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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.

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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.
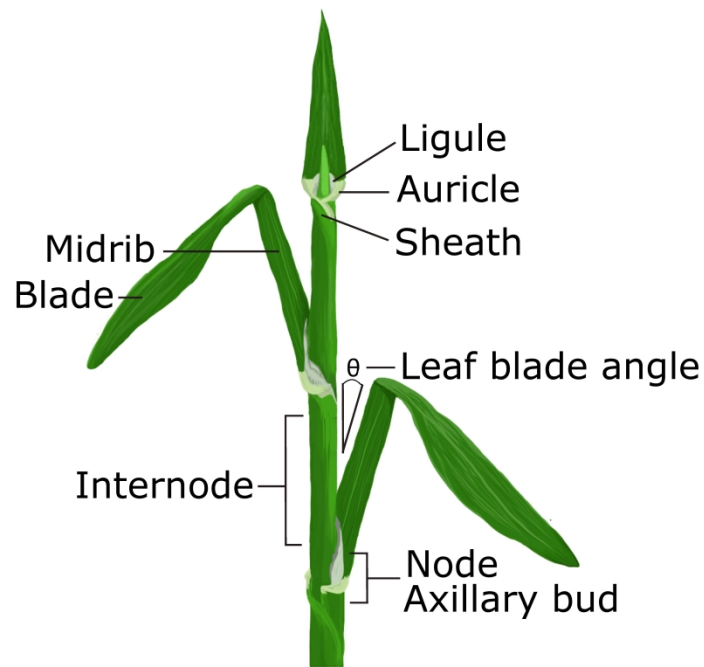
Figure 1.2 - Vegetative to Reproductive transition in cereals using wheat as an example. The wheat shoot apex transitions from a vegetative dome producing leaves into an elongating inflorescence lined with double ridges. The lower ridge arrests while the upper ridge goes on to produce spikelets lining 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).

