

First record on secondary pollen presentation in the Cucurbitaceae family

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Aim – Secondary pollen presentation in flowers has been described only in a few species across about 25 plant families. The first report of secondary pollen presentation in the Cucurbitaceae family is given here.

Key result – *Sechium talamancensis*, endemic to high elevations in Costa Rica, presents nearly 39% of its pollen secondarily on the distal ends of its petals. The remaining pollen is presented on the anthers, the primary pollen presenters.

Significance – Closely related and commercially important congeners of *S. talamancensis* do not show secondary pollen presentation. Potential selective advantages of the phenomenon that differentiates *S. talamancensis* from its lower elevation congeners are discussed.

Key words – Cucurbitaceae, *Sechium talamancensis*, secondary pollen presentation.

INTRODUCTION

Secondary pollen presentation, the display of pollen on floral parts other than the anthers, is a rare phenomenon reported from only about 25 distantly-related flowering plant families (Yeo 1993, Howell et al. 1993). The function of secondary pollen presentation varies greatly. Presentation of pollen on a surface other than the primary pollen presenter may protect pollen from desiccation or exploitation, aid cross- or self-pollination, and increase the efficiency of pollen delivery (Yeo 1993, Howell et al. 1993). The placement of pollen for secondary pollen presentation may also serve to extend the male phase of a flower through the protection and regulated release of pollen grains (Howell et al. 1993). Further, the increased efficiency of pollination due to secondary pollen presentation may select for lower investment in ovules per locule (Ladd 1994).

The mechanism, and position of placement of pollen on the secondary presenters, provide insights on the selective advantage and evolution of secondary pollen presentation. Howell et al. (1993) identified nine types of secondary pollen presentation based on the organ where pollen was presented, whether the pollen was exposed or not, and how the pollen was received by the secondary pollen presenter. Pollen has been shown to be secondarily presented on nearly all structures of a flower including the perianth, filaments, and style. There is also high variation in the specific mechanism of application of secondary pollen presentation except that nearly all secondary pollen presenters receive pollen from anthers

dehiscing introrsely during the development and anthesis of a flower (Howell et al. 1993).

Here I report the presence of secondary pollen presentation in *Sechium talamancensis* (Wunderlin) C. Jeffrey (Cucurbitaceae). This is the first record of secondary pollen presentation in the Cucurbitaceae family.

MATERIALS AND METHODS

This research was performed in July 2013 in a montane oak forest in Costa Rica, San José Province at the Cuericí Biological Station (elevation: 2,585 m a.s.l, coordinates: 09°33'N, 83°40'W). In this locality *Sechium talamancensis* (Cucurbitaceae) is abundant. *Sechium talamancensis* is a monoecious tendrillate vine (fig. 1A) endemic to Costa Rica, found from 1,500 to 2,800 m a.s.l (Krings & Braham 2005). Its structure and habit is similar to its lower elevation congeners, economically important *S. edule* (Jacq.) Swartz (locally known as chayote) and *S. tacaco* (Pittier) C. Jeffrey. Staminate flowers of *S. talamancensis* are borne on axillary panicles (fig. 1B) (Krings & Braham 2005). The flowers are actinomorphic and pentamerous. The corolla tube is wide open, exposing ten nectaries that are sunken into the base of the hypanthium. The nectaries produce large amounts of nectar, often visible as large droplets (fig. 1C). The inner surfaces of the flower are covered with glandular hairs. Staminate flowers have five fused stamens culminating in partly-fused anther lobes. Pistillate flowers arise from the same axil as staminate inflorescences. The corolla, calyx and nectaries

of the pistillate flowers are similar to that in staminate flowers. Pistillate flowers have a fusiform ovary and a capitate stigma. During the study period pistillate flowers at the study site had matured into fruits. Therefore, receptive pistillate flowers could not be observed to investigate the process of pollen transfer.

To confirm initial observations of secondary pollen presentation in *S. talamancensis*, I surveyed a total of 41 staminate flowers from eight inflorescences in three vines that were at least 50 m from each other. In each open flower I recorded the presence of pollen on the tip of the petals (fig. 1C). Next, I quantified the pollen displayed on the anthers (primary pollen presenter) and petals (secondary pollen presenter) of five haphazardly selected flowers from the three *S. talamancensis* vines. To quantify the pollen presented on anthers, all the pollen grains on the anthers of a flower were mixed in a water-filled Petri dish (99 mm diameter) containing four haphazardly placed cover glasses (22 × 22 mm). The number of pollen grains within the area of each cover glass was counted under a microscope, averaged, and extrapolated for the area of the Petri dish. To quantify the pollen grains presented on all five petals of each flower, the pollen grains on two petals of a flower were counted under a microscope, averaged, and multiplied by five. The mean ± standard error (SE) of the estimated total number of pollen (sum of pollen on primary and secondary pollen presenters) and pollen on secondary presenter per flower are reported. Care was taken to ensure that pollen did not transfer between the primary and secondary pollen presenter during sampling. However, possible differences in pollen numbers due to removal or deposition by visiting pollinators prior to sampling could not be accounted for.

