic tiller growth where plants show prostrate

growth at tillering stage but decrease tiller angle later on, is an appealing trait to balance benefits and costs of erect tiller angle. Dynamic tiller growth allows for a larger area for photosynthetic accumulation and competition with weeds (68), and may help adapt winter wheat where snow covering prostrate plants protects against freezing (134). In agreement, barley dynamic tillering locus *V-V-HD* only exhibits a prostrate growth habit when sown in winter (431).

Tiller angle is determined by redistribution of auxin signals involved in shoot gravitropism pathways, and accordingly, genes regulating auxin transport control tiller angle in rice (45, 116, 199). For example, modulating polar auxin transport (PAT) by suppressing auxin efflux transporters PIN-FORMED 1a (PIN1a) or enhancing PIN2 increases tiller angle (45, 405) while LAZY1 (LA1) directly enhances PAT to widen tiller angle (150, 154, 414, 423, 433). Overexpression of *OsBRXL4*, a member of the plant-specific Brevis Radix (BRX), widens tiller angle by promoting the nuclear localization of LA1, essential for its function (206). Amino acid substitutions in two conserved residues in the Arabidopsis LA1 ortholog switched shoot gravitropism from negative (upward bending) to positive (downward bending)(415), highlighting LA1 mechanisms and potential rational engineering of conserved regions of *LA1* to control tiller angle. Besides LA1, three QTL loci in rice, *TILLER ANGLE CONTROL1* (*TAC1*), *TAC3* and *D2*, also control tiller angle and were selected during japonica domestication (79). In addition, starch-deficient mutants with defective ADP-glucose pyrophosphorylase (AGP; OsAGPL1) activity and loci involved in SL also alter tiller angle (275, 309). Overall, these studies suggest that tiller angle is a complex trait which should be further explored in different agronomic environments.

3.2 Tiller number

Since each leaf normally develops one axillary meristem, tiller number reflects the number of basal leaves on the primary stem giving rise to secondary shoots, which themselves can produce tertiary shoots. The decision for the bud to grow out or not is environmentally influenced and regulated through sugar availability and hormone signaling, with resource-limited conditions associated with bud dormancy. Several tillering mutants exhibit a higher number of fast-outgrowing leaves or fail to suppress outgrowing bracts (41, 252, 284, 374, 382) while variation in genes involved in auxin transport, BR, GA and SL pathways influence tiller outgrowth (7, 8, 74, 101, 133, 137, 159, 246, 320, 378, 405). Initiation and outgrowth of tillers is thus controlled by complex regulatory networks that respond to internal hormonal and environmental cues to control axillary meristem and bud fate.

Tillers form over three steps: axillary meristem initiation, axillary bud formation and bud outgrowth. In Arabidopsis, *KNOX* genes and genes encoding plant-specific GRAS family of transcription factors

such as *LATERAL SUPPRESSOR* (*LAS*) maintain meristematic potential during axillary meristem initiation (109). These appear partly conserved in cereals: for instance, loss of MONOCULM1 (MOC1), the rice ortholog of LAS, leads to dwarf, single stemmed rice plants due to a failure to form axillary buds, suggesting that MOC1 promotes both axillary meristem initiation and height (109, 202). The DELLA protein SLENDER RICE 1 (SLR1) protects MOC1 from degradation while GA promotes the degradation of SLR1, explaining why semi-dwarf rice cultivars of the Green Revolution show increased tiller number (207). MOC1 targets key branching genes including *SHORT INTERNODES* (*OsSHI*) encoding a zinc finger transcription factor and the rice orthologue of the master branching suppressor overexpressed in modern maize – the TCP transcription factor *TEOSINTE BRANCHED1* (*TB1*) (75, 341, 383). Inhibition of bud outgrowth by TB1 appears highly conserved, including in Arabidopsis (2), rice (FC1/OsTB1) (347), barley (*VULGARE SIX-ROWED* (VRS) 5) (290), wheat (70) and sorghum (SbTB1) (158). A duplicated *TB1* ortholog in rice, *OsTB2*, promotes tillering, potentially through OsTB1-OsTB2 physical interaction, and *OsTB2* variants increasing tiller number were selected during upland rice adaptation (231), exemplifying how close relatives of known tillering genes expand the allelic arsenal regulating this trait.

External, resource and long-distance signals from the shoot (auxin) and root (SL) are integrated by TB1 to control tillering (2, 28, 42, 81, 89, 157, 158, 339, 369, 377, 428). Besides MOC1, other upstream regulators of TB1 include Ideal Plant Architecture 1 (IPA1), a SPL transcription factor, which directly binds to the *OsTB1* promoter to suppress tillering (224). Disrupted miR156 recognition elevates IPA1 function and leads to increased lodging resistance and grain yield (149, 251). The rice CIRCADIAN CLOCK ASSOCIATED1 (OsCCA1) also represses tiller bud outgrowth through positive regulation of both OsTB1, IPA1, and the SL receptor DWARF14 (377) while SL signalling promotes *TB1* expression by regulating degradation of DWARF53 (D53), the rice orthologue of the Arabidopsis MORE AXILLARY GROWTH 2 (MAX2) (358) which can also directly interact to disrupt IPA1 transactivation (335). In contrast, BR signalling promotes tillering in rice through downstream transcription factors, including OsBZR1, which negatively regulates OsTB1 while bound by D53 (89). Since SL induces the degradation of D53-OsBZR1, SL and BR signalling appear to antagonistically regulate OsTB1, and thus tillering, by modulating protein stability.

3.3 Tiller perspectives

Variation in TB1 and its orthologs were selected during cultivation of barley, rice, wheat, and maize (70, 131, 341, 347), but downstream targets of TB1 also played key roles. For instance, TB1 directly regulates the *TASSELS REPLACE UPPER EARS1* (*TRU1*) gene, encoding a BOP protein, which was directly selected and overexpressed in modern maize (80). Interestingly, one of barley's two *BOP* genes, called

HvUNICULM4, acts at axil and leaf boundary regions to control axillary bud differentiation (349) although its relationship with barley TB1 (VRS5) is little explored. Similarly, *grassy tillers1*, another downstream target of TB1 likely selected in modern maize, encodes a *HOX1* gene necessary suppress bud outgrowth under shaded conditions, a regulatory relationship conserved between maize, sorghum and rice, although potentially via different photoreceptors (180, 391). These studies show that regulatory networks underlying master branching regulators, such as TB1, can represent important agronomic targets, especially given high stand densities of modern farming.

4 Flowering time

The primary shoot apex and tiller buds integrate innate developmental signals with environmental input to flower. Core gene domains and families regulating the vegetative to reproductive transition in cereals show some conservation with Arabidopsis but many molecular components appear less conserved. For instance, unlike Arabidopsis, cereals regulate flowering in separate stages from the control of vegetative to floral transition, the rate of development through intermediate stages and/or the time to heading. Since each of these stages influences final architecture, variation in flowering signals and networks played major roles in domestication, inflorescence diversification and in current productivity and projected yield in different climates.

4.1 Vegetative to reproductive development

The vegetative to reproductive transition is normally coordinated by environmental and seasonal changes (Fig 3A); however, many cereal varieties show spring and /or photoperiod insensitive growth habits without tight environmental regulation and cease leaf production earlier relative to the winter/ photoperiod sensitive varieties. While reduced vegetative biomass reduces yield potential, accelerated 'spring' flowering is adaptive in harsh conditions (freezing, drought, high-temperature stress) shorten the growing season, and enables the expansion of wheat and barley cultivation. Cereals use partial or direct counterparts of flowering pathways best known in Arabidopsis, including age, vernalization, photoperiod and gibberellin pathways, but are classified differently.

4.2 Vernalization pathway

Cereals such as wheat and barley use vernalization to delay flowering until after the cold winters typical of temperate climates. Accordingly, this pathway seems absent in tropical cereals (e.g. maize and rice) although homologues of vernalization genes have developmental roles (394). The vernalization pathway, using hexaploid wheat gene names as the example (Figure 4.1), centres around

a MADS-box transcription factor gene called *VERNALIZATION 1* (*VRN1*) (362) whose expression is low during autumn, and the grass-specific *VERNALIZATION 2* (*VRN2*) loci, comprising two genes, *ZCCT1* and *ZCCT2* (220). With the arrival of cold temperatures and short days (SDs), the normally long day (LD) activated expression of *VRN2* decreases while *VRN1* expression increases. VRN1 then activates the expression of *VERNALIZATION 3* (*VRN3*) (also called *FLOWERING LOCUS T –like 1* (*FT-1*)), (65) whose protein likely moves to the apex where it orchestrates the transition, as in Arabidopsis and rice (54). Allelic variation in all these genes shows strong signatures of selection and contributes to variation in the duration and optimal temperatures of vernalization. For instance, dominant mutations in *VRN1's* promoter or intron 1 that increase *VRN1* expression, weaken low temperature requirements and produce a spring habit. In diploid and tetraploid wheat, null mutations in *VRN2* also remove the vernalization requirement, as does overexpression of *VRN3* (*FT1*) (228). Additional genes are involved but their interaction in the pathway is unclear. For further vernalization pathway details please see Temperature Control of Plant Development (272). <Figure 4.1 near here>

Temperature directly regulates VRN1 at multiple levels, akin to vernalisation pathways in Arabidopsis (21): before cold exposure, GLYCINE RICH RNA-BINDING PROTEIN 2 (GRP2), an RNA-binding protein, binds and inhibits accumulation of *VRN1* mRNA but vernalization-dependent modifications on GRP2, recognised by VERNALIZATION-RELATED 2, interferes with this binding (400). SNPs in the GRP2 binding site of *VRN-A1* vary the vernalization requirement (166), suggesting possible breeding values. Characterising more loci may help fine-tune the vernalization response to slow development under warmer climates, accelerate it following colder winters, and provide intermediate requirements in extremely variable winter temperatures.

4.3 Photoperiod pathway

The photoperiod pathway in cereals is also adaptive and directed by selection. Wheat and barley are ancestral LD plants, requiring long photoperiods to trigger flowering, whereas rice is a SD plant, requiring less than 13.5 h of daylight to trigger flowering. Similar to the vernalization pathway, the photoperiod pathway works through a single gene, *PHOTOPERIOD 1* (*PPD1*) whose expression is regulated by light, via PHYTOCHROME C (PHYC), and the circadian clock (322). Mutations in this pathway alter flowering time in crops: for instance, tetraploid wheat lacking *PHYC* flower much later under long-days (Chen et al 2014) whilst mutations in the *PPD-D1* promoter of hexaploid wheat change its circadian regulation resulting in a photoperiod-insensitive vegetative to reproductive transition (20, 322, 366). *CONSTANS-like* (*CO-like*) genes also contribute to photoperiod regulation in wheat and barley, although not to the same extent as in Arabidopsis (214). Additionally, *PPD2* (suggested to be *FT3*) predominantly functions in SD regulation in barley and wheat (115, 182, 436)

while HvFT3/ PPD2-H2 alleles in barley promote flowering even without full vernalization, an adaptive advantage under Mediterranean-like conditions (39). Furthermore, *HvFT3* has a role regulating spikelet initiation (258)(discussed in 5.1). Taken together, combining the major growth response alleles, such as *PPD1* and *VRN1*, with minor genetic loci may help fine-tune adaptation both of flowering time and floral architecture to specific climates.

In rice, SDs promote flowering using a similar genetic framework with a *CO-like* gene *HEADING DATE 1* (*HD1*) regulating *FT-like HEADING DATE 3A* (*HD3A*) and *RICE FLOWERING LOCUS T 1* (*RFT1*) gene expression. Interestingly the CCT-domain protein in rice most similar to VRN2 (wheat) and GHD7 (barley), OsEARLY FLOWERING 3, activates expression of a rice-specific protein EHD1 under SDs and represses Os*GHD7* under LDs (427). Exploiting these genes, and additional LD-promoting loci (342) could expand rice cultivation to more northern regions. Modulating photoperiod, along with vernalization, requirements could help adjust cereal cultivation according to new climate patterns.

4.4 Timing of emergence

In contrast to the rapid vegetative to floral switch in Arabidopsis, the transition in cereals can occur weeks or even months before heading, with intermediate steps differentially regulated. For instance, many cereals undergo the floral transition under SDs, but require inductive LDs for the inflorescence to emerge, as in barley where florets initiated under SD ultimately abort without LD conditions (69). Of the many emergence time QTLs identified in cereals, some are also vegetative to floral transition QTLs, such as *VRN1* and *PPD1*, which could reflect indirect effects on emergence caused by earlier transition delays and/or that the same genes regulate both transition and emergence. The second hypothesis is better supported, not only by VRN1 (193) but also by the *EARLY MATURITY LOCUS 8* (*HvEAM8)* where selection for impaired function accelerates the floral transition and emergence under SDs and LDs irrespective of the *PPD1* allele, enabling photoperiod insensitive flowering in temperate regions (5, 92, 418, 436).

4.5 Flowering time perspectives

Compared to Arabidopsis, monocots have a vastly expanded *FT-like* gene family with some members showing species-specific regulation (107, 115, 258, 283) as in the temperate grass-specific miR5200 mediated photoperiodic control of two *FTs* (*FT1* and *FT2*) (242, 395). Defining *FT-like* gene function, their interactions and environmental regulation may help understand the functional consequences of allelic variation and expand their agronomic use. Variation in *CENTRORADIALIS* (*HvCEN*), a member of PEBP-family containing the *FT* genes, and orthologous to the flowering repressor and *FT*-antagonist *TERMINAL FLOWER1* (*TFL1*), correlates with the expansion of the cultivation range of spring barley

(53, 156, 173). Mutations in *HvCEN* accelerate progression through spikelet initiation, decreasing spikelet number but only under LD, potentially due to released HvCEN antagonism of FT1 (22). New work in rice also supports that TFL1 competes with FT1 for binding sites in 14-3-3 proteins to control both flowering time and spikelet and panicle branch number (156). FT1 also affects the number of fertile spikelets in barley and wheat by modifying the rate and duration of spikelet initiation (23, 69), while increased dosage of TaTB1 promotes paired spikelet formation in wheat by directly interacting FT1 to delay inflorescence development (70). Thus, beyond their roles in flowering time, *FT-like* genes represent important targets for modulating phases of inflorescence development before spikelet fate, thereby influencing important yield components, including branch, spikelet and floret number, a role likely relevant in the field, as shown by *PPD1* regulation of spikelet number via *TaFT2* (107). Defining how FT-like proteins interact with other factors regulating inflorescence meristem behaviour, discussed in the next section, will further add to the complex regulatory networks controlling developmental timing.

5 Inflorescences

While cereal leaf morphology is broadly conserved, cereal inflorescences are remarkably diverse, reflecting differences in branching, meristem identity and fertility (26). In the Triticeae, such as wheat, barley and rye, rows of axillary meristems are initiated which almost immediately acquire spikelet meristem identity, forming single, unbranched spikes lined with pedicellate spikelets. However, axillary meristems in most cereals undergo rounds of branching before terminating in a spikelet meristem, as in the looser panicles of rice and oats, or develop into a specialised branching meristem such as the spikelet paired meristems (SPMs) in panicoid grasses such as sorghum, millet and maize, the latter also producing separate male and female inflorescences (Figure 5.1). Since branching normally stops when axillary meristems acquire spikelet fate and the potential to produce florets, branching decisions are linked with inflorescence productivity, as are floret number and fertility (104, 106, 179, 292, 307, 376). Here, we discuss recent advances of fundamental and agricultural significance. <Figure 5.1 near here>

5.1 Inflorescence meristems and branching

Mutant studies indicate that the size of the shoot apex influences branching potential. Across plants, disruptions in CLAVATA/EMBRYO SURRONDING REGION-like (CLE) mobile peptide signalling cascades that normally restrict meristem size by inhibiting *WUSCHEL-HOMEOBOX-like* (*WOX*) gene expression, lead to enlarged shoot tips with extra branching (27). The interplay between size and branching appears deeply conserved (170, 332) although expansion of *CLE* and *WOX* gene families in grasses,

coupled with functional studies in maize, millet and rice, suggests distinctive molecular circuitries (27, 386, 407, 432). Excitingly, existing and engineered variation in CLE-based signaling can increase inflorescence branch number (and yield potential) in cereals (25, 146, 363, 432) as shown by promoter-editing generation of weak *CLE* alleles in maize (218). Other components also influence meristem size and grain potential, such as the heterotrimeric G-proteins (368): the *dense panicle1* QTL exploited in rice results from an impaired function Gγ subunit allele which enlarges the inflorescence meristem and produces more grain (129, 404). Heterotrimeric G-proteins interact with CLV signalling and cytokinin metabolism to regulate meristematic activity and control panicle branching and grain number in rice (9, 181, 368). In addition, the GRF transcription factors which regulate leaf size (section 1.3.3) also increase axillary meristem size, branch and spikelet number (103).

Besides pathways controlling meristem size, other regulatory players also influence meristem branching. One of the best understood is the maize *ramosa* (*ra*) pathway where regulatory cascades involving three major genes *RA1-3* modulate KNOX to establish determinate spikelet identity and restrict branching (86, 100). While *RA1* and *RA3* appear specific to panicoids, *RA2* orthologs, which encode LATERAL ORGAN BOUNDARY (LOB) transcription factors, suppress branching in other cereals, including barley where HvRA2, called VRS4, works to maintain the unbranched spike form (178, 439). Strikingly, both maize and barley RA2 control TCP transcription factors, including *TB1* orthologs, whose impaired function also leads to branching (13, 58, 284, 286). In fact, suppression of inflorescence branching by *TB1* orthologs appears well conserved in maize, rice, barley and wheat (70, 131, 157, 290, 347) as is the specification of spikelet versus branching identity via the boundary-expressed APETALA2-ERF FRIZZY PANICLE (FZY) factors (49, 66, 71, 72, 130, 175, 285, 317). Quantitative variation upstream from the rice *FZY* locus represses *FZY* expression via BZR1, causing delayed spikelet fate, prolonged branching identity and substantial increases in yield, another example of phase timing modulating crop productivity (16), while another QTL in a distal *FZY* promoter reduces *FZY* expression and increases branch and grain number (384). Selection of variation in expression of *FZY* and *CLE* variation suggests a promising strategy to directly engineer yield, and point to boundary areas around axillary meristems as potential organising centres coordinating meristem fate and influencing yield components (27). For instance, defective BR boundary accumulation in sorghum lead to spikelet branching and the conversion of sterile branches into grain-setting spikelets (412). Taken together, central regulatory cascades, their control of hormone pathways and interactions across meristem boundaries regulate cereal inflorescence meristem potential.

