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Fruit set increases with maleness in the andromonoecious *Acacia caven*

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ABSTRACT

In long-lived plants, sexual expression can be highly variable in time and space. The extent to which sexual dimorphism of flowers is expressed in the same or in separate individuals, may have implications for the plants' dependence on pollen vectors, the compatibility of the pollen received, and the potential for setting fruit. Here, we account for variability in sexual expression in the small tree *Acacia caven*, which produces hermaphrodite and male flowers on the same or in separate individuals. We focus on whether individual sexual expression influences fruit set, which latter has been reported to be extremely low in this species. Individual sexual expression, estimated as the hermaphrodite: male flowers ratio was variable both within and among plants across two reproductive seasons. Though male flower production could be very high (up to 99% of the flowers), all trees produced both flower types within the same individual, thus confirming andromonoecy in this species. More interestingly, hermaphrodite: male flowers ratio had a negative effect on fruit set. This pattern was consistent across two reproductive seasons and suggests that maleness should favor female function. Similar trends found in other plant species with the same sexual system support the hypothesis that male flowers of andromonoecious species may contribute to reduce self-pollen interference compared with hermaphrodite flowers. By favoring the deposition of compatible pollen grains and increasing fruit set, maleness would then help to maintain andromonoecy in this and other andromonoecious species.

Introduction

Lability in sexual expression is common in dioecious and monoecious perennial angiosperm species (Korpelainen, 1998). The sexual expression of a plant as a whole is determined by sex variability of individual flowers, therefore, changes in the relative abundance of functionally male vs. functionally female flowers within a plant will determine plants' sexual expression at a given time. Compared with animals, sexual expression in long-lived plants may vary during their lifetime, and both environmental and genetic factors have been shown to trigger changes in sexual expression under natural and artificial conditions (Diggle et al., 2011). In co-sexual plants (i.e., two sexes present in the same individual of hermaphrodite or monoecious species) sexual expression can vary with size (e.g., Calviño and Galetto, 2010), age (e.g., Nanami et al., 2004), and the successional stage of the community (Litrico et al., 2005). But irrespective of the mechanism driving change in sexual expression, there are direct consequences for fruiting success, reinforcing the link between sex allocation strategies and plant reproductive output. For instance, when two sexual morphs are present, changes in the male: female ratio modify pollen availability and can limit seed production in several dioecious plants (reviewed by de Jong et al., 2005). Moreover, in co-sexual plants, some flower morphs may be more effective attracting pollinators than others (Podolsky, 1992). When this occurs, a reduction in the percentage of the most attractive flower morph (e.g., male flowers) may lower fruit set (e.g., Schelssman et al., 2004). Therefore, variable sexual expression may account for fruiting success in plants with different sexual systems.

For a single species, the impact of sexual expression on fruiting success would depend on whether allocation to male and female structures occurs in the same or different individuals and on sexual expression variability. Spatial separation of male and female structures determines pollinator dependence, and usually, as the spatial separation of sexual structures increases, the plants' dependence on pollen vectors to set fruits becomes stronger. Accordingly, dioecious species have higher pollinator dependence than

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Table 1
Location and sample sizes of the eight studied populations of *Acacia caven*.

Site (population codes)	Year	Latitude	Longitude	Altitude (m a.s.l.)	Number of plants	Number of inflorescences collected per plant/year
BO	2006	31°19′46.89″ S	64°17′21.49″ W	466	8	15
MZ	2006	31°15′32.93″ S	64°18′1.83″ W	552	14	15
UQ	2006	31°14′2.29″ S	64°19′48.06″ W	619	9	18
LQIII	2006	31° 9′11.29 ″ S	64°20′28.85″ W	832	16	18
LQN	2008/2010	31° 9′09.31″ S	64°20′43.12″ W	857	10	20
LR	2008/2010	31°45′25.05″ S	64°27′26.16″ W	712	10	20
LM	2008/2010	31° 9′40.34″ S	64°21′03.67″ W	867	10	20
SD	2008/2010	31°10′57.09″ S	64°15′40.05″ W	649	10	20

monoecious species (Bond, 1994). Furthermore, for monoecious species whose sexual expression is variable, fruiting success will depend on the interplay between the relative proportion of functionally female flowers at a given time, and the successful pollination of these flowers. Changes in sexual expression over time and space will have diverse consequences for the plants' reproductive success and, therefore, for the probability to contribute locally to the seed pool.

