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Gene Expression in the Early Floral Meristem

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INTRODUCTION

The differential expression of genetic information facilitates the regulation of complex developmental pathways. Thus, to understand the control of morphogenesis, it is essential that the patterns of developmentally regulated gene activity and the basis for this regulation be determined. Perhaps the clearest illustration of the potential of this type of investigation comes from the analysis of early embryogenesis in Drosophila (reviewed by Akam, 1987; Ingham and Arias, 1992; St Johnston and Nüsslein-Volhard, 1992; Wilkens, 1993). The descriptions of gene expression patterns during Drosophila embryogenesis revealed the genetic mechanisms underlying the control of anterior–posterior axis determination and showed that the cellular specification of segment boundaries in the embryo occurs long before segmentation is manifest. In recent years, the Drosophila studies have demonstrated that the molecular basis for the developmental regulation of embryonic gene activity is complex and diverse, including transcriptional, post-transcriptional, and translational control mechanisms as well as mechanisms related to the structural organization of chromatin (see Wilkens, 1993).

The analysis of developmentally regulated gene expression in plants should be equally exciting and informative, especially when applied to the study of meristem function. Meristems are the site of all postembryonic organ initiation in angiosperms, yet we understand very little about how meristems function. In this review, I will discuss several patterns of meristem gene expression that occur during the vegetative-to-floral transition, and I will examine what these patterns reveal about the control of floral meristem initiation. Several other recent reviews discuss the evidence that alterations in meristem gene activity are associated with the transition from vegetative to floral development (Bernier, 1988; Kelly and Meeks-Wagner, 1993).

CONTROL OF MERISTEM ACTIVITY THROUGHOUT THE VEGETATIVE-TO-FLORAL TRANSITION

Floral meristems are generally produced after an extended period of vegetative growth. During vegetative growth, the apical meristem is the source of lateral vegetative branches and leaves. In response to internal or external cues, the vegetative phase ends with the initiation of inflorescence and floral development (see Bernier et al., 1993, this issue). Inflorescences can be classified as determinate or indeterminate. Determinate inflorescences, which are found in plants such as tobacco, are characterized by the formation of a terminal flower. By contrast, indeterminate inflorescences, which are found in Antirrhinum and Arabidopsis, are characterized by growth from a regenerative apical inflorescence meristem that remains undifferentiated throughout development. The inflorescence meristems of indeterminate plants also give rise to bracts, lateral floral branches, and determinate floral meristems.

It is possible to represent shoot meristem activity in angiosperms as a progression of overlapping developmental stages: vegetative → inflorescence → floral (V → I → F) (see Wetmore et al., 1959; Lang, 1965). The related activities of vegetative, inflorescence, and floral meristems are revealed by the existence of single-gene mutations, such as the *clavata* mutations of Arabidopsis, that disrupt meristem function throughout all phases of development (Koornneef et al., 1983; Leyser and Furner, 1992; Shannon and Meeks-Wagner, 1993). As diagrammed in Figure 1A, some basic developmental programs may remain fixed throughout the vegetative, inflorescence, and floral stages, while other basic programs may be modified to facilitate changes in meristem function during the V → I → F progression. Finally, some programs are likely to be stage specific, and thus unique to a particular developmental stage. Interactions between these different types of developmental programs would permit the coordination of common and stage-specific meristem activities throughout plant growth.