5.2 Spikelets, florets and fertility

Spikelets form axillary floret meristems off an extending rachilla axis. Spikelet number, arrangement and productivity varies across species, reflecting different phyllotactic and determinacy patterns (Figure 5.1). For example, rice and maize inflorescences bear spikelets on spiral branches but spikes arrange spikelets along alternate nodes. However, while wheat spikelets are solitary, barley shows a distinctive spikelet arrangement with each spike node making a triple spikelet cluster of a central spikelet flanked by two sterile lateral spikelets. In maize, spikelet arrangement is sex-specific where the ears bear multiple rows of paired spikelets and the male tassel branches display spikelet pairs in alternate rows (161, 243). In addition, spikelets generate either a fixed number of florets, for example two for maize and one for barley and rice, or a variable number, such as in wheat and Brachypodium which generate an indeterminate number of florets, many of which remain sterile. Inflorescence termination can also differ: the wheat spike which terminates in a single spikelet compared to the barley spike that indeterminately produces spikelets before arresting. Increasing the number of florets produced in determinate spikelets as well as preventing floret abortion are major breeding targets. For example, modulating spikelet determinacy and indeterminacy in rice can produce so-called 'multifloret' spikelets bearing two or three florets (292, 294), a promising avenue to increase grain production (292).

Central developmental checkpoints during later inflorescence formation involves the progression from indeterminate spikelet to determinate floret meristem as well as the differentiation of the floret meristem into perianth and sexual floret organs (6, 160). In addition to *FT-like* genes, the *APETALA2-like* (*AP2L*) transcription factors and their limitation by microRNA172 (miR172), appears crucial to regulate these transitions, mediated in part by controlling rachilla elongation and *MADS*-box genes, especially the *LEAFY HULL STERILE1*-(*LHS1*)-like *SEPALLATA* genes (31, 50–52, 60, 62, 110, 183, 184, 187, 237, 238, 325, 328, 333, 336). For instance, the *SUPERNUMERARY BRACT* (*SNB*) and *INDETERMINATE SPIKELET1* (*IDS1*) *AP2L*-genes in rice establish perianth organ identity and accelerate the spikelet to floret meristem identity transitions by promoting *LHS1*-like *OsMADS1* expression (57, 147, 163, 183, 273, 287, 288), a role conserved in barley and wheat (61, 325, 429). HvMADS1 also has a role in preventing spike branching at high temperatures (194), although whether this involves HvAP2Ls is unclear.

Fertility depends on correct floret organ differentiation and function, with grain set additionally dependent on successful pollination and grain maturation. Floret meristems first form opposing lemma and palea hulls which enclose the stamens and single-ovary carpel with style and stigma; in addition, small sacs called lodicules, in between the stamens and lemma, enlarge at anthesis to open

the lemma hinge and facilitate pollen transfer into the floret (160, 316). Based on orthologous gene expression, lodicules appear analogous to petals, consistent with their pollination role, while hull organs likely represent outer perianth organs (221, 413). Molecular circuits controlling floret organs show conservation with the ABCDE gene model proposed to explain dicot flower development (316) where class 'A' gene activity defines the outer perianth (sepals), 'AB', the inner perianth (petals), 'BC', the stamens, 'C', the carpel, and 'CD' the ovule, with the 'E' class genes contributing to all functions (136, 350). ABCDE genes encode MADS-box transcription factors, except for the class 'A' *AP2Ls* which encode AP2-domain transcription factors (151). Unsurprisingly, aberrant floret development and fertility loss in cereals results from impaired ABCDE gene function (36, 82, 83, 195, 353, 408).

Transcriptomic studies in barley revealed suites of *MADS*-box genes expressed in fertile flowers, many of which appear downregulated in sterile lateral spikelets and potentially downstream of the *VULGARE SIX-ROWED* spike (*VRS*) loci which cause lateral floral arrest shortly after lemma primordium formation in wild type 'two-rowed' barley (32, 69, 213, 352, 439). Defective alleles in *VRS1* and *VRS5* allow continued lateral development and fertility, and were selected during cultivation to generate so-called 'six-row' barley (176, 225, 243, 290). Additional *VRS* alleles lead to partial six-row or *intermedium* phenotypes which can combine to generate novel six-rowed architectures with improved grain uniformity, important for malting grain (439). *VRS3* encodes a histone demethylase (33, 370) but all other cloned *VRS* genes encode DNA-binding transcription factors, some of which are orthologous to branching regulators: *VRS1* (*HvHOX1*) encodes a HD-ZIP (176); *VRS4* encodes the RA2 LOB (178); *VRS2* encodes a SHORT INTERNODES (SHI) transcriptional regulator (417); and *VRS5* encodes barley TB1 (290). Interestingly, TB1 in maize also arrests female sex organs in male tassels (131). Consistent with their branching roles in other grasses, *VRS* alleles influence traits other than row-type such as tillering and spike/spikelet determinacy (178, 209, 417, 439), which also show potential yield benefits in novel higher order *VRS* combinations (439). Upregulated by HvRA2 (VRS4), HvVRS3 and HvTB1 (VRS5), VRS1 is the central downstream integrator of lateral floret infertility (370, 439). Elements of this network function in other cereals, such as the *VRS1* ortholog *Grain Number Increase 1* (*TaHOX1*) in wheat which inhibits floret outgrowth during rachilla development and whose impaired function alleles were selected for increased fertile floret number per spikelet (304). *VRS1*/*HvHOX1*, and its paralog *HvHOX2*, originated from an ancestral gene duplication event. While the function of HvHOX2 is present in most cereals, impaired *HvHOX1* and *TaHOX1* were both selected to increase grain number in barley and wheat, respectively (304, 306). However, in barley, the *Vrs1.t1* allele, underlying the *DEFICIENS* (*DEF*) locus, leads to super suppression of the lateral spikelets and preferentially occurs in specific germplasm, potentially to facilitate resource allocation to enlarge the

central grain (305). Mining the VRS network may improve grain parameters in modern cultivars through controlling floret fertility as well as other architectural traits (439).

Recent work also showed that *AP2L* genes contribute to late perianth, carpel and post-fertilisation development. Ease of hull shedding was positively selected or the hulls themselves or glume bracts have been greatly reduced and/or softened during domestication to increase harvest. In rice, the *APL2 SHAT1* is important for abscission zone development at the base of the lemma (430) while in wheat, miR172-resistant alleles of *TaAP2L5* (the *Q* domestication gene) lead to more easily shed grain due to softer and altered shaped glumes (62, 91, 110, 328). AP2Ls in wheat and barley reduce lodicule swelling, and in cultivars with enhanced APL2 function, often due to disrupted miR172 regulation, show cleistogamy or 'closed' flowering due to unexpanded lodicules, a trait commonly selected to maintain germplasm (1, 61, 125, 262). Double fertilisation of the ovary generates the embryo and endosperm which develop enclosed by maternal ovary tissue. This includes specialised transfer tissues, the integuments (which make the testa or seed coat) and the ovary wall or pericarp, forming the grain fruit or caryopsis (392) which elongates and expands to fill the void between the floret hulls (30), the dimensions of which are proposed to physically limit grain size in rice (196, 197). Multiple rice grain size QTL control hull cell number and/or expansion (232, 291, 293, 299, 326, 334, 385, 426), including *SNB* which restricts floret hull cell expansion (148, 234). Important new work showed that the *HvAP2* gene in barley not only constrains hull, lodicule and pericarp length but also limits integument and maternal transfer tissues proliferation and persistence, associated with promoting endosperm growth (325), consistent with roles in Arabidopsis where AtAP2 restricts integument cell expansion, seed size and seed mass (151, 254, 274). Thus, HvAP2 seems to control both floret shape and grain dimensions while selection of allelic variation in *AP2L* genes was associated with improved grain traits (148, 325, 401), pointing to a possible role of modulation of AP2L function and/or their *MADS-box* targets as important during selection for changes in spikelet and grain during cereal cultivation and potential routes to select for improved grain features.

5.3 Inflorescence perspectives

Defining the functions of more *GRF-GIF-mir396*, *CLE*, *LRR* and *WOX* genes, especially in the temperate cereals, will point to existing and novel routes to modify meristem size and shape for agronomic benefit. Understanding the relationship between floret morphology and grain parameters, as well as stacking of alleles controlling specific branching events, may also point to novel pathways for directed selection for crop improvement.

6 The stem

In cereals, compressed vegetative stem internodes dramatically lengthen acropetally during the flowering phase (160, 300) (Figure 1.2). Overly tall stems are prone to lodge or fall over while semi-dwarf varieties lodge less as well as partition less carbon into vegetative biomass, benefits which contributed to the vast yield improvements of the Green Revolution.

Intercalary meristems just about each stem node drive internode elongation, a strategy only found in monocots with sheathing leaf bases (93). Each internode grows through successive phases from intercalary proliferation, coupled proliferation-expansion to a final expansion stage (277) while remaining enclosed by the leaf sheaths whose earlier elongation provides structural support (167, 269). The peduncle internode can extend longer than the flag leaf sheath to push the inflorescence out, often coincident or shortly after anthesis. Increasing GA levels and/or responsiveness, which leads to degradation DELLA growth-suppressing transcription factors (344), are long known to promote the cell division and expansion necessary for internode elongation, including intercalary growth (162, 300, 301). Elevated GA signalling causes precocious and ectopic internode elongation in cereals (135) while defects in GA metabolism or signalling cause dwarfism, including in Green Revolution cereal varieties (281). For example, a major semi-dwarfing locus in rice, *semidwarf-1*, encodes a GA 20-oxidase (GA20ox) enzyme critical for GA biosynthesis whose defective alleles cause semi-dwarfism (337). The *REDUCED HEIGHT* wheat semi-dwarfs (TaRHT-B1 and -D1) show reduced responsiveness to GA (98) due to truncated, constitutively-active DELLAs (279, 281), as well as changes in flowering time as do polymorphisms in the orthologous maize gene, *DWARF 8* (354).Defects in BR metabolism or signalling underlie other semi-dwarfing alleles (40, 121). Mutations in the barley *uzu* (*HvBRI1*) locus and in the BR biosynthetic genes – *HvBRD* (*BR 6-OXIDASE*), *HvCPD* (*BRASSINOSTEROID C-23 HYDROXYLASE*) and *HvDIM* (*DIMINUTO*) - all show similar phenotypes, including erect and small leaves as well as reduced stature (74). Defective BR signalling is more commonly associated with reduced cell elongation (12, 47, 123, 346), yet loss of function *BRI1* also causes improper formation of the intercalary meristem (410). BR interacts with GA metabolism and signalling to control growth (14, 102, 200, 359) although these interactions are sensitive to developmental context (308).

Study of other semi-dwarf alleles points to a regulatory role for hormone transport in and out of the intercalary meristem. Defective alleles of maize and sorghum genes encoding an ATP-binding cassette type B1 (ABCB1) auxin efflux transporter leads to short, thick internodes (259) with abnormal nodal vasculature, while defective auxin transport out of the intercalary meristem in maize correlates with reduced intercalary proliferation (171). As internode elongation is specifically linked to reproductive development in cereals (268), understanding vascular patterning and transport dynamics in intercalary meristems both before and during elongation may help reveal mechanistic links

coordinating internode elongation with flowering. For instance, control of nodal patterning in maize by BLH transcription factors is crucial for proper intercalary proliferation (365) while inflorescence-derived auxin appears necessary for GA biosynthesis in the barley internode (393) with GA actively mobilised to the intercalary region in rice (250). Specific regulation in different parts of the cereal stem may also be relevant: for instance, the rice *ELONGATED UPPERMOST INTERNODE* gene encodes an enzyme which deactivates GA specifically in the peduncle internode (435), while a gibberellin 2-oxidase, which also deactivates GA, encoded by the *SHORTENED BASAL INTERNODES* gene, specifically limits basal internode expansion (212). New work also shows that two FT-like flowering signals in rice control GA signalling in intercalary regions to synchronise internode growth with the flowering transition (108). Taken together, modification in hormone metabolism, transport and signalling appear key to linking and modulating internode growth in cereals during flowering and further understanding of these pathways may reveal new ways to control stem growth in cereal crops to improve yield.

6.1 Stem perspectives

Finding new routes to semi-dwarfism is important since the green revolution alleles have undesirable pleiotropy, such as reduced seed germination and vigour (261). Studying other components which specifically regulate internode growth may help us selectively control internode growth. For example, BR activates OsMIR396d expression while OsGRF6 promoted GA biosynthesis and signalling suggests that miR396-GRF coordinates a dynamic interplay between BR and GA, consistent with impaired elongation and intercalary activity from GRF and GIF defects (165, 208). Other miRNA modules also influence internode growth. In barley, *ZEOCRITON* (*ZEO*) alleles encoding miRNA172-resistant *HvAP2* transcripts delay the transition to floret development (125) and prolong weakened intercalary proliferation, block final expansion and accelerate vascularisation leading to dwarfism and severely dense spikes (277). *ZEO* leads to reduced GA responsiveness, but also elevated jasmonate (JA) phytohormone-related gene expression and JA sensitivity; since JA antagonises GA-promoted growth (112), miR172 may restrict HvAP2 activity to dampen the JA pathway and allow for rapid GA-promoted internode elongation at flowering (277). Taken together, miRNA regulated transcription factors such as the GRF-GIFs and AP2Ls may be important mediators of hormonal crosstalk to link floral progression and internode development.

7 Below ground

The root system is essential to the plant's sessile lifestyle by providing structural support, facilitating and sensing soil water and nutrients and through responding to biotic and abiotic stresses. Accordingly, root systems are vital to crop performance, resiliency and yield. Understanding how roots sense and perceive changes in the soil, combined with accurate phenotyping, is important to learn how plants adapt to their environment and for genetic improvement of crop root systems.

7.1 Root architecture

Cereals, including, wheat, barley, rice and maize, develop a fibrous root system composed of a primary root and different side root types, some of which are shared with taproot systems such as lateral and adventitious roots, as well as seminal and crown roots not present in taproot systems (Figure 7.1) (10, 55, 248). Root system architecture is flexible and adjusts to environmental conditions. Ideal root ideotypes for enhanced water and nitrate uptake can be combined in different ways to specific benefits. For example, one ideotype consists of shallow growth angles, thin diameters, many lateral roots and long root hairs which mainly captures water and nutrients such as phosphorus (P), potassium (K) and ammonium from the top soil; a second ideotype has a steep growth angle, large diameter and a few laterals in combination with many lateral branches arising from the crown roots which enable deeper rooting (230). Understanding the molecular and genetic mechanisms which control rooting architectures may provide breeders with genetic handles to improve crop resiliency and performance. <Figure 6.1 near here>

Studies point to both common and divergent regulation of cereal root architecture (63, 122, 174, 248). For instance, auxin/cytokinin homeostasis, well known to regulate Arabidopsis roots, appears to extend into cereals since high levels of auxin reduces root length and differentiation of the stem cell niche (marked by accumulation of starch granules) in maize and rice, similar to Arabidopsis (67, 77, 210, 381). However, new studies suggest differences in barley. For instance, in barley, stem cell niche differentiation is not marked with starch as in Arabidopsis and columella stem cells do not differentiate upon application of CLE peptides that normally promote this event (169, 338). Additionally, low auxin levels enhance Arabidopsis root growth but barley lacked this response (168). However, some network elements such as the PLETHORA (PLT) transcription factors, which along with auxin function in stem cell niche maintenance in Arabidopsis, may be conserved since the barley *HvPLT1* homologue is expressed similarly (3, 99, 168, 236). Also, separate roles in the root, shoot and panicle development of PIN1 homologs in rice suggest that cereals show possible functional divergence in auxin transport (64, 204, 380). In addition, barley contains eleven members of the *CYTOKININ OXIDASES/DEHYDROGENASES* (*CKX*) gene family involved in cytokinin degradation, with

two involved in root morphology (105, 390). New reporters for auxin and cytokinin may soon reveal more insights about hormone regulation and distribution during root (and shoot) development in barley and other cereals (168).

7.2 Interaction with above ground traits

Long-distance signals transmitted between the shoot and root in response to environmental changes are essential for plant growth and development (172). Shoot and root traits also show coordinated responses. For instance, in wheat most root traits negatively correlate with spikes per area, grains per spike and thousand grain weight while seminal root traits show a positive correlation with thousand grain weight (403). Similarly, overexpressing the wheat *MORE ROOT* (*TaMOR*) gene in rice resulted in an enlarged root system and increased grain yield (191). Genes involved in developmental timing also impact on root development. For example, compared to spring alleles, winter alleles of *TaVRN1* correlate with increased root length at anthesis likely due to the prolonged vegetative growth (372), suggesting that TaVRN1 may coordinate aerial and below ground architecture. Similarly, the barley RING-type E3 ubiquitin ligases *HvYRG1* and *HvYRG2,* phylogenetically closely related to the GRAIN WEIGHT 2 gene that controls grain size in rice and wheat (19, 186), also function in root growth. Reduced expression of *HvYRG1* accelerated heading time, prolonged the grain-filling period and stimulated in root growth while *HvYRG2* downregulation delayed flowering time and reduce the root system (437). In rice, *FPF4 (flowering-promoting factor 4)*, both promotes flowering time and flower development while influencing root development by modulating auxin homeostasis (114). Altogether, these studies point to important roles below ground for genes traditionally associated with flowering time.

7.3 Root perspectives

Roots are essential for uptake of nutrients and anchoring of the plant. Root architecture between monocots and dicots differs, although the principles of auxin and cytokinin transport, and downstream responsive genes show conservation (168). As such, understanding the molecular mechanisms that underly these different read-outs will provided a fundamental basis to understand, and possibly manipulate, root development and its interaction with the environment and above ground traits.

8 Summary and Overall Perspectives

Modern breeding continues to modify inflorescence architecture and developmental timing in cereals to improve yield. Nonetheless, projected rates of increased grain demand coupled with climate change present enormous challenges to global food security. Exploiting and generating novel changes

in cereal architecture may improve yield. The explosion of plant genomic resources, including those for traditionally recalcitrant cereals such as barley, holds exciting potential, especially with new advances in gene editing (298), to reveal the underlying mechanisms regulating variation in reproductive architecture, both within and between species. We hope this review showcases both conserved and novel pathways to direct this research.

