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Control of grass inflorescence form by the fine-tuning of meristem phase change

Junko Kyozuka, Hiroki Tokunaga and Akiko Yoshida

The grass inflorescence is interesting from the points of view of development and evolution. In the grass family, flowers are produced on small branches called spikelets. The recent isolation of regulators of spikelet meristem (SM) identity has shed new light on development and the evolution of the gene networks involved. The timing of SM specification is mediated by the combinatorial functions of these regulators, and determines the grass inflorescence form. Furthermore, tight links between meristem cell proliferation, maintenance of meristem indeterminacy, and suppression of the spikelet identity are being uncovered.

Addresses
Graduate School of Agriculture and Life Sciences, University of Tokyo, Yayoi, Bunkyo, Tokyo 113-8657, Japan

Corresponding author: Kyozuka, Junko (akyozuka@mail.ecc.u-tokyo.ac.jp)

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Introduction

Inflorescence structures result from the activities of meristems. The fate of a meristem is specified at its initiation and sequentially changes as the plant develops (Figure 1 and Box 1). Among the series of phase changes that may occur at a meristem, the transition to floral meristem (FM) is special because the FM is the determinate and final phase at which the meristem stops its activity. Therefore, in most plants, the basic structure of the inflorescence is defined by the spatial arrangement of the flowers. In grass species, however, the flowers (termed florets) are produced in small branches called spikelets [1,2]. The spikelet structure is found only in grass species, and grass flowers are always formed in spikelets. In some grass species, such as rice, each spikelet generates one flower (floret). In others, such as maize and wheat, there are two or more flowers per spikelet. Therefore, the spikelet meristem (SM) is considered as the determinate phase and the grass inflorescence structure is defined by the arrangement of spikelets rather than the arrangement of flowers. In this review we will focus on grass inflorescence development, especially as it occurs in rice (*Oryza sativa*).

A rice inflorescence has a branched structure and is classified as a panicle (Figure 2). After the transition to the reproductive phase, a vegetative shoot apical meristem (SAM) is transformed into a primary inflorescence meristem (IM), which then produces primary branches. The branch meristem (BM) produces several lateral meristems. Early lateral meristems acquire a BM identity and grow as secondary branches at proximal positions, while later lateral meristems are specified as SMs. All BMs at the top of each branch are eventually transformed into SMs. The pattern of branching is determined by the timing of the meristem phase shift from the BM to the SM. Delays in SM specification lead to reiterations of branching, resulting in larger inflorescences that could potentially produce more grain. Conversely, the acceleration of SM specification results in smaller inflorescences with fewer spikelets. Despite the huge variation in their forms, all grass inflorescences can be interpreted by this common logic based on their branching patterns.

Cell proliferation in the meristem correlates with prolonged branching activity

As the inflorescence structure is directly linked to grain number, genetic screening and QTL analyses have been extensively performed in rice, maize, barley, and other grasses to isolate genes involved in SM specification [3–8]. Some of the isolated genes are grass specific while others have non-grass counterparts that play roles in some aspects of development.

ABERRANT PANICLE ORGANIZATION1 (*APO1*) and *APO2*, orthologs of Arabidopsis *UNUSUAL FLORAL ORGANS* (*UFO*) and *LEAFY* (*LFY*), respectively, are major regulators of the rice inflorescence structure and identified in several independent studies [9•,10–13]. Loss-of-function mutations of these genes result in small inflorescences with less branching, due to the precocious specification of SM identity. *APO2* is indispensable for *APO1* function, while the level of *APO1* activity acts as a determinant for the meristem phase change. Increases in *APO1* expression (but not *APO2*) lead to prolonged indeterminate meristem fate and delays in SM specification (Figure 3). These phenotypes indicate that *APO1* and *APO2* maintain BM identity and suppress SM identity. On the other hand, in eudicot species the *UFO* and *LFY* orthologs promote determinate floral fate [14–17]. Thus, the functions of *APO1* and *APO2* appear to be opposite to those of *UFO* and *LFY*. Recent studies suggest that *LFY* orthologs might play a more general role in cell division

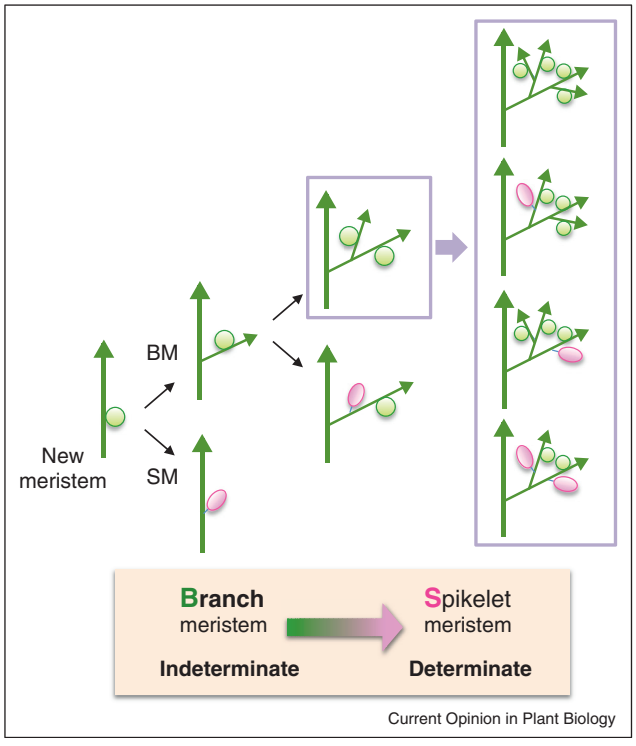
Box 1 Different types of meristems in rice inflorescence