The developmental programs that operate in the meristem direct growth processes such as the rate of primordium initiation, the phyllotaxy of emerging primordia, and the determinate or indeterminate developmental potential of the meristem (see Huala and Sussex, 1993, this issue). The spatial and temporal regulation of such developmental programs should be revealed by the expression patterns of genes related to each program. For instance, many of these patterns will reflect the known or hypothesized boundaries that occur in shoot meristems. As shown in Figure 1B, such boundaries include those of the meristematic cell layers (L1, L2, and L3); the central zone/peripheral zone interface, which is thought to distinguish the central apical initial cell population from the surrounding organogenic cell population; and the rib meristem boundary. However, because novel patterns of gene expression can precede the establishment of boundaries, it is likely that the use

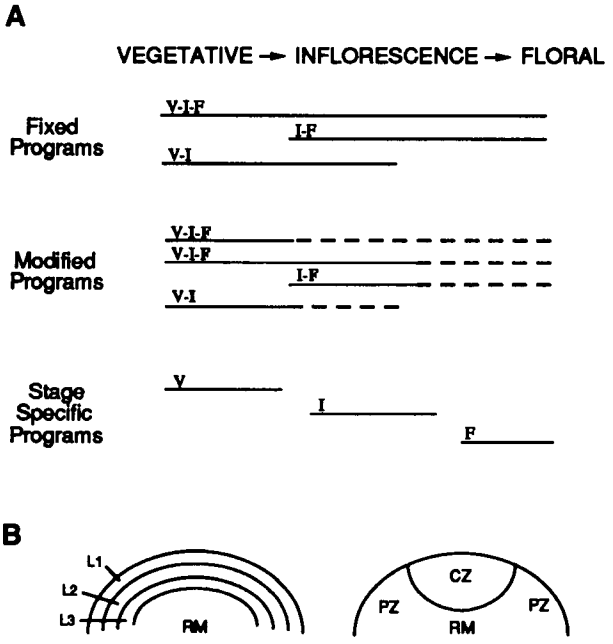

Figure 1. Shoot Meristem Function and Organization throughout the Vegetative-to-Floral Transition.

(A) Schematic representation of the various types of developmental programs that might occur in the shoot meristem during the V→I→F progression. Unmodified phases are represented by solid lines, and modified phases are represented by dashed lines.

(B) Diagrams showing the organization of the shoot meristem into cell layers (L1, L2, and L3) and functional zones (CZ, central zone; PZ, peripheral zone; RM, rib meristem). The central zone is defined by the relatively low mitotic index of cells in the central region of the meristem, and the peripheral zone is defined as the organogenic region of the meristem that is lateral to the central zone. The rib meristem is located at the base of the central zone and is comprised of cells that mainly divide in a transverse plane relative to the longitudinal axis of the stem.

of gene-specific probes will identify additional levels of functional organization within the meristem. Such information will be critical for understanding how meristem activity is regulated throughout the V → I → F transitions.

EVIDENCE FOR FIXED PATTERNS OF MERISTEM GENE EXPRESSION DURING THE VEGETATIVE-TO-FLORAL TRANSITION

As shown in Figure 2A, several genes have been cloned that display fixed patterns of mRNA or protein expression in vegetative, inflorescence, and floral meristems. cDNA cloning of genes expressed in tobacco shoot apices (Kelly et al., 1990) and in *Sinapis alba* shoot apices (Melzer et al., 1990) has resulted in the identification of genes transcribed in the shoot apex throughout plant development. The tobacco A3 clone was isolated by differential screening of a shoot apex cDNA library (Kelly et al., 1990). RNA gel blot analysis demonstrated that the A3 transcript is specific to the shoot apex and remains at a nearly constant level throughout development. Although the function of the single-copy A3 gene has yet to be determined, in situ hybridization results have shown that the A3 transcript is excluded from the L1 cell layer but is otherwise distributed uniformly throughout the remainder of the meristem at all stages of development (A. Kelly and D.R. Meeks-Wagner, unpublished results). Although A3 transcript is not detected in vegetative leaf tissues, a significant level of transcript is present in the parenchyma cells of the developing petals, stamens, and carpels (Kelly et al., 1990; A. Kelly and D.R. Meeks-Wagner, unpublished results). This suggests that although the expression pattern of A3 transcript is fixed in the meristem dome throughout plant growth, the initiation of floral development permits A3 expression in positions outside the dome. The accumulation of A3 transcript in immature floral organs may reflect multiple functions for the A3 gene during plant development. Alternatively, it may reflect the maintenance of the "meristematic state" by a subpopulation of cells during the early stages of floral differentiation (see Pri-Hadash et al., 1992).