RESULTS

All the flowers surveyed (41 open flowers on eight inflorescences across three vines) showed secondary pollen presentation on the distal end of the petals (fig. 1C). The staminate flowers had a total of 3429.76 ± 823.88 pollen grains ($n = 5$). Of the total pollen grains, 38.52 ± 3.91 % pollen grains (1368.5 ± 360.69 pollen grains, $n = 5$) were presented on the secondary pollen presenter, the distal ends of each of the five petals. The pollen was presented in a single layer on both primary and secondary presenters. Observations of partially opened flowers showed dehiscent anthers, which had exposed pollen prior to anthesis.

DISCUSSION

S. talamancensis shows exposed secondary pollen presentation on the perianth of its staminate flowers. A considerable proportion of the total pollen produced by the flower (38.52 ± 3.91 %) is presented on the secondary pollen presenter, indicative of its selective advantage. The transfer of pollen from the primary to the secondary pollen presenter likely occurs prior to anthesis. Dehiscence of anther lobes prior to anthesis may allow pollen to stick to the glandular hairs on the distal surface of the petals. Also, the outward movement of petals during the process of anthesis may facilitate the attachment of pollen to the petals. The secondary pollen presentation in *S. talamancensis* falls under the category of 'perianth presenters with exposed pollen presentation' (Howell et al. 1993).

Exposed pollen presentation on the perianth is also seen in *Acrotriche serrulata* R.Br. (Ericaceae) (McConchie et al.

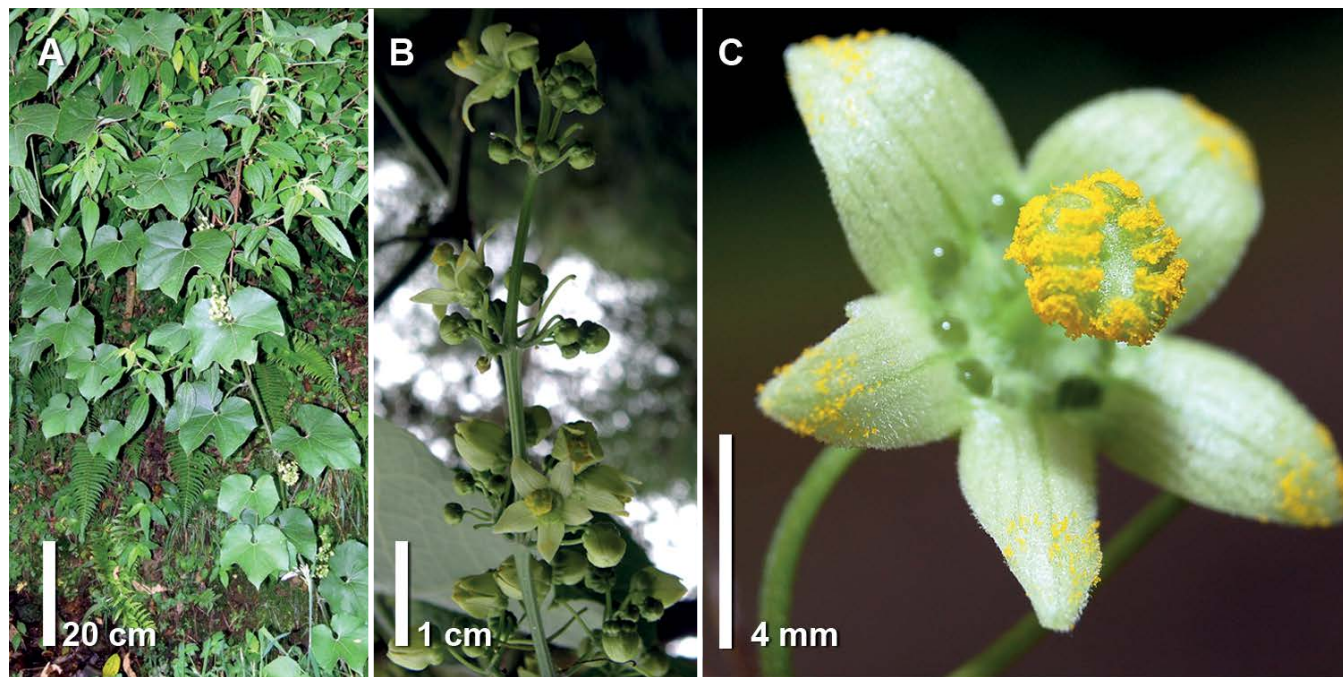


Figure 1 – *Sechium talamancensis*: A, habit; B, male inflorescence; C, staminate flower showing secondary pollen presentation on the distal end of each petal (courtesy of García-Robledo C.).