The shoot apical meristem (SAM) is converted to an inflorescence meristem (IM) after the transition to the reproductive phase. Then, the IM starts to initiate branch meristems (BM)s. Among the meristems that are generated from the BMs, early ones acquire BM identity and grow as next order branches while later ones are specified as determinate spikelet meristems (SMs). This pattern can be reiterated. The BMs themselves are eventually transformed into SMs after generating a certain number of branches and spikelets.

Abbreviations: IM: inflorescence meristem; BM: branch meristem; SM: spikelet meristem; FM: floral (floret) meristem.

and meristem development and that this function is more ancestral than its function in FM and floral organ development [18–20]. In addition to suppression of SM identity, *APO1* and *APO2* are involved in various other developmental processes including leaf growth, stem thickness, control of the intervals of leaf initiation and floral organ development [9•,10,21]. The ancestral role of *UFO* and *LFY* orthologs are probably exerted by *APO1* and *APO2*. The functions of *APO1* and *APO2* in the promotion of indeterminate BM fate likely derive from this ancestral role of *LFY*.

Figure 1



Concept of meristem identity specification. A new meristem (green circle), which then acquires the identity of a branch meristem (BM, green arrow) or a spikelet meristem (SM, pink oval). While the SM has a determinate developmental fate and grows as a spikelet, the BM is indeterminate and further produces new meristems that acquire either SM or BM identities.

A positive correlation between the degree of cell proliferation within each meristem and the overall degree of branching in the inflorescence is often observed in rice. In gain-of-function mutants of *APO1*, the meristem proliferates more vigorously than wild type (Figure 3) [10]. The enhanced proliferation is first observed during the reproductive transition concomitant with the onset of *APO1* and *APO2* expression in the meristem [10]. In contrast, the IMs are small in *apo1* and *apo2* loss-of-function mutants. *OsSPL14*, which encodes a *SQUAMOSA* promoter binding transcription factor, was shown to correspond to a gene called *WEALTHY FARMER'S PANICLE* (*WFP*)/*Ideal Plant Architecture1* (*IPA1*), a key QTL locus controlling the traits of fewer tillers and more grains [22,23]. In plants with higher *OsSPL14*/*WFP*/*IPA1* activity, the IM becomes bigger and the inflorescence contains more branches. *GRAIN NUMBER1a* (*GN1a*) was identified as a QTL gene that confers increases in grain number in high yield cultivars. *GN1a* encodes a cytokinin oxidase/dehydrogenase, which degrades cytokinin [24]. Cultivars with reduced *GN1a* mRNA levels produce large inflorescences with increased branches due to elevated cytokinin levels. The IM in these cultivars is also larger than normal. The correlation was also observed for the *DROUGHT AND SALT TOLERANCE* (*DST*) gene, which was shown to be a direct up-stream activator of *GN1a* expression [25•,26]. The function of *DST* is conserved in barley and wheat. In another example of the correlation between IM size and increased branching, the constitutive overexpression of *RCN* genes, rice orthologs of Arabidopsis *TERMINAL FLOWER1*, conferred highly branched, large inflorescence phenotypes [27]. This was accompanied by an overproliferation of meristem cells (Yasuno and Kyozuka, in preparation). Future analyses will reveal whether the prolonged indeterminate fate (delays in specifying SM identity) is a consequence of the enhanced meristem activity, and if so the mechanisms underlying such a link.

CLAVATA signaling affects meristem size and the number of organs produced in the inflorescence

The CLAVATA (CLV) signaling pathway, which regulates stem cell homeostasis in apical meritems, is basically conserved in grass species [28–31]. The maize *thick tassel dwarf1* (*td1*) and *fasciated ear2* (*fea2*) genes are the closest homologs of Arabidopsis *CLV1* and *CLV2*, respectively [29,32]. Mutations in these genes result in extensive overproliferation of stem cells and meristem fasciation. This leads to increases in the numbers of kernel rows and spikelet density [33•]. Recently it was shown that a stem cell restricting signal from a CLV receptor is transmitted by the α subunit of a heterotrimeric GTP binding protein encoded by maize *COMPACT PLANT2* (*CT2*) [34••]. In *ct2* loss-of-function mutants, the