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 ($\theta$) 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.
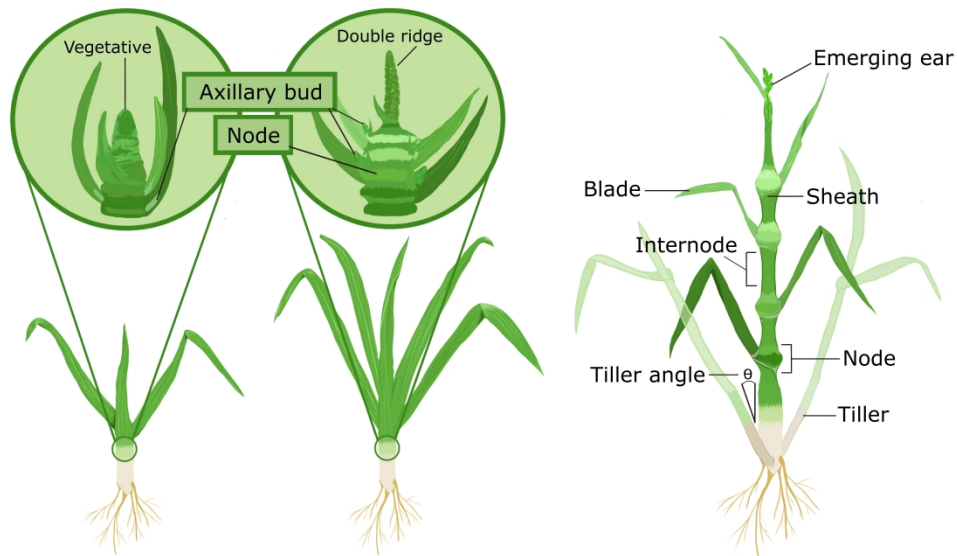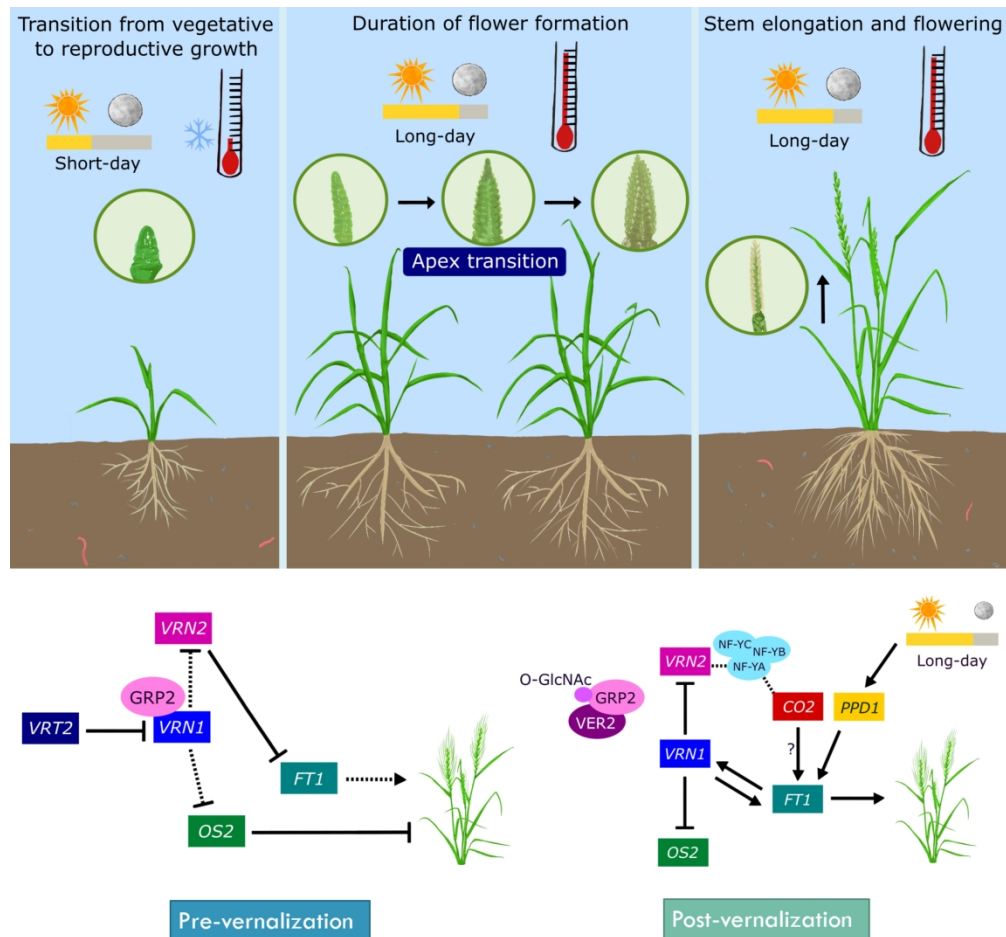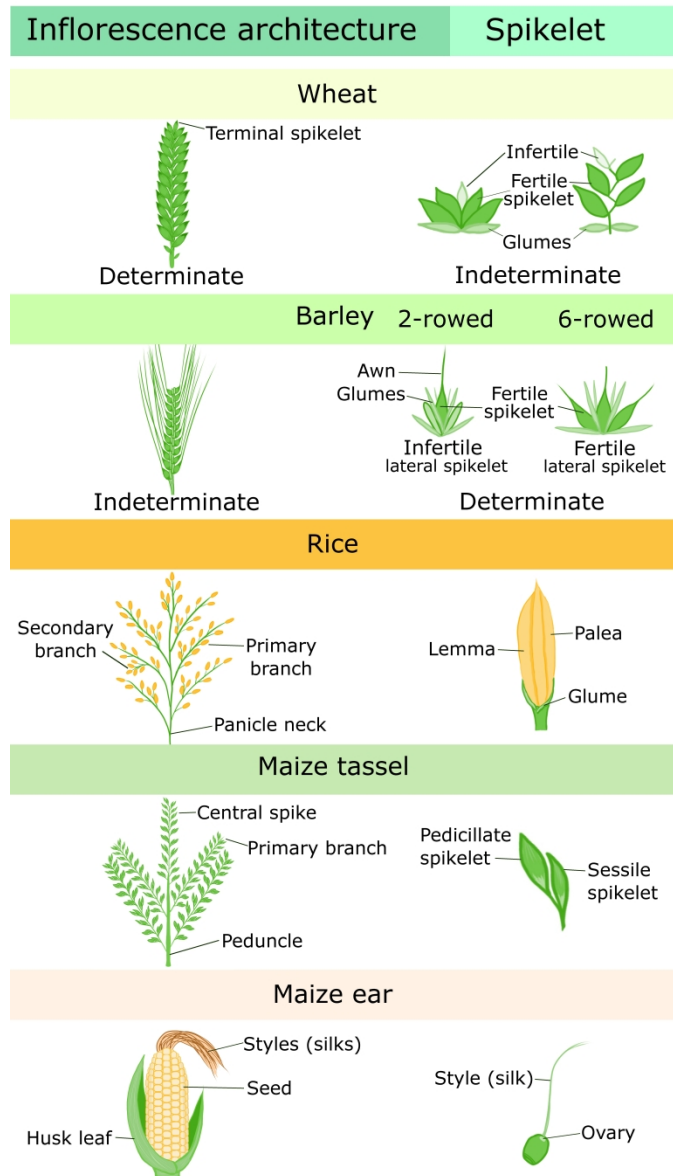
231x347mm (600 x 600 DPI)