Acacia caven (Molina) Molina (Fabaceae) is one of the most widespread tree species of sub-tropical South America, occurring between 18 and 37°S in all dry areas of the Chaco (Aronson, 1992). In central Argentina, *A. caven* has a mass flowering at the end of winter (August) when it is the most important floral resource in the community (Ashworth, 2004; Baranelli et al., 1995). Given that hermaphrodite and male flowers are usually present in the same plant, *Acacia caven* first was reported to be andromonoecious (Aronson, 1992). But male individuals (i.e., with functionally male flowers only) do occur in both Chilean and Argentinian populations (Baranelli et al., 1995; Peralta et al., 1992). Plants of Argentinian populations characterized as male ones were able to produce some fruits (Baranelli et al., 1995), but whether fruitless trees in this study were male or hermaphrodite individuals with unsuccessful pollination is unknown. Furthermore, and contrasting with its widespread distribution, *A. caven* fruit set can be extremely low and highly variable, including several trees that do not set fruit at all (Ashworth, 2004; Baranelli et al., 1995). Insufficient and inadequate pollination by animals may certainly limit fruit production in *A. caven* due to high self-incompatibility (Peralta et al., 1992). Nevertheless, the usually high pollination intensity registered in populations from central Argentina, provides evidence that pollen quantity is not the limiting factor for low fruit set in this species (nearly 70% of hermaphrodite flowers per tree are usually pollinated, Ashworth, 2004).

One way to increase fruit production is to avoid self-pollination by reducing sexual interference with the production of unisexual flowers (Barrett, 2002). Particularly, the abundance and the spatial distribution of male and hermaphrodite flowers within a plant (e.g., whether unisexual flowers are located in the same or in different inflorescences/plants) may influence fruit set. Accordingly, the location of male flowers on separate individuals would influence fruit set in *A. caven.* But more importantly, it may reveal the existence of androdioecious populations (hermaphrodite and male individuals) of *A. caven* with male trees unable to set fruits. Because male plants of androdioecious species exclusively are functioning as a pollen source, the simultaneous occurrence of male and hermaphrodite plants will have direct consequences for the persistence of sexual morphs in the population (Panell, 2002). Here, we account for sexual expression variability in *Acacia caven* by studying the hermaphrodite: male flower ratio in different plants and populations, and by following sexual expression and fruit production in the same focal trees over different reproductive events. The specific aims of this study were: (i) to analyze how are hermaphrodite and male flowers distributed within and between *A. caven* trees, (ii) to test the temporal variation in sexual expression, and (iii) to test the effect of hermaphrodite: male flowers ratio on fruit set.

Material and methods

In central Argentina, *Acacia caven* (Molina) Molina begins flowering at the end of winter (August) just before the summer rains, with pods being ripe 6 months later. Flowering is profuse, and pollination is carried out by native bees, wasps and flies, being the exotic bee *Apis mellifera* the most common (Aguilar, 2005; Ashworth, 2004). Self-incompatibility, the lack of autonomous selfing and the absence of wind pollination give *A. caven* a strict dependence on pollinators to set fruits (Ashworth, 2004; Peralta et al., 1992). Flowers are nectarless and arranged in globular fragrant inflorescences (i.e., heads, Fig. 1) which can display hermaphrodite and functionally-male flowers by the arrest of the pistil during floral development. Hermaphrodite flowers are protogynous (Peralta et al., 1992). A head may display between 20 and 60 small yellow flowers with a variable percentage of hermaphrodite and male flowers (Baranelli et al., 1995; Peralta et al., 1992). Thus, three head types can be distinguished: male heads (i.e., those with male flowers only), hermaphrodite heads (hermaphrodite flowers only) and mixed heads which display both flower types.

All the studied populations are located at the eastern slope of Sierras Chicas Hills, Córdoba province, Argentina (Table 1). Vegetation composition was similar among the population stands and dominated by *Prosopis* spp. and *Litraea molleoides* in the tree layer. In the study area, most of the species flower between September and March, during summer rainfall, when precipitation may surpass 700 mm year^{-1}. The climate is warm temperate to subtropical, with mean annual temperatures of 19 °C (Zak et al., 2004).

Within plant variability in *A. caven* sexual expression was explored with a sample of 2380 heads collected from 88 individuals, distributed in eight populations, on different years (Table 1). Collection of heads was made by dividing the canopy into four equal sections and collecting between two to three heads from each section at the same height (between 1.5 and 2 m). Each head was dissected under a stereoscopic microscope to observe the gynoecium development and to categorize each flower as hermaphroditic or male. The hermaphrodite: male flowers ratio obtained from the head samples was used as a surrogate for sexual expression. Because in *Acacia* spp., the amount of pollen produced depends more on the hermaphrodite: male flowers ratio than on the number of polyads per flower/head (Kenrick, 2003), sexual expression can be estimated accurately by the floral sex ratio in these species.

The effect of sexual expression on fruit set was studied in 40 trees from four populations. Twenty inflorescences per plant were collected in 2008 and 2010 from each of these trees and sexual expression estimated as above. In 2009, a late frost killed many preformed inflorescences and no plants set fruit in any of the four focal populations that year. To estimate fruit set, segments of 70 cm length on three branches of a similar diameter (ca. 2 cm) were marked on each plant. Selected branches were distributed around