REFERENCES

1. Abdel-Ghani AH, Parzies HK, Omary A, Geiger HH. 2004. Estimating the outcrossing rate of barley landraces and wild barley populations collected from ecologically different regions of Jordan. *Theor. Appl. Genet.* 109(3):588–95
2. Aguilar-Martínez JA, Poza-Carrión C, Cubas P. 2007. Arabidopsis Branched1 acts as an integrator of branching signals within axillary buds. *Plant Cell*. 19(2):458–72
3. Aida M, Beis D, Heidstra R, Willemsen V, Blilou I, et al. 2004. The PLETHORA genes mediate patterning of the Arabidopsis root stem cell niche. *Cell*. 119(1):109–20
4. Alewell C, Ringeval B, Ballabio C, Robinson DA, Panagos P, Borrelli P. 2020. Global phosphorus shortage will be aggravated by soil erosion. *Nat. Commun.* 11(1):1–12
5. Alvarez MA, Tranquilli G, Lewis S, Kippes N, Dubcovsky J. 2016. Genetic and physical mapping of the earliness per se locus Eps-A m 1 in Triticum monococcum identifies EARLY FLOWERING 3 (ELF3) as a candidate gene. *Funct. Integr. Genomics*. 16(4):365–82
6. Arber A. 2010. *The Gramineae*. Cambridge: Cambridge University Press
7. Arite T, Iwata H, Ohshima K, Maekawa M, Nakajima M, et al. 2007. DWARF10, an RMS1/MAX4/DAD1 ortholog, controls lateral bud outgrowth in rice. *Plant J.* 51(6):1019–29
8. Arite T, Umehara M, Ishikawa S, Hanada A, Maekawa M, et al. 2009. d14, a Strigolactone-Insensitive Mutant of Rice, Shows an Accelerated Outgrowth of Tillers. *Plant Cell Physiol.* 50(8):1416–24
9. Ashikari M, Sakakibara H, Lin S, Yamamoto T, Takashi T, et al. 2005. Cytokinin oxidase regulates rice grain production. *Science.* 309(5735):741–45
10. Atkinson JA, Rasmussen A, Traini R, Voß U, Sturrock C, et al. 2014. Branching out in roots: uncovering form, function, and regulation. *Plant Physiol.* 166(2):538–50
11. Austin RB, FORD MA, EDRICH JA, HOOPER BE. 1976. Some effects of leaf posture on photosynthesis and yield in wheat. *Ann. Appl. Biol.* 83(3):425–46
12. Azpiroz R, Wu Y, LoCascio JC, Feldmann KA. 1998. An Arabidopsis brassinosteroid-dependent mutant is blocked in cell elongation. *Plant Cell*. 10(2):219–30
13. Bai F, Reinheimer R, Durantini D, Kellogg EA, Schmidt RJ. 2012. TCP transcription factor, BRANCH ANGLE DEFECTIVE 1 (BAD1), is required for normal tassel branch angle formation in maize. *Proc. Natl. Acad. Sci.* . 109(30):12225–30
14. Bai MY, Shang JX, Oh E, Fan M, Bai Y, et al. 2012. Brassinosteroid, gibberellin and phytochrome impinge on a common transcription module in Arabidopsis. *Nat. Cell Biol.* 14(8):810–17
15. Bai MY, Zhang LY, Gampala SS, Zhu SW, Song WY, et al. 2007. Functions of OsBZR1 and 14-3-3

proteins in brassinosteroid signaling in rice. *Proc. Natl. Acad. Sci. U. S. A.* 104(34):13839–44

16. Bai X, Huang Y, Hu Y, Liu H, Zhang B, et al. 2017. Duplication of an upstream silencer of FZP increases grain yield in rice. *Nat. Plants*. 3(11):885–93

17. Bauer B, von Wirén N. 2020. Modulating tiller formation in cereal crops by the signalling function of fertilizer nitrogen forms. *Sci. Rep.* 10(1):1–11

18. Becraft PW, Bongard-Pierce DK, Sylvester AW, Poethig RS, Freeling M. 1990. The liguleless-1 gene acts tissue specifically in maize leaf development. *Dev. Biol.* 141(1):220–32

19. Bednarek J, Boulaflous A, Girousse C, Ravel C, Tassy C, et al. 2012. Down-regulation of the TaGW2 gene by RNA interference results in decreased grain size and weight in wheat. *J. Exp. Bot.* 63(16):5945–55

20. Bentley AR, Horsnell R, Werner CP, Turner AS, Rose GA, et al. 2013. Short, natural, and extended photoperiod response in BC2F4 lines of bread wheat with different Photoperiod-1 (Ppd-1) alleles. *J. Exp. Bot.* 64(7):1783–93

21. Berry S, Dean C. 2015. Environmental perception and epigenetic memory: mechanistic insight through FLC. *Plant J.* 83(1):133–48

22. Bi X, van Esse W, Mulki MA, Kirschner G, Zhong J, et al. 2019. CENTRORADIALIS interacts with FLOWERING LOCUS T -Like genes to control floret development and grain number. *Plant Physiol.* 180(2):1013–30

23. Boden SA, Cavanagh C, Cullis BR, Ramm K, Greenwood J, et al. 2015. Ppd-1 is a key regulator of inflorescence architecture and paired spikelet development in wheat. *Nat. Plants*. 1:

24. Bolduc N, O'Connor D, Moon J, Lewis M, Hake S. 2012. How to Pattern a Leaf. *Cold Spring Harb. Symp. Quant. Biol.* . 77:47–51

25. Bommert P, Nagasawa NS, Jackson D. 2013. Quantitative variation in maize kernel row number is controlled by the FASCIATED EAR2 locus. *Nat. Genet.* 45(3):334–37

26. Bommert P, Satoh-Nagasawa N, Jackson D, Hirano H-Y. 2005. Genetics and evolution of inflorescence and flower development in grasses. *Plant Cell Physiol.* 46(1):69–78

27. Bommert P, Whipple C. 2018. Grass inflorescence architecture and meristem determinacy. *Semin. Cell Dev. Biol.* 79:37–47

28. Booker J, Sieberer T, Wright W, Williamson L, Willett B, et al. 2005. MAX1 encodes a cytochrome P450 family member that acts downstream of MAX3/4 to produce a carotenoid-derived branch-inhibiting hormone. *Dev. Cell*. 8(3):443–49

29. Bossinger G. 2009. Segments (Phytomers). In *Encyclopedia of Life Sciences*. Chichester: John Wiley & Sons, Ltd

30. Brinton J, Uauy C. 2019. A reductionist approach to dissecting grain weight and yield in wheat. *J. Integr. Plant Biol.* 61(3):337–58

31. Brown RH, Bregitzer P. 2011. A Ds Insertional Mutant of a Barley miR172 Gene Results in Indeterminate Spikelet Development. *Crop Sci.* 51(4):1664–72

32. Bull H, Casao MC, Zwirek M, Flavell AJ, Thomas WTB, et al. 2017. Barley SIX-ROWED SPIKE3 encodes a putative Jumonji C-type H3K9me2/me3 demethylase that represses lateral spikelet fertility. *Nat. Commun.* 8(1):936

33. Bull H, Casao MC, Zwirek M, Flavell AJ, Thomas WTB, et al. 2017. Barley SIX-ROWED SPIKE3

encodes a putative Jumonji C-type H3K9me2/me3 demethylase that represses lateral spikelet fertility. *Nat. Commun.* 8(1):936

34. Byrne ME, Simorowski J, Martienssen RA. 2002. ASYMMETRIC LEAVES1reveals knox gene redundancy in Arabidopsis. *Development*. 129(8):1957 LP – 1965

35. Cal AJ, Sanciangco M, Rebolledo MC, Luquet D, Torres RO, et al. 2019. Leaf morphology, rather than plant water status, underlies genetic variation of rice leaf rolling under drought. *Plant. Cell Environ.* 42(5):1532–44

36. Callens C, Tucker MR, Zhang D, Wilson ZA. 2018. Dissecting the role of MADS-box genes in monocot floral development and diversity. *J. Exp. Bot.* 69(10):2435–59

37. Cao H, Chen S. 1995. Brassinosteroid-induced rice lamina joint inclination and its relation to indole-3-acetic acid and ethylene. *Plant Growth Regul.* 16(2):189–96

38. Cao Y, Zeng H, Ku L, Ren Z, Han Y, et al. 2020. ZmIBH1-1 regulates plant architecture in maize. *J. Exp. Bot.* 71(10):2943–55

39. Casao MC, Karsai I, Igartua E, Gracia MP, Veisz O, Casas AM. 2011. Adaptation of barley to mild winters: A role for PPDH2. *BMC Plant Biol.* 11(1):164

40. Castorina G, Persico M, Zilio M, Sangiorgio S, Carabelli L, Consonni G. 2018. The maize lilliputian1 (lil1) gene, encoding a brassinosteroid cytochrome P450 C-6 oxidase, is involved in plant growth and drought response. *Ann. Bot.* 122(2):227–38

41. Chang SH, Tan CM, Wu CT, Lin TH, Jiang SY, et al. 2018. Alterations of plant architecture and phase transition by the phytoplasma virulence factor SAP11. *J. Exp. Bot.* 69(22):5389–5401

42. Chatfield SP, Stirnberg P, Forde BG, Leyser O. 2000. The hormonal regulation of axillary bud growth in Arabidopsis. *Plant J.* 24(2):159–69

43. Che R, Tong H, Shi B, Liu Y, Fang S, et al. 2016. Control of grain size and rice yield by GL2-mediated brassinosteroid responses. *Nat. Plants*. 2(1):15195

44. Chen XX, Zhang W, Liang XY, Liu YM, Xu SJ, et al. 2019. Physiological and developmental traits associated with the grain yield of winter wheat as affected by phosphorus fertilizer management. *Sci. Rep.* 9(1):1–12

45. Chen Y, Fan X, Song W, Zhang Y, Xu G. 2012. Over-expression of OsPIN2 leads to increased tiller numbers, angle and shorter plant height through suppression of OsLAZY1. *Plant Biotechnol. J.* 10(2):139–49

46. Cho S-H, Yoo S-C, Zhang H, Pandeya D, Koh H-J, et al. 2013. The rice narrow leaf2 and narrow leaf3 loci encode WUSCHEL-related homeobox 3A (OsWOX3A) and function in leaf, spikelet, tiller and lateral root development. *New Phytol.* 198(4):1071–84

47. Choe S, Noguchi T, Fujioka S, Takatsuto S, Tissier CP, et al. 1999. The Arabidopsis dwf7/ste1 mutant is defective in the delta7 sterol C-5 desaturation step leading to brassinosteroid biosynthesis. *Plant Cell*. 11(2):207–21

48. Chono M, Honda I, Zeniya H, Yoneyama K, Saisho D, et al. 2003. A Semidwarf Phenotype of Barley uzu Results from a Nucleotide Substitution in the Gene Encoding a Putative Brassinosteroid Receptor. *Plant Physiol.* 133(3):1209–19

49. Chuck G. 2002. The Control of Spikelet Meristem Identity by the branched silkless1 Gene in Maize. *Science.* 298(5596):1238–41

50. Chuck G, Meeley RB, Hake S. 1998. The control of maize spikelet meristem fate by the APETALA2-like gene indeterminate spikelet1. *Genes Dev.* 12(8):1145–54

51. Chuck G, Meeley R, Hake S. 2008. Floral meristem initiation and meristem cell fate are regulated by the maize AP2 genes ids1 and sid1. *Development*. 135(18):3013–19

52. Chuck G, Meeley R, Irish E, Sakai H, Hake S. 2007. The maize tasselseed4 microRNA controls sex determination and meristem cell fate by targeting Tasselseed6/indeterminate spikelet1. *Nat. Genet.* 39(12):1517–21

53. Comadran J, Kilian B, Russell J, Ramsay L, Stein N, et al. 2012. Natural variation in a homolog of Antirrhinum CENTRORADIALIS contributed to spring growth habit and environmental adaptation in cultivated barley. *Nat. Genet.* 44:1388–92

54. Corbesier L, Vincent C, Jang S, Fornara F, Fan Q, et al. 2007. FT Protein Movement Contributes to Long-Distance Signaling in Floral Induction of Arabidopsis. *Science.* 316(5827):1030–33

55. Coudert Y, Périn C, Courtois B, Khong NG, Gantet P. 2010. Genetic control of root development in rice, the model cereal. *Trends Plant Sci.* 15(4):219–26

56. Dai M, Hu Y, Zhao Y, Liu H, Zhou D-X. 2007. A WUSCHEL - LIKE HOMEOBOX Gene Represses a YABBY Gene Expression Required for Rice Leaf Development. *Plant Physiol.* 144(1):380–90

57. Dai Z, Wang J, Zhu M, Miao X, Shi Z. 2016. OsMADS1 Represses microRNA172 in Elongation of Palea/Lemma Development in Rice. *Front. Plant Sci.* 7(DECEMBER2016):1891

58. de Souza Moraes T, van Es SW, Hernández-Pinzón I, Kirschner GK, van der Wal F, et al. 2021. The TCP transcription factor HvTB2 heterodimerizes with VRS5(HvTB1) and controls spike architecture in barley. *bioRxiv*. 2021.04.14.439785

59. De Vos D, Nelissen H, AbdElgawad H, Prinsen E, Broeckhove J, et al. 2020. How grass keeps growing: an integrated analysis of hormonal crosstalk in the maize leaf growth zone. *New Phytol.* 225(6):2513–25

60. Debernardi JM, Greenwood JR, Jean Finnegan E, Jernstedt J, Dubcovsky J. 2020. APETALA 2-like genes AP2L2 and Q specify lemma identity and axillary floral meristem development in wheat. *Plant J.* 101(1):171–87

61. Debernardi JM, Greenwood JR, Jean Finnegan E, Jernstedt J, Dubcovsky J. 2020. *APETALA 2*-like genes *AP2L2* and *Q* specify lemma identity and axillary floral meristem development in wheat. *Plant J.* 101(1):171–87

62. Debernardi JM, Lin H, Chuck G, Faris JD, Dubcovsky J. 2017. microRNA172 plays a crucial role in wheat spike morphogenesis and grain threshability. *Development*. 144(11):1966–75

63. Del Bianco M, Kepinski S. 2018. Building a future with root architecture. *J. Exp. Bot.* 69(22):5319–23

64. Dello Ioio R, Nakamura K, Moubayidin L, Perilli S, Taniguchi M, et al. 2008. A genetic framework for the control of cell division and differentiation in the root meristem. *Science.* 322(5906):1380–84

65. Deng W, Casao MC, Wang P, Sato K, Hayes PM, et al. 2015. Direct links between the vernalization response and other key traits of cereal crops. *Nat. Commun.* 6:5882

66. Derbyshire P, Byrne ME. 2013. MORE SPIKELETS1 is required for spikelet fate in the inflorescence of Brachypodium. *Plant Physiol.* 161(3):1291–1302

67. Di Mambro R, De Ruvo M, Pacifici E, Salvi E, Sozzani R, et al. 2017. Auxin minimum triggers the developmental switch from cell division to cell differentiation in the Arabidopsis root. *Proc. Natl. Acad. Sci.* 114(36):E7641–49

68. Didon UME. 2002. Variation Between Barley Cultivars in Early Response to Weed Competition. *J. Agron. Crop Sci.* 188(3):176–84

69. Digel B, Pankin A, von Korff M. 2015. Global Transcriptome Profiling of Developing Leaf and Shoot Apices Reveals Distinct Genetic and Environmental Control of Floral Transition and Inflorescence Development in Barley. *Plant Cell*. 27(9):2318–34

70. Dixon LE, Greenwood JR, Bencivenga S, Zhang P, Cockram J, et al. 2018. TEOSINTE BRANCHED1 Regulates Inflorescence Architecture and Development in Bread Wheat (Triticum aestivum). *Plant Cell*. 30(3):563–81

71. Dobrovolskaya O, Pont C, Sibout R, Martinek P, Badaeva E, et al. 2015. FRIZZY PANICLE drives supernumerary spikelets in bread wheat. *Plant Physiol.* 167(1):189–99

72. Dobrovolskaya OB, Amagai Y, Popova KI, Dresvyannikova AE, Martinek P, et al. 2017. Genes WHEAT FRIZZY PANICLE and SHAM RAMIFICATION 2 independently regulate differentiation of floral meristems in wheat. *BMC Plant Biol.* 17(2):15–27

73. Dockter C, Gruszka D, Braumann I, Druka A, Druka I, et al. 2014. Induced Variations in Brassinosteroid Genes Define Barley Height and Sturdiness, and Expand the Green Revolution Genetic Toolkit. *Plant Physiol.* 166(4):1912–27

74. Dockter C, Gruszka D, Braumann I, Druka A, Druka I, et al. 2014. Induced variations in brassinosteroid genes define barley height and sturdiness, and expand the green revolution genetic toolkit. *Plant Physiol.* 166(4):1912–27

75. Doebley J, Stec A, Hubbard L. 1997. The evolution of apical dominance in maize. *Nature*. 386(6624):485–88

76. Doebley JF, Gaut BS, Smith BD. 2006. The molecular genetics of crop domestication. *Cell*. 127(7):1309–21

77. Dolan L, Janmaat K, Willemsen V, Linstead P, Poethig S, et al. 1993. Cellular organisation of the Arabidopsis thaliana root. *Development*. 119(1):71–84

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

79. Dong H, Zhao H, Xie W, Han Z, Li G, et al. 2016. A Novel Tiller Angle Gene, TAC3, together with TAC1 and D2 Largely Determine the Natural Variation of Tiller Angle in Rice Cultivars. *PLoS Genet.* 12(11):e1006412–e1006412

80. Dong Z, Li W, Unger-Wallace E, Yang J, Vollbrecht E, Chuck G. 2017. Ideal crop plant architecture is mediated by tassels replace upper ears1, a BTB/POZ ankyrin repeat gene directly targeted by TEOSINTE BRANCHED1. *Proc. Natl. Acad. Sci.* 114(41):E8656 LP-E8664

81. Dong Z, Xiao Y, Govindarajulu R, Feil R, Siddoway ML, et al. 2019. The regulatory landscape of a core maize domestication module controlling bud dormancy and growth repression. *Nat. Commun.* 10(1):3810

82. Dreni L, Jacchia S, Fornara F, Fornari M, Ouwerkerk PBF, et al. 2007. The D-lineage MADS-box gene OsMADS13 controls ovule identity in rice. *Plant J.* 52(4):690–99

83. Dreni L, Zhang D. 2016. Flower development: the evolutionary history and functions of the

AGL6 subfamily MADS-box genes. *J. Exp. Bot.* 67(6):1625–38

84. Duan P, Ni S, Wang J, Zhang B, Xu R, et al. 2016. Regulation of OsGRF4 by OsmiR396 controls grain size and yield in rice. *Nat. Plants*. 2(1):15203

85. Duvick DN. 2005. The Contribution of Breeding to Yield Advances in maize (Zea mays L.). . 86:83–145. Academic Press

86. Eveland AL, Goldshmidt A, Pautler M, Morohashi K, Liseron-Monfils C, et al. 2014. Regulatory modules controlling maize inflorescence architecture. *Genome Res.* 24(3):431–43

87. Fakorede MAB, Mock JJ. 1978. Changes in morphological and physiological traits associated with recurrent selection for grain yield in maize. *Euphytica*. 27(2):397–409

88. Fang J, Guo T, Xie Z, Chun Y, Zhao J, et al. 2021. The URL1–ROC5–TPL2 transcriptional repressor complex represses the ACL1 gene to modulate leaf rolling in rice. *Plant Physiol.*

