

Correlated evolution of flower size and seed number in flowering plants (monocotyledons)

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- **Background and Aims** Kin selection theory predicts that a parent may minimize deleterious effects of competition among seeds developing within ovaries by increasing the genetic relatedness of seeds within an ovary. Alternatively, the number of developing seeds could be reduced to one or a few. It has also been suggested that single or few seeded fruits may be correlated with small flowers, and multi-ovulate ovaries or many seeded fruits may be associated with large flowers with specialized pollination mechanisms. We examined the correlation between flower size and seed number in 69 families of monocotyledons to assess if correlations are significant and independent of phylogeny.
- **Methods** We first examined the effect of phylogenetic history on the evolution of these two traits, flower size and seed number, and then mapped correlations between them on the latest phylogenetic tree of monocotyledons.
- **Results** The results provide phylogenetically robust evidence of strong correlated evolution between flower size and seed number and show that correlated evolution of traits is not constrained by phylogenetic history of taxa. Moreover, the two character combinations, small flowers and a single or few seeds per fruit, and large flowers and many seeded fruits, have persisted in monocotyledons longer than other trait combinations.
- **Conclusions** The analyses support the suggestion that most angiosperms may fall into two categories, one with large flowers and many seeded fruits and the other with small flowers and single or few seeded fruits, and kin selection within ovaries may explain the observed patterns.

Key words: Kin selection, monocotyledons, flower size, seed number, evolution of correlated traits.

INTRODUCTION

Flowering plants exhibit a wide range of reproductive modes (Darwin, 1877; Stebbins, 1974; Barrett, 1992; Richards, 1997; Briggs and Walters, 2016). Correlations among reproductive traits have provided new explanations for the evolution of breeding systems (Bawa, 1980; Givinish, 1980; Felsenstein, 1985) and possibility of kin selection (Kress, 1981; Bawa, 2016), and sexual selection (Willson, 1979; Bawa, 1980) in plants. Kress (1981) noted correlations between polyads, or pollen aggregations, and multi-ovulate ovaries on the one hand, and between monads and ovaries with a single or a few ovules on the other. He invoked kin selection to explain the association between pollen aggregations with multi-ovulated ovaries, arguing that such associations increase the genetic relatedness of seeds developing within an ovary, thereby minimizing deleterious effects of competition among developing siblings.

Bawa (2016) extended the concept of kin selection to suggest that flowering plants may have followed two evolutionary trends: one that increases the genetic relatedness of seeds within multi-ovulate ovaries or many seeded fruits through evolution of specialized pollination mechanisms in large flowers, and the other a reduction in seed number to one or a few in small flowers pollinated by generalist insects or wind. Thus, he predicted

that kin selection may have generated two sets of contrasting correlated traits in flowering plants: (1) large flowers, pollen aggregations, specialist pollinators, synchronous arrival of pollen grains that interact to increase the genetic relatedness of seeds within fruits in multi-ovulate ovaries associated with the aforementioned floral traits, and (2) small flowers, a generalist mode of pollination including wind and water pollination that may interact to reduce sibling competition by decreasing seed number to one or a few within fruits.

For these two sets of correlations, critical are the correlations between: (1) small flowers and one or a few ovules per ovary or one or a few seeds per fruit, and (2) large flowers and multi-ovulate ovaries or many seeded fruits, because other correlated traits follow from these two traits.

Here, based on a broad survey of the monocotyledons (69 families), we demonstrate that an overwhelming majority of families show that large flower size is associated with multi-ovulate ovaries or multi-seeded fruits, and small flowers are associated with ovaries with a single or a few seeded fruits. We propose that most angiosperms may fall into one or the other category depending upon flower size and the associated seed number per fruit.

Further, we used modern comparative phylogenetic methods to: (1) determine if the evolution of flower size and seed

number in monocotyledons is constrained by phylogenetic relationships of taxa; (2) test the existence of correlated evolution between flower size and seed number; and (3) assess the most probable evolutionary route and directionality of flower size and seed number. Finally, we discuss these results in the context of kin selection, allometry and other explanations advanced to account for reduction in ovule or seed number in angiosperms.

We chose monocotyledons to address the above questions because they are a large and diverse group that have a widespread distribution, show variation in the traits of interest, and have an abundance of the data easily accessible in one place (Friedman and Barrett, 2009). The analyses were done at the family level because for the overwhelming majority of families, the analysed traits appear to be specific to families, with little variation among genera within families.

Our results are significant and novel in two respects. First and foremost, if such correlations hold in other groups of plants, most of the flowering plants may fall into two broad groups based on flower size and ovule and seed number. Although several authors have highlighted the correlations among flower size, mode of pollination and ovule number (Bawa, 1980, 2016; Burd et al., 2009; Friedman and Barrett, 2009, 2011), demonstration of contrasting sets of correlations among reproductive traits has been lacking. Secondly, the correlated evolution of flower size and seed number provides a possible new framework for examining the evolution of a range of reproductive traits from flower size and pollination mechanisms to seed number per fruit.

