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Andromonoecy and buzz pollination in *Solanum* species (Solanaceae) endemic to the Canary Islands

by

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Abstract

We investigated the pollination and reproductive biology of two Canary Island endemics, *Solanum vespertilio* and *S. lidii* (Solanaceae). We measured male function (pollen development), female function (fruit initiation) and spatial arrangement of reproductive parts within flowers and inflorescences. Furthermore, we observed flower visitors and monitored visitation rates. Both species of *Solanum* display andromonoecy: Long-styled flowers are functionally hermaphrodite and borne proximally on the inflorescences, while short-styled flowers are functionally male and borne distally on inflorescences. Large bees capable of buzzing were the main flower visitors. In particular, the endemic Canarian bumblebee, *Bombus terrestris canariensis*, was a frequent visitor and pollen vector of *S. vespertilio*.

Keywords: andromonoecy, buzz pollination, Canary Islands, *Solanum*.

Introduction

In the endemic flora of the Canary Islands (514 spp.), relatively few species show sexual dimorphism: heterostyly (one sp.) (Olesen & al., 2003); dioecy (16 spp.); monoecy, gynomoecy or gynodioecy (46 spp.) (Helfgott & al., 2000). Andromonoecy has not been reported. However, two endemic Canarian species of *Solanum*, *S. vespertilio* and *S. lidii*, bear short-styled and long-styled flowers on the same plant individual. Functionally they may be andromonoecious (Whalen & Costrich, 1986; Diggle, 1991; Diggle, 1994). Pollen is contained in sac-like poricidal anthers characteristic of buzz-pollination. This implies that pollen can only be removed from the anthers by thoracic muscle vibration of bees. However, to date no studies have investigated the pollination and re-

Resumen

Se estudiaron la polinización y biología reproductiva de dos especies endémicas de las Islas Canarias: *Solanum vespertilio* y *S. lidii* (Solanaceae). Se midieron la función masculina (desarrollo polínico), la función femenina (iniciación de fruto) y la disposición espacial de los órganos reproductivos, tanto en las flores como en las inflorescencias. Se registraron además los visitantes de las flores y su frecuencia. Ambos *Solanum* son andromonoicos: las flores con estilo largo son funcionalmente hermafroditas y proximales en las inflorescencias, mientras que las flores con estilo corto son funcionalmente masculinas y distales en la inflorescencia. Los visitantes más asiduos fueron grandes abejas y abejorros zumbadores. El abejorro endémico *Bombus terrestris canariensis*, en particular, fue un visitante frecuente y un vector de polen para *S. vespertilio*.

Palabras clave: andromonoecia, buzz pollination, Islas Canarias, *Solanum*.

productive systems of these rare endemic species. Here we address the questions: Does female function (fruit initiation) and male function (pollen development) differ between short and long styled flowers? What is the spatial arrangement of reproductive parts within and between flowers? Which insects visit the flowers, and which are potential pollinators?

Materials and methods

The two *Solanum* species of this study belong to the subgenus *Leptostemonum* section *Nycterium*. *Solanum lidii* Sunding is confined to Gran Canaria, while *S. vespertilio* Aiton is found on Tenerife and Gran Canaria. Both species are classified as vulnerable (Gómez Campo, 1996). The plants are small woody shrubs. Inflorescences are non-branching cymes in *S. lidii*, while secondary branching occurs in

S. vespertilio. The blue-purple corolla is weakly zygomorphic. Pollen is contained in yellow poricidal anthers borne on short filaments. The stamens are dimorphic, each flower having 3-4 stamens with short anthers on the dorsal side and one stamen with a long, slender anther on the ventral side of the flower. The style is filamentous and dimorphic (short or long), and deflected to the opposite side of the long stamen (enantiostyly) (unpubl.).

A small population of *S. lidii* consisting of four flowering plants was studied in Temisa, Gran Canaria (27°55'N, 15°30'W). Vegetation was a low xerophytic shrub. A population of *S. vespertilio* consisting of 20 plants was studied in the Anaga peninsula of Tenerife (28°32'N, 16°09'W). Vegetation was a shrub dominated by *Erica arborea* L., located at the borders of the laurel forest.

Pollen grains were analysed by SEM. Diameter of the tricolpate pollen grains was defined as the distance from one aperture to the opposite side through the centre of the pollen grain. Pollen diameter was measured in 10 pollen grains in each of the eight categories: short and long anthers of short-styled and long-styled flowers in each of the two species (Table 1). We tested female function of flowers by marking 49 short-styled flowers (six individuals) and 47 long-styled flowers (five individuals) of *S. vespertilio*. Fruit initiation was monitored two weeks later. Furthermore, we recorded numbers of long-styled and short-styled flowers, flower buds and fruits and their spatial arrangement within inflorescences in 60 inflorescences of *S. lidii* and in 11 inflorescences of *S. vespertilio*.

Flower-visitors of *S. lidii*, were observed on February 10th 2003, while *S. vespertilio* was observed on February 10th, March 11-12th and May 31st 2001, and March 15th and 28th 2003. Rates of visitation were monitored during three 1-h trials during the peak activity period of flower-visitors (10-15h) on March 15th 2003. Pollen load of the most frequent flower-visitors

(*Bombus terrestris canariensis* Perez, two specimens) were analysed by SEM.

