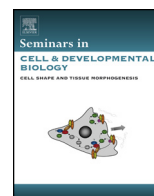




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Review

Grass inflorescence architecture and meristem determinacy

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ABSTRACT

The grass inflorescence is striking not only for its beauty and diversity, but also for its developmental complexity. While models of inflorescence architecture have been proposed in both eudicots and grasses, these are inadequate to fully explain the complex branching events that occur during the development of the grass inflorescence. Key to understanding grass inflorescence architecture is the meristem determinacy/indeterminacy decision, which regulates the number of branching events that occur. Here we review what has been learned about meristem determinacy from grass mutants with defects in inflorescence development. A picture is emerging of a complex network of signaling molecules and meristem identity factors that interact to regulate inflorescence meristem activity, many of which have been modified during crop domestication directly affecting yield traits.

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1. Introduction

Grasses have a striking diversity in their inflorescence architectures, in particular with respect to branching (see Fig. 1 for a limited sample of cultivated grass inflorescence diversity). Branching architecture can have important consequences in wild grass species both for wind pollination [1,2] as well as for the size and number of kernels. The diversity of branching architecture across the grass family raises basic developmental questions about molecular mechanisms that regulate branching and how those mechanisms evolve. Grass inflorescence architecture has also been modified during the independent domestication events of cereals such as wheat, rice, barley and maize [3] which together are responsible for the vast majority of the calories consumed by humans [4]. Careful investigation of the genetic regulation of grass inflorescence architecture reveals basic developmental patterning mechanisms as well as historical and possible future pathways to optimize yield in cereal crops. Fortunately the grass family is particularly well suited to address these basic and applied questions. The agronomic importance of cereals has led to the development of model species that span the broad diversity of grasses including maize (*Zea mays* ssp. *mays*), rice (*Oryza sativa*), barley (*Hordeum vulgare*) and more recently setaria (*Setaria italica*) and brachypodium (*Brachypodium distachyon*). A large collection of grass mutants affecting inflorescence architecture has provided key insights into the molecular mechanisms regulating inflorescence architecture. In addition, domestication QTL's directly effecting agronomic traits associated with inflorescence architecture have been cloned (See Supplemental Table S1).

A complete accounting for mature inflorescence architecture in grasses would need to consider a broad array of developmental processes including the regulation of branching (meristem initiation and determinacy), phyllotaxy changes, internode elongation, branch angle, and positional modification of inflorescence structures (e.g. male/female differentiation of spikelets and florets). While there has been recent progress along some of these fronts (see e.g. [5,6]), rather than provide a comprehensive review of these diverse phenomenon we have chosen to focus here on a more narrow question that we feel is at the core of the inflorescence architecture. Specifically, we will review meristem determinacy and how it is regulated during grass inflorescence development. A large number of genes controlling meristem determinacy have

emerged from genetic studies in grass models systems, particularly maize and rice, and many of these genes provide novel insights into inflorescence architecture beyond established models worked out in *Arabidopsis* and other eudicot species.

We will begin with a discussion of a central aspect of meristem determinacy, meristem size homeostasis. Although this has been carefully studied in *Arabidopsis*, novel insights have come from mutants in grasses identified primarily through their effect on inflorescence meristems. We will then discuss how meristem determinacy is regulated in the context of the grass inflorescence to provide diverse branching architectures. A central theme that frequently re-appears throughout our discussions of meristem size homeostasis and branching determinacy is the importance of mobile signals that interact in a complex network to regulate meristem activity.

2. Meristem size homeostasis

Branching is the production of new axillary meristems, and as such the regulation of branching is largely a matter of meristem activity. Throughout plant development meristems differ in the number of organs they are capable of generating (meristem determinacy) as well as the identity of the organs produced (meristem identity). The transition from a vegetative to a reproductive state defines the first step of inflorescence development. In the vegetative phase, the shoot apical meristem (SAM) is dominated by the production of leaves. As is the case for other angiosperms, in grasses a complex set of internal and environmental cues combine to signal a transition from vegetative SAM to an inflorescence meristem (IM) [7]. Morphologically, the first sign of the transition from SAM to IM is a rapid increase in meristem size, associated with a shift from distichous (two-ranked) phyllotaxy of the SAM, to polistichous (multi-ranked) phyllotaxy of the IM [8,9]. This meristem expansion is tightly regulated and perturbed in several rice and maize mutants with dramatic enlargement or fasciation of the IM. Interestingly, this transition to polistichous phyllotaxy was lost in pooid grasses (Fig. 1), which maintain the two-ranked phyllotaxy of the vegetative state [6]. This may explain the lack of fasciation mutants from pooid cereals in spite of a large collection of other inflorescence mutants in this clade. Investigation of maize and rice fasciation mutants has confirmed many aspects of meristem size homeostasis known from *Arabidopsis*, but has also underscored the importance of other factors whose role in meristem size regulation would have been missed otherwise.

2.1. The core CLV-WUS pathway

Research of the past two decades in *Arabidopsis* has shown that meristem size is regulated by a negative feedback loop also known as the *CLAVATA* (CLV) signaling pathway [10]. The current working model predicts that the stem cell promoting factor *WUSCHEL* (WUS), a homeodomain transcription factor, expressed in the organizing center (OC) of the meristem, coordinates stem cell fate by activating expression of *CLV3* only within cells belonging to the overlying central zone (CZ). CLV3 is a small mobile peptide and once processed and secreted is perceived by at least four different receptor complexes including CLV1 and BARELY ANY MERISTEM homo-dimers, and CLV2-CORYNE (CRN) hetero-dimers that upon activation stabilize the meristem stem cell population by signaling back to the OC to repress WUS expression, thereby completing the negative feedback loop. As stem cells divide within the central zone, their daughter cells are displaced laterally into the meristem's peripheral zone, where they become incorporated into differentiating organ primordia.

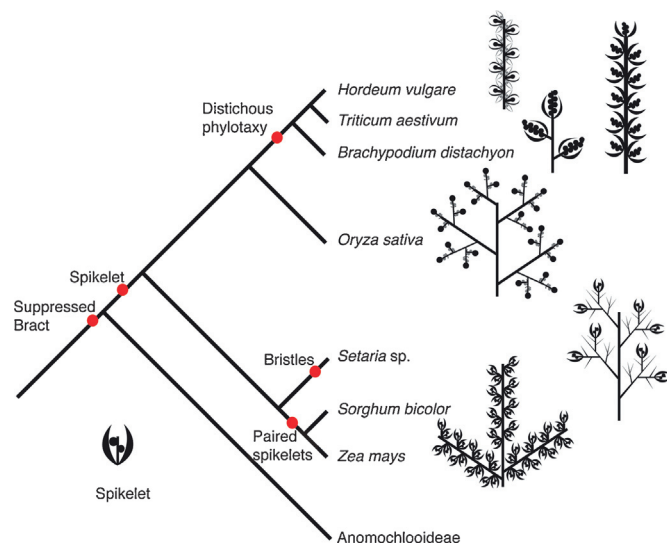


Fig. 1. Phylogeny of grasses and diverse inflorescence branching architectures of model grass species. Several major morphological transitions that characterize large clades are indicated on the phylogeny.

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