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REVIEW ARTICLE

Mechanisms and function of flower and inflorescence reversion

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Abstract

Flower and inflorescence reversion involve a switch from floral development back to vegetative development, thus rendering flowering a phase in an ongoing growth pattern rather than a terminal act of the meristem. Although it can be considered an unusual event, reversion raises questions about the nature and function of flowering. It is linked to environmental conditions and is most often a response to conditions opposite to those that induce flowering. Research on molecular genetic mechanisms underlying plant development over the last 15 years has pinpointed some of the key genes involved in the transition to flowering and flower development. Such investigations have also uncovered mutations which reduce floral maintenance or alter the balance between vegetative and floral features of the plant. How this information contributes to an understanding of floral reversion is assessed here. One issue that arises is whether floral commitment (defined as the ability to continue flowering when inductive conditions no longer exist) is a developmental switch affecting the whole plant or is a mechanism which assigns autonomy to individual meristems. A related question is whether floral or vegetative development is the underlying default pathway of the plant. This review begins by considering how studies of flowering in *Arabidopsis thaliana* have aided understanding of mechanisms of floral maintenance. *Arabidopsis* has not been found to revert to leaf production in any of the conditions or genetic backgrounds analysed to date. A clear-cut reversion to leaf production has, however, been described in *Impatiens balsamina*. It is proposed that a single gene controls whether *Impatiens* reverts or can maintain flowering when inductive conditions are removed, and it is inferred that this gene functions to control the synthesis or transport of a leaf-generated signal. But it is also argued that the susceptibility of *Impatiens* to reversion is a consequence of the meristem-based mechanisms controlling development of the flower in this species. Thus, in *Impatiens*, a leaf-derived signal is critical for completion of flowering and can be considered to be the basis of a plant-wide floral commitment that is achieved without accompanying meristem autonomy. The evidence, derived from *in vitro* and other studies, that similar mechanisms operate in other species is assessed. It is concluded that most species (including *Arabidopsis*) are less prone to reversion because signals from the leaf are less ephemeral, and the pathways driving flower development have a high level of redundancy that generates meristem autonomy even when leaf-derived signals are weak. This gives stability to the flowering process, even where its initiation is dependent on environmental cues. On this interpretation, *Impatiens* reversion appears as an anomaly resulting from an unusual combination of leaf signalling and meristem regulation. Nevertheless, it is shown that the ability to revert can serve a function in the life history strategy (perenniality) or reproductive habit (pseudovivipary) of many plants. In these instances reversion has been assimilated into regular plant development and plays a crucial role there.

Key words: Floral development, floral induction, floral maintenance, floral reversion, meristem, perenniality, pseudovivipary.

Introduction

Floral reversion is a return to leaf production after a period of flower development. A less strict definition is that there is a return to an earlier phase of development. There are two

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distinct types; inflorescence reversion in which vegetative development occurs after, or intercalated within, inflorescence development (Fig. 1) and flower reversion, in which the form of the flower itself is altered. The flower may be incomplete, with some parts replaced with leaves, or there may be proliferation after the formation of the normal complement of floral organs.

The most striking feature of reversion is its strong association with environmental conditions. This aspect of reversion is emphasized in Battey and Lyndon (1990). Reports of conditions causing reversion in various plant species are summarized in Table 1 of that review and more recent reports are presented here, as an up-date, in Table 1.

This review concentrates on the mechanisms and functions of flower and inflorescence reversion. Since 1990 there have been extensive studies of molecular mechanisms regulating flowering. The focus is on how this research (summarized in Table 2) informs understanding of reversion. Two plant species are considered in detail. The first is *Arabidopsis thaliana* which is small, has a rapid life cycle, a wide range of mutations, a completely sequenced genome and is, therefore, a model species for the study of flowering. Although reversions seen in this plant are from flower to inflorescence development and are therefore not true reversions to leaf production, the terminology, genetic interactions, and insight into floral maintenance derived from it are relevant to studies of reversion to leaf production.

The second species is *Impatiens balsamina*, in which the terminal flower reverts to leaf production consistently in response to transfer from inductive short days (SD) to long days (LD). The progress in identifying the genetic basis of this response is described.

The way in which findings for these two species relate to physiological, molecular, and *in vitro* reports of reversion in other plants is then discussed and the implications for the concept of floral commitment are considered. Finally, two cases are described in which reversion has a functional significance: perenniality and pseudovivipary.

Mechanisms of inflorescence and flower reversion

Arabidopsis thaliana

The transition to flowering in *Arabidopsis* is the culmination of a complex interaction of genes. The flowering time

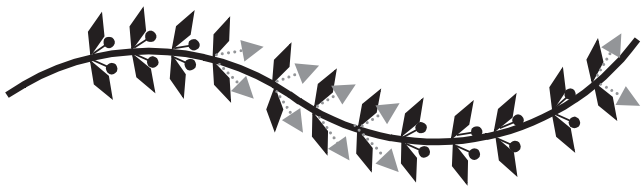

Fig. 1. Diagrammatic representation of inflorescence reversion. Filled circles represent flowers, filled triangles, vegetative axillary meristems.

Table 1. *Environmental causes of flower and inflorescence reversion (additional to those listed in Table 1. Battey and Lyndon, 1990)*