Melzer et al. (1990) used a similar cDNA cloning approach with the long-day (LD) plant *S. alba* to isolate clones of genes expressed in the shoot apex during the vegetative-to-floral transition. The three cDNA libraries screened were made from shoot apices harvested after 2, 5, or 10 days of inductive LD photoperiod. RNA dot blot analysis of several clones isolated from the day 2 and day 5 libraries demonstrated that transcripts for these genes were present in vegetative shoot apices as well as immature inflorescence apices. In situ hybridization analysis with clone pSFD5.04 showed hybridization to the peripheral zone of both inflorescence and early floral meristems (see Figure 2A). Thus, despite the differences in the developmental potential exhibited by indeterminate inflorescence meristems and determinate floral meristems, the expression pattern of the gene represented by clone pSFD5.04 is similar in both stages. Given this expression pattern, Melzer et al. (1990) suggested that the pSFD5.04 clone represents a peripheral zone meristem activity that, although involved in early floral meristem function, is not specific to floral organogenesis.

A final example of a fixed pattern of gene expression throughout the V → I → F progression is provided by the Knotted-1 (KN1) protein of maize. Dominant mutations of the *Knotted-1* (*Kn1*) gene, which encodes a protein with significant homology to the homeodomain proteins of animals (Vollbrecht et al., 1991), result in the proliferation of cells associated with leaf veins. Using a polyclonal antibody raised against full-length KN1 protein produced in *Escherichia coli*, Smith et al. (1992) reported that in wild-type plants the highest levels of KN1 protein occur in the shoot apical meristem. Lower levels of KN1 protein also occur in the undifferentiated provascular bundle cells and in the rib meristem of immature vegetative and floral shoots. KN1 protein has a similar pattern of expression in vegetative, inflorescence, and floral meristems: the protein is found throughout all cell layers of the meristem but is absent