1986). *Acrotriche serrulata* presents all its pollen secondarily on subterminal hairs on the petal lobes. The loading of pollen on the secondary pollen presenter in both *S. talamancensis* and *A. serrulata* occurs during anthesis. However, in *A. serrulata*, the introrsely dehiscent anthers deposit pollen on the subterminal hairs of the petals that are positioned between the pistil and anthers (McConchie et al. 1986). In *A. serrulata* secondary pollen presentation may serve to protect the pollen from being submerged in the large quantity of nectar that fills its corolla tube (McConchie et al. 1986). In contrast, *S. talamancensis* stamens form a central column with anthers facing the petals, and, during anthesis only a part of the total pollen load is deposited on the secondary pollen presenter. The remaining pollen is retained on the anthers.

Secondary pollen presentation in staminate flowers as seen in *S. talamancensis* also occurs in a few dioecious species in Proteaceae (genera *Aulax* and *Leucadendron*) (Ladd & Donaldson 1993, Ladd 1994) and Myristicaceae (genus *Myristica*) (Armstrong & Drummond 1986) families. Similar to *S. talamancensis*, staminate flowers of *Myristica fragrans* Houtt. form a central staminal column and during anthesis pollen is deposited both on the inner surface of the perianth throat and the apical portion of the staminal column (Armstrong & Drummond 1986).

Since *S. talamancensis* shows secondary pollen presentation on staminate flowers, this rules out the function of secondary pollen presentation to increase the distance between the site of pollen presentation and stigma (Yeo 1993). Instead this form of pollen presentation may provide multiple surfaces for deposition of pollen from the flower to the pollinating visitor (Yeo 1993). In *M. fragrans* beetles seek pollen grains in the staminate flowers that have a wider perianth throat than the pistillate flowers (Armstrong & Drummond 1986). The beetle's body is covered by pollen from the secondary pollen presenter. When the pollen-coated beetles visit mimetic pistillate flowers in search of pollen, the narrower perianth causes pollen to brush onto the stigma. In *A. serrulata*, secondary pollen presentation on the perianth may favour pollination mainly by ants and other insects that crawl on the petals before reaching the nectar source (Schneemilch et al. 2011). Secondary pollen presentation may serve similar functions in *S. talamancensis*. This can be tested through observation of its pollination biology and the morphology of pistillate flowers.

The lack of this phenomenon in the low elevation congeners of *S. talamancensis* (*S. edule* and *S. tacacao*) that have similar floral structures (Krings & Braham 2005) is puzzling. The selective advantage of presentation of pollen on primary and secondary surfaces in *S. talamancensis* could be due to the lack of specificity or high variability in the way pollinators arrive to the flower. The pollinators of *S. talamancensis* are not known. Congeneric and economically important *S. edule* that ranges from 0 to 2000 m a.s.l. is primarily pollinated by stingless bees in the genus *Trigonia* (Wille et al. 1983). Secondary pollinators include wasps. Wille et al. (1983) showed that with increase in elevation the primary pollinators of *S. edule* decreased while the secondary pollinators increased. Further, with increase in elevation

the abundance of the four most important primary pollinators reduced, and, their relative abundance shifted. Perhaps the elevation range at which *S. talamancensis* grows has physiological limitations on the pollinators of its lower elevation congeners. Therefore, secondary pollen presentation may be an adaptation to deposit pollen on a different suite of primary pollinators, under the phylogenetic constraints of the general floral morphology of the genus *Sechium*.

ACKNOWLEDGEMENTS

I thank Carlos Garcia-Robledo for help with field observations and their documentation, and two anonymous reviewers whose comments improved the manuscript. I thank the Organization for Tropical Studies and Cuerici Biological Station for logistical support. The research was supported by the Christian Lieding Scholarship Program and University of Nebraska-Lincoln School of Biological Sciences Special Funds.

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Manuscript received 26 Aug. 2014; accepted in revised version 6 Feb. 2015.

Communicating Editor: Elmar Robbrecht.