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Carpeloidy in flower evolution and diversification: a comparative study in Carica papaya and Arabidopsis thaliana

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INTRODUCTION

Flowers are the result of evolutionary innovations, which include bisexuality and determinate flower meristems. The origin of bisexuality from ancestors with indeterminate and unisexual axes of male or female structures relies on the location on the same flower axis of stamen and carpel structures. Determinate flowers result through internode compaction and production of a reduced and fixed number of reproductive organs (Bateman et al., 2006; Baum and Hileman, 2006).

One of the possible scenarios for the separation of stamen from carpel zones in compacted hermaphrodite flowers required the early specification of stamen and carpel identities by developmental homeostasis. The process may be a fundamental aspect of flower development that is hidden in most instances by developmental homeostasis.

Key words: Arabidopsis, Carica papaya, bisexual flowers, carpeloidy, ectopic ovules, evo-devo, feminization, floral development, sex conversion, sup1 mutants.

Background and Aims Bisexual flowers of Carica papaya range from highly regular flowers to morphs with various fusions of stamens to the ovary. Arabidopsis thaliana sup1 mutants have carpels replaced by chimeric carpel–stamen structures. Comparative analysis of stamen to carpel conversions in the two different plant systems was used to understand the stage and origin of carpeloidy when derived from stamen tissues, and consequently to understand how carpeloidy contributes to innovations in flower evolution.

Methods Floral development of bisexual flowers of Carica was studied by scanning electron microscopy and was compared with teratological sup mutants of A. thaliana.

Key Results In Carica development of bisexual flowers was similar to wild (unisexual) forms up to locule initiation. Feminization ranges from fusion of stamen tissue to the gynoecium to complete carpeloidy of antepetalous stamens. In A. thaliana, partial stamen feminization occurs exclusively at the flower apex, with normal stamens forming at the periphery. Such transformations take place relatively late in development, indicating strong developmental plasticity of most stamen tissues. These results are compared with evo-devo theories on flower bisexuality, as derived from unisexual ancestors. The Arabidopsis data highlight possible early evolutionary events in the acquisition of bisexuality by a patchy transformation of stamen parts into female parts linked to a flower axis-position effect. The Carica results highlight tissue-fusion mechanisms in angiosperms leading to carpeloidy once bisexual flowers have evolved.

Conclusions We show two different developmental routes leading to stamen to carpel conversions by late re-specification. The process may be a fundamental aspect of flower development that is hidden in most instances by developmental homeostasis.

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Inflorescence buds were dissected under a Wild MZ8 stereomicroscope (Leica, Wetzlar, Germany), dehydrated in an absolute ethanol–acetone series, and critical point dried with a K850 Critical Point Dryer (Emitech Ltd, Ashford, UK). Material was coated with platinum using a K575X sputter coater (Emitech Ltd) and observed with a Supra 55VP scanning electron microscope (LEO Electron Microscopy Ltd, Cambridge, UK).

For Arabidopsis, flower samples were mounted on slides covered with double-sided adhesive tape and photographed with a Leica MZ TLIII binocular system.

RESULTS

Floral development in staminate and pistillate Carica flowers

Ronse De Craene and Smets (1999) described the floral development of staminate and pistillate Carica. Early stages of flowers including the development of petals was highly similar between pistillate and staminate flowers. Subsequently, differences were found in the absence of the androecium in pistillate flowers, while pistillate flowers had massive ovaries with subequal carpellary lobes and strongly developed intruding parietal placenta. In staminate flowers two stamen whorls surround a central residual area which develops into a spear-like organ that Ronse De Craene and Smets (1999) interpreted as a pistillode. These elements constitute the reference system in the analysis of bisexual flowers below.