Species	Conditions causing flowering	Conditions causing reversion	Characteristics of reverted plants	Reference
Boronia megastigma	Cool temperature (17/9 °C day/night)	Transfer to warm temperature (25/17 °C day/night) 'Commitment' requires 11–15 weeks of cool temperature	Signs of reversion even when carpels formed. Young buds may form only leaf-like sepals before vegetative development. Older buds abort and are abscised. Vegetative growth may be found in axils of bracts below these buds	Day *et al.*, 1994
Eucalyptus lansdowneana F. Muell. & J. Brown subsp. *lansdowneana*	Enhanced by cold. Daylength insensitive?	Low solar radiation and short (0–5 weeks) cold treatment 15/10 °C	Not described	Moncur, 1992
Glycine max	Short days	Transfer to long days	Trifoliolate leaves initiated in 2/5 phyllotaxy after initiation of floral bracts	Washburn and Thomas, 2000
Hardenbergia violacea cv. Mini haha	Short days (<12.5 h) and cool temperature (15–18 °C)	Transfer to long days and/or warm temperature (22 °C)	Buds abort and vegetative shoot growth begins from adjacent tissue. Inflorescence reversion?	King, 1998
Lupinus angustifolius (some genotypes)	Vernalization of 2–4 weeks (5 °C)	Marginally too short a period of vernalization (much too short and plants do not flower)	Distortions of first flowers to appear. Next buds to appear have no petals, stamens, or carpels but short bracts. Later buds still form in axil of bract but give rise to leaves	Landers, 1995
Suaeda salsa	Short days (critical daylength 14 h)	Transfer to long days (16 h) after 4–6 SD cycles of 10 h	'succulent leaves grew up from the original flower bud'	Kefu *et al.*, 2002
Titanotrichum oldhamii	Natural populations flower in long days	Short days	Meristem fate can be flower, proliferation of bracts or bulbil formation depending on environment	Wang and Cronk, 2003
Whytockia bijieensis YZ Wang & ZY Li	High humidity and/or moderate temperature?	Low night temperature (12–14 °C) and low humidity (<75%)	Reversion after first sepals in first flower pair on inflorescence axis	Wang, 2001

Table 2. *Genetic causes of flower and inflorescence reversion*

Species	Gene	Gene type	Reversion phenotype	Expression pattern	Possible role	Reference
Arabidopsis thaliana	*Agamous-Like 24* (*AGL24*)	MADS	Constitutive expression: flower reversion to inflorescence development erupting from ovary	Shoot apical meristem and developing leaf primordia	WT: *LFY* and *AP1* must suppress *AGL24* which promotes inflorescence development	Yu *et al*., 2004
Arabidopsis thaliana	*Leafy* (*LFY*)	Novel class	*lfy-6* mutant grown in SD: normal flower but ovary ruptures and ectopic flower-bearing shoot grows out	Developing flower primordia and leaf primordia before flowering	See text for discussion	Okamuro *et al*., 1996
Arabidopsis thaliana	*Agamous* (*AG*)	MADS box	*ag-1* mutant grown in SD: flowers formed of several whorls sepal, petal, petal repeated, then reversion to inflorescence meristem	Inner whorls of floral meristem	See text for discussion	Okamuro *et al*., 1996
Lycopersicon esculentum Mill.	*Tomato MADS box 29* (*TM29*)	MADS; similarity to *SEPALLATA* genes of *Arabidopsis*	Cosuppression/antisense *TM29*: ectopic shoots of partial leaves, secondary flowers from fruit	Vegetative, inflorescence and floral meristems and all floral organs	*TM29* role in floral meristem identity, maintenance, floral organ and fruit development	Ampomah-Dwamena *et al*., 2002
Lycopersicon esculentum Mill.	*Single Flower Truss* (*SFT*)	Unknown	Mutant: inflorescence produces normal flowers initially then reverts to produce vegetative shoot in the position of the next flower	Unknown	Promoter of flowering (mutants are late flowering) and regulator of floral transition and vegetative development programme via *SP* gene	Molinero-Rosales *et al*., 2004
Petunia hybrida	*Floral Binding Protein 2* (*FBP2*)	MADS Similarity to *TM5* (tomato). *SEPALLATA*-like	Cosuppression *FBP2*: new inflorescences growing from axils of carpels	Petals, stamens, carpels	*FBP2* either (i) promotes floral transition, or (ii) represses inflorescence characteristics	Angenent *et al*., 1994
Zea mays	*Indeterminate Floral Apex 1* (*IFA1*) – double mutants with *ZAG1* or *IDS1*	Unknown	Double mutants: *ifa1, ids1*: return to earlier meristem type, spikelet becomes branch or spikelet pair meristem. *ifa1, zag1*: floral meristems become branch or spikelet meristems. Leaf-like glumes in spikelet, branching structures from centre of flower	Unknown	Regulation of meristem determinacy. *ifa1* mutants suffer loss of determinacy in spikelet, spikelet pair and floral meristems	Laudencia-Chingcuanco and Hake, 2002
Zea mays	*Indeterminate 1* (*ID1*)	Zinc finger transcription factor	Mutant is late flowering. Inflorescences have vegetative characteristics, plantlets grow out of spikelets	Immature leaves only	Promotes floral transition and maintenance, possibly by regulating synthesis/ transport of floral stimulus	Colasanti *et al*., 1998
Zea mays	*Zea FLO LFY 1* and *2* (*ZFL 1* and *2*)	*FLO/LFY* homologues	Mutants sometimes produce proliferous flowers and ectopic vegetative outgrowths	Vegetative meristem, some leaf primordia. Reproductive development	Similar role to *FLO/LFY* in the floral transition, meristem identity, phyllotaxy, floral organ identity regulation	Bomblies *et al*., 2003

genes control the response to the environment (light, daylength, temperature), autonomous/endogenous and hormonal signals. Integrator genes, at the intersection of these different pathways, regulate genes which control the transition to floral development in the meristem (Simpson and Dean, 2002). One concept of flowering time regulation proposes that the genetic pathways can be regarded as enabling and promoting (Boss *et al*., 2004). Promoting pathways, for example, the photoperiod pathway in which *CONSTANS* (*CO*) plays a key role, lead to the activation of the integrator genes, whereas enabling pathways regulate the expression of floral repressors, for example, *FLOWERING LOCUS C* (*FLC*), and regulate meristem competence to flower. It is envisaged that the balance between the enablers and the promoters shifts during the life cycle of the plant, in response to the environment and to endogenous signals; it also shifts in different plant species, accounting for both the diversity and adaptability of flowering responses (Boss *et al*., 2004).

Once the meristem has become directed to floral development, a final set of genes dictates the development of the organs of the flower (for a review see Jack, 2004); and the reproductive phase is completed with the cessation of growth of that meristem.

