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Branching Out: The *ramosa* Pathway and the Evolution of Grass Inflorescence Morphology

The recent cloning of two classical maize mutants, *ramosa1* (*ra1*) by Vollbrecht et al. (2005) and *ra2* by Bortiri et al. (2006) (in this issue of *The Plant Cell*), has identified a pathway that plays a fundamental role in inflorescence architecture in maize. The name *ramosa*, from the Latin ''ramus'' meaning ''branch,'' reflects the phenotype of the *ra* mutants, which have a highly branched inflorescence. Characterization of orthologs of *ra1* and *ra2* from other grasses suggests that the *ramosa* pathway has been involved in the morphological evolution of grass inflorescences (Vollbrecht et al., 2005; Bortiri et al., 2006). This commentary will discuss evolution of the *ramosa* pathway in the context of some of the concepts of evolution of development (evo-devo).

INFLORESCENCE MORPHOLOGY IN THE GRASSES

The *ramosa* pathway regulates inflorescence architecture in the grasses. The spikelet is the building block of the grass inflorescence (Figure 1) (Clifford, 1987). The spikelet is a short branch that encloses one or more florets within two leaf-like organs. Grasses differ from each other in their arrangement of branches, spikelets, and florets (Clifford, 1987). Therefore, genes that regulate this arrangement may have been involved in the evolution of the grasses (Kellogg, 2001). The majority of grasses bear spikelets singly. For example, grasses such as rice have many long branches bearing single spikelets (Figure 1C), while barley has a main spike bearing single spikelets (Clifford, 1987). The production of short branches bearing two spikelets is a derived trait of the Andropogoneae, a grass tribe comprising 1000 species, including maize, *Sorghum*, sugarcane, and *Miscanthus* (Grass Phylogeny Working Group, 2001; Kellogg, 2001; Mathews et al., 2002). For example, maize has long branches at the base of a main spike with spikelet pairs covering the long branches and main spike (Figure 1A) (McSteen et al., 2000), whereas *Sorghum* undergoes multiple orders of branching before producing spikelet pairs (Vollbrecht et al., 2005). Recent findings described below show that the *ramosa* pathway plays a critical role in imposing determinacy on the spikelet pair in the Andropogoneae (Vollbrecht et al., 2005; Bortiri et al., 2006).

THE *ramosa* PATHWAY

The *ra1* mutant was first described in 1912 (Gernart, 1912). *ra1* mutants affect branching in both the male (tassel) and female (ear) inflorescence (Nickerson and Dale, 1955). In the *ra1* tassel, there is a transformation of spikelet pairs (which are in effect short branches) into long branches bearing single or paired spikelets (Vollbrecht et al., 2005) (Figure 1B). The result is a tassel that instead of having a dramatic switch from long branch to short branch (spikelet pair) identity as in normal plants has a gradual switch with the branches getting shorter acropetally. The ear, which is usually unbranched, is highly branched in *ra1* mutants, resulting in reduced fertility. It is important to note that *ra1* is not required for spikelet pair meristem identity per se, as spikelet pairs do form on branches and at the apical part of the main spike. Rather, *ra1* is required for the abrupt switch to determinate growth that occurs when the inflorescence starts to produce spikelet pairs.

ra1 was cloned by transposon tagging with *Suppressor-mutator* and encodes a putative zinc finger transcription factor of the EPF class (Vollbrecht et al., 2005). Putative orthologs of *ra1* are found in closely related species in the Andropogoneae, such as *Sorghum* and *Miscanthus*. Although transcription factors of the EPF class are found in other species, a clear ortholog of *ra1* is not found in rice or *Arabidopsis*. In maize, *ra1* is expressed at the base of the axillary meristems that give rise to the spikelet pair in the inflorescence. There are four types of axillary meristem in the maize inflorescence, named after the structures they produce: the branch meristem, the spikelet pair meristem, the spikelet meristem, and the floral meristem (McSteen et al., 2000). *ra1* is not expressed in branch meristems but begins to be expressed as spikelet pair meristems initiate (Vollbrecht et al., 2005). *ra1* is not expressed in the spikelet pair meristem itself but is expressed in a region surrounding the base of the meristem. Later, *ra1* is expressed at the base of spikelet meristems where it is not known to play a role. It is proposed that *ra1* expression imposes determinacy on spikelet pair meristems. The absence of *ra1* in spikelet pair meristems of *ra1* mutants causes them to become indeterminate producing additional spikelets. Moreover, the absence of *ra1* expression in branch meristems of wild-type tassels may allow them to be indeterminate.

