Stability of the floral structure in Leguminosae with flag versus non-flag blossom

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Summary: This work is dedicated to the problem of natural variability of flowers with different types of symmetry. We focus on a comparative study of floral merism in Leguminosae with mono- and polysymmetric flowers. With few exceptions, most of the analyzed species exhibit a certain level of variation. Generally, monosymmetric flowers appear more stable than polysymmetric; variability of monosymmetric flowers with three types of petals (flag blossom) is lower than in monosymmetric flowers with two types of petals. Adaxial structures are more constant than abaxial ones, and no fluctuations are found in gynoecium morphology in pentamerous and pentacyclic leguminous flowers. We discuss these phenomena in light of the existing concept of genetic control of floral symmetry.

The variability, a basic capacity of living things to change, is the main factor which makes them subject to natural selection. Because of this, some variants appear inadaptive and become eliminated, while others are found either bringing more benefits or having the same adaptive potential as previously existing ones.

Compared to animals, ontogeny of plants is very flexible with many inducible shifts and numerous switches between different developmental trajectories. In most cases, the exact number of serially homologous structures (lateral roots, leaflets in compound leaf, flowers per inflorescence, petals in corolla, ovules in carpel, etc.) is of little or no significance. As a result, the morphology which is considered 'normal' comprises a range of variation rather than a certain set of exact numbers and values. Although these numbers and values are under genetic control (and hence under pressure of selection), a significant degree of variation independent from the genotype, often within the same individual, can be observed.

Possibly, the only example of structure which requires the *exact* number of counterparts in plants is the monosymmetric (zygomorphic) flower, where all elements interact in a special way. Any fluctuations in morphology of such flower are inadaptive, so the risk of such fluctuations needs to be diminished.

The phenomenon of meristic changes in floral morphology has been known for long and different interpretations of it exist (Ronse De Craene 2016). Genetic control of floral zygomorphy was precisely dissected in a model species, *Antirrhinum majus* L. (Plantaginaceae; Almeida et al. 1997) and seems more or less conserved in angiosperms (Preston & Hileman 2009). Some mutations affecting size of floral meristem (FM) may cause changes in merism even in a monosymmetric flower (Sinjushin 2016). However, degree of natural variability in flowers with different types of symmetry in wild-type plants requires deeper examination. To characterize merism variations in dependence on floral symmetry, we focused on legumes (Leguminosae = Fabaceae s.l.), the family displaying an outstanding diversity of floral structure. The basic type of the leguminous flower
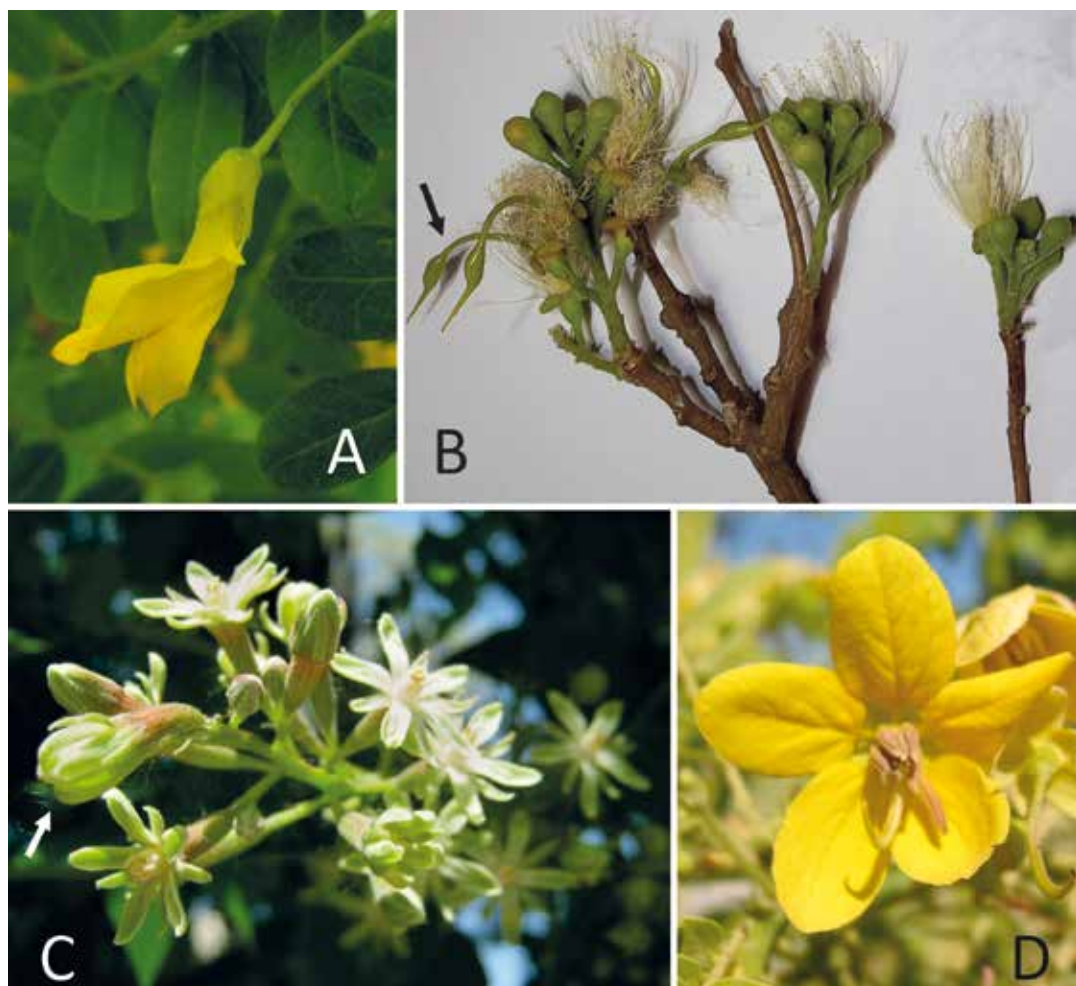
Figure 1. Some of species examined. A – *Caragana arborescens*; B – *Cordyla pinnata* (arrow = carpel on long gynophore); C – *Gymnocladus dioicus* (arrow = terminal flower); D – *Senna surattensis*.