89. Fang Z, Ji Y, Hu J, Guo R, Sun S, Wang X. 2020. Strigolactones and Brassinosteroids Antagonistically Regulate the Stability of the D53–OsBZR1 Complex to Determine FC1 Expression in Rice Tillering. *Mol. Plant*. 13(4):586–97

90. FAO. 2015. FAO cereal supply and demand brief

91. Faris JD, Simons KJ, Zhang Z, Gill BS. 2005. The wheat super domestication gene Q. In *Wheat Information Service*

92. Faure S, Turner AS, Gruszka D, Christodoulou V, Davis SJ, et al. 2012. Mutation at the circadian clock gene EARLY MATURITY 8 adapts domesticated barley (Hordeum vulgare) to short growing seasons. *Proc. Natl. Acad. Sci.* 109(21):8328 LP – 8333

93. Fisher JB, French JC. 1978. Internodal meristems of monocotyledons: further studies and a general taxonomic survey. *Ann. Bot.* 42:41–50

94. Foster T, Yamaguchi J, Wong BC, Veit B, Hake S. 1999. Gnarley1 Is a Dominant Mutation in the knox4 Homeobox Gene Affecting Cell Shape and Identity. *Plant Cell*. 11(7):1239 LP – 1252

95. Freeling M, Hake S. 1985. Developmental genetics of mutants that specify knotted leaves in maize. *Genetics*. 111(3):617–34

96. Fuller DQ, Allaby R. 2018. Seed Dispersal and Crop Domestication: Shattering, Germination and Seasonality in Evolution Under Cultivation. In *Annual Plant Reviews online*, pp. 238–95. Chichester, UK: John Wiley & Sons, Ltd

97. Furbank RT, Sharwood R, Estavillo GM, Silva-Perez V, Condon AG. 2020. Photons to food: genetic improvement of cereal crop photosynthesis. *J. Exp. Bot.* 71(7):2226–38

98. Gale M, Youssefian S. 1985. Dwarfing genes in wheat. In *Progress in Plant Breeding*, ed G Russell, pp. 1–35. London: Butterworth

99. Galinha C, Hofhuis H, Luijten M, Willemsen V, Blilou I, et al. 2007. PLETHORA proteins as dose-dependent master regulators of Arabidopsis root development. *Nature*. 449(7165):1053–57

100. Gallavotti A, Long JA, Stanfield S, Yang X, Jackson D, et al. 2010. The control of axillary meristem fate in the maize ramosa pathway. *Development*. 137(17):2849–56

101. Gallavotti A, Yang Y, Schmidt RJ, Jackson D. 2008. The relationship between auxin transport and maize branching. *Plant Physiol.* 147(4):1913–23

102. Gallego-Bartolomé J, Minguet EG, Grau-Enguix F, Abbas M, Locascio A, et al. 2012. Molecular mechanism for the interaction between gibberellin and brassinosteroid signaling pathways in Arabidopsis. *Proc. Natl. Acad. Sci. U. S. A.* 109(33):13446–51

103. Gao F, Wang K, Liu Y, Chen Y, Chen P, et al. 2015. Blocking miR396 increases rice yield by shaping inflorescence architecture. *Nat. Plants*. 2(1):1–9

104. Gao X-Q, Wang N, Wang X-L, Zhang XS. 2019. Architecture of Wheat Inflorescence: Insights from Rice. *Trends Plant Sci.* 24(9):802–9

105. Gasparis, Przyborowski, Kała, Nadolska-Orczyk. 2019. Knockout of the HvCKX1 or HvCKX3 Gene in Barley (Hordeum vulgare L.) by RNA-Guided Cas9 Nuclease Affects the Regulation of Cytokinin Metabolism and Root Morphology. *Cells*. 8(8):782

106. Gauley A, Boden SA. 2019. Genetic pathways controlling inflorescence architecture and development in wheat and barley. *J. Integr. Plant Biol.* 61(3):296–309

107. Gauley A, Boden SA. 2021. Stepwise increases in FT1 expression regulate seasonal progression of flowering in wheat (Triticum aestivum). *New Phytol.* 229(2):1163–76

108. Gómez-Ariza J, Brambilla V, Vicentini G, Landini M, Cerise M, et al. 2019. A transcription factor coordinating internode elongation and photoperiodic signals in rice. *Nat. Plants*. 5(4):358–62

109. Greb T, Clarenz O, Schäfer E, Müller D, Herrero R, et al. 2003. Molecular analysis of the LATERAL SUPPRESSOR gene in Arabidopsis reveals a conserved control mechanism for axillary meristem formation. *Genes Dev.* 17(9):1175–87

110. Greenwood JR, Finnegan EJ, Watanabe N, Trevaskis B, Swain SM. 2017. New alleles of the wheat domestication gene Q reveal multiple roles in growth and reproductive development. *Development*. 144(11):1959–65

111. Guo M, Thomas J, Collins G, Timmermans MCP. 2008. Direct Repression of KNOX Loci by the ASYMMETRIC LEAVES1 Complex of Arabidopsis. *Plant Cell*. 20(1):48–58

112. Guo Q, Major IT, Howe GA. 2018. Resolution of growth–defense conflict: mechanistic insights from jasmonate signaling. *Curr. Opin. Plant Biol.* 44:72–81

113. Guo W, Chen L, Herrera-Estrella L, Cao D, Tran L-SP. 2020. Altering Plant Architecture to Improve Performance and Resistance. *Trends Plant Sci.* 25(11):1154–70

114. Guo Y, Wu Q, Xie Z, Yu B, Zeng R, et al. 2020. OsFPFL4 is Involved in the Root and Flower Development by Affecting Auxin Levels and ROS Accumulation in Rice (Oryza sativa). *Rice*. 13(1):1–15

115. Halliwell J, Borrill P, Gordon A, Kowalczyk R, Pagano ML, et al. 2016. Systematic Investigation of FLOWERING LOCUS T-Like Poaceae Gene Families Identifies the Short-Day Expressed Flowering Pathway Gene, TaFT3 in Wheat (Triticum aestivum L.). *Front. Plant Sci.* 7:857

116. Harmoko R, Yoo JY, Ko KS, Ramasamy NK, Hwang BY, et al. 2016. N-glycan containing a core α1,3-fucose residue is required for basipetal auxin transport and gravitropic response in rice (Oryza sativa). *New Phytol.* 212(1):108–22

117. Hay A, Kaur H, Phillips A, Hedden P, Hake S, Tsiantis M. 2002. The Gibberellin Pathway Mediates KNOTTED1-Type Homeobox Function in Plants with Different Body Plans. *Curr. Biol.* 12(18):1557–65

118. He Z, Zeng J, Ren Y, Chen D, Li W, et al. 2017. OsGIF1 Positively Regulates the Sizes of Stems,

Leaves, and Grains in Rice. *Front. Plant Sci.* 8:1730

119. Hedden P. 2003. The genes of the Green Revolution. *Trends Genet.* 19(1):5–9

120. Hepworth SR, Zhang Y, McKim S, Li X, Haughn GW. 2005. BLADE-ON-PETIOLE–Dependent Signaling Controls Leaf and Floral Patterning in Arabidopsis. *Plant Cell*. 17(5):1434–48

121. Hirano K, Kawamura M, Araki-Nakamura S, Fujimoto H, Ohmae-Shinohara K, et al. 2017. Sorghum DW1 positively regulates brassinosteroid signaling by inhibiting the nuclear localization of BRASSINOSTEROID INSENSITIVE 2. *Sci. Rep.* 7(1):126

122. Hochholdinger F, Yu P, Marcon C. 2018. Genetic Control of Root System Development in Maize

123. Hong Z, Ueguchi-Tanaka M, Shimizu-Sato S, Inukai Y, Fujioka S, et al. 2002. Loss-of-function of a rice brassinosteroid biosynthetic enzyme, C-6 oxidase, prevents the organized arrangement and polar elongation of cells in the leaves and stem. *Plant J.* 32(4):495–508

124. Horton P. 2000. Prospects for crop improvement through the genetic manipulation of photosynthesis: morphological and biochemical aspects of light capture. *J. Exp. Bot.* 51(suppl_1):475–85

125. Houston K, McKim SM, Comadran J, Bonar N, Druka I, et al. 2013. Variation in the interaction between alleles of HvAPETALA2 and microRNA172 determines the density of grains on the barley inflorescence. *Proc. Natl. Acad. Sci.* 110(41):16675–80

126. Hu J, Wang Y, Fang Y, Zeng L, Xu J, et al. 2015. A Rare Allele of GS2 Enhances Grain Size and Grain Yield in Rice. *Mol. Plant*. 8(10):1455–65

127. Hu M, Lv S, Wu W, Fu Y, Liu F, et al. 2018. The domestication of plant architecture in African rice. *Plant J.* 94(4):661–69

128. Huang L-J, Luo J, Wang Y, Li N. 2021. From Green Revolution to Green Balance: The Nitrogen and Gibberellin Mediated Rice Tiller Growth. *Plant Signal. Behav.*, p. 1917838

129. Huang X, Qian Q, Liu Z, Sun H, He S, et al. 2009. Natural variation at the DEP1 locus enhances grain yield in rice. *Nat. Genet.* 41:494

130. Huang Y, Zhao S, Fu Y, Sun H, Ma X, et al. 2018. Variation in the regulatory region of FZP causes increases in secondary inflorescence branching and grain yield in rice domestication. *Plant J.* 96(4):716–33

131. Hubbard L, McSteen P, Doebley J, Hake S. 2002. Expression patterns and mutant phenotype of teosinte branched1 correlate with growth suppression in maize and teosinte. *Genetics*. 162(4):1927–35

132. Huijser P, Schmid M. 2011. The control of developmental phase transitions in plants. *Dev.* . 138(19):4117–29

133. Hussien A, Tavakol E, Horner DS, Muñoz-Amatriaín M, Muehlbauer GJ, Rossini L. 2014. Genetics of Tillering in Rice and Barley. *Plant Genome*. 7(1):

134. Hyles J, Bloomfield MT, Hunt JR, Trethowan RM, Trevaskis B. 2020. Phenology and related traits for wheat adaptation. *Heredity (Edinb).* 125(6):417–30

135. Ikeda A, Ueguchi-Tanaka M, Sonoda Y, Kitano H, Koshioka M, et al. 2001. slender rice, a constitutive gibberellin response mutant, is caused by a null mutation of the SLR1 gene, an ortholog of the height-regulating gene GAI/RGA/RHT/D8. *Plant Cell*. 13(5):999–1010

136. Irish V. 2017. The ABC model of floral development. *Curr. Biol.* 27(17):R887–90

137. Ishikawa S, Maekawa M, Arite T, Onishi K, Takamure I, Kyozuka J. 2005. Suppression of Tiller Bud Activity in Tillering Dwarf Mutants of Rice. *Plant Cell Physiol.* 46(1):79–86

138. Ishiwata A, Ozawa M, Nagasaki H, Kato M, Noda Y, et al. 2013. Two WUSCHEL-related homeobox Genes, narrow leaf2 and narrow leaf3, Control Leaf Width in Rice. *Plant Cell Physiol.* 54(5):779–92

139. Isidro J, Knox R, Clarke F, Singh A, DePauw R, et al. 2012. Quantitative genetic analysis and mapping of leaf angle in durum wheat. *Planta*. 236(6):1713–23

140. Itoh J-I, Hibara K-I, Sato Y, Nagato Y. 2008. Developmental role and auxin responsiveness of Class III homeodomain leucine zipper gene family members in rice. *Plant Physiol.* 147(4):1960–75

141. Itoh J-I, Nonomura K-I, Ikeda K, Yamaki S, Inukai Y, et al. 2005. Rice Plant Development: from Zygote to Spikelet. *Plant Cell Physiol.* 46(1):23–47

142. Jackson D, Veit B, Hake S. 1994. Expression of maize KNOTTED1 related homeobox genes in the shoot apical meristem predicts patterns of morphogenesis in the vegetative shoot. *Development*. 413(2):405–13

143. Jang S, An G, Li H-Y. 2017. Rice Leaf Angle and Grain Size Are Affected by the OsBUL1 Transcriptional Activator Complex. *Plant Physiol.* 173(1):688 LP – 702

144. Jang S, Shim S, Lee YK, Lee D, Koh H-J. 2021. Major QTLs, qARO1 and qARO9, Additively Regulate Adaxial Leaf Rolling in Rice. *Front. Plant Sci.* 12:64

145. Jasinski S, Piazza P, Craft J, Hay A, Woolley L, et al. 2005. KNOX action in Arabidopsis is mediated by coordinate regulation of cytokinin and gibberellin activities. *Curr. Biol.* 15(17):1560–65

146. Je B Il, Gruel J, Lee YK, Bommert P, Arevalo ED, et al. 2016. Signaling from maize organ primordia via FASCIATED EAR3 regulates stem cell proliferation and yield traits. *Nat. Genet.* 48(7):785–91

147. Jeon JS, Jang S, Lee S, Nam J, Kim C, et al. 2000. leafy hull sterile1 is a homeotic mutation in a rice MADS box gene affecting rice flower development. *Plant Cell*. 12(6):871–84

148. Jiang L, Ma X, Zhao S, Tang Y, Liu F, et al. 2019. The APETALA2-Like Transcription Factor SUPERNUMERARY BRACT Controls Rice Seed Shattering and Seed Size. *Plant Cell*. 31(1):17–36

149. Jiao Y, Wang Y, Xue D, Wang J, Yan M, et al. 2010. Regulation of OsSPL14 by OsmiR156 defines ideal plant architecture in rice. *Nat. Genet.* 42(6):541–44

150. Jiao Z, Du H, Chen S, Huang W, Ge L. 2021. LAZY Gene Family in Plant Gravitropism. *Front. Plant Sci.* 11:2096

151. Jofuku KD, den Boer BGW, Van Montagu M, Okamuro JK. 1994. Control of Arabidopsis flower and seed development by the homeotic gene APETALA2. *Plant Cell*. 6(9):1211–25

152. Johnston R, Leiboff S, Scanlon MJ. 2015. Ontogeny of the sheathing leaf base in maize (Zea mays). *New Phytol.* 205(1):306–15

153. Johnston R, Wang M, Sun Q, Sylvester AW, Hake S, Scanlon MJ. 2014. Transcriptomic Analyses Indicate That Maize Ligule Development Recapitulates Gene Expression Patterns That Occur during Lateral Organ Initiation. *Plant Cell Online* . 26(12):4718–32

154. Jones JW, Adair CR. 1938. A “lazy” mutation in rice. *J. Hered.* 29(8):315–18

155. Jöst M, Hensel G, Kappel C, Druka A, Sicard A, et al. 2016. The INDETERMINATE DOMAIN Protein BROAD LEAF1 Limits Barley Leaf Width by Restricting Lateral Proliferation. *Curr. Biol.* 26(7):903–9

156. Kaneko-Suzuki M, Kurihara-Ishikawa R, Okushita-Terakawa C, Kojima C, Nagano-Fujiwara M, et al. 2018. TFL1-like proteins in rice antagonize rice FT-like protein in inflorescence development by competition for complex formation with 14-3-3 and FD. *Plant Cell Physiol.* 59(3):458–68

157. Kebrom TH, Brutnell TP, Finlayson SA. 2010. Suppression of sorghum axillary bud outgrowth by shade, phyB and defoliation signalling pathways. *Plant, Cell Environ.* 33(1):48–58

158. Kebrom TH, Burson BL, Finlayson SA. 2006. Phytochrome B represses Teosinte Branched1 expression and induces sorghum axillary bud outgrowth in response to light signals. *Plant Physiol.* 140(3):1109–17

159. Kebrom TH, Spielmeyer W, Finnegan EJ. 2013. Grasses provide new insights into regulation of shoot branching. *Trends Plant Sci.* 18(1):41–48

160. Kellogg EA. 2015. *Flowering Plants. Monocots*, Vol. XIII. Cham: Springer International Publishing AG. 1–416 pp.

161. Kellogg EA, Camara PEAS, Rudall PJ, Ladd P, Malcomber ST, et al. 2013. Early inflorescence development in the grasses (Poaceae). *Front. Plant Sci.* 4(JUL):250

162. Kende H, van der Knaap E E van der, Cho H-T. 1998. Deepwater rice: A model plant to study stem elongation. *Plant Physiol.* 118(4):1105–10

163. Khanday I, Yadav SR, Vijayraghavan U. 2013. Rice LHS1/OsMADS1 Controls Floret Meristem Specification by Coordinated Regulation of Transcription Factors and Hormone Signaling Pathways. *Plant Physiol.* . 161(4):1970–83

164. Khew C-Y, Teo C-J, Chan W-S, Wong H-L, Namasivayam P, Ho C-L. 2015. Brassinosteroid insensitive 1-associated kinase 1 (OsI-BAK1) is associated with grain filling and leaf development in rice. *J. Plant Physiol.* 182:23–32

165. Kim JH. 2019. Biological roles and an evolutionary sketch of the GRF-GIF transcriptional complex in plants. *BMB Rep.* 52(4):227–38

166. Kippes N, Chen A, Zhang X, Lukaszewski AJ, Dubcovsky J. 2016. Development and characterization of a spring hexaploid wheat line with no functional VRN2 genes. *Theor. Appl. Genet.* 129(7):1417–28

167. Kirby EJM, Appleyard M, Simpson N a. 1994. Co-ordination of stem elongation and Zadoks growth stages with leaf emergence in wheat and barley. *J. Agric. Sci.* 122(01):21

168. Kirschner GK, Stahl Y, Imani J, von Korff M, Simon R. 2018. Fluorescent reporter lines for auxin and cytokinin signalling in barley (Hordeum vulgare). *PLoS One*. 13(4):e0196086

169. Kirschner GK, Stahl Y, Von Korff M, Simon R. 2017. Unique and Conserved Features of the Barley Root Meristem. *Front. Plant Sci.* 8:1240

170. Kitagawa M, Jackson D. 2019. Control of meristem size. *Annu. Rev. Plant Biol.* 70:269–91

171. Knöller AS, Blakeslee JJ, Richards EL, Peer WA, Murphy AS. 2010. Brachytic2/ZmABCB1 functions in IAA export from intercalary meristems. *J. Exp. Bot.* 61(13):3689–96

172. Ko D, Helariutta Y. 2017. Shoot–Root Communication in Flowering Plants. *Curr. Biol.* 27(17):R973–78

173. Kobayashi Y, Kaya H, Goto K, Iwabuchi M, Araki T. 1999. A Pair of Related Genes with Antagonistic Roles in Mediating Flowering Signals. *Science.* 286(5446):1960 LP – 1962

174. Koevoets IT, Venema JH, Elzenga JTM, Testerink C. 2016. Roots Withstanding their Environment: Exploiting Root System Architecture Responses to Abiotic Stress to Improve Crop Tolerance. *Front. Plant Sci.* 07(AUG2016):1335