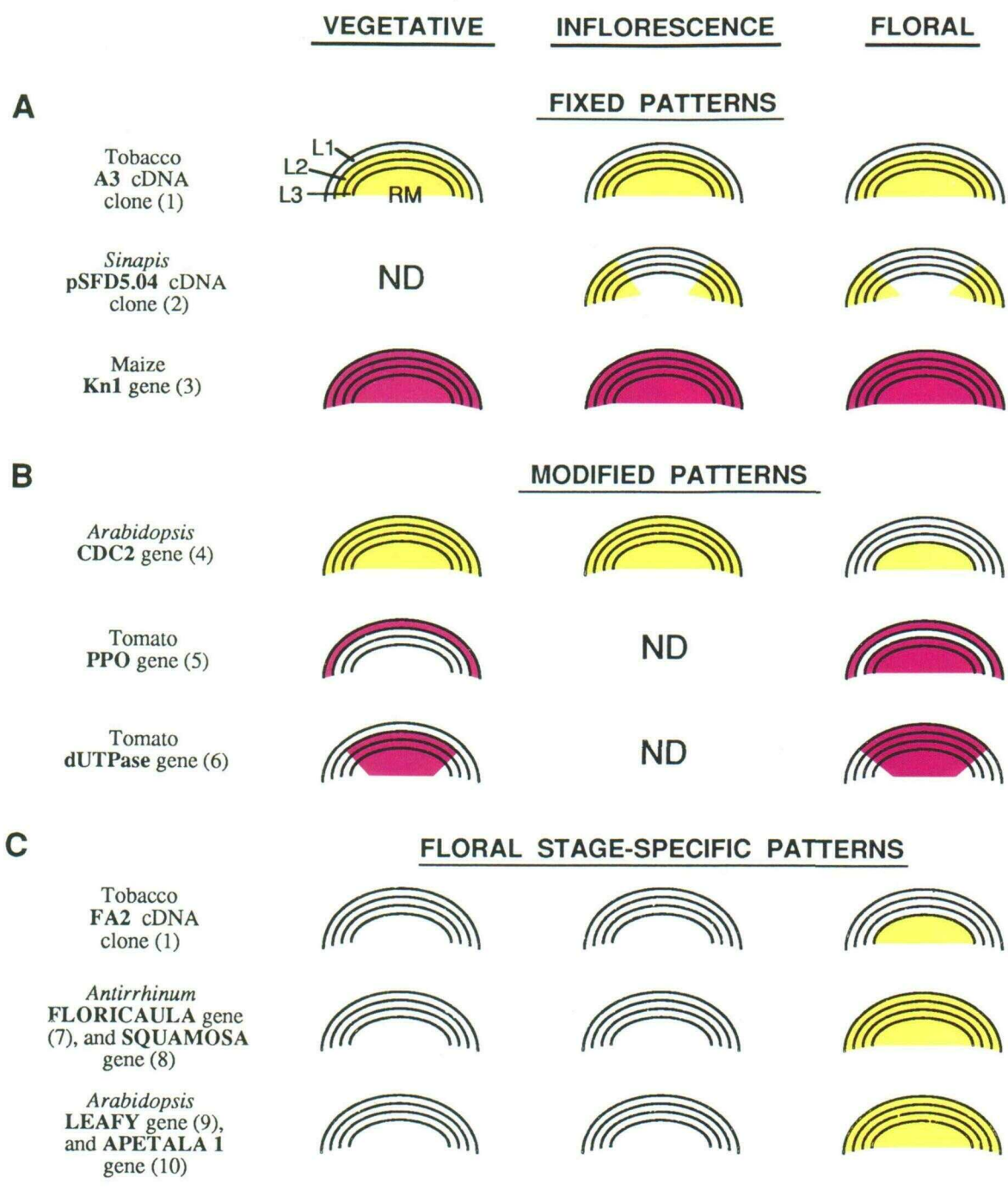

Figure 2. Examples of Gene Expression Patterns in Shoot Meristems during the Vegetative-to-Floral Transition.

Diagrams of vegetative, inflorescence, and floral meristems as described in Figure 1B.

(A) Fixed patterns of gene expression.

(B) Modified patterns of gene expression.

(C) Floral stage–specific patterns of gene expression.

Patterns indicated in yellow represent RNA localization by in situ hybridization, and patterns indicated in purple represent protein localization by antibodies. The L1, L2, and L3 cell layers and the rib meristem (RM) are represented as indicated in the first panel. (1) A. Kelly and D.R. Meeks-Wagner, unpublished results; (2) Melzer et al. (1990); (3) Smith et al. (1992); (4) Martinez et al. (1992); (5) Shahar et al. (1992); (6) Pri-Hadash et al. (1992); (7) Coen et al. (1990); (8) Huijser et al. (1992); (9) Weigel et al. (1992); and (10) Mandel et al. (1992).

from the peripheral zone cells that are specified to initiate organ primordia. This fixed pattern of expression suggests that KN1, in combination with other gene products, regulates development by specifying the meristematic state of cells (Smith et al., 1992). This idea is supported by the observation that KN1 protein is present in the cells of the floral meristem until the termination of meristem activity by the development of the ovule primordium (Smith et al., 1992).

EVIDENCE FOR MODIFIED PATTERNS OF MERISTEM GENE EXPRESSION DURING THE VEGETATIVE-TO-FLORAL TRANSITION

While some meristem-related developmental programs are likely to be fixed throughout the vegetative-to-floral transition, other programs may be modified during the V → I → F progression. The alteration of basic developmental programs would allow for subtle changes in meristem activity during the different stages of plant development. For example, the V → I transition is often accompanied by a decrease in plastochron duration and an increase in internodal distances. Because similar changes in plant growth can be imposed upon vegetative development by altering the growth conditions, it seems likely that such changes would simply require the modification of existing developmental programs. The modification of such programs may be revealed by changes in meristem gene expression.