is pentamerous and pentacyclic, so we attempted to reveal degrees and patterns of variability of flower structure in legumes with distinct floral morphology.

Materials and methods

Plant material (flowers and floral buds) was collected from 11 legume species (Table 1) representing diverse floral structures (Fig. 1). In all cases, we gathered every certain sample from a single individual plant to minimize intraspecific genetic differences. Only of a few species we investigated several samples from different individuals or localities. A minimum of 100 flowers were examined in most samples, either freshly collected or preserved in 70% ethanol. All statistical treatment was carried out using Microsoft Excel (Microsoft Inc.) and Statistica 7 (Statsoft Inc.).

Results

Variations in organ number

Only three of fifteen samples appeared fully uniform (Table 2), viz. *Caragana*, *Lupinus* and one sample of *Styphnolobium*. Other species exhibited a certain degree of variation of some or all

Table 1. List of species used for survey.

Species	Subfamily (sensu LPWG 2017): clade (sensu Bruneau et al. 2001; Cardoso et al. 2013)	Locality
Gleditsia triacanthos L.	Caesalpinoideae: Caesalpinieae	Botanical Garden of the Southern Federal University, Rostov-on-Don
Gymnocladus dioicus (L.) K. Koch	Caesalpinoideae: Caesalpinieae	Botanical Garden of the Lomonosov Moscow State University
Senna surattensis (Burm. f.) H. Irwin & Barneby	Caesalpinioideae: Cassieae	Egypt (ornamental)
Cercis canadensis L.	Cercidoideae: Cercideae	Botanical Garden of the Southern Federal University, Rostov-on-Don
Cordyla pinnata (A. Rich.) Milne-Redh.	Papilionoideae: Amburaneae	Parc national du Mali, Bamako, Mali
Styphnolobium japonicum (L.) Schott	Papilionoideae: *Cladrastis* clade	Truskavets, W Ukraine (ornamental); Botanical Garden of the Southern Federal University, Rostov-on-Don
Amorpha fruticosa L.	Papilionoideae: Amorpheae	Botanical Garden of the Southern Federal University, Rostov-on-Don
Caragana arborescens Lam.	Papilionoideae: Hedysareae	Moscow city (ornamental)
Galega orientalis Lam.	Papilionoideae: Inverted Repeat Lacking-Clade	Dubki, Odintsovo district, W Moscow Region
Lathyrus pratensis L.	Papilionoideae: Fabeae	S.N. Skadovskii Zvenigorod Biological Station, Odintsovo district, W Moscow Region
Lupinus polyphyllus Lindl.	Papilionoideae: Genisteae	