175. Komatsu M, Chujo A, Nagato Y, Shimamoto K, Kyozuka J. 2003. FRIZZY PANICLE is required to prevent the formation of axillary meristems and to establish floral meristem identity in rice spikelets. *Development*. 130(16):3841–50

176. Komatsuda T, Pourkheirandish M, He C, Azhaguvel P, Kanamori H, et al. 2007. Six-rowed barley originated from a mutation in a homeodomain-leucine zipper I-class homeobox gene. *Proc. Natl. Acad. Sci.* 104(4):1424–29

177. Kong F, Zhang T, Liu J, Heng S, Shi Q, et al. 2017. Regulation of Leaf Angle by Auricle Development in Maize. *Mol. Plant*. 10(3):516–19

178. Koppolu R, Anwar N, Sakuma S, Tagiri A, Lundqvist U, et al. 2013. Six-rowed spike4 (Vrs4) controls spikelet determinacy and row-type in barley. *Proc. Natl. Acad. Sci. U. S. A.* 110(32):13198–203

179. Koppolu R, Schnurbusch T. 2019. Developmental pathways for shaping spike inflorescence architecture in barley and wheat. *J. Integr. Plant Biol.* 61(3):278–95

180. Kumar V, Kim SH, Adnan MR, Heo J, Jeong JH, et al. 2021. Tiller Outgrowth in Rice (Oryza sativa L.) is Controlled by OsGT1, Which Acts Downstream of FC1 in a PhyB-Independent Manner. *J. Plant Biol.* 64(5):417–30

181. Kurakawa T, Ueda N, Maekawa M, Kobayashi K, Kojima M, et al. 2007. Direct control of shoot meristem activity by a cytokinin-activating enzyme. *Nature*. 445(7128):652–55

182. Laurie DA, Pratchett N, Snape JW, Bezant JH. 1995. RFLP mapping of five major genes and eight quantitative trait loci controlling flowering time in a winter× spring barley (Hordeum vulgare L.) cross. *Genome*. 38(3):575–85

183. Lee D-Y, An G. 2012. Two AP2 family genes, SUPERNUMERARY BRACT (SNB) and OsINDETERMINATE SPIKELET 1 (OsIDS1), synergistically control inflorescence architecture and floral meristem establishment in rice. *Plant J.* 69(3):445–61

184. Lee DY, Lee J, Moon S, Park SY, An G. 2007. The rice heterochronic gene SUPERNUMERARY BRACT regulates the transition from spikelet meristem to floral meristem. *Plant J.* 49(1):64–78

185. Lee J, Park J-J, Kim SL, Yim J, An G. 2007. Mutations in the rice liguleless gene result in a complete loss of the auricle, ligule, and laminar joint. *Plant Mol. Biol.* 65(4):487–99

186. Lee KH, Park SW, Kim YJ, Koo YJ, Song JT, Seo HS. 2018. Grain width 2 (GW2) and its interacting proteins regulate seed development in rice (Oryza sativa L.). *Bot. Stud.* 59(1):23

187. Lee Y-S, Lee D-Y, Cho L-H, An G. 2014. Rice miR172 induces flowering by suppressing OsIDS1 and SNB, two AP2 genes that negatively regulate expression of Ehd1 and florigens. *Rice*. 7(1):31

188. Leiboff S, Strable J, Johnston R, Federici S, Sylvester AW, Scanlon MJ. 2021. Network analyses

identify a transcriptomic proximodistal prepattern in the maize leaf primordium. *New Phytol.* 230(1):218–27

189. Lenhard M. 2017. Plant Development: Keeping on the Straight and Narrow and Flat. *Curr. Biol.* 27(23):R1277–80

190. Lev-Yadun S, Gopher A, Abbo S. 2000. The Cradle of Agriculture. *Science.* 288(5471):1602 LP – 1603

191. Li B, Liu D, Li Q, Mao X, Li A, et al. 2016. Overexpression of wheat gene TaMOR improves root system architecture and grain yield in Oryza sativa. *J. Exp. Bot.* 67(14):4155–67

192. Li C, Li Y, Shi Y, Song Y, Zhang D, et al. 2015. Genetic control of the leaf angle and leaf orientation value as revealed by ultra-high density maps in three connected maize populations. *PLoS One*. 10(3):e0121624

193. Li C, Lin H, Chen A, Lau M, Jernstedt J, Dubcovsky J. 2019. Wheat VRN1 , FUL2 and FUL3 play critical and redundant roles in spikelet development and spike determinacy. *Development*. 146(14):

194. Li G, Kuijer HNJ, Yang X, Liu H, Shen C, et al. 2021. MADS1 maintains barley spike morphology at high ambient temperatures. *Nat. Plants*. 7(8):1093–1107

195. Li H, Liang W, Hu Y, Zhu L, Yin C, et al. 2011. Rice MADS6 Interacts with the Floral Homeotic Genes SUPERWOMAN1 , MADS3 , MADS58 , MADS13 , and DROOPING LEAF in Specifying Floral Organ Identities and Meristem Fate. *Plant Cell*. 23(7):2536–52

196. Li N, Li Y. 2016. Signaling pathways of seed size control in plants. *Curr. Opin. Plant Biol.* 33:23–32

197. Li N, Xu R, Li Y. 2019. Molecular Networks of Seed Size Control in Plants. *Annu. Rev. Plant Biol.* 70(1):435–63

198. Li P-F, Cheng Z-G, Ma B-L, Palta JA, Kong H-Y, et al. 2014. Dryland Wheat Domestication Changed the Development of Aboveground Architecture for a Well-Structured Canopy. *PLoS One*. 9(9):e95825

199. Li P, Wang Y, Qian Q, Fu Z, Wang M, et al. 2007. LAZY1 controls rice shoot gravitropism through regulating polar auxin transport. *Cell Res.* 17(5):402–10

200. Li Q-F, Wang C, Jiang L, Li S, Sun SSM, He J-X. 2012. An interaction between BZR1 and DELLAs mediates direct signaling crosstalk between brassinosteroids and gibberellins in Arabidopsis. *Sci. Signal.* 5(244):ra72

201. Li S, Gao F, Xie K, Zeng X, Cao Y, et al. 2016. The OsmiR396c-OsGRF4-OsGIF1 regulatory module determines grain size and yield in rice. *Plant Biotechnol. J.* 14(11):2134–46

202. Li X, Qian Q, Fu Z, Wang Y, Xiong G, et al. 2003. Control of tillering in rice. *Nature*. 422(6932):618–21

203. Li X, Wu P, Lu Y, Guo S, Zhong Z, et al. 2020. Synergistic Interaction of Phytohormones in Determining Leaf Angle in Crops. *Int. J. Mol. Sci.* 21(14):5052

204. Li Y, Zhu J, Wu L, Shao Y, Wu Y, Mao C. 2019. Functional Divergence of PIN1 Paralogous Genes in Rice. *Plant Cell Physiol.* 60(12):2720–32

205. Li Z, Li B, Liu J, Guo Z, Liu Y, et al. 2016. Transcription factors AS1 and AS2 interact with LHP1 to repress KNOX genes in Arabidopsis. *J. Integr. Plant Biol.*

206. Li Z, Liang Y, Yuan Y, Wang L, Meng X, et al. 2019. OsBRXL4 Regulates Shoot Gravitropism and Rice Tiller Angle through Affecting LAZY1 Nuclear Localization. *Mol. Plant*. 12(8):1143–56

207. Liao Z, Yu H, Duan J, Yuan K, Yu C, et al. 2019. SLR1 inhibits MOC1 degradation to coordinate tiller number and plant height in rice. *Nat. Commun.* 10(1):2738

208. Liebsch D, Palatnik JF. 2020. MicroRNA miR396, GRF transcription factors and GIF co-regulators: a conserved plant growth regulatory module with potential for breeding and biotechnology. *Curr. Opin. Plant Biol.* 53:31–42

209. Liller CB, Neuhaus R, von Korff M, Koornneef M, van Esse W, Zeng D. 2015. Mutations in Barley Row Type Genes Have Pleiotropic Effects on Shoot Branching. *PLoS One*. 10(10):e0140246

210. Lim J, Helariutta Y, Specht CD, Jung J, Sims L, et al. 2000. Molecular analysis of the SCARECROW gene in maize reveals a common basis for radial patterning in diverse meristems. *Plant Cell*. 12(8):1307–18

211. Lin W -c. 2003. The Arabidopsis LATERAL ORGAN BOUNDARIES-Domain Gene ASYMMETRIC LEAVES2 Functions in the Repression of KNOX Gene Expression and in Adaxial-Abaxial Patterning. *Plant Cell*. 15(10):2241–52

212. Liu C, Zheng S, Gui J, Fu C, Yu H, et al. 2018. Shortened Basal Internodes Encodes a Gibberellin 2-Oxidase and Contributes to Lodging Resistance in Rice. *Mol. Plant*. 11(2):288–99

213. Liu H, Li G, Yang X, Kuijer HNJ, Liang W, Zhang D. 2020. Transcriptome profiling reveals phase-specific gene expression in the developing barley inflorescence. *Crop J.* 8(1):71–86

214. Liu H, Zhou X, Li Q, Wang L, Xing Y. 2020. CCT domain-containing genes in cereal crops: flowering time and beyond. *Theor. Appl. Genet.* 133(5):1385–96

215. Liu JM, Park SJ, Huang J, Lee EJ, Xuan YH, et al. 2016. Loose Plant Architecture1 (LPA1) determines lamina joint bending by suppressing auxin signalling that interacts with C-22-hydroxylated and 6-deoxo brassinosteroids in rice. *J. Exp. Bot.* 67(6):1883–95

216. Liu K, Cao J, Yu K, Liu X, Gao Y, et al. 2019. Wheat TaSPL8 Modulates Leaf Angle Through Auxin and Brassinosteroid Signaling. *Plant Physiol.* 181(1):179–94

217. Liu K, Xu H, Liu G, Guan P, Zhou X, et al. 2018. QTL mapping of flag leaf-related traits in wheat (Triticum aestivum L.). *Theor. Appl. Genet.* 131(4):839–49

218. Liu L, Gallagher J, Arevalo ED, Chen R, Skopelitis T, et al. 2021. Enhancing grain-yield-related traits by CRISPR–Cas9 promoter editing of maize CLE genes. *Nat. Plants*. 7(3):287–94

219. Liu L, Sun G, Ren X, Li C, Sun D. 2015. Identification of QTL underlying physiological and morphological traits of flag leaf in barley. *BMC Genet.* 16(1):29

220. Liuling Y, Artem L, Ann B, Gabriela T, Wusirika R, et al. 2004. The Wheat VRN2 Gene Is a Flowering Repressor Down-Regulated by Vernalization. *Science.* 303(5664):1640–44

221. Lombardo F, Yoshida H. 2015. Interpreting lemma and palea homologies: a point of view from rice floral mutants. *Front. Plant Sci.* 6:61

222. Long SP, ZHU X, Naidu SL, Ort DR. 2006. Can improvement in photosynthesis increase crop yields? *Plant. Cell Environ.* 29(3):315–30

223. Lu Y, Meng Y, Zeng J, Luo Y, Feng Z, et al. 2020. Coordination between GROWTH-REGULATING FACTOR1 and GRF-INTERACTING FACTOR1 plays a key role in regulating leaf growth in rice.

BMC Plant Biol. 20(1):200

224. Lu Z, Yu H, Xiong G, Wang J, Jiao Y, et al. 2013. Genome-wide binding analysis of the transcription activator ideal plant architecture1 reveals a complex network regulating rice plant architecture. *Plant Cell*. 25(10):3743–59

225. LUNDQVIST U, ABEBE B, LUNDQVIST A. 1989. Gene interaction of induced intermedium mutations of two-row barley. *Hereditas*. 111(1):37–47

226. Luo M, Yu C-W, Chen F-F, Zhao L, Tian G, et al. 2012. Histone deacetylase HDA6 is functionally associated with AS1 in repression of KNOX genes in arabidopsis. *PLoS Genet.* 8(12):e1003114

227. Luo X, Zheng J, Huang R, Huang Y, Wang H, et al. 2016. Phytohormones signaling and crosstalk regulating leaf angle in rice. *Plant Cell Rep.* 35(12):2423–33

228. Lv H, Zheng J, Wang T, Fu J, Huai J, et al. 2014. The maize d2003, a novel allele of VP8, is required for maize internode elongation. *Plant Mol. Biol.* 84(3):243–57

229. Lv LH, Zhao M, Zhao JR, Tao HB, Wang P. 2008. Canopy structure and photosynthesis of summer maize under different nitrogen fertilizer application rates. *Sci. Agric. Sin.* 41(9):2624–32

230. Lynch JP. 2013. Steep, cheap and deep: an ideotype to optimize water and N acquisition by maize root systems. *Ann. Bot.* 112(2):347–57

231. Lyu J, Huang L, Zhang S, Zhang Y, He W, et al. 2020. Neo-functionalization of a Teosinte branched 1 homologue mediates adaptations of upland rice. *Nat. Commun.* 11(1):725

232. Lyu J, Wang D, Duan P, Liu Y, Huang K, et al. 2020. Control of Grain Size and Weight by the GSK2-LARGE1/OML4 Pathway in Rice. *Plant Cell*. 32(6):1905–18

233. Ma DL, Xie RZ, Niu XK, Li SK, Long HL, Liu YE. 2014. Changes in the morphological traits of maize genotypes in China between the 1950s and 2000s. *Eur. J. Agron.* 58:1–10

234. Ma X, Feng F, Zhang Y, Elesawi IE, Xu K, et al. 2019. A novel rice grain size gene OsSNB was identified by genome-wide association study in natural population. *PLOS Genet.* 15(5):e1008191

235. Magne K, Liu S, Massot S, Dalmais M, Morin H, et al. 2020. Roles of BdUNICULME4 and BdLAXATUM-A in the non-domesticated grass Brachypodium distachyon. *Plant J.* 103(2):645–59

236. Mähönen AP, Tusscher K Ten, Siligato R, Smetana O, Díaz-Triviño S, et al. 2014. PLETHORA gradient formation mechanism separates auxin responses. *Nature*. 515(7525):125–29

237. Malcomber ST, Kellogg EA. 2004. Heterogenous expression patterns and separate roles of the SEPALLATA gene LEAFY HULL STERILE1 in grasses. *Plant Cell*. 16(7):1692–1706

238. Malcomber ST, Preston JC, Reinheimer R, Kossuth J, Kellogg EA. 2006. Developmental Gene Evolution and the Origin of Grass Inflorescence Diversity. In *Advances in Botanical Research*. 44:425–81. Academic Press

239. Mantilla-Perez MB, Salas Fernandez MG. 2017. Differential manipulation of leaf angle throughout the canopy: current status and prospects. *J. Exp. Bot.* 68(21–22):5699–5717

240. Mathan J, Singh A, Jathar V, Ranjan A. 2019. Anatomical features, efficient photosystem, and Rubisco activity contribute to high leaf photosynthesis in wild rice. *bioRxiv*, p. 754887

241. Matsuoka M, Ichikawa H, Saito A, Tada Y, Fujimura T, Kano-Murakami Y. 1993. Expression of a

rice homeobox gene causes altered morphology of transgenic plants. *Plant Cell*. 5(9):1039 LP – 1048

242. McKeown M, Schubert M, Preston JC, Fjellheim S. 2017. Evolution of the miR5200-FLOWERING LOCUS T flowering time regulon in the temperate grass subfamily Pooideae. *Mol. Phylogenet. Evol.* 114:111–21

243. McKim SM, Koppolu R, Schnurbusch T. 2018. Barley Inflorescence Architecture. , pp. 171–208. Springer, Cham

244. McKim SM, Stenvik G-E, Butenko MA, Kristiansen W, Cho SK, et al. 2008. The BLADE-ON-PETIOLE genes are essential for abscission zone formation in Arabidopsis. *Development*. 135(8):1537–46

245. McMullen MD, Kresovich S, Villeda HS, Bradbury P, Li H, et al. 2009. Genetic Properties of the Maize Nested Association Mapping Population. *Science.* 325(5941):737 LP – 740

246. McSteen P. 2009. Hormonal Regulation of Branching in Grasses. *Plant Physiol.* 149(1):46–55

247. Mekonnen MM, Hoekstra AY. 2018. Global Anthropogenic Phosphorus Loads to Freshwater and Associated Grey Water Footprints and Water Pollution Levels: A High-Resolution Global Study. *Water Resour. Res.* 54(1):345–58

248. Meng F, Xiang D, Zhu J, Li Y, Mao C. 2019. Molecular Mechanisms of Root Development in Rice. *Rice*. 12(1):1

249. Milla R, Matesanz S. 2017. Growing larger with domestication: a matter of physiology, morphology or allocation? *Plant Biol.* 19(3):475–83

250. Milne RJ, Perroux JM, Rae AL, Reinders A, Ward JM, et al. 2017. Sucrose transporter localization and function in phloem unloading in developing stems. *Plant Physiol.* 173(2):1330–41

251. Miura K, Ikeda M, Matsubara A, Song X-J, Ito M, et al. 2010. OsSPL14 promotes panicle branching and higher grain productivity in rice. *Nat Genet*. 42(6):545–49

252. Miyoshi K, Ahn BO, Kawakatsu T, Ito Y, Itoh JI, et al. 2004. PLASTOCHRON1, a timekeeper of leaf initiation in rice, encodes cytochrome P450. *Proc. Natl. Acad. Sci. U. S. A.* 101(3):875–80

253. Mock JJ, Pearce RB. 1975. An ideotype of maize. *Euphytica*. 24(3):613–23

254. Modrusan Z, Reiser L, Feldmann KA, Fischer RL, Haughn GW. 1994. Homeotic Transformation of Ovules into Carpel-like Structures in Arabidopsis. *Plant Cell*. 6(3):333–49

255. Moon J, Candela H, Hake S. 2013. The Liguleless narrow mutation affects proximal-distal signaling and leaf growth. *Development*. 140(2):405–12

256. Moreno MA, Harper LC, Krueger RW, Dellaporta SL, Freeling M. 1997. liguleless1 encodes a nuclear-localized protein required for induction of ligules and auricles during maize leaf organogenesis. *Genes Dev.* . 11(5):616–28

257. Muehlbauer GJ, Fowler JE, Girard L, Tyers R, Harper L, Freeling M. 1999. Ectopic Expression of the Maize Homeobox Gene Liguleless3 Alters Cell Fates in the Leaf1. *Plant Physiol.* 119(2):651–62

258. Mulki MA, Bi X, von Korff M. 2018. FLOWERING LOCUS T3 controls spikelet initiation but not floral development. *Plant Physiol.* 178(3):1170–86

259. Multani DS, Briggs SP, Chamberlin MA, Blakeslee JJ, Murphy AS, Johal GS. 2003. Loss of an

MDR Transporter in Compact Stalks of Maize br2 and Sorghum dw3 Mutants. *Science.* 302(5642):81 LP – 84