Figure 2B shows several examples of meristem gene expression patterns that are modified during the vegetative-to-floral transition. Martinez et al. (1992) used in situ hybridization to characterize the expression of the Arabidopsis *CDC2* gene in vegetative, inflorescence, and floral meristems. The Arabidopsis *CDC2* gene was identified as a DNA clone that complements *cdc2* mutants of *Schizosaccharomyces pombe* or *cdc28* mutants of *Saccharomyces cerevisiae* (Ferreira et al., 1991; Hirayama et al., 1991). Because the yeast *CDC2* gene encodes a protein kinase (p34) that functions in the control of the G1- to S-phase transition of the mitotic cell cycle (see Nurse, 1990), the Arabidopsis *CDC2* gene is likely to be an important regulator of cell division in shoot meristems. In Arabidopsis, *CDC2* transcript is uniformly distributed throughout all layers of the vegetative and inflorescence apical meristems, including the rib meristem regions (Martinez et al., 1992). However, the pattern of *CDC2* gene expression is significantly different in early floral meristems, where the transcript is absent from the surface layers (L1, L2, and L3) and is present at high levels in the cells of the rib meristem and the developing pedicel.

Given that both vegetative and inflorescence meristems of Arabidopsis function in an indeterminate manner, the similarity in *CDC2* expression at these stages is not surprising. In fact, the *CDC2* expression pattern corresponds to the pattern of mitotic activity observed in mature vegetative and inflorescence meristems (Bernier, 1962; Brown et al., 1964; Besnard-Wibaut, 1970). The pattern of *CDC2* expression appears to be modified during the I → F transition. High levels of *CDC2* transcript in the rib meristem and developing pedicel may reflect the increased mitotic and metabolic activity in this region during floral meristem initiation (Vaughn, 1955; Wetmore et al., 1959; Bonner et al., 1991). Martinez et al. (1992) also noted that the expression pattern of *CDC2* in the early floral meristem is the reciprocal of the pattern displayed by several of the floral homeotic genes, and they suggested that antagonistic interactions between *CDC2* and the homeotic genes may determine these expression patterns.

Using arrested floral meristems from the cauliflower-like inflorescence of the tomato *anantha* mutant, Lifschitz and coworkers raised polyclonal antibodies to two proteins (P2 and P18) that are abundant in *anantha* floral meristems (Pri-Hadash et al., 1992; Shahar et al. 1992). The corresponding genes were isolated by using the antibodies to screen cDNA expression libraries made from meristem RNA. DNA sequence analysis suggests that the P2 gene encodes a polyphenoloxidase (PPO) or tyrosinase (Shahar et al., 1992). Immunolocalization studies showed that P2 protein is primarily localized in the L1 cell layer of the vegetative apical meristem, although low levels of protein occur throughout the L2 and L3 cell layers as well as in the rib meristem. By contrast, early floral meristems accumulate P2 protein in the L1 and L3 cell layers and in the rib meristem but not in the L2 cell layer. P2 protein is also absent from the provascular tissue of the immature flower. In situ hybridization with P2 cDNA sequences showed that the pattern of P2 transcript accumulation is the same as the pattern of P2 protein accumulation, suggesting that P2 protein distribution during the vegetative-to-floral transition is controlled at the transcriptional level (Shahar et al., 1992).