Results and discussion

Reproductive system

Pollen grains were developed in both long-styled and short-styled flowers. We found no differences in structure or size of pollen grains of short-styled and long-styled flowers within species (Table 1). Furthermore, no differences were found between pollen from short and long anthers within flowers (Table 1). Whether pollen viability differs remains to be investigated. Of the 49 marked short-styled flowers of *S. vespertilio*, 45 had withered and showed no fruit initiation, while four could not be found two weeks after flowering. Of the 47 marked long-styled flowers, 40 (85%) showed fruit initiation, while seven had withered. Thus, both species were functionally andromonoecious, short-styled flowers being functionally male and long-styled flowers being functionally hermaphrodite. Andromonoecy is common among species of the subgenus *Leptostemonum* (Symon, 1979; Whalen & Costrich, 1986).

In both Canarian *Solanum* species, flowers open in sequence, one or two at a time, from the proximal to the distal end of an inflorescence. Fruits were borne proximally on the inflorescences, followed by long-styled flowers, long-styled flower buds, short-styled flowers, short-styled flower buds and flower buds of indeterminable style length in sequence towards the distal end. This floral arrangement is typical of andromonoecious *Solanum* species (Whalen & Costrich, 1986). Andromonoecy combined with temporal segregation in flowering of male and hermaphrodite flowers may promote out-crossing (Coleman & Coleman, 1982; Anderson & Symon, 1989). Cross pollination may be further enhanced by enantiostyly, which facilitates pollen transfer between mirror-image flowers (Bowers, 1975; Dulberger, 1981)

Table 1. Diameter of pollen grains (Mean \pm SD, N = 10).

Species	Flower type	Long anther	Short anthers	U-test (P) ^a
<i>Solanum lidii</i>	long-styled	20.6 \pm 0.6 μ m	20.5 \pm 0.9 μ m	0.34 n.s.
	short-styled	20.1 \pm 0.7 μ m	19.7 \pm 1.1 μ m	0.80 n.s.
	U-test (P) ^b	1.55 n.s.	1.55 n.s.	
<i>Solanum vespertilio</i>	long-styled	20.0 \pm 0.7 μ m	19.9 \pm 0.6 μ m	0.42 n.s.
	short-styled	20.6 \pm 0.8 μ m	20.2 \pm 1.0 μ m	0.42 n.s.
	U-test (P) ^b	1.71 n.s.	1.59 n.s.	

^a Mann-Whitney U-test of difference in pollen diameter between long and short anthers within flowers. P > 0.05 = n.s.

^b Mann-Whitney U-test of difference in pollen diameter between flowers of different style length. P > 0.05 = n.s.

Pollination

As in most other species of *Solanum*, only large insects capable of buzzing can remove pollen from the anthers and function as pollen vectors (Symon, 1979). For *S. lidii*, only one female individual of *Amegilla* Friese sp. (Apidae) was observed buzzing the flowers during the observation period. Small bees of the genus *Lasioglossum* Curtis (Halictidae) and small beetles (*Meligethes* Stephens sp.) were observed on the anthers, possibly searching for pollen. However, the latter two species did not buzz, nor did they touch the stigma in long-styled flowers, and thus they were not effective pollinators.

In *S. vespertilio*, the Canarian bumblebee, *Bombus t. canariensis*, was a regular visitor. The bumblebees were observed buzzing the flowers from early morning to late afternoon. *Bombus t. canariensis* was the only insect, which regularly visited the flowers of *S. vespertilio* (0.15-0.24 visits/flower/h). During a visit, bumblebees grasped the short stamens firmly with the mandibles and legs, while making a high-pitched sound. Bite marks were regularly seen on the short stamens of old flowers. Although bumblebees did not collect pollen from the long stamen, the apical pore of this anther and the stigma of long-styled flowers often touched the dorsal side of the bee during a visit. SEM analysis revealed that many *Solanum* pollen grains were deposited on both the upper and lower parts of the abdomen, while few adhered to the head.

Other less frequent visitors were *Apis mellifera* L. (0-0.04 visits/flower/h), *Anthophora alluaudi* Perez (Apidae) (0-0.01 visits/flower/h) and *Lasioglossum chalcodes* Brulle (Halictidae). The behaviour of *Anthophora alluaudi* on *Solanum* flowers was similar to that of *B. t. canariensis*. In contrast, *Apis mellifera* was unable to buzz the anthers, and did not touch the stigma of long-styled flowers. *Lasioglossum chalcodes* buzzed the short anthers, but was not sufficiently large to contact the tip of the long anther and stigma during a visit. Thus, the latter two species are poor pollen vectors.

The pollinator fauna of oceanic islands is usually less diverse compared to mainland areas. In particular, large-bodied, specialised flower-visitors are rare (Barrett, 1996). The small potential pollinator pool of the Canarian *Solanum* species may be due to the limited number of large bees capable of buzzing, which inhabit the islands. In comparison, *Solanum rostratum* Dunal and *S. elaeagnifolium* L. growing in a continental desert region (Arizona, USA) are visited frequently by several species of pollen collecting bees (eight and nine spp., respectively) (Linsley & Cazier, 1963). *Solanum elaeagnifolium* is a close relative of *S. vespertilio* (Bohs & Olmstead, 2001).

Although *B. t. canariensis* was the only frequent visitor of *S. vespertilio*, it is a reliable pollinator under various climatic conditions. On many occasions during fieldwork in the Canary Islands, we have observed active *B. t. canariensis* individuals. Weather conditions at which *B. t. canariensis* was foraging ranged from 9°C in rainy weather to 29°C in sunny and windy weather (Y. L. Dupont & C. Skov, unpubl. data). Furthermore, *B. t. canariensis* visits at least 88 different plant species (30 families) in the Canary Islands, and most likely is an important pollinator of many endemic plants (Hohmann & al., 1993). It may thus be regarded as a keystone pollinator species.

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