260. Nagasawa N, Miyoshi M, Sano Y, Satoh H, Hirano H, et al. 2003. SUPERWOMAN1 and DROOPING LEAF genes control floral organ identity in rice. *Development*. 130(4):705–18

261. Nagel M, Behrens A-K, Börner A. 2013. Effects of *Rht* dwarfing alleles on wheat seed vigour after controlled deterioration. *Crop Pasture Sci.* 64(9):857–64

262. Nair SK, Wang N, Turuspekov Y, Pourkheirandish M, Sinsuwongwat S, et al. 2010. Cleistogamous flowering in barley arises from the suppression of microRNA-guided HvAP2 mRNA cleavage. *Proc. Natl. Acad. Sci.* 107(1):490–95

263. Nardmann J, Ji J, Werr W, Scanlon MJ. 2004. The maize duplicate genes narrow sheath1 and narrow sheath2 encode a conserved homeobox gene function in a lateral domain of shoot apical meristems. *Development*. 131(12):2827–39

264. Nardmann J, Werr W. 2012. The invention of WUS-like stem cell-promoting functions in plants predates leptosporangiate ferns. *Plant Mol. Biol.* 78(1–2):123–34

265. Nelissen H, Eeckhout D, Demuynck K, Persiau G, Walton A, et al. 2015. Dynamic Changes in ANGUSTIFOLIA3 Complex Composition Reveal a Growth Regulatory Mechanism in the Maize Leaf. *Plant Cell*. 27(6):1605 LP – 1619

266. Nelissen H, Gonzalez N, Inzé D. 2016. Leaf growth in dicots and monocots: so different yet so alike. *Curr. Opin. Plant Biol.* 33:72–76

267. Nelissen H, Rymen B, Jikumaru Y, Demuynck K, Van Lijsebettens M, et al. 2012. A Local Maximum in Gibberellin Levels Regulates Maize Leaf Growth by Spatial Control of Cell Division. *Curr. Biol.* 22(13):1183–87

268. Nicholls PB, May LH. 1964. Studies on the growth of the barley apex. II. on the initiation of internode elongation in the inflorescence. *Aust. J. Bioi. Sci.* 17:619–30

269. Niklas KJ. 1990. The Mechanical Significance of Clasping Leaf Sheaths in Grasses: Evidence from Two Cultivars of Avena sativa. *Ann. Bot.* 65(5):505–12

270. Ning J, Zhang B, Wang N, Zhou Y, Xiong L. 2011. Increased Leaf Angle1, a Raf-Like MAPKKK That Interacts with a Nuclear Protein Family, Regulates Mechanical Tissue Formation in the Lamina Joint of Rice. *Plant Cell*. 23(12):4334 LP – 4347

271. O'Connor DL, Runions A, Sluis A, Bragg J, Vogel JP, et al. 2014. A Division in PIN-Mediated Auxin Patterning during Organ Initiation in Grasses. *PLOS Comput. Biol.* 10(1):e1003447

272. O'Connor K, González-Suárez P, Dixon LE. 2020. Temperature Control of Plant Development. In *Annual Plant Reviews online*, pp. 563–606. Wiley

273. Ohmori S, Kimizu M, Sugita M, Miyao A, Hirochika H, et al. 2009. MOSAIC FLORAL ORGANS1, an AGL6-like MADS box gene, regulates floral organ identity and meristem fate in rice. *Plant Cell*. 21(10):3008–25

274. Ohto M -a., Fischer RL, Goldberg RB, Nakamura K, Harada JJ. 2005. Control of seed mass by APETALA2. *Proc. Natl. Acad. Sci.* 102(8):3123–28

275. Okamura M, Hirose T, Hashida Y, Yamagishi T, Ohsugi R, Aoki N. 2013. Starch reduction in rice stems due to a lack of OsAGPL1 or OsAPL3 decreases grain yield under low irradiance during ripening and modifies plant architecture. *Funct. Plant Biol.* 40(11):1137–46

276. Ort DR, Merchant SS, Alric J, Barkan A, Blankenship RE, et al. 2015. Redesigning photosynthesis to sustainably meet global food and bioenergy demand. *Proc. Natl. Acad. Sci.* 112(28):8529 LP – 8536

277. Patil V, McDermott HI, McAllister T, Cummins M, Silva JC, et al. 2019. APETALA2 control of barley internode elongation. *Development*. 146(11):

278. Pendleton JW, Smith GE, Winter SR, Johnston TJ. 1968. Field Investigations of the Relationships of Leaf Angle in Corn (Zea mays L.) to Grain Yield and Apparent Photosynthesis1. *Agron. J.* 60(4):422–24

279. Peng J, Harberd NP. 1997. Gibberellin deficiency and response mutations suppress the stem elongation phenotype of phytochrome-deficient mutants of Arabidopsis. *Plant Physiol.* 113(4):1051 LP – 1058

280. Peng J, Richards DE, Hartley NM, Murphy GP, Devos KM, et al. 1999. "Green revolution" genes encode mutant gibberellin response modulators. *Nature*. 400(6741):256–61

281. Peng J, Richards DE, Hartley NM, Murphy GP, Devos KM, et al. 1999. "Green revolution" genes encode mutant gibberellin response modulators. *Nature*. 400(6741):256–61

282. Phelps-Durr TL, Thomas J, Vahab P, Timmermans MCP. 2005. Maize rough sheath2 and Its Arabidopsis Orthologue ASYMMETRIC LEAVES1 Interact with HIRA, a Predicted Histone Chaperone, to Maintain knox Gene Silencing and Determinacy during Organogenesis. *Plant Cell*. 17(11):2886–98

283. Pieper R, Tomé F, Pankin A, von Korff M. 2021. FLOWERING LOCUS T4 delays flowering and decreases floret fertility in barley. *J. Exp. Bot.* 72(1):107–21

284. Poursarebani N, Seidensticker T, Koppolu R, Trautewig C, Gawroński P, et al. 2015. The genetic basis of composite spike form in barley and 'miracle-wheat.' *Genetics*

285. Poursarebani N, Seidensticker T, Koppolu R, Trautewig C, Gawroński P, et al. 2015. The Genetic Basis of Composite Spike Form in Barley and 'Miracle-Wheat.' *Genetics*. 201(1):155–65

286. Poursarebani N, Trautewig C, Melzer M, Nussbaumer T, Lundqvist U, et al. 2020. COMPOSITUM 1 contributes to the architectural simplification of barley inflorescence via meristem identity signals. *Nat. Commun.* 11(1):1–16

287. Prasad K, P. S, Kumar S, Kushalappa K, Vijayraghavan U. 2001. Ectopic expression of rice OsMADS1 reveals a role in specifying the lemma and palea, grass floral organs analogous to sepals. *Dev. Genes Evol.* 211(6):281–90

288. Prasad K, Parameswaran S, Vijayraghavan U. 2005. OsMADS1, a rice MADS-box factor, controls differentiation of specific cell types in the lemma and palea and is an early-acting regulator of inner floral organs. *Plant J.* 43(6):915–28

289. Preece C, Livarda A, Christin P-A, Wallace M, Martin G, et al. 2017. How did the domestication of Fertile Crescent grain crops increase their yields? *Funct. Ecol.* 31(2):387–97

290. Ramsay L, Comadran J, Druka A, Marshall DF, Thomas WTB, et al. 2011. INTERMEDIUM-C, a modifier of lateral spikelet fertility in barley, is an ortholog of the maize domestication gene TEOSINTE BRANCHED 1. *Nat. Genet.* 43(2):169–72

291. Ren D, Hu J, Xu Q, Cui Y, Zhang Y, et al. 2018. FZP determines grain size and sterile lemma fate in rice. *J. Exp. Bot.* 69(20):4853–66

292. Ren D, Li Y, He G, Qian Q. 2020. Multifloret spikelet improves rice yield. *New Phytol.* 225(6):2301–6

293. Ren D, Rao Y, Leng Y, Li Z, Xu Q, et al. 2016. Regulatory Role of OsMADS34 in the Determination of Glumes Fate, Grain Yield, and Quality in Rice. *Front. Plant Sci.* 7(DECEMBER2016):1853

294. Ren D, Yu H, Rao Y, Xu Q, Zhou T, et al. 2018. 'Two-floret spikelet' as a novel resource has the potential to increase rice yield. *Plant Biotechnol. J.* 16(2):351–53

295. Richards RA. 2000. Selectable traits to increase crop photosynthesis and yield of grain crops. *J. Exp. Bot.* 51(suppl_1):447–58

296. Richardson AE, Hake S. 2018. Drawing a Line: Grasses and Boundaries. *Plants (Basel, Switzerland)*. 8(1):4

297. Rodríguez D, Andrade FH, Goudriaan J. 1999. Effects of phosphorus nutrition on tiller emergence in wheat. *Plant Soil*. 209(2):283–95

298. Rönspies M, Dorn A, Schindele P, Puchta H. 2021. CRISPR–Cas-mediated chromosome engineering for crop improvement and synthetic biology. *Nat. Plants*. 7(5):566–73

299. Ruan B, Shang L, Zhang B, Hu J, Wang Y, et al. 2020. Natural variation in the promoter of TGW2 determines grain width and weight in rice. *New Phytol.* 227(2):629–40

300. Sachs RM. 1965. Stem Elongation. *Annu. Rev. Plant Physiol.* 16(1):73–96

301. Sachs RM, Lang A, Bretz CF, Roach J. 1960. Shoot histogenesis: subapical meristematic activity in a caulescent plant and the action of gibberellic acid and Amo-1618. *Am. J. Bot.* 47(4):260–66

302. Sadok W, Lopez JR, Zhang Y, Tamang BG, Muehlbauer GJ. 2020. Sheathing the blade: significant contribution of sheaths to daytime and nighttime gas exchange in a grass crop. *plant cell Environ.* 43(8):1844–61

303. Sakamoto T, Morinaka Y, Ohnishi T, Sunohara H, Fujioka S, et al. 2006. Erect leaves caused by brassinosteroid deficiency increase biomass production and grain yield in rice. *Nat. Biotechnol.* 24(1):105–9

304. Sakuma S, Golan G, Guo Z, Ogawa T, Tagiri A, et al. 2019. Unleashing floret fertility in wheat through the mutation of a homeobox gene. *Proc. Natl. Acad. Sci.* 116(11):5182–87

305. Sakuma S, Lundqvist U, Kakei Y, Thirulogachandar V, Suzuki T, et al. 2017. Extreme suppression of lateral floret development by a single amino acid change in the VRS1 transcription factor. *Plant Physiol.* 175(4):1720–31

306. Sakuma S, Pourkheirandish M, Matsumoto T, Koba T, Komatsuda T. 2010. Duplication of a well-conserved homeodomain-leucine zipper transcription factor gene in barley generates a copy with more specific functions. *Funct. Integr. Genomics*. 10(1):123–33

307. Sakuma S, Schnurbusch T. 2020. Of floral fortune: tinkering with the grain yield potential of cereal crops. *New Phytol.* 225(5):1873–82

308. Salazar-Henao JE, Lehner R, Betegón-Putze I, Vilarrasa-Blasi J, Caño-Delgado AI. 2016. BES1 regulates the localization of the brassinosteroid receptor BRL3 within the provascular tissue of the Arabidopsis primary root. *J. Exp. Bot.*

309. Sang D, Chen D, Liu G, Liang Y, Huang L, et al. 2014. Strigolactones regulate rice tiller angle by

attenuating shoot gravitropism through inhibiting auxin biosynthesis. *Proc. Natl. Acad. Sci. U. S. A.* 111(30):11199–204

310. Satterlee JW, Scanlon MJ. 2019. Coordination of Leaf Development Across Developmental Axes. *Plants*. 8(10):433

311. Satterlee JW, Strable J, Scanlon MJ. 2020. Plant stem-cell organization and differentiation at single-cell resolution. *Proc. Natl. Acad. Sci.* 117(52):33689 LP – 33699

312. Scanlon MJ, Freeling M. 1998. The narrow sheath leaf domain deletion: a genetic tool used to reveal developmental homologies among modified maize organs. *Plant J.* 13(4):547–61

313. Scanlon MJ, Schneeberger RG, Freeling M. 1996. The maize mutant narrow sheath fails to establish leaf margin identity in a meristematic domain. *Development*. 122(6):1683 LP – 1691

314. Schneeberger R, Tsiantis M, Freeling M, Langdale JA. 1998. The rough sheath2 gene negatively regulates homeobox gene expression during maize leaf development. *Development*. 125(15):2857–65

315. Schneeberger RG, Becraft PW, Hake S, Freeling M. 1995. Ectopic expression of the knox homeo box gene rough sheath1 alters cell fate in the maize leaf. *Genes Dev.* 9(18):2292–2304

316. Schrager-Lavelle A, Klein H, Fisher A, Bartlett M. 2017. Grass flowers: An untapped resource for floral evo-devo. *J. Syst. Evol.* 55(6):525–41

317. Schreiber AW, Shi B-J, Huang C-Y, Langridge P, Baumann U. 2011. Discovery of barley miRNAs through deep sequencing of short reads. *BMC Genomics*. 12(1):129

318. Semiarti E, Ueno Y, Tsukaya H, Iwakawa H, Machida C, Machida Y. 2001. The ASYMMETRIC LEAVES2 gene of Arabidopsis thaliana regulates formation of a symmetric lamina, establishment of venation and repression of meristem-related homeobox genes in leaves. *Development*. 128(10):1771–83

319. Senapati N, Semenov MA. 2020. Large genetic yield potential and genetic yield gap estimated for wheat in Europe. *Glob. Food Sec.* 24:100340

320. Shaaf S, Bretani G, Biswas A, Fontana IM, Rossini L. 2019. Genetics of barley tiller and leaf development. *J. Integr. Plant Biol.* 61(3):226–56

321. Sharman BC. 1942. Developmental anatomy of the shoot of Zea mays L. *Ann. Bot.* 6(22):245–82

322. Shaw LM, Turner AS, Laurie DA. 2012. The impact of photoperiod insensitive Ppd-1a mutations on the photoperiod pathway across the three genomes of hexaploid wheat (Triticum aestivum). *Plant J.* 71(1):71–84

323. Shimano S, Hibara K, Furuya T, Arimura S, Tsukaya H, Itoh J-I. 2018. Conserved functional control, but distinct regulation, of cell proliferation in rice and Arabidopsis leaves revealed by comparative analysis of GRF-INTERACTING FACTOR 1 orthologs. *Development*. 145(7):dev159624

324. Shindo M, Yamamoto S, Shimomura K, Umehara M. 2020. Strigolactones Decrease Leaf Angle in Response to Nutrient Deficiencies in Rice. *Front. Plant Sci.* 11:135

325. Shoesmith JR, Solomon CU, Yang X, Wilkinson LG, Sheldrick S, et al. 2021. APETALA2 functions as a temporal factor together with BLADE-ON-PETIOLE2 and MADS29 to control flower and grain development in barley. *Development*. 148(5):dev194894

326. Si L, Chen J, Huang X, Gong H, Luo J, et al. 2016. OsSPL13 controls grain size in cultivated rice. *Nat. Genet.* 48(4):447–56

327. Simkin AJ, López-Calcagno PE, Raines CA. 2019. Feeding the world: improving photosynthetic efficiency for sustainable crop production. *J. Exp. Bot.* 70(4):1119–40

328. Simons KJ, Fellers JP, Trick HN, Zhang Z, Tai Y-S, et al. 2006. Molecular characterization of the major wheat domestication gene Q. *Genetics*. 172(1):547–55

329. Sinclair TR, Sheehy JE. 1999. Erect Leaves and Photosynthesis in Rice. *Science.* 283(5407):1455 LP – 1455

330. Sinha N, Hake S. 1990. Mutant characters of Knotted maize leaves are determined in the innermost tissue layers. *Dev. Biol.* 141(1):203–10

331. Sirault XRR, Condon AG, Wood JT, Farquhar GD, Rebetzke GJ. 2015. "Rolled-upness": phenotyping leaf rolling in cereals using computer vision and functional data analysis approaches. *Plant Methods*. 11(1):1–11

332. Somssich M, Je B Il, Simon R, Jackson D. 2016. CLAVATA-WUSCHEL signaling in the shoot meristem. *Development*. 143(18):3238–48

333. Song G, Sun G, Kong X, Jia M, Wang K, et al. 2019. The soft glumes of common wheat are sterile-lemmas as determined by the domestication gene Q. *Crop J.* 7(1):113–17

334. Song X-J, Huang W, Shi M, Zhu M-Z, Lin H-X. 2007. A QTL for rice grain width and weight encodes a previously unknown RING-type E3 ubiquitin ligase. *Nat. Genet.* 39(5):623–30

335. Song X, Lu Z, Yu H, Shao G, Xiong J, et al. 2017. IPA1 functions as a downstream transcription factor repressed by D53 in strigolactone signaling in rice. *Cell Res.* 27(9):1128–41

336. Sormacheva I, Golovnina K, Vavilova V, Kosuge K, Watanabe N, et al. 2015. Q gene variability in wheat species with different spike morphology. *Genet. Resour. Crop Evol.* 62(6):837–52

337. Spielmeyer W, Ellis MH, Chandler PM. 2002. Semidwarf (sd-1), "green revolution" rice, contains a defective gibberellin 20-oxidase gene. *Proc. Natl. Acad. Sci. U. S. A.* 99(13):9043–48

338. Stahl Y, Simon R. 2009. Is the arabidopsis root niche protected by sequestration of the CLE40 signal by its putative receptor ACR4? *Plant Signal. Behav.* 4(7):634–35

339. Stirnberg P, Chatfield SP, Leyser HMO. 1999. AXR1 acts after lateral bud formation to inhibit lateral bud growth in Arabidopsis. *Plant Physiol.* 121(3):839–47

340. Strable J, Wallace JG, Unger-Wallace E, Briggs S, Bradbury PJ, et al. 2017. Maize YABBY Genes drooping leaf1 and drooping leaf2 Regulate Plant Architecture. *Plant Cell*. 29(7):1622–41

341. Studer A, Zhao Q, Ross-Ibarra J, Doebley J. 2011. Identification of a functional transposon insertion in the maize domestication gene tb1. *Nat. Genet.* 43(11):1160–63

342. Subudhi PK, De Leon TB, Tapia R, Chai C, Karan R, et al. 2018. Genetic interaction involving photoperiod-responsive Hd1 promotes early flowering under long-day conditions in rice. *Sci. Rep.* 8(1):2081

343. Sun Q, Li TY, Li DD, Wang ZY, Li S, et al. 2019. Overexpression of Loose Plant Architecture 1 increases planting density and resistance to sheath blight disease via activation of PIN-FORMED 1a in rice. *Plant Biotechnol. J.* 17(5):855–57