The *LEAFY* (*LFY*) gene has been identified as a key regulator in the flowering process (Weigel *et al*., 1992; Weigel and Nilsson, 1995). It is an integrator in the terminology of Boss *et al*. (2004). *LEAFY* has its primary role in controlling the switch from inflorescence development to floral development and is up-regulated in response to inductive long day (LD) conditions and gibberellins (GA) (Blazquez *et al*., 1998). Acting with *WUSCHEL* (*WUS*), a homeodomain gene, it activates *AGAMOUS* (*AG*) (Parcy *et al*., 1998; Busch *et al*., 1999). *AG* is a MADS-box transcription factor which controls the development of stamens and carpels in the flower (Yanofsky *et al*., 1990) and also provides the 'stop' function to growth when flowering is complete, by repressing *WUS* (Fig. 2a; Lohmann *et al*., 2001; Lenhard *et al*., 2001). Along with the *CLAVATA* (*CLV*) genes, *WUS* plays a key role in maintaining a population of undifferentiated cells in the meristem (Fletcher, 2002; Tooke and Battey, 2003).

CLV and *WUS* maintain meristem function by regulating the accumulation of undifferentiated cells in the face of their loss to a differentiated state (Fig. 2b; Schoof *et al*., 2000). Much less is known about the molecular mechanisms which ensure that floral development is maintained in the meristem.

In *Arabidopsis*, failure to maintain the floral state leads to a form of flower reversion in which an inflorescence grows out from a flower. It is rare that this occurs in wild-type *Arabidopsis*, although it may occur at a low frequency in the first flowers formed in a Landsberg *erecta* background in SD (Okamuro *et al*., 1996). However, reversions to inflorescence development are frequently

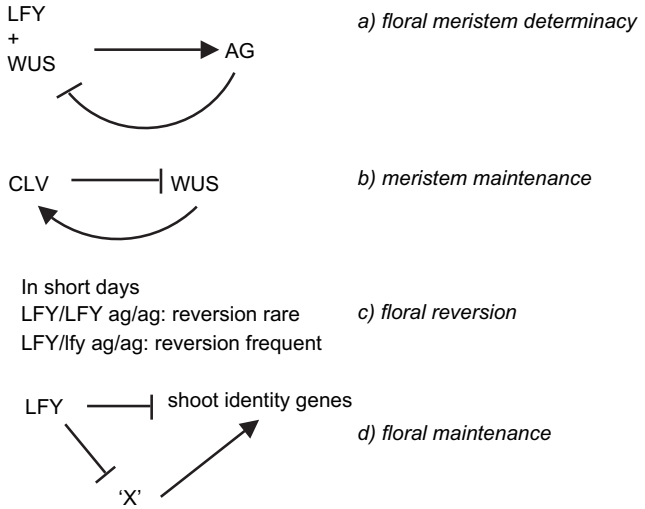

Fig. 2. Genetic pathways of meristem maintenance and determinacy in *Arabidopsis thaliana*. (a) Floral meristem determinacy: *AGAMOUS* (*AG*), a MADS-box *c* function gene specifying stamen and carpel identity, prevents further growth of the flower by shutting down meristem cell accumulation through repression of *WUS. ag* mutants produce indeterminate flowers. *LFY* and *WUS* promote expression of *AG* (Lohmann *et al*., 2001; Lenhard *et al*., 2001). (b) Meristem maintenance: the size of the expression domain of *WUSCHEL* (*WUS*), which promotes stem cell identity, is controlled by *CLAVATA* (*CLV*). The pool of meristematic cells is maintained by a self-regulating system with *WUS* promoting expression of *CLV3* (Schoof *et al*., 2000; Fletcher, 2002). (c) Floral reversion: *LEAFY* (*LFY*) is able to reduce reversion frequency independently of *AG* as shown by the rarity of reversion in a homozygous *LFY* background (Parcy *et al*., 2002). (d) Floral maintenance: in this model of floral maintenance *LFY* acts directly or via an intermediate factor ('X') to repress shoot identity genes, such as *TERMINAL FLOWER 1* (*TFL1*) (Parcy *et al*., 2002). *LFY* also represses *AGAMOUS LIKE 24* (*AGL24*), a promoter of inflorescence identity (Yu *et al*., 2004).

found in heterozygous *lfy-6* and homozygous *ag-1* mutants grown under SD conditions (Okamuro *et al*., 1996), indicating that *LFY* and *AG* are critical to floral maintenance in *Arabidopsis*. The key role of *LFY* is demonstrated by the much greater frequency of reversion in *ag* mutants in a heterozygous *LFY* background (*LFY lfy, ag ag*) than in a homozygous *LFY* background (*LFY LFY, ag ag*). This result also reveals that the ability of *LFY* to maintain flowering can be independent of *AG* (Fig. 2c; Parcy *et al*., 2002). Furthermore, experiments with a *LFY:VP16* transgene suggest that floral maintenance is achieved through transcriptional repression of shoot identity genes such as *TERMINAL FLOWER 1* (*TFL1*). *LFY* interacts with other, currently unknown factors to bring this about (Parcy *et al*., 2002). It is also thought to act as a transcriptional repressor of *AGAMOUS-LIKE 24. AGL24* is a promoter of inflorescence fate. It is a MADS-box gene expressed in vegetative plants and in the transition to flowering. Overexpression of *AGL24* results in reversion to inflorescence development presumably because *LFY* and *APETALA1* (*AP1*) are unable to suppress it completely. In the reversion of *lfy-6* mutants, *AGL24* is found to be weakly suppressed (Fig. 2d; Yu *et al*., 2004).

Although floral maintenance of *Arabidopsis* can be ascribed, in part, to transcriptional repression of shoot or inflorescence identity genes by *LFY*, both heterozygous *lfy-6* mutants and *ag-1* mutants only revert when grown in SD or when *ag* mutations are combined with a mutation in the photoperiod pathway (Okamuro *et al*., 1996; Mizukami and Ma, 1997), which are less inductive conditions for this quantitative long-day plant. One explanation for this is that *LFY* is only expressed at a low level in weakly inductive conditions and this may reduce its capacity to repress shoot identity genes. Okamuro *et al*. (1996) were able to suppress SD-induced reversion of *ag-1* and heterozygous *lfy-6* mutants by blocking phytochrome activity (using a *hy-1* mutant background) or increasing gibberellins (endogenously in a *spindly* mutant background or by exogenous application). Night break treatments were also effective in causing some degree of suppression. A GA-mediated signal could be a requirement for floral maintenance and might operate by promoting expression of *LFY* or genes downstream of *LFY* or by suppressing shoot identity genes.