floral whorls (Fig. 2). Table 2 indicates that coefficients of variation (C.V.) of overall floral organ numbers are unequal in different species.

Patterns of variation in organ numbers appear almost similar in all studied species:

I) calyx is less stable than corolla;

II) androecium, either outer or inner whorl, is the least stable domain in flower;

III) gynoecium is invariable in all species with pentacyclic flowers.

Notably, there are three types of structures which were (almost) never found unstable in number, viz. two adaxial sepals (Fig. 2A, B), adaxial petal and carpel. We recorded only one flower of *Amorpha* with two petals which, however, might result from a fusion of two independent FMs. Carpel was always single and properly oriented in all cases except for *Cordyla*. We included this unusual plant in our investigations although its flowers are not pentamerous and pentacyclic comparing with the other studied species.

Sometimes, organs appeared anomalously fused (Fig. 2D, E). When two (or more) structures were discernible (e.g. basing on venation pattern), they were counted as separate units.

One of the factors contributing to floral (in)stability may be the genotype of a certain individual or influence of a certain environment. This may explain the contrasting results of counts in flowers of *Styphnolobium japonicum* in two localities (Table 2).

Table 2. Variation of floral organ number in selected species. ✳ polysymmetric, ↓ monosymmetric, ◎ spiral arrangement. The overall C.V. of number of floral organs is given in bold italics in cells with species name. This parameter was calculated only for species with full set of organs in the pentacyclic flower.