344. Sun T. 2008. Gibberellin Metabolism, Perception and Signaling Pathways in Arabidopsis. *Arab.*

B. 2008(6):e0103

345. Sun X, Cahill J, Van Hautegem T, Feys K, Whipple C, et al. 2017. Altered expression of maize PLASTOCHRON1 enhances biomass and seed yield by extending cell division duration. *Nat. Commun.* 8(1):14752

346. Sun Y, Fan X-Y, Cao D-M, Tang W, He K, et al. 2010. Integration of brassinosteroid signal transduction with the transcription network for plant growth regulation in Arabidopsis. *Dev. Cell*. 19(5):765–77

347. Takeda T, Suwa Y, Suzuki M, Kitano H, Ueguchi-Tanaka M, et al. 2003. The OsTB1 gene negatively regulates lateral branching in rice. *Plant J.* 33(3):513–20

348. Tang Y, Liu H, Guo S, Wang B, Li Z, et al. 2018. OsmiR396d Affects Gibberellin and Brassinosteroid Signaling to Regulate Plant Architecture in Rice. *Plant Physiol.* 176(1):946–59

349. Tavakol E, Okagaki R, Verderio G, Vahid SJ, Hussien A, et al. 2015. The barley Uniculme4 gene encodes a BLADE-ON-PETIOLE-like protein that controls tillering and leaf patterning. *Plant Physiol.* 168(1):164–74

350. Theißen G, Melzer R, Rümpler F. 2016. MADS-domain transcription factors and the floral quartet model of flower development: linking plant development and evolution. *Development*. 143(18):3259 LP – 3271

351. Theodoris G, Inada N, Freeling M. 2003. Conservation and molecular dissection of ROUGH SHEATH2 and ASYMMETRIC LEAVES1 function in leaf development. *Proc. Natl. Acad. Sci. U. S. A.*

352. Thiel J, Koppolu R, Trautewig C, Hertig C, Kale SM, et al. 2021. Transcriptional landscapes of floral meristems in barley. *Sci. Adv.* 7(18):eabf0832

353. Thompson BE, Bartling L, Whipple C, Hall DH, Sakai H, et al. 2009. bearded-ear encodes a MADS box transcription factor critical for maize floral development. *Plant Cell*. 21(9):2578–90

354. Thornsberry JM, Goodman MM, Doebley J, Kresovich S, Nielsen D, Buckler ES. 2001. Dwarf8 polymorphisms associate with variation in flowering time. *Nat. Genet.* 28(3):286–89

355. Tian F, Bradbury PJ, Brown PJ, Hung H, Sun Q, et al. 2011. Genome-wide association study of leaf architecture in the maize nested association mapping population. *Nat. Genet.* 43(2):159–62

356. Tian J, Wang C, Xia J, Wu L, Xu G, et al. 2019. Teosinte ligule allele narrows plant architecture and enhances high-density maize yields. *Science.* 365(6454):658–64

357. Timmermans MCP. 1999. ROUGH SHEATH2: A Myb Protein That Represses knox Homeobox Genes in Maize Lateral Organ Primordia. *Science.* 284(5411):151–53

358. Tong H, Jin Y, Liu W, Li F, Fang J, et al. 2009. DWARF and LOW-TILLERING, a new member of the GRAS family, plays positive roles in brassinosteroid signaling in rice. *Plant J.* 58(5):803–16

359. Tong H, Xiao Y, Liu D, Gao S, Liu L, et al. 2014. Brassinosteroid regulates cell elongation by modulating gibberellin metabolism in rice. *Plant Cell*. 26(11):4376–93

360. Toriba T, Tokunaga H, Nagasawa K, Nie F, Yoshida A, Kyozuka J. 2020. Suppression of Leaf Blade Development by BLADE-ON-PETIOLE Orthologs Is a Common Strategy for Underground Rhizome Growth. *Curr. Biol.*

361. Toriba T, Tokunaga H, Shiga T, Nie F, Naramoto S, et al. 2019. BLADE-ON-PETIOLE genes

temporally and developmentally regulate the sheath to blade ratio of rice leaves. *Nat. Commun.* 10(1):619

362. Trevaskis B, Bagnall DJ, Ellis MH, Peacock WJ, Dennis ES. 2003. MADS box genes control vernalization-induced flowering in cereals. *Proc. Natl. Acad. Sci.* 100(22):13099 LP – 13104

363. Trung KH, Tran QH, Bui NH, Tran TT, Luu KQ, et al. 2020. A Weak Allele of FASCIATED EAR 2 (FEA2) Increases Maize Kernel Row Number (KRN) and Yield in Elite Maize Hybrids. *Agronomy*. 10(11):1774

364. Truong SK, McCormick RF, Rooney WL, Mullet JE. 2015. Harnessing Genetic Variation in Leaf Angle to Increase Productivity of Sorghum bicolor *Genetics*. 201(3):1229 LP – 1238

365. Tsuda K, Abraham-Juarez M-J, Maeno A, Dong Z, Aromdee D, et al. 2017. KNOTTED1 Cofactors, BLH12 and BLH14, Regulate Internode Patterning and Vein Anastomosis in Maize. *Plant Cell*. 29(5):1105–18

366. Turner A, Beales J, Faure S, Dunford RP, Laurie DA. 2005. The Pseudo-Response Regulator Ppd-H1 Provides Adaptation to Photoperiod in Barley. *Science.* 310(5750):1031–34

367. Ueno Y, Ishikawa T, Watanabe K, Terakura S, Iwakawa H, et al. 2007. Histone Deacetylases and ASYMMETRIC LEAVES2 Are Involved in the Establishment of Polarity in Leaves of Arabidopsis *Plant Cell*. 19(2):445 LP – 457

368. Urano D, Miura K, Wu Q, Iwasaki Y, Jackson D, Jones AM. 2016. Plant morphology of Heterotrimeric G protein mutants. *Plant Cell Physiol.* 57(3):437–45

369. van Es SW, Muñoz-Gasca A, Romero-Campero FJ, de los Reyes P, Tarancón C, et al. 2020. A gene regulatory network critical for axillary bud dormancy. *bioRxiv*. 2020.12.14.394403

370. van Esse GW, Walla A, Finke A, Koornneef M, Pecinka A, von Korff M. 2017. Six-Rowed Spike3 (VRS3) Is a Histone Demethylase That Controls Lateral Spikelet Development in Barley. *Plant Physiol.* 174(4):2397–2408

371. Verma A, Niranjana M, Jha SK, Mallick N, Agarwal P, Vinod. 2020. QTL detection and putative candidate gene prediction for leaf rolling under moisture stress condition in wheat. *Sci. Rep.* 10(1):18696

372. Voss-Fels KP, Robinson H, Mudge SR, Richard C, Newman S, et al. 2018. VERNALIZATION1 Modulates Root System Architecture in Wheat and Barley. *Mol. Plant*. 11(1):226–29

373. Waites R, Hudson A. 1995. phantastica: a gene required for dorsoventrality of leaves in Antirrhinum majus. *Development*. 121(7):2143–54

374. Walla A, Wilma van Esse G, Kirschner GK, Guo G, Brünje A, et al. 2020. An Acyl-CoA N-Acyltransferase regulates meristem phase change and plant architecture in Barley. *Plant Physiol.* 183(3):1088–1109

375. Wang B, Smith SM, Li J. 2018. Genetic Regulation of Shoot Architecture. *Annu. Rev. Plant Biol.* 69(1):437–68

376. Wang C, Yang X, Li G. 2021. Molecular Sciences Molecular Insights into Inflorescence Meristem Specification for Yield Potential in Cereal Crops Molecular Insights into Inflorescence Meristem Specification for Yield Potential in Cereal Crops. *Int. J. Mol. Sci*. 22:3508

377. Wang F, Han T, Song Q, Ye W, Song X, et al. 2020. The rice circadian clock regulates tiller

growth and panicle development through strigolactone signaling and sugar sensing. *Plant Cell*. 32(10):3124–38

378. Wang H, Chen W, Eggert K, Charnikhova T, Bouwmeester H, et al. 2018. Abscisic acid influences tillering by modulation of strigolactones in barley. *J. Exp. Bot.* 69(16):3883–98

379. Wang H, Wang H. 2015. The miR156/SPL Module, a Regulatory Hub and Versatile Toolbox, Gears up Crops for Enhanced Agronomic Traits. *Mol. Plant*. 8(5):677–88

380. Wang JR, Hu H, Wang GH, Li J, Chen JY, Wu P. 2009. Expression of PIN genes in rice (Oryza sativa L.): Tissue specificity and regulation by hormones. *Mol. Plant*. 2(4):823–31

381. Wang L, Chu H, Li Z, Wang J, Li J, et al. 2014. Origin and development of the root cap in rice. *Plant Physiol.* 166(2):603–13

382. Wang L, Sun S, Jin J, Fu D, Yang X, et al. 2015. Coordinated regulation of vegetative and reproductive branching in rice. *Proc. Natl. Acad. Sci.* 112(50):15504–9

383. Wang M, Le Moigne M-A, Bertheloot J, Crespel L, Perez-Garcia M-D, et al. 2019. BRANCHED1: A Key Hub of Shoot Branching

384. Wang S-S, Chung C-L, Chen K-Y, Chen R-K. 2020. A Novel Variation in the FRIZZLE PANICLE (FZP) Gene Promoter Improves Grain Number and Yield in Rice. *Genetics*. 215(1):243–52

385. Wang S, Wu K, Yuan Q, Liu X, Liu Z, et al. 2012. Control of grain size, shape and quality by OsSPL16 in rice. *Nat. Genet.* 44(8):950–54

386. Wang W, Li G, Zhao J, Chu H, Lin W, et al. 2014. DWARF TILLER1, a WUSCHEL-Related Homeobox Transcription Factor, Is Required for Tiller Growth in Rice. *PLoS Genet*. 10(3):e1004154

387. Wang Y, Lu J, Ren T, Hussain S, Guo C, et al. 2017. Effects of nitrogen and tiller type on grain yield and physiological responses in rice. *AoB Plants*. 9(2):

388. Watson DJ. 1952. The Physiological Basis of Variation in Yield. , ed AGBT-A in A Norman. 4:101–45. Academic Press

389. Weatherwax P. 1923. *The story of the maize plant*. University of Chicago Press

390. Werner T, Nehnevajova E, Köllmer I, Novák O, Stmad M, et al. 2010. Root-specific reduction of cytokinin causes enhanced root growth, drought tolerance, and leaf mineral enrichment in Arabidopsis and tobacco. *Plant Cell*. 22(12):3905–20

391. Whipple CJ, Kebrom TH, Weber AL, Yang F, Hall D, et al. 2011. grassy tillers1 promotes apical dominance in maize and responds to shade signals in the grasses. *Proc. Natl. Acad. Sci.* . 108(33):E506–12

392. Wilkinson LG, Bird DC, Tucker MR. 2018. Exploring the Role of the Ovule in Cereal Grain Development and Reproductive Stress Tolerance. In *Annual Plant Reviews online*, pp. 181–216. Wiley

393. Wolbang CM, Chandler PM, Smith JJ, Ross JJ. 2004. Auxin from the Developing Inflorescence Is Required for the Biosynthesis of Active Gibberellins in Barley Stems. *Plant Physiol.*

394. Woods DP, Ream TS, Bouché F, Lee J, Thrower N, et al. 2017. Establishment of a vernalization requirement in Brachypodium distachyon requires REPRESSOR OF VERNALIZATION1. *Proc. Natl. Acad. Sci.* 114(25):6623–28

395. Wu L, Liu D, Wu J, Zhang R, Qin Z, et al. 2013. Regulation of FLOWERING LOCUS T by a

microRNA in Brachypodium distachyon. *Plant Cell*. 25(11):4363–77

396. Wu X. 2009. Prospects of Developing Hybrid Rice with Super High Yield. *Agron. J.* 101(3):688–95

397. Wu X, Tang D, Li M, Wang K, Cheng Z. 2013. Loose Plant Architecture1, an INDETERMINATE DOMAIN protein involved in shoot gravitropism, regulates plant architecture in rice. *Plant Physiol.* 161(1):317–29

398. Wu Y, Zhao S, Li X, Zhang B, Jiang L, et al. 2018. Deletions linked to PROG1 gene participate in plant architecture domestication in Asian and African rice. *Nat. Commun.* 9(1):4157

399. Xiang J-J, Zhang G-H, Qian Q, Xue H-W. 2012. SEMI - ROLLED LEAF1 Encodes a Putative Glycosylphosphatidylinositol-Anchored Protein and Modulates Rice Leaf Rolling by Regulating the Formation of Bulliform Cells. *Plant Physiol.* 159(4):1488–1500

400. Xiao J, Xu S, Li C, Xu Y, Xing L, et al. 2014. O-GlcNAc-mediated interaction between VER2 and TaGRP2 elicits TaVRN1 mRNA accumulation during vernalization in winter wheat. *Nat. Commun.* 5(1):4572

401. Xie Q, Li N, Yang Y, Lv Y, Yao H, et al. 2018. Pleiotropic effects of the wheat domestication gene Q on yield and grain morphology. *Planta*. 247(5):1089–98

402. Xie Q, Mayes S, Sparkes DL. 2015. Carpel size, grain filling, and morphology determine individual grain weight in wheat. *J. Exp. Bot.* 66(21):6715–30

403. Xu F, Chen S, Yang X, Zhou S, Chen X, et al. 2021. Genome-Wide Association Study on Seminal and Nodal Roots of Wheat Under Different Growth Environments. *Front. Plant Sci.* 11:

404. Xu H, Zhao M, Zhang Q, Xu Z, Xu Q. 2016. The *DENSE AND ERECT PANICLE 1* (*DEP1*) gene offering the potential in the breeding of high-yielding rice. *Breed. Sci.* 66(5):659–67

405. Xu M, Zhu L, Shou H, Wu P. 2005. A PIN1 family gene, OsPIN1, involved in auxin-dependent adventitious root emergence and tillering in rice. *Plant Cell Physiol.* 46(10):1674–81

406. Xu P, Ali A, Han B, Wu X. 2018. Current Advances in Molecular Basis and Mechanisms Regulating Leaf Morphology in Rice. *Front. Plant Sci.* 9:1528

407. Xu W, Tao J, Chen M, Dreni L, Luo Z, et al. 2017. Interactions between FLORAL ORGAN NUMBER4 and floral homeotic genes in regulating rice flower development. *J. Exp. Bot.*

408. Yamaguchi T, Lee DY, Miyao A, Hirochika H, An G, Hirano HY. 2006. Functional diversification of the two C-class MADS box genes OSMADS3 and OSMADS58 in Oryza sativa. *Plant Cell*

409. Yamaguchi T, Nagasawa N, Kawasaki S, Matsuoka M, Nagato Y, Hirano H-Y. 2004. The YABBY Gene DROOPING LEAF Regulates Carpel Specification and Midrib Development in Oryza sativa. *Plant Cell*. 16(2):500–509

410. Yamamuro C, Ihara Y, Wu X, Noguchi T, Fujioka S, et al. 2000. Loss of Function of a Rice brassinosteroid insensitive1 Homolog Prevents Internode Elongation and Bending of the Lamina Joint. *Plant Cell*. 12(9):1591 LP – 1605

411. Yanai O, Shani E, Dolezal K, Tarkowski P, Sablowski R, et al. 2005. Arabidopsis KNOXI proteins activate cytokinin biosynthesis. *Curr. Biol.* 15(17):1566–71

412. Yang J, Thames S, Best NB, Jiang H, Huang P, et al. 2018. Brassinosteroids Modulate Meristem Fate and Differentiation of Unique Inflorescence Morphology in Setaria viridis. *Plant Cell*. 30(1):48–66

413. Yoshida H. 2012. Is the lodicule a petal: Molecular evidence? *Plant Sci.* 184:121–28

414. Yoshihara T, Spalding EP. 2017. LAZY genes mediate the effects of gravity on auxin gradients and plant architecture. *Plant Physiol.* 175(2):959–69

415. Yoshihara T, Spalding EP. 2020. Switching the direction of stem gravitropism by altering two amino acids in Atlazy1. *Plant Physiol.* 182(2):1039–51

416. Yoshikawa T, Tanaka S-Y, Masumoto Y, Nobori N, Ishii H, et al. 2016. Barley *NARROW LEAFED DWARF1* encoding a WUSCHEL-RELATED HOMEOBOX 3 (WOX3) regulates the marginal development of lateral organs. *Breed. Sci.* 66(3):416–24

417. Youssef HM, Eggert K, Koppolu R, Alqudah AM, Poursarebani N, et al. 2017. VRS2 regulates hormone-mediated inflorescence patterning in barley. *Nat. Genet.* 49(1):157–61

418. Zakhrabekova S, Gough SP, Braumann I, Muller AH, Lundqvist J, et al. 2012. Induced mutations in circadian clock regulator Mat-a facilitated short-season adaptation and range extension in cultivated barley. *Proc. Natl. Acad. Sci.* 109(11):4326–31

419. Zhang D, Sun W, Singh R, Zheng Y, Cao Z, et al. 2018. GRF-interacting factor1 Regulates Shoot Architecture and Meristem Determinacy in Maize. *Plant Cell*. 30(2):360–74

420. Zhang G-H, Xu Q, Zhu X-D, Qian Q, Xue H-W. 2009. SHALLOT-LIKE1 is a KANADI transcription factor that modulates rice leaf rolling by regulating leaf abaxial cell development. *Plant Cell*. 21(3):719–35

421. Zhang J, Ku LX, Han ZP, Guo SL, Liu HJ, et al. 2014. The ZmCLA4 gene in the qLA4-1 QTL controls leaf angle in maize (Zea mays L.). *J. Exp. Bot.* 65(17):5063–76

422. Zhang L-Y, Bai M-Y, Wu J, Zhu J-Y, Wang H, et al. 2009. Antagonistic HLH/bHLH Transcription Factors Mediate Brassinosteroid Regulation of Cell Elongation and Plant Development in Rice and Arabidopsis. *Plant Cell*. 21(12):3767–80

423. Zhang N, Yu H, Yu H, Cai Y, Huang L, et al. 2018. A Core Regulatory Pathway Controlling Rice Tiller Angle Mediated by the LAZY1-Dependent Asymmetric Distribution of Auxin. *Plant Cell*. 30(7):1461–75

424. Zhang W, Tan L, Sun H, Zhao X, Liu F, et al. 2019. Natural Variations at TIG1 Encoding a TCP Transcription Factor Contribute to Plant Architecture Domestication in Rice. *Mol. Plant*. 12(8):1075–89

425. Zhang X, Davidson EA, Mauzerall DL, Searchinger TD, Dumas P, Shen Y. 2015. Managing nitrogen for sustainable development. *Nature*. 528(7580):51–59