In the late flowering *Arabidopsis* ecotype *Sy-0*, the interaction of the gene *AERIAL ROSETTE 1* (*ART1*) with flowering time genes *FLC* and *FRIGIDA* (*FRI*) gives a phenotype defined by an enlarged basal rosette of leaves, aerial rosettes in the axils of cauline leaves, and inflorescence and flower reversion. Here, flowering time genes affect plant morphology as well as the transition to flowering. The phenotype is attributed to a deficiency of floral signals or poor competence to respond to them (Poduska *et al*., 2003).

The importance of floral signal transport has been underlined by the report that the flowering time gene *CO* of *Arabidopsis* regulates the synthesis or transport of a floral signal (An *et al*., 2004). The expression of *CO* in the phloem is sufficient to induce flowering, partly through cell-autonomous activation of *FLOWERING LOCUS T* (*FT*) and partly by an *FT*-independent pathway. The FT protein itself may move between cells or regulate synthesis of a floral signal. Notably, one possible target for *FT* in the meristem may be *AP1* (Ruiz-Garcia *et al*., 1997) which Hempel *et al*. (1997) consider a consistent marker of commitment, always expressed after floral determination has been achieved in *Arabidopsis*. Gisel *et al*. (2002) have found that the point of floral commitment in *Arabidopsis* correlates with a reduction in the movement of a symplastic tracer from leaf to meristem; this finding might implicate a repressor in the flowering process. Movement of symplastic tracer resumes on further floral development.

Impatiens balsamina

Initial research using mixed seed (giving plants with a range of flower colours) indicated that *Impatiens balsamina* cv. Dwarf Bush Flowered is a short day (SD) plant in which the majority of plants revert to leaf production when transferred to long day (LD) conditions (Battey and Lyndon, 1984, 1990). An association of reversion with flower colour was noted, red-flowered plants giving a completely consistent reversion response (Battey, 1985). Red-flowered plants were therefore used for detailed molecular analysis of the reversion response described next. It was also noted, however, that purple-flowered plants consistently showed continued flower development even in non-inductive LD (Battey, 1985). These purple-flowered plants provided a useful resource for later physiological (Tooke *et al*., 1998) and genetic analysis (described below).

With red-flowered plants, more short day (SD) cycles cause more of the flower to form before the return to leaf initiation (Pouteau *et al*., 1997). For example, 5 SD is usually sufficient to bring about a change to whorled phyllotaxy, the loss of axillary structures, and the development of patches of pigment on bract-like leaves. With 8 SD plants are able to develop petals before reverting. The reverted meristem, whilst producing leaves, retains some level of floral determination as the leaves are produced in whorls and without axillary meristems and rapid reflowering occurs on transfer back to inductive conditions (Battey and Lyndon, 1986). A transition to a vegetative spiral phyllotaxy with associated axillary meristems is seen much later (Battey, 1985). It is worth noting, however, that even under constant SD conditions, in which a complete flower is formed, the growth pattern of the meristem is only weakly determinate and reiteration from the gynoecium can occur (Pouteau *et al*., 1997, 1998). Analysis of the expression patterns of *Impatiens* homologues of *LFY* and *AP1* (*Imp-LFY* and *Imp-AP1*) has shown that *Imp-AP1* expression is associated with petal development and that *Imp-LFY* is expressed in the meristem in an unchanging pattern through vegetative, flowering, and reverting development (Pouteau *et al*., 1997). Vegetative expression of *LFY* without up-regulation upon floral induction has been described in tobacco where it is not associated with reversion (Kelly *et al*., 1995).

Physiological experiments show that reversion of *Impatiens* results from the failure of a leaf-derived signal to be supplied to the meristem during flower formation (Pouteau *et al*., 1997). There is evidence to show that the meristem responds quantitatively to this leaf signal. Whilst plants revert if deprived of the signal, reduced signal may maintain flowering, but alter the form of the flower. Restricting the number of leaves (through their removal) which can perceive the inductive SD conditions results in flowers which may contain up to double the number of petals of the undefoliated controls (Tooke and Battey, 2000). Flower development appears to be prolonged by limited leaf-derived inductive signal; one interpretation of this is that this signal promotes the transition to C function.

In the purple-flowered line of *Impatiens*, plants continue to flower when transferred from SD to LD, but removal of the induced leaves (those unfolded in SD) causes reversion

(Tooke *et al*., 1998). This indicates that a crucial difference between the flowering (purple-flowered) and reverting (red-flowered) lines is the ability of leaves to produce an inductive signal in the absence of inductive conditions. Thus, leaves of the flowering line deliver to the meristem a vital floral maintenance factor, either by self-perpetuation of the initial SD signal or by production of an autonomous signal in LD.

In recent work, the flowering (purple-flowered) and reverting (red-flowered) lines have been crossed to address the genetic basis for this difference. An unexpected result of this study is the appearance, in the F_1 and F_2 generations, of a novel reflowering line which neither continues to flower normally nor becomes fully reverted (to ongoing leaf initiation) when transferred from SD to LD (Fig. 3). The terminal flower in the reflowering phenotype is generally anomalous. Figure 4A and B show plants with prominent and numerous bract-like organs, whilst plants in Fig. 4C and D have excessive numbers of petals. In the subtlest cases of reflowering there is little internode elongation on reversion and plants display varying degrees of phyllody before continuing flower development.

In each progeny tested, 5SD+LD treatment produces three phenotypes: reverting, flowering, and reflowering. However, responses are not uniform, contrasting with the parental genotypes where phenotype is invariant and true-breeding, and variation has been found between experiments (F Tooke and N Battey, unpublished data).