Flower development in Carica perfect bisexual flowers

Flowers are enclosed by a bract and two bracteoles. Five sepals are rapidly initiated in a 2/5 sequence starting on the abaxial side next to the bract (Fig. 1A, D). The sepals grow into massive subequall lobes enclosing the bud in a quincuncial aestivation. The five petal lobes arise almost simultaneously and undergo strongly contorted growth by unequal development (Fig. 1B, C). Petals develop into highly asymmetric organs with an inner section intruding between the developing stamens and an outer layer enveloping a neighboring inner invagination of an adjacent petal (Fig. 1C). Stamens initiate immediately following common basal growth below the petals. They develop on the periphery of a flattened apex. Initiation of anteseopal stamens proceeds the antepetalal stamens, but often stamens on the abaxial side of the flower arise before those on the adaxial side (Fig. 1E, F). The androecium is diplostemonous with the anteseopal stamens overlapping the antepetalal stamens (Fig. 1F, H). This is caused by the continuing growth of a common primordium lifting stamens and petals into a tube (Figs 1F, H). This two-tiered arrangement of the stamens is maintained and developing stamens form a long tube around the developing ovary. In later stages hairy filaments are produced leading to erect tetrasporangiate stamens (Fig. 3A–C). The central apical area differentiates into a bulging pentagon and five carpellary lobes develop simultaneously on the periphery (Figs 1G and 2A). They grow upwards as five carpels around a central residue (Fig. 2B, C). Carpels often have an unequal shape or develop irregularly (Fig. 2B–D). While a
common lower tube leads to a saccate ovary, the carpellary lobes remain apically separate and develop into stylar lobes (Figs 2D and 3A). A characteristic shape resembling antlers is finally achieved at maturity. Compared with unisexual flowers of Carica, the ovary of a bisexual flower resembles an elongated pear.
Stamen feminization in Carica flowers occurs through invasive stamen–carpel fusion

We now compare the development of perfect bisexual flowers with floral material from the same cultivar showing highly variable flowers, ranging from fully hermaphrodite morphs to strongly altered teratological flowers.

In a large number of cases (45% of 30 nearly mature flowers investigated), flowers depart from the wild-type situation by being much more distorted, showing a range of transitional morphologies between ovary and stamens. Distortions appear at the time of carpellary locule differentiation by the invagination of antepetalous stamens into the carpellary

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**Fig. 2.** Differentiation of organs in bisexual Carica papaya without (A–D) and with (E–H) carpel–stamen fusion. (A) Initiation of five carpels on apical meristem; all stamens removed. (B) Lateral view of differentiation of peripheral carpels. (C) Apical view of development of carpellary locules; antesepalous stamens removed. (D) Development of stigmatic lobes on top of ovary; note the tube with fused petals and stamens surrounding the ovary. (E,F) Apical and lateral view of two buds at differentiation of carpellary locules. Note scars of antepetalous stamen invading carpel zone (arrows). (G,H) Two views of abnormal buds showing invading antepetalous stamens fused with ovary (arrow). Note hybrid fused stamen–carpels and the development of normal filaments of antesepalous stamens.

Abbreviations: Ap, antepetalous stamen; As, antesepalous stamen; C, carpel or stigmatic lobe. Scale bars = 100 µm.
FIG. 3. Carpeloidy in preanthetic buds of *Carica papaya*. (A) Lateral view of partly dissected perfect bisexual flower showing elongated ovary and two levels of stamens. (B) Lateral view of similar stage but with incompletely developed ovary showing fusion scar on one side (arrow). Similar pistillodes are typical for wild-type male flowers. (C) Lateral view of abnormal bud with extensive fusion between aberrant antepetalous stamens and ovary. Note stigmatic-shaped appendages on antepetalous stamens. (D) Apical view of flower with partly feminized antepetalous stamens fused to carpellar tissue. (E) Transverse section through composite ovary–stamen structure. Note the extensive fusion of carpellar and stamen tissue. (F) Lateral view of compound ovary–stamen structure with no evidence of staminal tissue. Arrow points to carpel slit. (G) Lateral view of two stamens; the left with extralocular ovules; the right with normal anther removed. (H,I) Lateral views of feminized stamens. In H note basal ovules and apical remnants of anthers (arrow); in I note lower ovules and higher stigmatic tissue (arrow). Abbreviations: Ap, antepetalous stamen; As, antesepalous stamen; C, carpel or stigmatic lobe. Scale bars: (A, C, D, F) = 100 μm; (B, E, G, H, I) = 200 μm.
This invasion occurs by sideways concrescence of ovary and antepetalous stamens (Fig. 2E–G) and corresponds to an invasion of stamen-origin tissue into the confines of the ovary (Fig. 4A–G). This was visible during development as a postgenital fusion of young stamens with the developing carpels (Fig. 2E, F). Fusion of stamens with the ovary appears to different degrees; sometimes one side of the flower produces anthers, while the other side becomes completely transformed by fusions with no clear anthers visible (Figs 2H and 3D). The ovary can also appear underdeveloped without clear stigmatic lobes, although ovule primordia are visible (Fig. 3B). In other cases, concrescence is almost complete without evidence of anther tissue (Figs 3C–F and 4D, E, G–I). While antepetalous stamens are fused with the ovary, the antesepalous stamens remain free and produce filaments (Figs 2H, 3C–E and 4D). The fusion of antepetalous stamens is accompanied by a transformation of anthers into plate-like stigmatic lobes (Figs 2G, H, 3C–D, F and 4G–J). In some cases monstrosities arise with slit-like holes (Fig. 3D, F, arrows), hybrid organs with external stylar tissue and anthers (Figs 3D, I and 4B, C, G) or ovule-producing appendages with remnants of sterile anthers (Fig. 3G–I). In most cases fusion was unequal as one or more stamens could be left out (Fig. 4D, G, J). In only a few cases did we find flowers corresponding to the pentandria type with an equal fusion of antepetalous stamens to the ovary apparently producing outwardly bulging carpels (Figs 3E and 4E).