There is evidence that *ra1* may function by controlling a mobile signal. Characterization of unstable alleles shows that sectors of wild-type tissue can confer a wild-type phenotype over a limited distance (Vollbrecht et al., 2005). Moreover, *ra1* is expressed in a boundary expression domain surrounding rather than within the meristem. One possibility is that the RA1 protein itself moves between cells. Another possibility is that *ra1* may control a hormonal signal. If a hormone is involved, then a possible candidate is gibberellic acid (GA), which has been implicated in the regulation of tassel branch number in maize. Application of high levels of GA reduces branch number in normal tassels and suppresses the phenotype of *ra1* mutant tassels (Nickerson, 1959, 1960). Paradoxically, some of the GA-deficient mutants have fewer tassel branches, and a low level of ectopically

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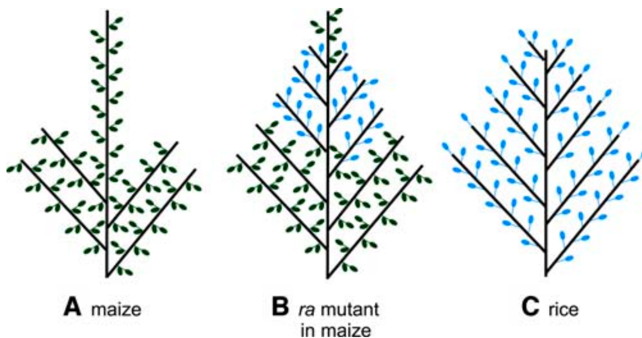

Figure 1. Simplified Schematic of Inflorescence Morphology in Maize and Rice Compared with the Phenotype of the *ra* Mutants in Maize.

(A) Maize has long branches at the base of a main spike. Short branches called spikelet pairs cover the main spike and the branches. Note the dramatic switch from long branches to short branches on the main spike.
(B) In the *ra1* and *ra2* mutants in maize, spikelet pairs on the main spike are converted into long branches bearing single spikelets or mixtures of single spikelets and spikelet pairs. Note that the *ra* mutants also produce an increased number of long branches bearing spikelet pairs, which have not been drawn for the sake of simplicity.
(C) Rice has many long branches bearing single spikelets.
Thick black lines represent the main spike and the lateral branches, green paired ovals represent paired spikelets, and blue ovals represent single spikelets. The diagram is simplified to illustrate the differences in branching pattern and presence of single versus paired spikelets but does not represent the total number of branches or spikelets.

applied GA actually promotes tassel branching in these mutants (Evans and Poethig, 1995). Therefore, the role of GA in tassel branching, and its interaction with the *ramosa* pathway, remains to be resolved. Moreover, other hormones have also been implicated in tassel branching. For example, application of auxin also reduces the number of tassel branches in wild-type plants (Heslop-Harrison, 1960). Thus, the role of hormones in branching of the maize inflorescence may be complex.