Analysis of F_1, F_2 and backcross progeny supports a single gene hypothesis as the simplest explanation for the observed phenotypes. Under this hypothesis the parent flowering line is AA and the reverting line, aa. The heterozygous genotype Aa has the novel reflowering phenotype but is leaky so that some of this genotype flower or, less frequently, revert. The effects of gene A appear to be dosage-dependent such that AA plants are largely unaffected by the switch from SD to LD; Aa plants undergo a brief reversion period (then reflower) and aa plants revert completely. Although the parent purple- and red-flowered lines are consistent in their flowering and reverting responses, their F_2 progeny show clearly that flower colour and reversion response are not genetically linked. Therefore, in the F_2 generation, whilst a plant may be of genotype aa, the flower colour would not necessarily be red.

When combined with the previously described data on leaf signalling in purple- and red-flowered *Impatiens* (Pouteau *et al*., 1997; Tooke *et al*., 1998), these results suggest that in *Impatiens* a single gene controls the daylength-independent synthesis/transport of a leaf signal. The effect of the signal on floral development is quantitative (as described above) and this could, in part, explain the 'leakiness' of the heterozygous phenotype. In the absence of this function, the signal fails to reach the meristem in non-inductive conditions. Consistent with this, the purple-flowered line of *Impatiens* (that continues to flower in non-inductive LD unless its leaves are removed) can flower eventually in LD, whereas the SD requirement is absolute in the red-flowered line. Thus the occurrence of reversion in LD correlates with an inactive daylength-independent pathway.

This interpretation leads to the conclusion that, in *Impatiens*, floral commitment is a consequence of continued supply of leaf-derived floral signal to the meristem (see also Hempel *et al*., 2000). But can this conclusion, that floral commitment is leaf-derived, be applied generally to other species? One possibility is that the susceptibility of *Impatiens* to revert in such a clear-cut manner results from the loss of floral signal combined with a peculiarity in the downstream, flower development process. Thus, in most other species a large number of interacting pathways give a generalized stability to flowering that leads to commitment or determination. A process with such a high degree of molecular redundancy may be inherently difficult to reverse once it has been initiated. Floral commitment may therefore be different in character from stable epigenetic changes that occur in plant development, such as vernalization. The underlying regulation of vernalization is now being revealed, and it is clearly brought about in a highly specific way (Gendall *et al*., 2001; Sung and Amasino, 2004).

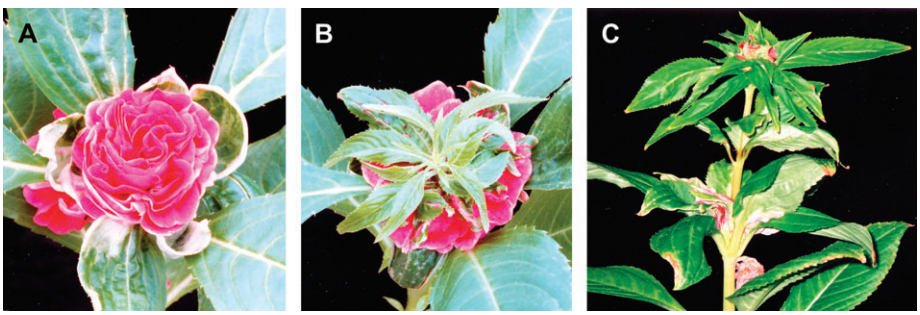

Fig. 3. Flowering, reverting and reflowering responses of *Impatiens* after 5 SD+LD treatment. (A) Top view of terminal flower showing flowering response. (B) Top view of reverting terminal flower. (A) and (B) show the typical responses observed in the parent lines, whilst (C) shows a novel reflowering phenotype in some of the progeny, in which a terminal flower is produced, but after an earlier phase of floral development and reversion.

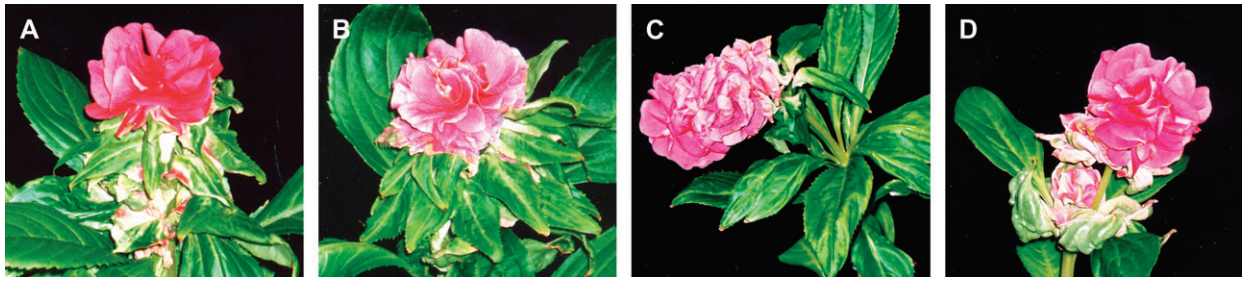

Fig. 4. Reflowering plants (after 5 SD+LD). (A, B) Prominent and numerous bracts. (C, D) Terminal flowers containing numerous petals. The plant in (C) produced 97 petals before the first stamen. (Terminal flowers which develop under SD conditions have approximately 20 petals.)

If this interpretation is correct, the failure of *Arabidopsis* to revert completely (i.e. to leaf production) may be the result of genetic redundancy in the multiple flowering pathways. In *Impatiens* it appears that a leaf-derived signal constantly regulates floral development at the meristem. The question that this analysis begs, however, is why floral development in *Impatiens* is so dependent on the leaf signal. This is discussed further in the Conclusions section of this review.