The P18 protein, which was also identified as an abundant protein in *anantha* meristems, was found to be a dUTPase by both DNA sequence analysis and by a biochemical assay for dUTPase activity (Pri-Hadash et al., 1992). dUTPase catalyzes the hydrolysis of dUTP to dUMP, which is a precursor of thymidine diphosphate; dUTPase is thus involved in the regulation of DNA metabolism in eukaryotes. Using an anti-P18 antibody, Pri-Hadash et al. (1992) showed that in vegetative meristems the P18 protein is abundant throughout the L2 and L3 cell layers of the meristem and the rib meristem but is absent from the L1 cell layer of the meristem. P18 protein is also localized to the provascular cells of the shoot apex. In early floral meristems, however, P18 protein accumulates in the L1 cell layer as well as in the L2 and L3 cell layers; it also accumulates in the rib meristem and in the provascular cells. This modification in the pattern of P18 expression is likely to be in anticipation of a specific, but unknown, role for the P18 dUTPase in the developing flower. Indeed, in immature flower buds the P18 protein is predominantly localized to the surface cell layers of the developing anthers, the pericarp, and the ovules, whereas there is no detectable P18 protein in the L1 cell layer of developing vegetative leaves.

EVIDENCE FOR FLORAL STAGE-SPECIFIC GENE EXPRESSION

Floral meristem function is dependent on the establishment of developmental pathways that operate specifically during the floral stage. These floral-specific pathways regulate growth processes such as floral phyllotaxy and internode elongation and direct the initiation of floral organ primordia. Such pathways are likely to be controlled by genes whose expression is specific to the floral stage and may be influenced by the activity of genes that display fixed or modified expression during the V → I → F progression. The following discussion of stage-specific gene activity will be limited to several examples of gene expression in the early floral meristem.

Using a differential cDNA screening approach, Kelly et al. (1990) isolated clones of several tobacco genes whose transcript levels in the shoot apex increase as the plant progresses through the V → I → F transitions. Clone FA2 displayed a dramatic increase in transcript accumulation in floral shoot apices. RNA gel blot analysis failed to detect FA2 RNA in leaves and roots but revealed high levels of FA2 transcript in immature sepals, petals, stamens, and pistils. As diagrammed in Figure 2C, in situ hybridization experiments have shown that FA2 transcript accumulates to high levels in the rib meristem region of the early tobacco floral meristem and in the cells of the developing pedicel of the immature tobacco flower (A. Kelly and D.R. Meeks-Wagner, unpublished results). This pattern is the reciprocal of that observed for the floral meristem identity genes of Antirrhinum (Coen et al., 1990; Huijser et al., 1992) and Arabidopsis (Mandel et al., 1992; Weigel et al., 1992) and is very similar to the pattern described for the floral meristem localization of the Arabidopsis *CDC2* transcript (Martinez et al., 1992; see Figure 2B). However, sequence analysis has shown that FA2 is not a *CDC2* homolog.

The developmental program(s) that function in the incipient floral meristem confer floral identity to these meristem cells. Genes that regulate floral meristem identity in Antirrhinum and Arabidopsis have been identified by mutations that cause the partial transformation of flowers into inflorescence shoots (reviewed by Schwarz-Sommer et al., 1990; Coen and Meyerowitz, 1991). Recently, several of these genes have been cloned, and their patterns of expression have been analyzed by in situ hybridization to vegetative, inflorescence, and floral meristems. Two cloned genes that function as important regulators of floral meristem identity in Antirrhinum are *FLORICAULA* (*FLO*) (Coen et al., 1990) and *SQUAMOSA* (*SQUA*) (Huijser et al., 1992). In Arabidopsis, the *LEAFY* (*LFY*) gene encodes a putative protein with an amino acid sequence very similar to that predicted for the *FLO*-encoded protein (Weigel et al., 1992), whereas the *APETALA1* (*AP1*) gene potentially encodes a putative protein similar to the *SQUA*-encoded protein (Mandel et al., 1992). *FLO* and *LFY* are unique (single-copy) genes, and the putative FLO and LFY proteins possess amino acid motifs that suggest that they function as transcriptional regulators (Coen et al., 1990; Weigel et al., 1992). *SQUA* and *AP1* are members of the multigene family of MADS-box transcriptional regulators (Huijser et al., 1992; Mandel et al., 1992).

