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Review

Genes and functions controlled by floral organ identity genes

Robert Sablowski*

Cell and Developmental Biology, John Innes Centre, Norwich Research Park, Norwich NR4 7UH, United Kingdom

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ABSTRACT

Floral organ identity genes specify the identity of floral organs in a manner analogous to the specification of body segments by *Hox* genes in animals. Different combinations of organ identity genes co-ordinate the expression of genes required for the development of each type of floral organ, from organ initiation until final differentiation. Here, I review what is known about the genes and functions subordinate to the organ identity genes. The sets of target genes change as organ development progresses and ultimately organ identity genes modify the expression of thousands of genes with a multitude of predicted functions, particularly in reproductive organs. However, genes involved in transcriptional control and hormone functions feature prominently among the early and direct targets. Functional analysis showed that control of organ-specific tissues and structures can be delegated to specialised intermediate regulators, but organ identity genes also fine-tune genes with general roles in shoot organ development, consistent with the notion that organ identity genes modify a core leaf-like developmental program. Future challenges include obtaining data with cellular resolution, predictive modelling of the regulatory network, and quantitative analysis of how organ identity genes and their targets control cell behaviour and ultimately organ shape.

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1. Introduction

The control of floral organ identity is one of the most striking examples of how regulatory genes determine plant structure (reviewed by [1,2]). Each of the four types of floral organs (sepals, petals, stamens and carpels) is specified by a unique combination of regulatory genes. In Arabidopsis, sepal development is guided by *APETALA1* (*AP1*) combined with any of four *SEPALLATA* (*SEP1–SEP4*) genes; petals are specified by *AP1*, *SEP1–3*, *APETALA3* (*AP3*) and *PISTILLATA* (*PI*); stamens develop under the control of *AP3*, *PI*, *SEP1–3* and *AGAMOUS* (*AG*), while the combination of only *AG* and *SEP1–3* directs carpel formation. These gene combinations are not only necessary, but sufficient for the development of floral organs: if the required set is artificially expressed outside flowers, leaves are transformed into the corresponding floral organs [3,4]. Conversely, in mutants that are unable to specify any type of floral organ, flowers are made of leaf-like organs [5,6]. These results are consistent

Abbreviations: *AG*, *AGAMOUS*; *AGL5*, *AGAMOUS-like 5*; *AP1*, *APETALA1*; *AP3*, *APETALA3*; ARF, auxin response factor; *ATH1*, *ARABIDOPSIS THALIANA HOMEOBOX GENE1*; *ATX1-2*, *ARABIDOPSIS TRITHORAX1-2*; bHLH, basic helix-loop-helix; bZIP, basic leucine zipper; ChIP, chromatin immunoprecipitation; ChIP-chip, ChIP followed by oligonucleotide chip analysis; ChIP-seq, ChIP followed by deep sequencing of immunoprecipitated DNA; DAD1, *DEFECTIVE IN ANTHER DEHISCENCE1*; *DEF*, *DEFICIENS*; *GA4*, *GA-REQUIRING 4*; GFP, green fluorescent protein; *GNC*, *GATA, NITRATE INDUCIBLE, CARBON METABOLISM-INVOLVED*; *GNL*, *GNC-LIKE*; GUS, β-glucuronidase; Hox, homeobox; JA, jasmonic acid; *JAG*, *JAGGED*; MADS, MCM1, AG, DEF, SRF; MPSS, massively parallel sequence signature; NAC, NAM, ATAF1-2, CUC1-2; *NAP*, *NAM-LIKE, ACTIVATED BY AP3/PI*; *NUB*, *NUBBIN*; PHA-4, pharynx-4; *PI*, *PISTILLATA*; *SEP1/2/3/4*, *SEPALLATA 1/2/3/4*; *SHP1/2*, *SHATTERPROOF1/2*; *SPL*, *SPOROCYTELESS*; *STY1/2*, *STYLISH1/2*; TCP, TB1, CYC, PCF1-2.

* Tel.: +44 1603 450530; fax: +44 1603 450045.
E-mail address: robert.sablowski@bbsrc.ac.uk.

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with the idea proposed by Goethe more than 200 years ago that floral organs and leaves are variations of the same basic type of organ [2].

The ability of floral organ identity genes to replace one organ type with another and their combinatorial action mirror the function of *Hox* genes, which specify the identity of body segments in animals [7,8]. Another similarity with *Hox* genes is that the floral organ identity genes control all stages of development of the body parts they specify, from initiation, through morphogenesis to cell differentiation [9,10]. In both cases, expression patterns are maintained throughout development by auto-regulation and by chromatin modification. Both *Hox* and floral organ identity genes encode transcription factors, but belong to unrelated families (homeodomain and MADS families, respectively). Thus the parallels between organ identity and *Hox* genes are a clear example of convergent evolution, with similar developmental strategies executed by unrelated sets of genes [11].