Species (no. of examined flowers)	Organ number (min – *mode* – max; C.V. in parentheses)				
	Sepals	Petals	Outer stamens	Inner stamens	Carpels
Gleditsia triacanthos male, tree 1 (n = 109)	✳ 2 – *3* – 5 (21.93%)	✳ 2 – *3* – 5 (21.59%)	–	–	–
G. triacanthos male, tree 2 (n = 105)	✳ 1 – *3* – 6 (32.14%)	✳ 2 – *3* – 5 (21.84%)	✳ 1 – *3* – 5 (22.27%)	✳ 1 – *3* – 5 (33.50%)	–
G. triacanthos hermaphrodite (n = 103) **15.27%**	✳ 2 – *3* – 5 (24.80%)	✳ 2 – *4* – 5 (19.24%)	✳ 1 – *3* – 5 (32.76%)	✳ 1 – *3* – 5 (31.56%)	1 – *1* – 1 (0.00%)
Gymnocladus dioicus hermaphrodite (n = 24) **3.63%**	✳ 4 – *5* – 6 (7.11%)	✳ 5 – *5* – 6 (6.59%)	✳ 5 – *5* – 6 (5.55%)	✳ 5 – *5* – 6 (7.97%)	1 – *1* – 1 (0.00%)
G. dioicus male (n = 159)	✳ 3 – *5* – 6 (9.34%)	✳ 4 – *5* – 7 (6.94%)	✳ 4 – *5* – 6 (6.13%)	✳ 4 – *5* – 6 (6.57%)	–
Senna surattensis (n = 44) **2.40%**	◎ 5 – *5* – 5 (0.00%)	◎ 5 – *5* – 6 (3.00%)	✳ 5 – *5* – 7 (7.11%)	✳ 5 – *5* – 5 (0.00%)	1 – *1* – 1 (0.00%)
Cercis canadensis (n = 203) **1.96%**	↓ 5 – *5* – 6 (3.11%)	↓ 5 – *5* – 5 (0.00%)	↓ 5 – *5* – 5 (0.00%)	↓ 5 – *5* – 5 (0.00%)	1 – *1* – 1 (0.00%)
Cordyla pinnata (n = 23)	–	–	✳ 86 – *107* – 114 (7.01%)		1 – *1* – 2 (33.95%)
Styphnolobium japonicum Truskavets (n = 75) **5.58%**	↓ 5 – *5* – 5 (0.00%)	↓ 4 – *5* – 7 (8.26%)	↓ 5 – *5* – 7 (12.05%)	↓ 5 – *5* – 7 (9.67%)	1 – *1* – 1 (0.00%)
S. japonicum Rostov (n = 145) **0.00%**	↓ 5 – *5* – 5 (0.00%)	↓ 5 – *5* – 5 (0.00%)	↓ 5 – *5* – 5 (0.00%)	↓ 5 – *5* – 5 (0.00%)	1 – *1* – 1 (0.00%)
Amorpha fruticosa (n = 166) **6.48%**	↓ 5 – *5* – 7 (6.95%)	↓ 1 – *1* – 2 (7.72%)	✳ 4 – *5* – 7 (6.47%)	✳ 5 – *5* – 6 (4.29%)	1 – *1* – 1 (0.00%)
Caragana arborescens (n = 113) **0.00%**	↓ 5 – *5* – 5 (0.00%)	↓ 5 – *5* – 5 (0.00%)	↓ 5 – *5* – 5 (0.00%)	↓ 5 – *5* – 5 (0.00%)	1 – *1* – 1 (0.00%)
Galega orientalis (n = 101) **7.65%**	↓ 5 – *5* – 7 (3.96%)	↓ 5 – *5* – 7 (3.96%)	↓ 5 – *5* – 7 (3.96%)	↓ 5 – *5* – 7 (3.96%)	1 – *1* – 1 (0.00%)
Lathyrus pratensis (n = 126) **0.97%**	↓ 5 – *5* – 5 (0.00%)	↓ 5 – *5* – 5 (0.00%)	↓ 5 – *5* – 5 (0.00%)	↓ 4 – *5* – 5 (1.78%)	1 – *1* – 1 (0.00%)
Lupinus polyphyllus (n = 100) **0.00%**	↓ 5 – *5* – 5 (0.00%)	↓ 5 – *5* – 5 (0.00%)	↓ 5 – *5* – 5 (0.00%)	↓ 5 – *5* – 5 (0.00%)	1 – *1* – 1 (0.00%)