During inflorescence development, *FLO* and *SQUA* transcripts accumulate throughout the early floral meristem (see Figure 2C) as well as in the young bracts that subtend maturing floral buds (Coen et al., 1990; Huijser et al., 1992). *FLO* and *SQUA* expression continues in all floral organs except the stamens. The *FLO* transcript is present only during the early stages of floral organ initiation, whereas *SQUA* transcript persists through later stages of flower development. In situ hybridizations have not detected *FLO* and *SQUA* transcripts in inflorescence meristems; the absence of *FLO* and *SQUA* transcripts from the vegetative meristem is inferred from RNA gel blot analysis. In the early floral meristem, *FLO* and *SQUA* are expressed throughout all cell layers and meristematic regions. Significant levels of transcript accumulate as soon as the flower primordium becomes physically distinguished in the axil of the developing bract. Given the similarity in the early expression of *FLO* and *SQUA*, Huijser et al. (1992) investigated whether *SQUA* is expressed in *flo* mutants. RNA gel blot analysis revealed nearly normal levels of *SQUA* transcript in the inflorescence of a *flo* mutant and of *FLO* transcript in the inflorescence of a *squa* mutant. Thus, *FLO* and *SQUA* appear not to regulate each other at the transcriptional level. However, it is possible that the combinatorial action of the *FLO* and *SQUA* gene products regulates the expression of other genes in the early floral meristem.

A very similar picture has emerged for the *LFY* and *AP1* genes of Arabidopsis. *LFY* and *AP1* transcripts are localized to early floral meristems and to immature floral organs but are not detected in inflorescence meristems (Mandel et al., 1992; Weigel et al., 1992). In situ hybridization has shown that *LFY* expression first occurs in the cells of the emerging floral meristem and then continues in all regions of the early floral meristem (see Figure 2C). *LFY* transcript remains at significant levels in all floral organs through the early stages of flower development (Weigel et al., 1992). *AP1* transcript shows a similar pattern of accumulation in the early floral meristem of Arabidopsis (Mandel et al., 1992). Unlike *LFY* transcripts, *AP1* transcripts are detected only in the sepal and petal primordia of the the developing flower (Mandel et al., 1992). As found with *FLO* and *SQUA* of Antirrhinum, the expression of *LFY* in the early floral meristem of Arabidopsis is not dependent upon wild-type *AP1* function (Weigel et al., 1992).

PATHWAYS THAT REGULATE GENE EXPRESSION IN THE EARLY FLORAL MERISTEM

Gene expression in the early floral meristem is apparently the sum of fixed, modified, and stage-specific patterns such as those described above. The existence of fixed and modified patterns of gene activity suggests that early floral meristem

development is related to genetically controlled processes that also function in vegetative and inflorescence meristems. Given the sequential progression of angiosperm development, finding evidence for genetically controlled processes that operate in the shoot meristem throughout plant growth is not surprising. Thus, it is possible that vegetative and inflorescence meristem function is distinguished from early floral meristem function primarily by the activity of the floral stage–specific genes.

Although this is an appealing hypothesis, the evidence for strict floral stage–specific gene activity is not unequivocal. For example, although FA2 transcripts are not detected in tobacco vegetative meristems by in situ hybridization, their presence has been clearly demonstrated by quantitative polymerase chain reaction (PCR) analysis (A. Kelly and D.R. Meeks-Wagner, unpublished results). Furthermore, transcripts of the tobacco homolog of *FLO* and *LFY*, the Tob-*FLO* gene, accumulate to a significant level in vegetative meristems as well as in floral meristems (A. Kelly and D.R. Meeks-Wagner, unpublished results). Although there is no evidence that the Tob-*FLO* gene is functionally equivalent to either the *FLO* or *LFY* gene, Tob-*FLO* is a single-copy gene that shares extensive sequence identity with both genes (A. Kelly and D.R. Meeks-Wagner, unpublished results). Perhaps further analysis of *FLO* and *SQUA* activity in Antirrhinum and of *LFY* and *AP1* activity in Arabidopsis will reveal developmentally significant vegetative expression of these genes.