The *ra2* mutant was first reported in 1935 (Emerson et al., 1935; Hayes, 1939). *ra2* mutants have a very similar tassel branching phenotype as *ra1*, but there are also clear differences. In the tassel, *ra2* branches are borne at a more upright angle, and spikelets are borne on elongated pedicels compared with *ra1* mutants or the wild ype. Moreover, the ears of *ra2* are less severely affected than *ra1* (Nickerson and Dale, 1955; Vollbrecht et al., 2005; Bortiri et al., 2006). The cloning of *ra2* from maize and related grasses is described in this issue of *The Plant Cell* (Bortiri et al., 2006). A point of interest is that although *ra1* was cloned the traditional way in maize (by transposon tagging), *ra2* is one of the first genes to be cloned by map-based cloning in maize. The first published example was the cloning of *teosinte glume architecture1* (Wang et al., 2005). Both of these cases made use of colinearity with the rice genome, but walking in maize should become easier when the maize genome sequence is completed (Chandler and Brendel, 2002).

ra2 encodes a putative LOB domain–containing transcription factor (Bortiri et al., 2006). Orthologs of *ra2* are found in sorghum, rice, and barley, unlike *ra1*, which is found in sorghum but not rice (Bortiri et al., 2006). Phylogenetic analysis shows that the closest homolog of *ra2* in *Arabidopsis* is *ASYMMETRIC LEAVES2-LIKE4*, but the C terminus is completely different in the two genes. *ra2* is expressed earlier than *ra1* and is in fact one of the earliest genes to be expressed during axillary branching in maize inflorescence development. *ra2* is expressed in the anlagen of the branch meristem and spikelet pair meristem and disappears as the meristems grow. *ra2* is also expressed when the spikelet meristem initiates. *ra2* is conserved in its expression in branches and spikelets of sorghum, barley, and rice, suggesting that it also plays an important role in these species (Bortiri et al., 2006).

Evidence from both expression data and double mutant analysis suggests that *ra2* acts upstream of *ra1* (Vollbrecht et al., 2005; Bortiri et al., 2006). As discussed above, *ra2* mutants have a tassel phenotype very similar to *ra1*, but the ear is less severely affected. Double mutants between *ra2* and a weak allele of *ra1* have a greatly enhanced ear phenotype, suggesting that *ra2* and *ra1* act in the same pathway. Convincing evidence was provided by RNA gel blot analysis and RNA in situ hybridization experiments, which showed that *ra1* expression is reduced in *ra2* mutants (Vollbrecht et al., 2005; Bortiri et al., 2006). Therefore, *ra2* is proposed to regulate *ra1*. Although it has not been shown that their interaction is direct, there is some evidence that *ra2* may be involved in transcriptional activation of *ra1* (Bortiri et al., 2006). However, as *ra1* is not expressed everywhere that *ra2* is expressed, there must be additional factors involved in the regulation of *ra1*.

EVOLUTION OF THE *ramosa* PATHWAY

The central premise of evo-devo is that changes in the overall morphology of organisms can be traced to early changes in development and in particular to changes in genes controlling development (Carroll et al., 2005). As transcription factors control many developmental processes, it is common to find that diversification of morphology between closely related organisms has involved changes in (1) how transcription factors are regulated or (2) how transcription factors interact with their target genes (Doebley and Lukens, 1998; Carroll et al., 2005). Another powerful mechanism in evo-devo is (3) co-option, whereby transcription factors are co-opted for a new purpose in a different species (Carroll et al., 2005). I discuss the evolution of the *ramosa* pathway in the context of some of these major mechanisms of evo-devo. I refer the reader to additional recent reviews for other examples of evo-devo in plants (Friedman et al., 2004; Kellogg, 2004; Irish and Litt, 2005; Piazza et al., 2005).

Changes in How Transcription Factors Are Regulated

A common mechanism of evo-devo is changes in the regulation of genes controlling development (Carroll et al., 2005). For

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example, spectacular changes in the body plans of animals (arthropods and vertebrates) correlate with shifts in the expression pattern of *Hox* genes (Averof and Patel, 1997; Cohn and Tickle, 1999). Also, striking changes in plant architecture correlate with changes in the level of *teosinte branched1* expression during the domestication of maize from teosinte (Doebley et al., 1997).