Variations in organ type

In some cases, we recorded organs of hybrid nature. For example, we found rare cases of petalization of stamen or sepal in several species. In one sample of *Styphnolobium* (Truskavets, Ukraine), some stamens were petaloid (with single anther or dilated filament) or carpelloid (with unusual pubescence and/or stigmatic tissue in apical part). The given survey was mainly focused on variations in floral merism, so we counted such unusual organs as stamens if they clearly belonged to an androecial domain and had unambiguous signs of staminal origin.
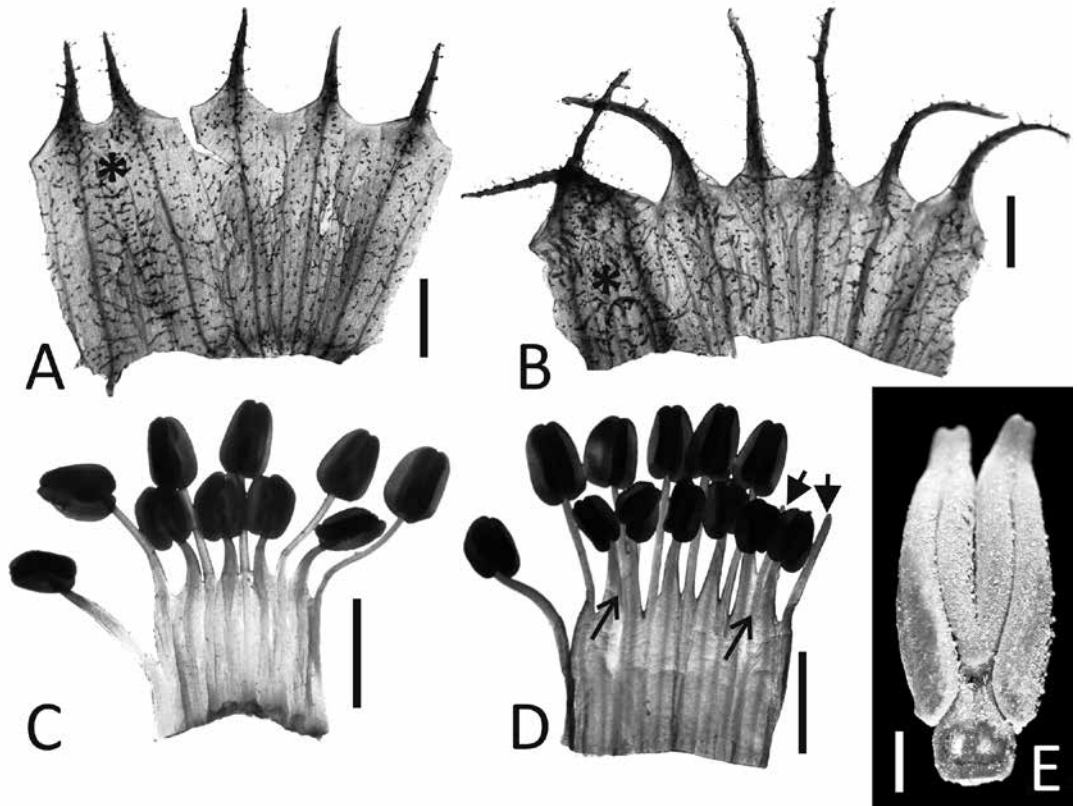
Figure 2. Some variations in floral structure in legumes. A–D – *Galega orientalis*; E – *Senna surattensis*. A – normal pentamerous calyx; B – anomalous heptamerous calyx; asterisk = adaxial side; C – pentamerous androecium; D – heptamerous androecium; vexillar stamen is on the left side of image; arrowheads = outer whorl stamens with anthers lost during dissection; arrows = unusual fusion of stamens; E – anomalous stamen with two anthers on a solitary filament. Scale bars = 1 mm.

In certain genera (e.g. *Senna*), some stamens lacked the anther, i.e. they were converted to staminodes. Inner stamens of flowers of *Cordyla* usually had thinner filaments and often lacked anthers. Such staminodes were counted as stamens, as they are patterned within the androecium.

Other types of variation

We found variations in sex of flowers in *Gymnocladus*, *Gleditsia* and *Cordyla*. Male trees of dioecious *G. dioicus* produced flowers of smaller size with a suppressed gynoecium development. So, we could not study gynoecium morphology in male flowers in detail. The hermaphrodite flowers were of larger size, united in less ramified inflorescences and had both stamens and carpels. Trees of *G. triacanthos* also appeared either hermaphroditic or male. Flowers of *C. pinnata* were gathered in simple racemes, but only a proximal part of the inflorescence produced fully developed carpels on long gynophores (Fig. 1B). Oppositely, the distal flowers had gynoecia suppressed in development and senescing by anthesis. However, the precise number of carpels could be estimated in *Cordyla*.

Some species also exhibited a variation in aestivation mode. For example, one of the abaxial petals in *Cercis*, either right or left, partly overlapped another abaxial petal. This feature seems defined either randomly or, more probably, conditioned by the position of a certain flower

in the inflorescence with respect to other flowers. Ratio between right- and left-sided flowers significantly corresponded to 1 : 1 (102 : 97, chi-square test, $p = 0.723$). A similar mode of variation was recorded in *Styphnolobium*, where ratio between right- and left-sided flowers also was 1 : 1 (54 : 53, chi-square test, $p = 0.923$). In *Senna* with spiral arrangement of calyx and corolla, this spiral also exhibited chirality, either clockwise or counterclockwise. No precise counts were made in this species for a given trait, but both types co-occur in the same inflorescence. Size variations, unless clearly resulting from organ fusion, were not taken into account.

