



Ontogeny, variation and evolution of inflorescence in tribe Fabeae (Fabaceae) with special reference to genera *Lathyrus*, *Pisum* and *Vavilovia*



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ABSTRACT

The present study reports the inflorescence ontogeny and morphology in tribe Fabeae (Fabaceae) addressing the evolutionary trends of selected inflorescence features in clade *Lathyrus–Pisum–Vavilovia*. In all three mentioned genera, the whole inflorescence in annual taxa comprises an open shoot bearing frondose leaves subtended by simple racemes. This shoot exhibits a pendulum symmetry which results from skewed position of leaves initiating at shoot apex. During floral initiation in a model species, i.e., *Vicia cracca*, numerous flowers are produced on these racemes but later most of them degrade and only a small portion (<4%) of previously initiated flowers result in production of mature fruits. This many-flowered state is derived from a single- or few-flowered one typical for the most basal representatives of this clade. The single-flowered state strongly correlates with annual life form and arises repeatedly during evolution of tribe Fabeae. The adaptive values of different inflorescence types are discussed.

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Introduction

In angiosperms, the inflorescence structure is predetermined by mode of pollination, fruit and seed dispersal and other factors. Inflorescences are conventionally subdivided into simple and compound, the former producing flowers on the main shoot, while the latter are characterized with flowers born also on axes of higher order than the main (Endress, 2010). Two possible ways to investigate evolutionary tendencies in inflorescence ontogeny are possible. The first is to analyze inflorescence variation in a group of related taxa. The second is to uncover genetic mechanisms underlying the inflorescence development with usage of mutation analysis. To date, certain success was reached during more than two decades of studies on two model plant species, *Arabidopsis thaliana* (L.) Heynh. (Brassicaceae) and *Antirrhinum majus* L. (Plantaginaceae). However, both species produce the simple inflorescence, so a genetic control of a compound inflorescence either is subjected to wide approximations, or needs other model objects. The members of legume family, Fabaceae, can serve as a model for such studies, as many of them produce compound inflorescences

and some species are considered as models in plant biology for long time. Although still lacking the complete genome sequence, the pea plant (*Pisum sativum* L.) is among the most traditional and finely studied legume species. Numerous genes disturbing its compound inflorescence ontogeny are known (Singer et al., 1999).

From the phylogenetic point of view, the pea is nested within a large clade including numerous species of the species-rich vetching genus (*Lathyrus*) together with a monotypic genus *Vavilovia* which belong to tribe Fabeae (Schaefer et al., 2012). Most representatives of this tribe are characterized with a double raceme with flowers borne on a racemose stalk (peduncle) in axils of bracts which can be missing in some species. The stalks themselves are subtended by frondose leaves on a main indeterminate shoot. In most accessions of the pea, flower number on axillary racemes does not exceed two.

Even in single- or two-flowered pea inflorescences, the remarkable phenomenon of pendulum inflorescence symmetry is evident (Sinjushin, 2013). It results in left–right alteration of chirality of subsequent axillary racemose inflorescences with respect of their position on a shoot. Such type of symmetry was reported in different clades of Fabaceae and also beyond this family (reviewed by Prenner, 2013).

However, in the whole *Lathyrus–Pisum–Vavilovia* clade, the polymorphism of inflorescence structure is much wider than in pea itself. In some species the peduncle of an axillary raceme is

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very short, while in other it can be very long. This feature is of taxonomic interest for vetches, as they are subdivided into subgenera *Vicia*, *Hypechusa* (Alef.) Stankev. (both with shortened or reduced peduncle), and *Cracca* (Medik.) Gams (with long peduncles) (Repjev et al., 1999). The number of flowers in a raceme ranges between one and few dozens. Flower size also strongly varies between species of a clade.

Data on genetic control of these traits are controversial. In pea, the number of flowers per axillary raceme was reported to be controlled by either two (Lamprecht, 1947) or one (Singer et al., 1999) gene(s). A chromosome aberration causing formation of two flowers instead of one was described in *L. sativus* L. (Talukdar, 2013). Inflorescence length also seems to be inherited as a quantitative trait in pea (Lamprecht, 1949). A single semidominant mutation affecting flower size was reported in given species (Lamprecht, 1963). The heritable variations in flower number and raceme length underlie the existing polymorphism of sweet pea (*L. odoratus* L.) cultivars but their genetic basis seems unclear (Fleming et al., 1925; Parsons and Mikic, 2011).

Obviously, genotypes of faboid legumes with altered flower number, flower size and inflorescence length are of significant practical interest. Introduction of certain mutations in genotypes of cultivated pea, vetches, lentils and vetchlings might contribute to productivity or to decorativeness of the ornamental forms. Except this, understanding the correlations between phylogenetic position and inflorescence features can shed some light on the evolutionary and ontogenetic tendencies in tribe Fabeae and, more generally, in angiosperms. The whole tribe is usually interpreted as transient from insect-pollinated to self-pollinating habit (reviewed in Repjev et al., 1999) but the role of inflorescence structure in this process has not been indicated. Relations between different inflorescence parameters and their ontogenetic dynamics are hence of special interest. We focused on three inflorescence parameters (see below) which are supposed to have contribution into attractiveness for pollinators and hence are expected to be under natural selection.