Hand-sectioned flowers with such bulging carpels showed that stamen–carpel fusions must have occurred in most cases between the margins of developing primary carpels and the adaxial epidermis of the filaments (Figs 2C, E–H, 3B and 4A–C). As a result the feminized stamens alternate with true carpels at the exterior of the central carpellary locule (Fig. 3C, E). In addition, connective and/or anther tissues can take part in the fusion process (Figs 2G, H and 4A–C), with, for example, tissue proliferation occurring from the anther interlocular space (Fig. 4C). In fully feminized fused stamens no trace of anther tissue is visible and circular cavities filled with ovules were produced centrally, representing miniature locular cavities around the central ovary and a dorsal vascular bundle in a similar position as normal carpels (Fig. 4D–F).

In conclusion, the results show that early stages of development were found to be highly conservative and similar to dioecious C. papaya, indicating that the developmental alterations commence after organ initiation, with stamens switching their developmental fate during morphogenesis. Despite the relatively variable occurrence of carpeloidy, we define the critical stage as locule differentiation in antepetalous stamens.

### DISCUSSION

This comparative study of carpeloidy in two plant species shows distinct developmental mechanisms which result in stamen–carpel conversions: (1) stamen feminization through antepetalous stamen–carpel fusion in Carica and (2) stamen feminization exclusively at the flower meristem centre in Arabidopsis, with stamens at the periphery of the meristem being wild-type. In the two species, such transformations mediated through apparently distinct cellular processes occurred at relatively late stages of stamen development, indicating strong developmental plasticity of various stamen tissues towards acquisition of female traits, including ovule formation.

In Carica, our observations on hermaphrodite flower development showed no clear-cut differences from wild morphs (see Ronse De Craene and Smets, 1999) until after stamen initiation, indicating that feminization is not linked to homeosis. In subsequent stages, hermaphrodite flower meristems and buds apparently lack space, as the basal common zone surrounding the pistillode in staminate flowers is less constricted compared with hermaphrodite flowers where the ovary bulges.
up and occupies the limited space. Compared with wild pistillate *Carica* flowers, the initiation of carpels in hermaphrodite flowers is irregular with different sizes of carpel primordia. This and the intruding, invasive growth of the stamens during differentiation suggest that tissue pressure in a closed space favours fusion of inner antepetalous stamens and

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**Fig. 4.** Carpelloidy in preanthetic buds of *Carica papaya* (cont.). (A–C) Lateral views of bisexual flowers with variable stamen–carpel fusions showing the role played by the adaxial side of stamen filaments in the process (A, B; black arrows). Connective cells are also involved, the result being aberrantly shaped anthers with associated invading tissue growth (B, C; white arrows). (D–F) Transverse sections of entirely feminized stamens fused to the gynoecium. The corresponding carpeloid structures appear as regular locules alternating with the genuine carpels and bear apparently normal ovules. The lobes and cavity of the genuine ovary can be seen in the centre (D, E). In D four feminized stamens are fused to the ovary. Arrows point to dorsal vascular bundles. (E) Slightly older bud showing the secondary locules and central ovary with ovules. (F) Detail of secondary locule of D. (G) Top view of partly sectioned ovary with feminized stamens. Partly fused aberrant stamen bearing stigmatic tissue is visible at top (arrow); the remaining stamens are indistinguishable from carpellar tissue and bear stigmatic papillae. (H, I) Lateral and top views of entirely feminized stamens fused to the gynoecium. In I incomplete fusion and transformation of two antepetalous stamens.