Discussion

Among studied material, two basic types of floral symmetry were found, viz. polysymmetric (*Gleditsia*, *Gymnocladus*, *Cordyla*, *Senna*) and monosymmetric (other genera). Floral mono-symmetry is generally acquired by the developmental gradient in expression of certain genes, the most important of them being *CYCLOIDEA* and *DICHOTOMA* (PRESTON & HILEMAN 2009). *CYC* is expressed in the adaxial domain of developing FM in many taxa (PRESTON & HILEMAN 2009). When expression of *CYC* is missing, the flower becomes abnormally polysymmetric with a more variable merism, as it was repeatedly demonstrated in some model species, the best investigated being a snapdragon, *Antirrhinum majus* (ALMEIDA et al. 1997). The adaxial domain in pentamerous monosymmetric leguminous flowers is distinguishable by special petal differentiation (vexillum in papilionoid legumes or vexilloid petal in some caesalpinioids like *Cercis*) and some other features, such as a free vexillar stamen in diadelphous androecium. The other four petals can develop in a similar way (a case of *Styphnolobium*) or clearly divide into lateral and abaxial petals (as in many papilionoids having wings and keel). This list seems more or less comprehensive although in different tribes similar floral morphology could be acquired by different evolutionary pathways.

Polysymmetric flowers

Four of examined species have fully or partly polysymmetric flowers. *G. triacanthos* and *G. dioicus* have two pentamerous whorls of free stamens (at least in functionally male flowers), while in flowers of *C. pinnata* numerous stamens cannot be assigned to discernible whorls (Fig. 1B, C). Perianth members in *S. surattensis* are arranged in a spiral way. Sepals as well as petals differ only in size, while all perianth structures are fully bilaterally symmetric (Fig. 1D).

All four species have a remarkable high level of floral instability (Table 2). In *Gleditsia* and *Gymnocladus*, only the gynoecium is stable and always monomerous. However, some flowers in *Cordyla* occasionally produce bicarpellate gynoecia, which never seem to result in a dimerous fruit. TUCKER (1991) reported the 'chaotic' characters of *Gleditsia* flowers such as variable sizes of FMs resulting in unstable merism, loosely controlled order of floral development and initiation of primordia on FM, variations in sex of flowers, etc.

Although no special survey on the expression of *CYC*-like genes in any of these species has been conducted to date, one may expect that fate of adaxial domain of their FMs is not governed specially (Fig. 3A). This explains both polysymmetry and high level of instability; however, the latter phenomenon seems to be evolutionarily tolerated due to the former one.

One more feature which contributes to overall instability of flowers in *Gleditsia* and *Gymnocladus* is the presence of a terminal flower, a phenomenon untypical of most legumes (Fig. 1C). A terminal position of flower is incompatible with its monosymmetry but it is possible in taxa with
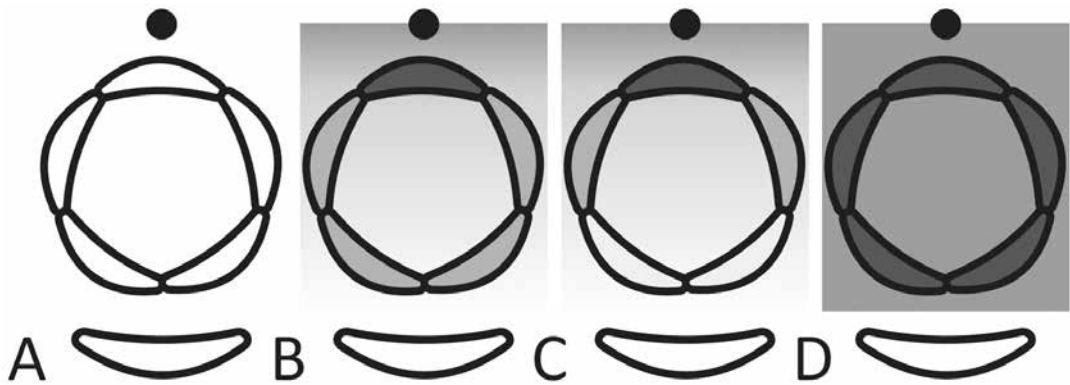
Figure 3. Variability of symmetry of the pentamerous corolla in legumes (see text for the explanation). Petals of polysymmetric corolla are shown in white, adaxial petal in dark grey, lateral petals in grey, abaxial petals in light grey. White arc = bract. Grey background denotes gradient of concentrations of certain morphogenes.