The present study was dedicated to analysis of ontogeny and evolutionary trends involving in quantitative features of inflorescence in the *Lathyrus–Pisum–Vavilovia* clade. The aims of this study can be outlined as (1) to investigate the ontogeny of inflorescence in a model species of tribe Fabeae, with special reference to origin of inflorescence symmetry, and (2) to study inflorescence morphometric parameters in this clade and search for correlations between phylogeny and morphological features.

Materials and methods

Plant material

The herbarium specimens (see Supplementary Material) of *Lathyrus*, *Pisum* and *Vavilovia* were used for morphological examination and for making the digital photographs for further measuring. The species were chosen according to the list from Schaefer et al. (2012). We treated *Pisum* as including only two species (*P. sativum* and *P. fulvum* Sibth. & Sm.) and *Vavilovia* as monotypic in consistency with our earlier results (Sinjushin and Demidenko, 2010). For comparison, we also examined some specimens of *Vicia* formerly placed in *Lathyrus*-related genus *Orobis*. Except these, some living materials were examined, viz. species inhabiting the territory of the S.N. Skadovskii Zvenigorod Biological Station of Moscow State University (Western Moscow region, Russia; N 55,698°, E 36,725°) and species from living collection of the Genetics Dept. of M.V. Lomonosov Moscow State University. Plants were cultivated on an experimental plot on a territory of the Zvenigorod Biological Station in 2012–2013 field seasons.

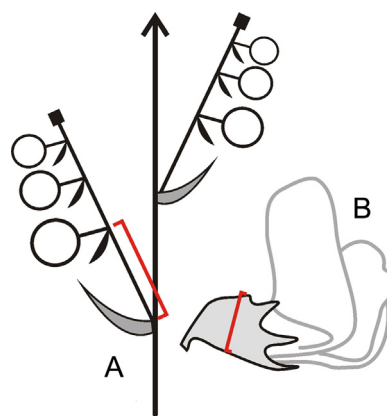


Fig. 1. The parameters scored in quantitative analysis of inflorescence in tribe Fabeae (measured parameters are marked). (A) Length of peduncle. (B) Calyx width.

Measurements

All measurements were carried out using Measure 2.0 (C Thing Software, USA) program on digital images of herbarium specimens. Minimum three measurements were made for all parameters on every specimen. For analysis, three parameters were scored: peduncle length (distance from the leaf axil to the place of first flower attachment, Fig. 1A), number of flowers per raceme, and flower size. When examining the available literature sources, few parameters characterizing flower size were found: distance from the calyx base to the standard tip (Etcheverry et al., 2012), flower weight (Galloni et al., 2007), etc. None of these parameters seemed convenient for estimation of flower size in herbarium materials, so we scored the calyx width, i.e., distance from adaxial incisures to abaxial side of the calyx (Fig. 1B). Calyx is also persistent at fruiting stage, thus making this parameter available for scoring on wider range of herbarium material.

The raceme length was also measured for the developmental dynamics on living plants of two species, *L. sativus* (single-flowered raceme) and *L. tuberosus* (few-flowered raceme). Distance from the leaf axil to the pedicel of the first flower was measured on living plants every day (Fig. 2). It was recorded that the raceme almost stops elongation at anthesis, so we used only flowering and fruiting specimens for measurements.

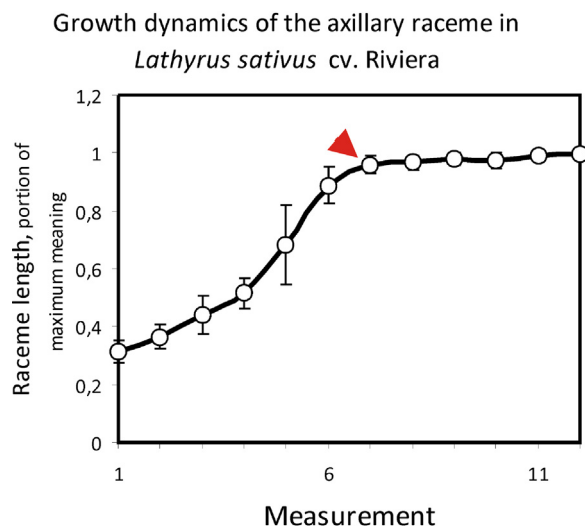


Fig. 2. The dynamics of length of peduncle in *Lathyrus sativus* cv. Riviera (mean ± S.D.). Arrowhead indicates the time of flower opening.

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