Abbreviations: Ap, antepetalous stamen; As, antesepalous stamen; St, stigmatic lobe. Scale bars: (A–E, H, I) = 1 mm; (F, G) = 200 μm.
FIG. 5. Carpeloidy in the Arabidopsis sup1 mutant. (A) Lateral view of a wild-type flower with sepals and petals removed. Five of six stamens and one valve, style and stigma are visible. (B) sup1 mutant flower with sepals and petals removed. Most stamens are wild-type and have liberated their pollen. Two stamens with enlarged connective (arrows) tissue, indicating weak feminization. A carpelloid structure has formed with narrow base and style and stigma. (C–L) All stamens shown were located at the flower centre, the remainder have been removed, with scars and nectaries visible on the flower bud dome. The pollen sacs, when present, are yellow or brownish. The common trends in feminized stamens are filament fasciation, connective tissue expansion, anther reduction, and production of ectopic ovules and/or stigmatic tissues. (C) Two stamens with weak feminization phenotypes. To the right, the stamen with a compact filament is topped by stigmatic tissue. The connective tissue has expanded. To the left, only one pollen sac is recognizable, two ovules and stigmatic papillae being produced. (D) Two stamens viewed from adaxial (D1) and abaxial (D2) sides. (D1) The stamen at the left has a medium-to-strongly feminized phenotype, lacks pollen sacs and is terminated by a compact green anther-like region topped with stigmatic tissue and one ovule-like structure. The stamen at the right has a weak feminized phenotype, producing stigmatic papillae at its top. The pollen sacs are reduced in size. (D2) The distal abaxial region of the two stamens is greenish and corresponds to a hypertrophied carpelloid connective tissue. (E) Two stamens, a weakly feminized to the right (producing one ovule on the filament) and a medium feminized to the left, producing a row of ovules along the expended connective tissue and the filament. Only one pollen sac is recognizable (asymmetric feminization); one theca has dedifferentiated. (F) A strongly feminized stamen with hypertrophied filament. The distal connective tissue has formed, and as an extension, a long and narrow carpelloid structure topped with stigmatic papillae. Two reduced brownish split thecae (aborted pollen sacs) with green carpelloid and stigmatic expansions are visible at the transition region between the filament and the central stigmatoid structure. (G) A strongly feminized stamen viewed from its adaxial (G1) and abaxial (G2) sides. (G1) The hypertrophied filament and connective tissue are producing rows of ovules and green carpelloid tissues topped with stigmatic papillae at distinct positions. The pollen sacs are reduced in number. The structure is fused at its base with a neighbouring curling stamen. (G2) The abaxial side shows the hypertrophied filament extending into a club-shaped valve structure. (H) A strongly feminized stamen with very compact and expanded filament and hypertrophied connective with two rows of ovules along the vasculature and the two narrow-sized pollen sacs undergoing dedifferentiation (as indicated by tissue colour at lateral positions, the latter being ‘resorbed’). (I–L) Details of stamen feminization. (I) A stamen with weak feminization phenotype producing two ovules with typical sup morphology located at the base of the anther and at the distal part of the filament. (J) A medium feminized stamen with hypertrophied filament and extended connective tissue forming a laminar structure topped with stigmatic papillae. Two reduced thecae with ectopic ovules at their base. Pollen sacs are reduced in number and size. (K) A medium feminized stamen with expanded greenish connective tissue topped with stigmatic papillae. Reduced abortive pollen sacs are present on both sides. (L) A medium feminized stamen with expended filament, vasculature and connective. Two rows of ovules are formed along the vasculature. The theca on the left is reduced and may undergo dedifferentiation. Scale bars = 125 μm.
carpels, with a transformation of the former into carpels as a result (also see Sieber et al., 2000 and below).