If the floral stage–specific genes are active during earlier stages of development, then it will be necessary to consider the possibility that early floral meristem function is determined by the modification of developmental programs that operate during vegetative and inflorescence meristem development. Such modifications could be controlled by genetically defined pathways that regulate the timing of floral initiation. Mutations that alter the timing of the vegetative-to-floral transition are common. For example, at least a dozen Arabidopsis genes have been identified by mutations that cause a late-flowering phenotype (Koornneef et al., 1983), and mutations in several other genes cause an early flowering phenotype (Shannon and Meeks-Wagner, 1991; Zagotta et al., 1992). Furthermore, by altering the environmental conditions under which wild-type plants are grown, it is possible to create phenocopies of most of the floral timing mutants. This suggests that these genetically defined pathways are themselves responsive to the environment, an attribute that would permit flowering plants to coordinate the progression through the V → I → F stages with changes in growth conditions. Thus, it is possible that genes that control major aspects of early floral meristem development, such as *FLO* and *SQUA* of Antirrhinum and *LFY* and *AP1* of Arabidopsis, are directly regulated by environmentally sensitive pathways.

Evidence in support of this idea comes from the analysis of meristem fate in plants possessing combinations of mutant alleles for the *LFY*, *AP1*, and *TERMINAL FLOWER1* (*TFL1*) genes of Arabidopsis. Plants homozygous for recessive *tfl1* mutant alleles are early flowering (Shannon and Meeks-Wagner, 1991) and produce a terminal floral meristem on each inflorescence axis (Shannon and Meeks-Wagner, 1991; Alvarez et al., 1992). Genetic analysis indicates that *TFL1* prevents the wild-type inflorescence meristem from acquiring floral meristem identity by negatively regulating the *LFY* and *AP1* developmental pathways in the inflorescence meristem (Shannon and Meeks-Wagner, 1993). This is consistent with the observations that *LFY* (Weigel et al., 1992) and *AP1* (Mandel et al., 1992) transcripts are not detected by in situ hybridization in the inflorescence meristem of wild-type plants.

FUTURE PROSPECTS

In the past few years, a variety of experimental approaches have led to the characterization of gene expression patterns in the early floral meristem. It is clear that many, and perhaps all, of the genes thus far characterized as being active in early floral meristems are also expressed in vegetative and inflorescence meristems. This may reflect the sequential nature of meristem ontogeny during plant development. A high degree of relatedness among the developmental programs that operate in the meristem throughout the plant life cycle may account for the observation that the reversion of floral meristem development to vegetative meristem development can be achieved by environmental shocks, such as abrupt changes in photoperiod or temperature, even when the shocks occur very late in flower bud development (Krishnamoorthy and Nanda, 1968; Battey and Lyndon, 1990). This situation greatly challenges our ability to frame the V → I → F progression in terms of a genetically controlled progression of developmental determination as proposed for early Drosophila embryogenesis.

To understand the genetic control of floral meristem initiation, it will be important to continue to identify and characterize genes expressed in shoot meristems during the various stages of plant development. One goal of this work should be to determine the earliest occurrence of true floral stage–specific gene expression. Another goal should be to search for genes that are down regulated during the I → F transition. The examination of floral meristem initiation has been largely from the point of view of meristem-expressed genes that are active in the early floral meristem, yet it is equally important to determine which genes are rendered inactive upon the I → F transition. The continued isolation of mutations that affect inflorescence development and the early stages of floral development will also be critical to defining the genetic pathways that regulate early floral meristem function. The roles of such genes can then be assessed by both genetic analysis and gene expression studies. Finally, the analysis of the molecular mechanisms that control early floral meristem gene expression will be important for elucidating the regulatory relationships between meristem gene activity and plant development. It will be interesting to learn whether the mechanisms that regulate the patterns of early floral meristem gene expression are directly responsive to the environmental cues that control the timing of the vegetative-to-floral transition.

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