Other cases of reversion

Strong evidence that a leaf-derived signal controls flowering in *Zea mays* is provided by the *id1* mutant which is late flowering and displays vegetative characteristics in the inflorescence (Colasanti *et al*., 1998). The *ID1* gene is only expressed in immature leaves, yet controls flowering at the meristem. This suggests that it plays a role in the synthesis or transport of a leaf-derived signal which induces and maintains flowering. In *Pisum*, flowering and reversion have been explained in terms of a 'balance model' with some similarities to the enabler and promoter interactions proposed for *Arabidopsis* (Boss *et al*., 2004). Flower initiation in *Pisum* occurs when a threshold promoter:inhibitor ratio is exceeded through the activity of several independent loci (Murfet, 1971; Weller *et al*., 1997). A fine balance exists though, and reversion can be observed in one specific genotype (lf E Sn). 'Transient flowering' occurs on grafting variants of this genotype. Flowering is followed to varying extents by reversion and then a subsequent stable floral state. The shifting promoter:inhibitor dynamics within the plant as, for example, the scion grows larger or the inhibitory potential decays as the plant ages could explain this result (Murfet, 1971). Partial induction has also been described in this species; 'bracteose malformed inflorescences' develop if the number of inductive cycles is suboptimal (Murfet, 1985).

Floral determination in vitro

If reversion is considered to result from a lack of determination (commitment) in meristem developmental fate (Huala and Sussex, 1993), evidence on the general character of the determination process is relevant to it. Determination can be tested through experiments involving propagation of the plant, bud, meristem or cell in question, away from conditions (or signal sources) that induce inflorescence or floral fate (Huala and Sussex, 1993). *In vitro* culture is preferable to grafting for meristem and cell studies because it allows complete isolation and thus some control on growth conditions, for example, number of leaves, hormonal type/level, and nutrient sources (McDaniel *et al*., 1992; Donnison and Francis, 1994).

Irish and Nelson (1991) have shown that the determination of inflorescence meristems can occur separately from that of flower primordia. *Zea mays* inflorescence meristems grown *in vitro* produced indeterminate vegetative structures with inflorescence phyllotaxy. Unless floral organ development had been initiated before isolation, meristems did not continue with normal flower (tassel) development. From this and related work it has become necessary to define a meristem by its phyllotaxy and other growth patterns and not the identity of organs it produces (Irish and Nelson, 1991; Huala and Sussex, 1993). For individual cells, determination can occur in a completely isolated meristem, in a meristem surrounded by a critical number of primordia, or outside the meristem (e.g. *Nicotiana* stem segments) (Singer and McDaniel, 1987; Ferguson *et al*., 1991; Irish and Nelson, 1991; Huala and Sussex, 1993).

These results indicate that determination can occur at plant, meristem, primordium, and cell (even non-meristem cell) level with different requirements for each type of organizational unit or plant species. This could account for the organ mosaics observed in *Impatiens* and *Arabidopsis* in response to environmental and genetic manipulation, respectively (Battey and Lyndon, 1984, 1988; Ng and Yanovsky, 2001).

In vitro work has led to the suggestion that, in environment-responsive plants, non-reversion could be a result of the plants' capacity to prevent flowering in weak inductive conditions (Donnison and Francis, 1994). In this case, plants only flower when a threshold amount of signal has been received by the meristem. The timing of this event has been determined through *in vitro* meristem culture experiments in *Lolium temulentum* (McDaniel *et al*., 1991). These authors reported that the amount of

signal affects flowering speed and extent of floral development in isolated meristems in a quantitative manner up to a saturation/optimum point (36 h in LD). Suboptimal signal levels do not result in reversion but rather slower flowering and abnormal flowers. In plants following this pattern, intact meristems flower after evocation and determination has been achieved so they do not revert when transferred to non-inductive conditions.

Work with *Silene coeli-rosa* (Donnison and Francis, 1994) suggests that there is another group of environment-responsive plants that do not normally revert, but do show reversion when the meristem is isolated from the plant. This observation is taken to indicate the continued need for signals from the whole plant for complete flowering. Floral determination occurs sequentially in the different whorls. Insufficient induction in these plants results in reversion after the last determined whorl. It has been suggested that intact meristems in these plants may not be permanently committed to flowering, but do not revert in non-inductive conditions because of a consistent supply of signals from the leaves.

In environment-neutral plants like *Nicotiana tabacum* and *Zea mays*, *in vitro* studies have shed light on the effect of age and node number on meristem phase change from juvenile to adult or vegetative to reproductive (Irish and Nelson, 1991; Irish and Jegla, 1997). The leaves act as a source of determination signal to the apical meristem and this signal is constantly necessary up to a certain stage. Meristems not receiving enough signal from the leaves or cultured too early will revert to juvenile (or vegetative) growth (Irish and Jegla, 1997).

Meristem developmental plasticity

Reversion requires of the plant a flexibility to switch from floral to vegetative or inflorescence development. In *Titanotrichum oldhamii*, floral meristems may appear identical up to the 'loaf' stage of meristem development, but have the capacity beyond this point to take on one of three fates; floral, bulbil cluster, or a proliferation of bracts. The latter two are a form of reversion from flowering which tends to occur at the end of the season (Wang and Cronk, 2003). How is this flexibility achieved? One explanation could be that a subset of cells in the meristem retains an undifferentiated or vegetative identity which is reasserted on reversion. Another is that cells which are initially assigned a floral fate regain the ability to become vegetative.

In the *Arabidopsis lfy-6* mutant (described earlier) *in situ* hybridization experiments, designed to analyse the origin of the ectopic shoot, reveal that cells of the meristem and even some of those in the growing ectopic shoot express the floral organ identity gene *AG*. This implies that cells that are initially floral are reprogrammed during reversion (Okamuro *et al*., 1996). This form of reprogramming may take place at a very subtle level. Hempel *et al*. (1997) have found that, although a plant may remain outwardly vegetative in appearance, it belies a 'flowering bias' detectable as a transient increase in the expression of *LFY* and *AGL8*.

In wild-type *Zea mays*, expression of *KNOTTED1* (*KN1*), a meristem-based gene is not detected during ovule development. *Zea mays ifa1* mutants suffer a loss of determinacy of all the usually determinate meristems (spikelet pair, spikelet, floral meristems) (Laudencia-Chingcuanco and Hake, 2002) and in these plants *KN1* expression reappears in a group of cells in the centre of the ovule. Thus meristematic fate appears to be regained at a molecular level.