Characterization of *ra1* expression within the Andropogoneae shows that changes in *ra1* expression correlate with changes in morphology (Vollbrecht et al., 2005). *Miscanthus* has a similar morphology to maize in that long branches and spikelet pairs are formed. However, in *Miscanthus*, there are more long branches relative to maize, and this correlates with a delay in the onset of *ra1* expression. *Sorghum* is highly branched relative to maize and produces spikelet pairs only after multiple rounds of branching. This phenotype correlates with a delay in peak *ra1* expression compared with maize and *Miscanthus*. Thus, expression of *ra1* is correlated with the imposition of determinate spikelet pair meristem identity in *Miscanthus* and *Sorghum*. Hence, *ra1* is likely playing a similar role in these species (Vollbrecht et al., 2005).

Although changes in the expression of *ra1* correlate with changes in morphology in the Andropogoneae, it is challenging to determine whether a gene is truly changed in its timing when the experiments are done in different species. Vollbrecht and coworkers performed an in-depth analysis comparing expression data to morphological data at different stages of development in the three species. This is similar to the challenge of experiments that have been done in mice, chicks, and fish, whereby changes in the timing of *Hox* gene expression were correlated with differences in body plans using markers of vertebrate development as a guide (Burke et al., 1995; Anand et al., 2003). One way of getting around the issue of timing (or developmental stage) when comparing gene expression in different organisms is to perform transgenic experiments of the type that are used routinely in animal studies (Belting et al., 1998; Anand et al., 2003; Carroll et al., 2005). For example, the sorghum *ra1* promoter could be linked to a reporter gene and transformed into maize to determine if its expression truly occurs later than the native maize *ra1* gene. These experiments would also answer the question of whether the changes in the timing of *ra1* expression in sorghum are due to changes in the sorghum promoter or *trans*-acting factors upstream of the promoter. If the activity of the sorghum promoter was delayed in maize, then this would imply that changes had occurred in the *cis*-regulatory region of *ra1* in sorghum, opening the door to experiments to determine the exact molecular basis of the change in *cis*-regulation. A starting point, which has been used in both animals and plants, would be to compare the regulatory regions of *ra1* from different species to identify conserved noncoding sequences potentially important in function (Shashikant et al., 1998; Kaplinsky et al., 2002).

Many evo-devo stories start with a correlation between morphology and gene expression pattern (Bharathan et al., 2002). Whether changes in gene expression are causative of morphological change requires further testing, again, usually with transgenic experiments (Kim et al., 2003). Frequently, evo-devo stories in both plants and animals end here due to limitations in the ability to transform nonmodel organisms. A great advantage of the grasses is that many, including rice, sorghum, maize, and barley, can be transformed. Whether changes in the timing of *ra1* expression are causative of the evolutionary change in morphology in these species could be tested in further studies. For example, can expression of the maize *ra1* gene in sorghum decrease branching? The results of these experiments would be very exciting because evidence of causation is rare in evo-devo.

Changes in How Transcription Factors Interact with Their Target Genes

A few evo-devo case studies have shown that changes in the coding regions of transcription factors can alter their interaction with downstream targets (Galant and Carroll, 2002; Ronshaugen et al., 2002; Maizel et al., 2005). This approach requires determining the direct target genes of transcription factors, which is very powerful for understanding the evolution of developmental pathways. A recent article beautifully illustrates this approach. *LEAFY* (*LFY*) regulates flower development in *Arabidopsis*, but the function of *LFY* in other species differs (Maizel et al., 2005). In an elegant series of microarray experiments, Maizel and coworkers showed that alterations in the DNA binding domain of *LFY* in flowering plants have resulted in *LFY* having different targets in different species. Therefore, evo-devo in the *LFY* pathway has involved changes in the coding region of *LFY*.

ra1 and *ra2* also have differences in their coding regions compared with gene family members in *Arabidopsis. ra1* has an invariant amino acid change in the zinc finger DNA binding domain compared with EPF zinc fingers in rice and *Arabidopsis* (Vollbrecht et al., 2005). Moreover, all grass *ra2* genes have a specific C-terminal putative activation domain that is absent from LOB genes in *Arabidopsis* (Bortiri et al., 2006). Therefore, members of the LOB and EPF gene families in the grasses may have different targets and, hence, different functions from their eudicot relatives. Identification of the direct target genes of the *ramosa* pathway will be important in unraveling the evolution of this pathway.