This fusion is variable and gradual, with identities of antepetalous stamens occasionally maintained on one side of the flower or with a complete transformation and immersion of stamens into carpellary tissue. The various degrees of carpeloidy we observed were variably associated with remaining male attributes, such as small sterile anthers. In this respect, Lassoudière (1969) distinguished, as we describe in detail here, (1) cases with hypertrophied filaments (i.e. fasciation) and more or less developed anthers, (2) cases with the development of a carpellary cavity by the curvature of the filament bearing a terminal anther and (3) cases with flowers with complete absorption of stamens into the ovary tissues. The last appeared as small-scale carpels with a dorsal vascular bundle in a similar position to that of normal carpels (Fig. 4D). Various authors have concentrated on these different types, as they determine the shape of fruits produced, which is of commercial significance (e.g. Storey, 1958, 1969).

The precise nature of carpeloidy at the cellular level in Carica remains to be analysed. The conversion process occurs rapidly upon stamen–carpel contact and is complete most of the time, i.e. all stamen tissues undergo feminization. The genetic nature of carpeloidy in Carica remains to be understood, possibly within the framework of the genetic system for sex determination, which rests on five pairs of sex-determining genes in the sixth chromosome (Purseglow, 1968). Interestingly, Ackerman et al. (2008) have investigated the differential expression profile of three B-class genes in the triocious papaya (bearing male, female and hermaphrodite flowers), suggesting that B-class genes are the main targets of the sex-determination system. Their and our study combined could stimulate further work on the role of B-class genes – extended to C-class and SUP genes – in the development of carpeloidy in Carica at specific stages and in tissues undergoing fusion.

Postgenital organ fusions have been investigated in a number of species and show that (1) fused organs, organ deformations and protrusions of epidermal cells developed at positions with high mechanical compression, (2) an intact cutin layer prevented fusions between different plant organs and was therefore necessary for normal epidermal differentiation and organ formation, and (3) the junctions of the fusions contained pectic polysaccharides (Sieber et al., 2000) and that diffusible factors were involved (Siegel and Verbeke, 1989). Furthermore, analysis of the genetic bases of the process has made much progress in identifying several of the genes involved in Arabidopsis (Lolle et al., 1998; Pruitt et al., 2000; Krolilok et al., 2003).

In Arabidopsis, we show that carpeloidy in sup1 stamens also arises during stamen development. The transformed structures have an overall stamen morphology, indicating that they had been initiated as stamens (and have genuine stamen identity) and maintain a recognizable stamen organization plan. Female attributes were generated on or from recognizable stamen tissues, namely connective, filament and anther apical region, and, more rarely, from micro-sporangial tissues, which all can exhibit a hypertrophied growth. None of these mosaic morphologies seems to result from stamen–carpel postgenital fusions, because early carpel parts, such as valves, have been only occasionally observed in our analysis in the strongly feminized phenotypes. Instead, stigmatic and ovule tissues, which differentiate latest during gynoecium morphogenesis, were formed directly and independently on stamen parts. Furthermore, the feminized structures undergoing such alterations were frequently symmetrical, which should not be the case in random fusions. In addition, the fact that SUP has been reported as being expressed in developing stamen (primordium, connective) and carpel (septum, ovules) tissues (Ito et al., 2003; Breuil-Broyer et al., 2004) may have significant relevance to these results for the understanding of carpeloidy in this species. We show that the mutation of this gene confers female attributes to stamen parts through filament fasciation, connective hypertrophy and anther reduction. Of note here, Warner et al. (2009) have shown by experimental manipulations of waterlily flowers that sepal and petal fates can switch very late in development and argue that sepalness and petalness in angiosperm history were not fixed to particular organs, but were primarily environmentally controlled.

The precise nature of carpeloidy at the cellular level in Arabidopsis remains to be understood, the conversion process occurring fast and being partial in sup1 mutants. The most spectacular and challenging issue is to analyse the conversion of the tissues close to the vascular strand along the filament and in the connective into regular ovule-producing tissues (placental?) and/or valve-like structures. Of note here, the results with petunia phsup1 mutant flowers in which feminized stamens exhibited excess proliferation of connective tissues around the vascular bundle (Nakagawa et al., 2004).