Two models have been proposed for the reversion phenotypes of *Petunia* plants with engineered cosuppression of the MADS-box *SEPALLATA*-like gene, *FBP2* (Table 2), in which new inflorescences grow from the axils of carpels. In the first model, the lack of *FBP2* means that floral commitment is slow to become established and the floral transition is incomplete, with some cells retaining inflorescence identity. An alternative model is that a floral meristem forms but the lack of *FBP2* results in a flower in which the inflorescence character is not completely suppressed (Angenent *et al*., 1994). The latter model has similarities to the mode of action of *LFY* in suppressing *TFL1* and *AGL24* in *Arabidopsis*.

It is of note that *STMADS16*, a *Solanum tuberosum* MADS-box gene with a high degree of similarity to *AGL24*, appears to superimpose a vegetative programme onto a flowering plant. Whilst wild-type expression is confined to vegetative development, heterologous expression in *Nicotiana tabacum* results in phenotypic alterations to the flower, for example, longer internodes in the inflorescence, sepals replaced by leaves (Garcia-Morato *et al*., 2000).

A common theme to these molecular reports is that floral maintenance is achieved through repression of vegetative or inflorescence development, suggesting that these forms of development are a type of default pathway onto which flowering may be superimposed. Mutations in *ZFL1* and *ZFL2*, *LFY* homologues in *Zea mays*, can in older plants result in ectopic vegetative outgrowths from floral organs (Bomblies *et al*., 2003). This coexistence of vegetative and floral development is interpreted as a loss of an abrupt transition between the two phases of development. In *ifa1* mutants (see above), however, reversion is always to a distinct, specific and not mixed meristem type (Laudencia-Chingcuanco and Hake, 2002).

Function of flower and inflorescence reversion

Perenniality

One of the outstanding problems for plant developmental biologists is to provide a mechanistic account of life-history strategy. The regulation of individual developmental events, such as flowering, fruiting, and senescence is now relatively well-understood; so is the metabolic regulation that underpins day-to-day plant existence. But the

correlative controls that connect these two levels, and are so characteristic of plants (Woolhouse, 1983; Hensel *et al*., 1994; Noodén and Penney, 2001) are now ripe for renewed exploration. Viewed in this context, flowering of an individual meristem becomes part of a wider process, in which the fate of the whole plant is determined. In an annual such as *Arabidopsis*, flowering is irreversible, global, and leads to fruiting and plant death. The species is therefore monocarpic. Some ecotypes with a high vernalization requirement can behave as winter annuals, or biennials if spring-sown (Michaels and Amasino, 2000). Nevertheless, flowering still results in plant death. The majority of plant species, however, are perennial: flowering occurs locally and is associated with the senescence and death of only part of the individual (Battey and Tooke, 2002). Crucially, some meristems do not adopt a floral fate and therefore provide the basis for continued growth the next season. This polycarpic life-history requires global controls over meristem behaviour and organ development that are currently not well understood. Does reversion, allowing a return to the vegetative mode after flowering, have any relevance to life-history strategy?

There is little evidence that flower reversion has adaptive significance; it seems just to be a developmental abnormality. Inflorescence reversion, however, can provide a means for the individual axes of a plant to switch repeatedly between vegetative and reproductive development. An interesting example of this is the Ravenelle wallflower (Diomaiuto, 1988). Cold temperature (5 °C) is required for the first transition to flowering, and is also good for flower emergence. However, inflorescence reversion eventually takes place at this temperature and a second flowering phase will only occur after a period of at least 3 weeks at higher temperature (22 °C), followed by a return to cold conditions (5 °C). After studying this process for 5 years, Diomaiuto concluded that the cycling between vegetative and reproductive growth coincides with the warm and cold summer/winter conditions of temperate regions. Thus inflorescence reversion provides a mechanism for ensuring a polycarpic perennial life-history in this species.

In a similar way, individual shoots of the bottlebrush plant (*Callistemon*) revert to vegetative growth after the inflorescence phase, so that the form of the plant shows the history of successive flowering phases (Fig. 5). In another member of the Myrtaceae, *Metrosideros*, it has been proposed that the attainment of reproductive competence is a consequence of the tree reaching a certain degree of branching complexity (Clemens *et al*., 2002; Sismilich *et al*., 2003). Extreme branching complexity, however, leads to a reduction in the number of vegetative meristems and this threatens the capacity of the tree for further growth. In this situation, inflorescence reversion to vegetative growth occurs with increased frequency to generate new vegetative capacity (Sreekantan *et al*., 2001; J Clemens, personal communication). In this case, reversion emerges as an important mechanism for maintaining the balance between vegetative and reproductive development in the polycarpic perennial life-history strategy of the tree.

The crucial question in these examples of inflorescence reversion is: what is the nature of inflorescence identity? Is the inflorescence meristem different from the vegetative meristem in an important functional sense, in which case the (floral) fate of its axillary meristems would be a consequence of its altered developmental trajectory? Or is it just a meristem protected from adopting a floral fate? Based on studies with *Arabidopsis* (Bradley *et al*., 1997), *Lolium* (Jensen *et al*., 2001), and *Metrosideros* (Sreekantan *et al*., 2004), *TFL* is the obvious candidate for this protective role, and the mechanism for *TFL* suppression, without accompanying *LFY* up-regulation, then emerges as the key to inflorescence reversion.

Pseudovivipary

Flowering leads to sexual reproduction of the plant; yet in some cases this outcome to the flowering process is not inevitable and is under environmental control. Pseudovivipary is a form of inflorescence proliferation in which the flowering process is aborted and further development produces leafy shoots or bulbils. Pseudovivipary, therefore, provides an alternative means to reproduce. This asexual adaptation is particularly prominent in species growing in extreme environments. It is found in the recently glaciated areas of the Northern hemisphere and high latitudes in the Southern hemisphere (Moore and Doggett, 1976). Characteristics of the environments which favour pseudovivipary include high precipitation and humidity, strongly seasonal climates, high altitudes and latitudes (arctic, alpine), late-thawing habitats, or arid/semi-arid areas (Lee

Fig. 5. *Callistemon.* The inflorescence reverts to vegetative growth.

and Harmer, 1980; Molau, 1993; Elmqvist and Cox, 1996). Around 1.5% of tundra species can show pseudovivipary (Lee and Harmer, 1980; Walter, 1985) and in areas of Svalbard and the NW Queen Elizabeth Islands it is found in >10% of species (Lee and Harmer, 1980).