Changes in the targets of transcription factors may also be caused by changes in the *cis*-regulatory regions of their target genes (Carroll et al., 2005). An excellent example from plants is provided by the *CYCLOIDEA* (*CYC*) pathway. *CYC* is a TCP domain–containing transcription factor that regulates floral asymmetry in *Antirrhinum* by altering growth of organs in the upper region of the floral meristem (Luo et al., 1996). *RADIALIS* (*RAD*), a MYB domain–containing transcription factor, is a direct downstream target of *CYC* (Costa et al., 2005). Evolution of the interaction was analyzed in *Arabidopsis*, which has *CYC* and *RAD* homologs but has radially symmetrical flowers. Costa and

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coworkers showed that expression of *Antirrhinum CYC* in *Arabidopsis* cannot induce the *Arabidopsis RAD*-like genes because they do not have *CYC* binding sites in their regulatory regions. Therefore, evolution of the *CYC* pathway has involved changes in the target gene *RAD* and in particular changes in the *cis*-regulatory regions of *RAD*. Whether evolution of the *ramosa* pathway involves a direct interaction between *ra2* and *ra1* remains to be determined.

Co-Option

A common mechanism in evo-devo is co-option of transcription factors for different purposes in different tissues (Carroll et al., 2005). *ra1* plays a major role in spikelet pair meristem determinacy in the Andropogoneae but is not present in rice, which, correspondingly, does not have spikelet pairs. Maize and rice last shared a common ancestor ~50 million years ago near the base of the grass radiation, leading to a crucial question: Was *ra1* co-opted in the Andropogoneae or lost in rice? Answering this question will require identifying additional *ra1* homologs within the Andropogoneae, within the Oryzeae, and most importantly from a species basal to both lineages to determine if *ra1* was present prior to the divergence of the two groups. If *ra1* was lost in a lineage leading to rice, what were the steps that led to its loss? Was it initially no longer expressed and then became a pseudogene? If *ra1* is specific to the Andropogoneae, was the gene co-opted in the lineage leading to Andropogoneae for the evolution of the spikelet pair meristem? In the example described above, it was proposed that *RAD* had been co-opted in the *Antirrhinum* lineage through addition of *CYC* binding sites to the regulatory regions of *RAD* (Costa et al., 2005). In order to address the mechanism by which *ra1* may have been co-opted, further analysis of its upstream regulator(s) and regulatory sequences are required. In animals, co-option of multiple target genes and entire signaling pathways has been demonstrated (Weatherbee et al., 1998; Keys et al., 1999). Therefore, co-option sometimes requires changes to the *cis*-regulatory elements of multiple target genes, again emphasizing the importance of identifying the targets in the rest of the pathway.

CONCLUSIONS

The cloning of *ra1* and *ra2* from maize has identified a pathway regulating inflorescence morphology. Cloning of the putative orthologs of *ra1* and *ra2* from other species indicates that evolution of this pathway may have been involved in the evolution of inflorescence morphology. The grasses are a premier model system for evo-devo studies: there is tremendous diversity in inflorescence morphology, the phylogeny is well understood, and many species are transformable so hypotheses can be tested. Moreover, maize in particular is an excellent model system for studying selection as it was domesticated from its wild ancestor teosinte a mere 10,000 years ago (Doebley, 2004). Indeed, *ra1* was shown to have been a target of selection during maize domestication or improvement (Vollbrecht et al., 2005). Future studies to address the role of the *ramosa* pathway within maize, within the Andropogoneae, and within the grasses will be important in understanding the evolution of the grasses and furthermore will provide an understanding of the mechanisms of evo-devo.

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