polysymmetric flowers. Merism and phyllotaxis of such flower often differ from those of lateral flowers (ENDRESS 1987).

Polysymmetric flowers of legumes may serve as an interesting object for survey on correlation between different whorls. In the cruciferous model species *Arabidopsis thaliana* (L.) Heynh., perianth whorls as well as gynoecium and androecium are tightly coordinated (the concept of bipolar patterning sensu CHOOB & PENIN (2004)). This means that merism of pairs calyx+corolla and androecium+gynoecium fluctuates synchronously. However, in polysymmetric flowers of legumes other correlations were found. In hermaphroditic flowers of *G. dioicus*, the only reliable correlation ($p < 0.01$) existed between corolla and inner staminal whorl (Spearman test, $\rho = 0.737$). A similar pattern was found in male flowers (data not shown) with most robust correlations in pairs calyx+outer whorl of stamens and corolla+inner whorl of stamens. In male flowers of *G. triacanthos*, reliable correlations ($p < 0.01$) were found in pairs calyx+corolla, calyx+outer whorl of stamens and corolla+outer whorl of stamens (Spearman test, ρ comprising 0.629, 0.833 and 0.823, respectively). In hermaphroditic flowers of *G. triacanthos*, less robust correlations ($p < 0.05$) were found in pairs calyx+corolla and corolla+inner whorl of stamens (data not shown). These data demonstrate that in these two species opposed whorls are often correlated more strongly than alternating ones. One could hardly expect a patterning influence of a single carpel on any floral whorl as distinct from *Arabidopsis*.

Cordyla has unusual floral morphology compared to most papilionoids. It lacks any abaxial-adaxial polarity except for carpel orientation and does not show any sign of corolla (Fig. 1B). Its FM seemingly has no additional negative size regulation associated with a monosymmetry, which may explain development of a polymerous androecium and, in some cases, sufficient FM size to initiate more than one carpel. When two carpels are present, one (larger) is orientated typically, with its cleft to adaxial side, while another one (smaller) occupies lateral position with its cleft pointing more or less to the center of the receptacle. A polymerous gynoecium seems inadaptive, as only monomerous fruits develop. Some species in the related genus *Swartzia* such as *S. dipetala* normally develop two carpels, both often giving rise to twin pods (PAULINO et al. 2013). Such unstable morphology of gynoecium in *Cordyla* is a kind of evolutionary 'overshoot' which results from the loss of monosymmetry but does not bring any benefit.

One more way to secondarily acquire monosymmetry is available by ectopic expression of *CYC*-like gene(s) which define an adaxial domain of FM in monosymmetric flowers (Fig. 3D). Such shift was recorded in *Cadia purpurea* Forssk., which has all five petals of flag-like morphology and hence polysymmetry unusual for core genistoid clade in which this species is nested (Cɪᴛᴇʀɴᴇ et al. 2006). This case was classified as an innovative homeotic transformation rather than true reversal to the ancestral polysymmetry, but similar mechanisms may contribute to transitions between different types of floral symmetry. For example, Pᴇɴɴɪɴɢᴛᴏɴ et al. (2000) pointed at few cases of apparent reversal to a monosymmetry some of which may comprise the homeotic transformations as in *Cadia*.

Although no special counts on the floral stability in *Cadia* are available, one may expect this flower to be very stable, as *CYC*-mediated function of maintenance of FM size is not lost in this genus regardless of its unusual monosymmetry, but rather distributed throughout the whole FM.