The combinatorial action of floral organ identity genes is reflected by interactions between the encoded proteins [12,13]. Therefore it is believed that different complexes of MADS proteins are able to activate or repress the sets of genes required for the development of each type of floral organ. However, as in the case of *Hox* genes and in fact throughout developmental biology, a large unexplained gap remains between the molecular function of these transcriptional regulators and their striking phenotypic effects. To begin to understand how the activity of floral organ identity genes is translated into the cellular activities that actually build floral organs, we need to reveal the gene expression programme that is co-ordinated by these genes. Specific questions include:

- What kinds of genes and functions are controlled? Do the organ identity genes directly control genes involved in basic cellular functions, such as division, expansion and metabolism, or are these genes controlled indirectly through networks of regulatory genes and signalling molecules?
- How do organ identity genes modify the underlying leaf-like gene expression program? Do they activate sets of organ-specific of genes or do they modify the activity of genes with roles in multiple organs (for example, genes required for the differentiation of cell types that are common between organs)?
- How are different sets of target genes selected in different places and times? Much of the answer to this depends on understanding how organ identity genes function in combination with each other, with other transcription factors and with target promoters.

Here, I review our progress in identifying the targets of floral organ identity genes and how this has contributed to answering the questions above.

2. Identifying the targets of floral organ identity genes.

In the early days, candidate target genes were revealed by expression patterns or by low-throughput differential expression screens. The first example was *AGL5* (*AGAMOUS-like 5*, subsequently re-named *SHATTERPROOF2*, *SHP2*), which was identified as a target of *AG* because it was expressed specifically in carpels and not expressed in the *ag* mutant; furthermore, AG bound in vitro to the *SHP2* promoter and ectopic AG activated a *SHP2*:*GUS* reporter gene [14]. The first evidence of direct regulation *in vivo* came from a screen for changes in the floral mRNA population after post-translational activation of AP3, with indirect effects blocked by cycloheximide [15]. In this screen, *NAP* (*NAM-related*, *activated by AP3*/*PI*), which encodes a member of the NAC family of transcription factors, was identified as an immediate target of AP3 and PI during petal and stamen development.

The subsequent sequencing of the Arabidopsis genome and development of expression arrays allowed analysis of gene expression at a much larger scale. The most straightforward approach was to compare gene expression in different floral organ identity mutants. Zik and Irish used cDNA arrays covering about a fourth of all Arabidopsis genes to identify a set of genes downstream of AP3/PI, which was enriched for genes involved in stress responses and cell wall metabolism [16]. Wellmer et al. [17] used an array of floral cDNAs and a genome-wide oligonucleotide array to compare a wider range of mutants with organ identity changes. Their experiments revealed a small number of transcripts enriched in sepals (13) or petals (18), but a much larger set of genes expressed specifically in carpels (206) or stamens (1162), many of which are related to gametophyte development [18]. Genes involved in general cellular maintenance (DNA recombination, protein synthesis, protein folding) were under-represented, while functional classes such as embryonic development and cell wall modification were over-represented [17]. Massively parallel sequence signatures (MPSS) were also used to compare the transcriptomes of mutant flowers with wild-type flowers and vegetative tissues [19]. The stamen-enriched set identified by MPSS showed good agreement with the array experiments, but the overlap for other organ types was small; these discrepancies may result from the different criteria used to define organ-enrichment (mutants compared, baseline expression, statistical analysis). However, two common themes emerged from all experiments comparing gene expression in different organ types. First, the organ identity genes directly or indirectly influence a wide array of developmental and cellular processes. Second, the reproductive organs clearly have more specilaised developmental programs than perianth organs.

The experiments described above were concerned only with spatial differences in gene expression and corresponded mostly to late stages of organ development. Other papers were concerned with temporal changes in the transcriptome. Bey et al. [20] analysed gene expression during the final stages of sepal and petal development in Antirrhinum and used a temperature-sensitive allele of *DEFICIENS* (*DEF*, the snapdragon orthologue of *AP3*) to detect genes that responded rapidly after DEF was activated. They noted that 60% of differentially expressed genes were stage-specific and that at late stages of petal development DEF appears to mostly regulate genes involved in metabolism and cell differentiation. In contrast, a disproportionate number of genes preferentially activated during early bud development in Arabidopsis and rice encode transcription factors [21–24]. Genes involved in the synthesis and response to hormones (gibberellin, auxin) were also over-represented in the transcriptome of early buds [21–23]. The overall conclusions of these time course experiments were that the gene expression programme under the floral organ identity genes changes over time and that early stages include a large proportion of regulatory genes (Fig. 1). The larger number of genes with metabolic and transport functions expressed at later stages of development could reflect a change in the types of functions controlled by organ identity genes, or it could reflect the accumulation of indirect effects on gene expression. To distinguish between these possibilities, it was necessary to identify the direct targets of organ identity genes.

Although rapid response to a regulatory gene (as in the temperature shift experiments described above for DEF) is suggestive, proof of direct interaction requires chromatin immunoprecipitation (ChIP). Gomez-Mena et al. [21] used ChIP to confirm that the AG protein binds directly to some of its early target genes. This included *AG* itself, *AP3* and *SEP3*, showing that an auto-regulatory loop maintains expression of the organ identity proteins that are predicted to function as a multiprotein complex. More recently, a number of important insights came from using ChIP-chip and ChIP-seq to obtain a global view of the direct targets of SEP3 in the wild type and in the *ag* mutant [25]. SEP3 bound *in vivo* to a large number of

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