426. Zhang X, Wang J, Huang J, Lan H, Wang C, et al. 2012. Rare allele of OsPPKL1 associated with grain length causes extra-large grain and a significant yield increase in rice. *Proc. Natl. Acad. Sci.* 109(52):21534–39

427. Zhao J, Huang X, Ouyang X, Chen W, Du A, et al. 2012. OsELF3-1, an Ortholog of Arabidopsis EARLY FLOWERING 3, Regulates Rice Circadian Rhythm and Photoperiodic Flowering. *PLoS One*. 7(8):e43705

428. Zhao Y, Christensen SK, Fankhauser C, Cashman JR, Cohen JD, et al. 2001. A role for flavin monooxygenase-like enzymes in auxin biosynthesis. *Science.* 291(5502):306–9

429. Zhong J, van Esse GW, Bi X, Lan T, Walla A, et al. 2021. INTERMEDIUM-M encodes an HvAP2L-H5 ortholog and is required for inflorescence indeterminacy and spikelet determinacy in barley. *Proc. Natl. Acad. Sci.* 118(8):e2011779118

430. Zhou Y, Lu D, Li C, Luo J, Zhu B-F, et al. 2012. Genetic Control of Seed Shattering in Rice by the APETALA2 Transcription Factor SHATTERING ABORTION1. *Plant Cell*. 24(3):1034–48

431. Zhou Y, Zhou G, Broughton S, Westcott S, Zhang X, et al. 2018. Towards the identification of a gene for prostrate tillers in barley (Hordeum vulgare L.). *PLoS One*. 13(2):e0192263

432. Zhu C, Liu L, Crowell O, Zhao H, Brutnell TP, et al. 2021. The CLV3 Homolog in Setaria viridis Selectively Controls Inflorescence Meristem Size. *Front. Plant Sci.* 12:151

433. Zhu M, Hu Y, Tong A, Yan B, Lv Y, et al. 2021. LAZY1 Controls Tiller Angle and Shoot Gravitropism by Regulating the Expression of Auxin Transporters and Signaling Factors in Rice. *Plant Cell Physiol.* 61(12):2111–25

434. Zhu X-G, Long SP, Ort DR. 2010. Improving Photosynthetic Efficiency for Greater Yield. *Annu. Rev. Plant Biol.* 61(1):235–61

435. Zhu Y, Nomura T, Xu Y, Zhang Y, Peng Y, et al. 2006. ELONGATED UPPERMOST INTERNODE encodes a cytochrome P450 monooxygenase that epoxidizes gibberellins in a novel deactivation reaction in rice. *Plant Cell*. 18(2):442–56

436. Zikhali M, Wingen LU, Leverington-Waite M, Specel S, Griffiths S. 2017. The identification of new candidate genes Triticum aestivum FLOWERING LOCUS T3-B1 (TaFT3-B1) and TARGET OF EAT1 (TaTOE1-B1) controlling the short-day photoperiod response in bread wheat. *Plant. Cell Environ.* 40(11):2678–90

437. Zombori Z, Nagy B, Mihály R, Pauk J, Cseri A, et al. 2020. Ring-type e3 ubiqitin ligase barley genes (Hvyrg1–2) control characteristics of both vegetative organs and seeds as yield components. *Plants*. 9(12):1–15

438. Zuo S min, Zhang Y fang, Chen Z xiang, Jiang W, Feng M hui, Pan X biao. 2014. Improvement of Rice Resistance to Sheath Blight by Pyramiding QTLs Conditioning Disease Resistance and Tiller Angle. *Rice Sci.* 21(6):318–26

439. Zwirek M, Waugh R, McKim SM. 2019. Interaction between row-type genes in barley controls meristem determinacy and reveals novel routes to improved grain. *New Phytol.* 221(4):1950–65

FIGURE CAPTIONS

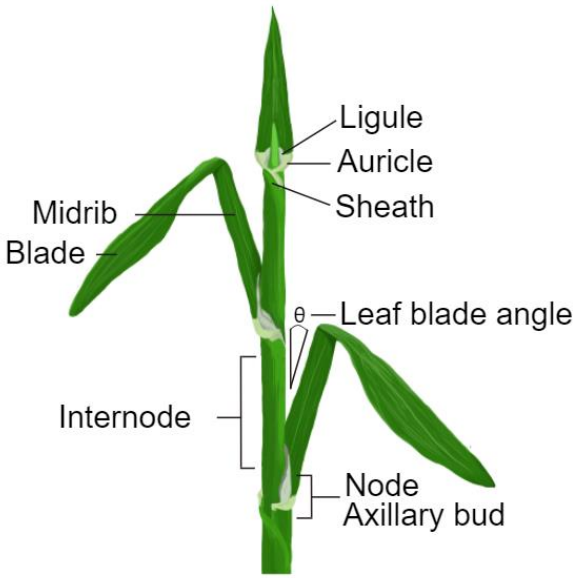


Figure 1.1 – The Vegetative Phytomer. Each phytomer consists of a node, a bud and underlying internode. Vegetative phytomer. Each node bears a leaf composed of a proximal sheath, boundary ligular region made up of the ligule and auricle, and a distal leaf blade. Leaf angle (θ) describes the angle between the leaf and main axis. Axillary buds form at the leaf-node axil and can grow into secondary shoots, called tillers. Internodes separate adjacent nodes.

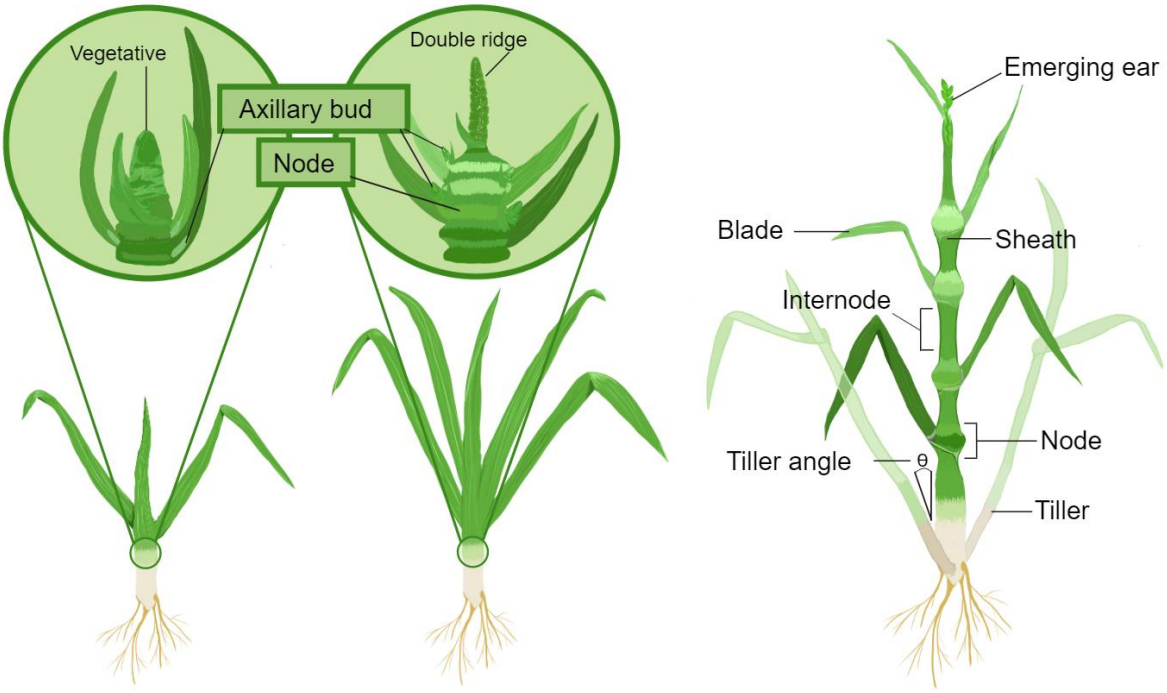
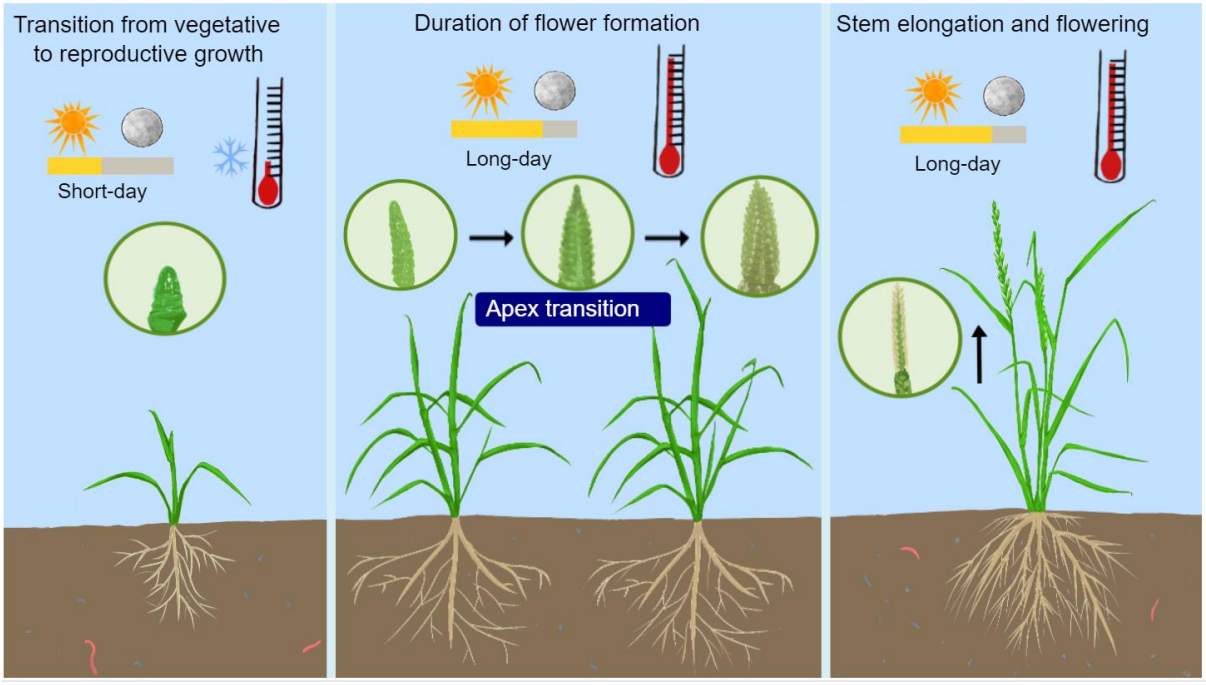


Figure 1.2 - Vegetative to Reproductive transition in cereals using wheat as an example. The wheat shoot apex transitions from a vegetative dome producing leaves into an elongating inflorescence lined with double ridges. The lower ridge arrests while the upper ridge goes on to produce spikelets lining the inflorescence axis. During flowering, the internodes underneath the apex elongate from bottom to top within the leaf sheaths. Final internode elongation pushes the ear out of the flag (last) leaf sheath. Axillary buds along elongated internodes remain dormant, while tillers grow out from nodes adjacent to unelongated basal internodes. Tiller angle describes the angle between the tiller and main stem.



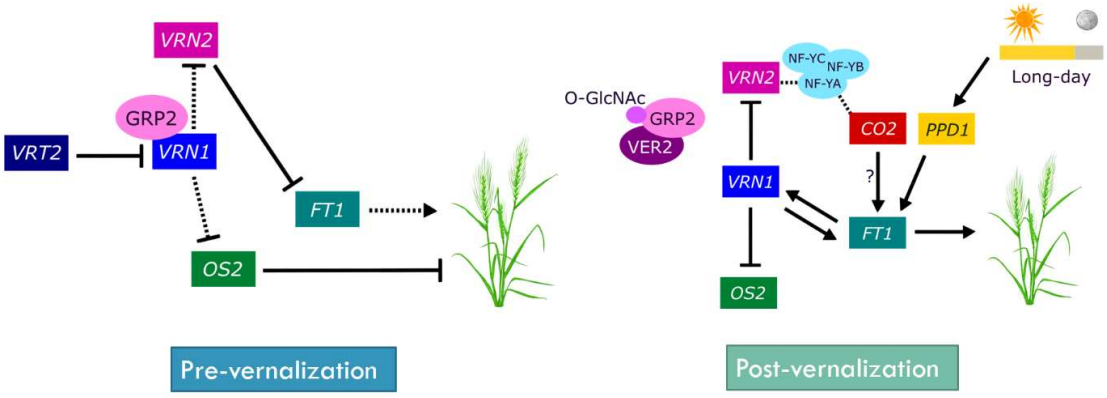


Figure 4.1 – Environmental control of flowering events. (A) Photoperiod and temperature influence multiple aspects of flowering including timing of the vegetative to reproduction transition, elongation of stem internodes and spike emergence from the flag leaf. (B) Molecular network of vernalisation in wheat. Pre-vernalization the repression of *FLOWERING LOCUS T* (*FT*) is via high levels of *VERNALIZATION 2* (*VRN2*) under long days and low levels of *VERNALIZATION 1* (*VRN1*). *VRN1* repression occurs via multiple molecular pathways including via binding of *VRN1* pre-mRNA via GRP2 and repression via *VEGETATIVE TO REPRODUCTIVE TRANSITION 2* (*VRT2*). With lowering temperatures and shorter days (post-vernalization) the repression of *FT1* via VRN2 decreases which also potentially increases the availability of CONSTANS 2 bound to NF-Y proteins which could increase *FT1* expression. Simultaneously, GRP2 is bound via VER2 and an O-GlcNAc modification which increases the availability of *VRN1* mRNA and so protein. Increased levels of VRN1 protein repress *VRN2* and other floral repressors, including *ODDSOC2* (*OS2*), and increase expression of *FT1*. Increased levels of VRN1 and FT1 lead to flowering.

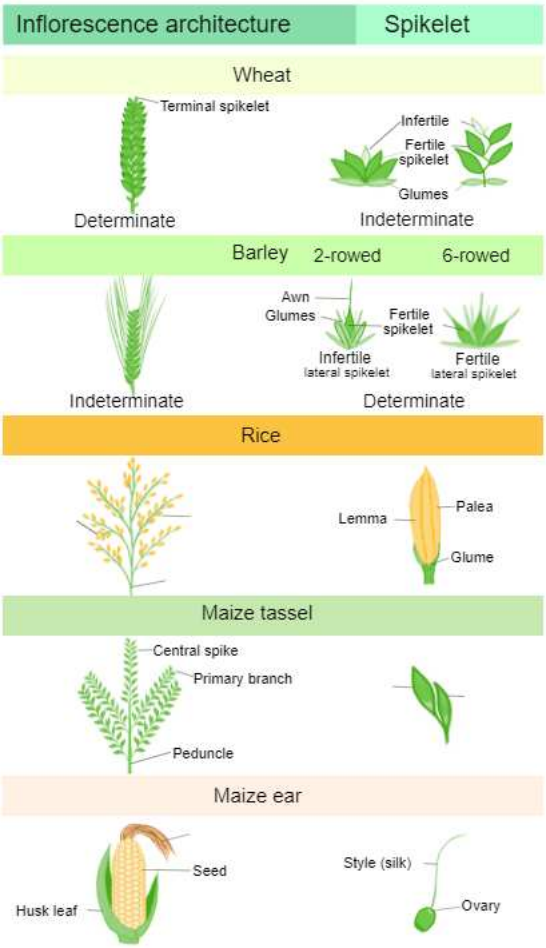


Figure 5.1. Inflorescence architecture and spikelet architecture of key cereal species. Wheat and barley form unbranched spikes. Wheat forms a determinate spike tipped with a terminal spikelet while barley continues to produce spikelets indeterminately from the spike tip. In the wheat spike, each node forms a single spikelet, flanked by glumes, which generates multiple florets indeterminately which only a few becoming fertile to set grain. In the barley spike, spikelets are also flanked by glumes but only ever form one floret. In two-rowed barley, each node forms a central fertile spikelet, setting a single grain, flanked by two infertile lateral spikelets. In six-rowed barley, the lateral spikelets are fertile and can also set grain. Rice forms a branched inflorescence called a panicle which forms primary and secondary branched. Each rice spikelet forms a single floret flanked by glumes. Like other florets, the rice floret has two opposing hulls: the lemma and palea. Maize forms male (tassel) and female (ear) inflorescences. The maize tassel is a branched inflorescence formed on top of the shoot axis and makes spikelet pairs of a sessile and more distal pedicellate spikelet. The maize ear forms rows of spikelet pairs where each floret's ovary style develops a long silk. The ear is wrapped by husk leaves from underlying compressed internodes.

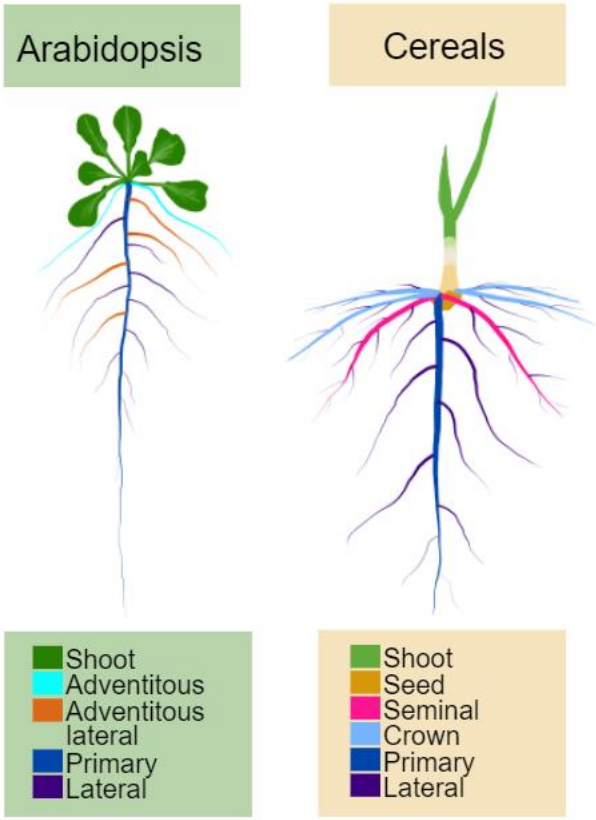


Figure 7.1 - Root system architecture of Arabidopsis compared to cereals. Arabidopsis has been used as a model species for dicotyledons. The root system is formed by different types of secondary roots, of which only the primary root is formed during embryogenesis. The lateral roots are formed post embryogenesis from pre-branch sites that are primed in the primary root meristem. The adventitious roots are formed de novo from non-root tissue. Additionally, the Arabidopsis root forms adventitious lateral roots, these are formed the novo from root tissue. The root system of cereals (monocotyledons) form two embryonic derived root types, the primary root and the seminal roots. After germination, the lateral roots are formed, which arise from the primary, seminal and the shoot-born crown roots (also called brace or nodal roots).