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.
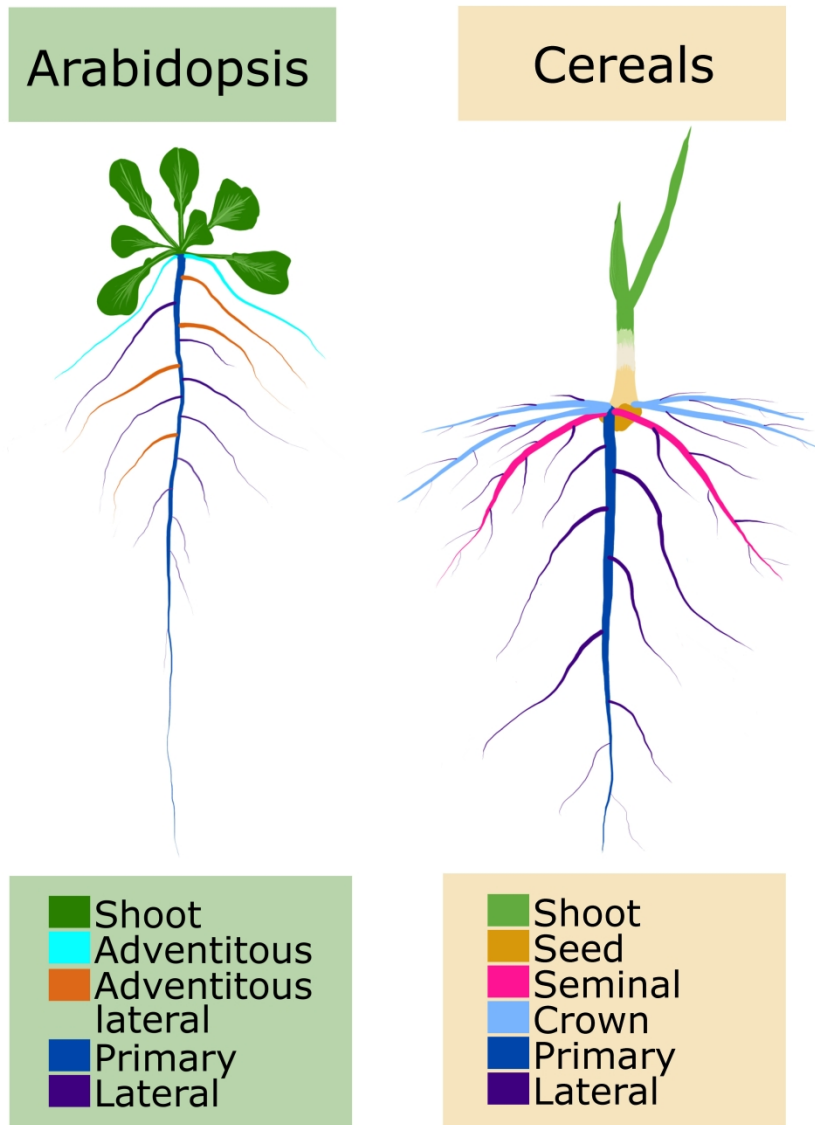
509x304mm (600 x 600 DPI)

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.

486x458mm (600 x 600 DPI)

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.

286x508mm (600 x 600 DPI)

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).

280x343mm (600 x 600 DPI)