Carpeloidy occurs in other Arabidopsis genetic backgrounds, such as the B-class gene mutations, which transform stamens into carpels, but – at the same time – transform petals into sepals in the majority of analysed alleles (Bowman et al., 1991; Krizek and Meyerowitz, 1996). We have concentrated our study on sup1, because the organ transformations associated with this mutation only affect the stamen–carpel balance. However, in both cases, B-class and SUP mutations participate in the same developmental process: acquisition of stamen and carpel identities in contingent territories via the expression of both appropriate combinations and/or concentrations of MADS-box transcription factors and of the male–female boundary factor, SUP (Bowman et al., 1992; Sakai et al., 2000).

Such considerations might be meaningful in the context of sup1 mutants undergoing carpeloidy at the floral meristem centre only. Altering SUP function appears to modify B-class gene activity at the floral meristem centre, which might interfere with female factors known to operate in that region, such as CRC, STK or SHP (Girin et al., 2009; Prunet et al., 2009), to name just a few. Work with the petunia phsup1 mutant showing that all stamens undergo weak feminization (Nakagawa et al., 2004) suggests that an altered class-B/C factor balance might suffice to provoke carpeloidy. This appears to be the case with alloplasmic lines of bread wheat exhibiting both carpeloidy and alteration of B-class gene expression (Hama et al., 2004).

In summary, the two species produce stamen-to-carpel transformations within defined genetic backgrounds. While in the bisexual Carica organ fusions represent the mechanism
underlying the sexual conversion, in the Arabidopsis sup1 context this process resulted from the formation of various female attributes directly on stamen parts. In both species, stamen filaments and connective tissues were the most responsive to feminization. In Carica, the ovules were formed, most of the time in locules along the vasculature, with ectopic ovules on the outside of transformed stamens also being observed. In Arabidopsis, the ovules were formed on the connective of or close to where the filament meets the connective tissue. More globally, the stamen developmental plasticity in the two plant systems appeared remarkably strong during organ differentiation.

Evo-devo implications

The results can now be placed within evo-devo scenarios of the derivation of flower bisexuality. The mostly male theory (MMT) predicts that the angiosperm flower is derived from the male reproductive structures of an ancestor, on which stamen–carpel fusions in the Carica system do not seem to directly contribute to the issue of the origin of bisexuality because they imply the pre-existence of bisexual flower meristems with compact internodes and whorls, enabling contact between stamen and carpel organs initiated at proximity and in a quite synchronous manner. However, the comparison of the Carica and Arabidopsis systems enabled us to identify common trends in stamen developmental plasticity, and in particular how ovules could form on stamen parts.

In contrast, the formation of ectopic ovules and stigma–style structures on developing stamens in Arabidopsis is highly relevant to the MMT because it implies that stamens have, in the absence of SUP, an intrinsic potential to sexual conversion and bisexuality in the absence of physical contacts with pre-existing female tissues. This indicates that somatic tissues of the A. thaliana stamen can switch developmental programmes locally and relatively late in development. The fact that such conversions occur at the flower meristem summit only, i.e. in the presumptive female domain, allows us to speculate that female factors mainly controlling ovule and style–stigma formation could have been specifically expressed in organs produced in that region of an ancestral male flower axis, with as a consequence the ectopic formation of female parts on bona fide male tissues.

In conclusion, our results show that carpeloidy has been expressed in different ways for morphological diversification during flower and fruit evolution. The Carica results highlight mechanisms that allow direct resource reallocation (for general trends see Wright and Meagher, 2003; Knight et al., 2006, and references therein) between male and female organs through (partial) sex conversion once bisexual flowers have evolved. The Arabidopsis results highlight possible early evolutionary events in the acquisition of bisexuality by transformation of stamen parts into female parts during stamen morphogenesis as a flower axis–position effect, i.e. in the distal region of the flower axis only. This process appears to support the basic claims of the MMT by a change in the expression of female differentiation factors within a male flower axis and on male organ structures. This differs from a reproductive organ identity switch during the initiation stage, i.e. a homeotic transformation, as claimed by the OOM theory.

Obviously, such bisexual organs were inefficient in nature in the short run and the formation of a fully functional bisexual flower would have required further optimizations. A better delimitation of the male–female boundary linked to more compact and determinate flower structures (Baum and Hileman, 2006; Solitis et al., 2007, and references therein) appears as a likely sequence of evolutionary events. We have shown that developmental plasticity during organ formation can circumvent such a sexual boundary constraint.

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LITERATURE CITED