The least stable floral domain like in *Arabidopsis* (Cʜᴏᴏʙ & Pᴇɴɪɴ 2004) is the one which develops last, i.e. androecium which was found initiating lately in most legumes (Tᴜᴄᴋᴇʀ 1984).

Monosymmetric flowers with two types of petals

Except for true terminal flowers, which are incompatible with a monosymmetry, every FM differentiates in a certain developmental gradient between subtending bract on the one side and active inflorescence apex on the other side (Fig. 3B, C). This gradient probably defines (but not results from) adaxial expression of *CYC*-like genes and proper position of the carpel with its cleft towards the adaxial side.

In model legumes like *Pisum* and *Lotus*, similar mutations are known, which result in differentiation of lateral (wing) petals in the same mode as abaxial (keel). Such mutation is called *keeled wings* (*k*) in garden pea and in *Lotus*, a phenotypically similar mutation in the orthologous gene *KEELED WINGS IN LOTUS 1* (*KEW1*) was described later (Fᴇɴɢ et al. 2006; Wᴀɴɢ et al. 2008). Intriguingly, gene *K* identified in pea appeared belonging to TCP family of transcription factors to which genes *CYC* and *DICH* belong (Wᴀɴɢ et al. 2008). Another ortholog of *CYC* in pea genome corresponds to gene *LOBBED STANDARD 1* (*LST1*). Mutants *lst1* exhibit unusual shape of the adaxial (standard) petal (Wᴀɴɢ et al. 2008). Mutants *lst*, *k lst* and yet unidentified *symmetric petals 1* (*syp1*) are remarkable because they have supernumerary floral organs (see Fig. 2a, b in Wᴀɴɢ et al. 2008). One may propose that genes encoding TCP transcription factors regulate different aspects of floral symmetry (abaxial vs. adaxial, differentiation of lateral domains) but also act as negative regulators of FM size, as it was unambiguously demonstrated for gene *CYC* (Gᴀᴜᴅɪɴ et al. 2000). That is why one may expect that the merism of monosymmetric flowers with three types of petal differentiation (Fig. 3C) and internal petal asymmetry would be more stable than in polysymmetric or in monosymmetric flowers with only two types of petals (Fig. 3B, as in *Stypnolobium*). That is the phenomenon, which we illustrated in Table 2.

From the regulatory point of view, secondary loss of all petals except for the adaxial one (*Amorpha*, *Dialium*, some species of *Swartzia*, etc.) comprises the same form of floral symmetry: four petals of five have the same ontogenetic fate. Investigations of Tᴜᴄᴋᴇʀ (1988) indicate that primordia of lateral and abaxial petals in flowers of *Amorpha* are initiated, but later suppressed and absent in mature flowers.

Monosymmetric flowers with three types of petals

Such floral morphology with distinctive 'flag-wings-keel-complex' is intuitively understood as typical for many papilionoids (*C. arborescens*, *G. orientalis*, *L. polyphyllus* and *L. pratensis*, in our analysis: Fig. 1A). A similar syndrome in some caesalpinioid legumes (*Cercis*) is interpreted as resulting from convergence (Tucker 2002).

We found a remarkably low level of variation in either number or position of organs in this group (Table 2). Flowers with pronounced monosymmetry have a specific pattern of expression of *CYC*-like genes, which was found restricted to an adaxial domain in model legume species (Feng et al. 2006; Citerne et al. 2006). This explains a higher level of stability compared to taxa having polysymmetric flowers together with an outstanding stability of adaxial floral parts (see above).

Conclusion

Based on the results of counts in leguminous flowers with different types of floral symmetry, the following conclusions can be postulated.

I) Polysymmetric flowers are generally more variable than monosymmetric, while monosymmetric flowers with three types of petals are more stable than those with two types of petals. This is most probably connected with negative regulation of FM size by proteins of TCP family, which also control floral symmetry.

II) Numbers of floral organs in opposed whorls are more strongly correlated than in adjacent whorls, at least in polysymmetric flowers.

III) Adaxial floral domain and monocarpellate gynoecium are the most stable floral parts in the leguminous flower.

Acknowledgements

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