MATERIALS AND METHODS

We analysed 69 out of 74 monocotyledon families in the phylogeny of the group of Hertweck et al. (2015). We used the ultrametric tree from r8s (Sanderson, 2003) that was trimmed to one example per monocotyledon family (Hertweck et al., 2015). We used a dated phylogenetic tree because, in a dated tree, the branch length is proportional to absolute age of taxa and not to evolutionary rate, and, further, it allows a comparison of alternative scenarios of temporal divergence on phylogenetic trees. Thus, one can explicitly test the alternative models of trait evolution on a temporal scale and,

indeed, most methods for reconstructing trait evolution require a dated phylogeny (O'Meara et al., 2006; Slater et al., 2012). Data for the two traits, flower size and seed number, were collected from diverse sources including Kubitzki (1998), Watson and Dallwitz (1992), *Flora of Ecuador* (Anderson and Harling, 2000), *Flora of China* (Wu et al., 2009) and various other sites on the world wide web (Supplementary Data Table S1). The two traits were coded as binary values. Five families out of the 74 showed a lot of variation in flower size and seed number (Table 1). The comparative phylogenetic methods used have limitation of integrating variable (polymorphic) character states in the analysis, therefore the variable families were excluded further from the analysis.

Flower size

Flower size was recorded from Watson and Dallwitz (1992), Kubitzki (1998) and images from the world wide web. Kubitzki (1998) and Watson and Dallwitz (1992) specifically mention for families if the flowers are small or inconspicuous. In such cases, we noted the flowers as small, and further verified the size by examining the images in Kubitzki (1998) and Google images. The small flowers appeared to be under 10 mm along the longest dimension – in most cases much smaller. Interestingly, Vamosi et al. (2003) also use 10 mm as the cut-off point for 'small inconspicuous flowers'. We further validated our categorization of flower size by generating a random list of 35 out of the 69 families analysed. For these 35 families that included 142 genera and 642 species, we compiled information on flower size from the *Flora of Ecuador* (Anderson and Harling, 2000) and *Flora of China* (Wu et al., 2009), two of the few floras that mention flower size. *Flora of Ecuador* (Anderson and Harling, 2000) described 13 out of the 69 monocotyledon families and included 31 genera and 123 species, and the *Flora of China* (Wu et al., 2009) provided data for an additional 111 genera and 519 species for the sampled families.

For these 35 families, we sampled the first 20 genera. In most cases, however, the number of genera was much smaller than 20 and, in such cases, we sampled all the genera. From each genus, we sampled the first ten species or, if there were less

TABLE 1. Monocotyledon families categorized according to a combination of two traits (flower size and ovule or seed number)

Families	Total number	Flower size and seed or ovule number
Acoraceae, Anarthriaceae, Arecaceae, Asparegaceae, Boryaceae, Centrolepidaceae, Commelinaceae, Cymodoceaceae, Cyperaceae, Dasyopogonaceae, Dioscoreaceae, Eceidicoleaceae, Eriocaulaceae, Flagellariaceae, Hanguanaceae, Joinvilleaceae, Juncaginaceae, Lanariaceae, Pandanaceae, Poaceae, Potamogetonaceae, Restionaceae, Rhipogonaceae, Smilacaceae, Thurniaceae, Triuridaceae, Typhaceae, Zosteraceae	28	Small flower and single or few seeded fruits
Campynemataceae, Colchicaceae, Cyranthaceae, Juncaceae, Tecophilaeaceae, Tofieldiaceae, Alstoemeriaceae, Amaryllidaceae, Blandfordiaceae, Bromeliaceae, Burmanniaceae, Butomaceae, Cannaceae, Corsiaceae, Costaceae, Doryanthaceae, Haemodoraceae, Hypoxidaceae, Iridaceae, Ixioliriaceae, Liliaceae, Lowiaceae, Mayacaceae*, Musaceae, Nartheciaceae, Orchidaceae, Petrosaviaceae, Petermanniaceae, Philesiaceae, Philydraceae, Pontederiaceae, Stemonaceae, Strelitziaceae, Velloziaceae, Xeronemataceae, Xyridaceae*, Zingiberaceae	6 31	Small flowers and many seeded fruits Large flower and many seeded fruits
Alismataceae, Heliconiaceae, Marantaceae, Asphodelaceae	4	Large flowers and single or few seeded fruits
Araceae, Asteliaceae, Hydrocharitaceae, Melanthiaceae, Rapateaceae	5	Could not categorize due to variation in seed number or flower size

*Although we treated Xyridaceae and Mayacaceae as large flowered families based on Kubitzki (1998), the data from the *Flora of China* indicated ambiguity with respect to flower size. Hence we repeated the analyses treating these two families as with both small and large flowers. The results from these analyses were the same.