Species which show pseudovivipary are generally perennials and very often grasses, for example, *Festuca vivipara*, *Poa alpina vivipara*, *Deschampsia alpina* (Molau, 1993; Elmqvist and Cox, 1996). Late-flowering can also be a factor and may be a key to the developmental process and its advantages. In studying reproductive strategies of Tundra plants, Molau (1993) suggests that late-flowering makes time a limiting resource. Many mechanisms for outbreeding (e.g. reduced self-compatibility) are available to the time-unlimited early-flowering species, but such selection processes could be reduced for species in late-thawing habitats. These late-flowering plants take a seed-risking (selfing) rather than a pollen-risking (dispersal) strategy (Molau, 1993). Expanding this idea, vegetative reproduction, by means of reversion to leafy shoot production, could be viewed as further insurance of successful reproduction. As Latting (1972) suggests, pseudovivipary offers a means to cope with short growing seasons by allowing rapid plant establishment.

In developmental terms there are two main ways in which pseudovivipary occurs; proliferation may be achieved by lemma elongation to form the first leaf of the plantlet, as is the case in *Deschampsia*, or by transformation of the spikelet to a leafy shoot (*Festuca ovina*, *Poa alpina*, *Poa bulbosa*) (Moore and Doggett, 1976). A distinction can be drawn between proliferations giving rise to leaves after flowering spikelets (reversion) and those akin to 'vegetative inflorescences' (incomplete flowering) (Battey and Lyndon, 1990).

In grasses showing pseudoviviparous development it is induced by marginal LD induction, i.e. weakly inductive conditions (Heide, 1994). In some cases it has been assimilated as a heritable response, but it is not usually an irreversible pattern of development beyond environmental influence (Evans, 1964). Habitually pseudoviviparous grasses can be induced to flower (although flowering is not completely normal) given optimal inductive conditions (Heide, 1994). Since floral initiation can occur, meristem competence to respond to floral promotion appears to be established. Latting (1972) described pseudovivipary as, 'an expression of the shifting balance of factors controlling vegetative or floral development'. It is the promotion of the shift towards floral development which appears weak. There are similarities here with the reversion of *Impatiens balsamina*. Given optimal inductive conditions (continuous SD), *Impatiens* will flower and produce seed yet, even as it does so, the ability to proliferate is evident in the reiterative growth of the gynoecium. Abandoning flowering to produce a leafy shoot is the result of weak induction. Perhaps, as proposed for *Impatiens*, pseudoviviparous development is a feature of plants lacking sufficient genetic redundancy to commit the plant to flowering. Here, the vulnerability of floral development to environmental conditions ensures flowering always results in reproduction, either sexual or asexual.

Conclusions

The recent studies of flowering of *Arabidopsis thaliana* have been a guide to the principal components of the reversion process and have presented clear models of how floral maintenance might be achieved. Interestingly, reversion of *Arabidopsis* is never a complete return to vegetative development. The relative difficulty of obtaining reversion, and the residual floral characteristics when it does occur may be a consequence of the genetic redundancy in flowering pathways of this plant.

In this case, 'floral commitment' may just be a consequence of the stability conferred on flowering in *Arabidopsis*, a process that once started has many different routes to completion. The early establishment of 'commitment' in *Arabidopsis* (Bradley *et al*., 1997), and the utility of certain genes as markers for it (e.g. *AP1*, Hempel *et al*., 1997), do not constitute proof that it is a specifically regulated step. In fact, the single gene mutations in *Arabidopsis* giving rise to reversion to inflorescence development do so only when plants are grown in weakly-inductive SD conditions.

In *Impatiens balsamina*, genetic analysis of a red-flowered line which reverts to vegetative development, and a purple-flowered line which maintains flowering when removed from inductive conditions, suggests that a single gene controls these different responses. Evidence from *Impatiens* contributes to the continuing physiological question as to the site of regulation of floral commitment. In accordance with results from analysis of the maize *id1* mutant and certain *in vitro* studies, flowering in *Impatiens* appears to be controlled by a leaf-derived signal, operating in a quantitative manner to promote flowering. The striking reversion at the meristem when the supply of leaf signal is shut off is a consequence of the organization of flower development. Thus, both the flowering and reverting lines require the leaf-derived signal to complete flowering; the difference is that in the flowering line the production/transport of the signal does not depend on continued inductive conditions (Tooke *et al*., 1998; Hempel *et al*., 2000). *Impatiens* may lack the level of redundancy required for the commitment of the meristem which is present in *Arabidopsis*. The reverted meristem shows some significant floral characteristics: the leaves are in floral (whorled) phyllotaxy and lack axillary meristems. This suggests that the floral development programme fails at the stage of floral organ differentiation.

One difference between *Arabidopsis* and *Impatiens* is the expression pattern of *LFY* and its *Impatiens* homologue *IMP-LFY. IMP-LFY* is not up-regulated during flowering and the expression level remains constant through vegetative growth,

flowering, and reversion. This low level of expression may be insufficient either to activate or to repress the *Impatiens* homologues of *AG* or *AGL24*. The examples above demonstrate that these genes have a role in floral meristem determinacy in *Arabidopsis*, and that a low level of *LFY* expression is key to a number of the instances of reversion.

The final stage of floral determinacy, conferred by *AG*, may also be a factor in the reiteration of growth from the gynoecium in *Impatiens*. The limited expression of *IMP-LFY*, and possibly the *Impatiens AG* homologue, may in part be responsible for the plasticity of floral formula in the terminal flower. The leaf-derived signal would then be required to act in promoting flowering in the absence of the decisive control by *IMP-LFY*.

The genetic mechanisms underlying floral maintenance show a close association with environmental factors. Their vulnerability to weakly-inductive conditions or their mutation can lead to strikingly anomalous flowering. These characteristics appear to be able to attune reproductive habit to ecological niche, allowing prominence of vegetative development over floral. In this way meristems can be conserved for a perennial lifecycle or for reproduction by asexual means rather than by seed.

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