

Autonomous self-pollination and pseudo-fruit set in South African species of *Eulophia* (Orchidaceae)

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Abstract

Autonomous self-pollination is surprisingly common among orchids and is thought to provide reproductive assurance when pollinators are scarce. During investigations of the reproductive biology of the orchid genus *Eulophia*, consistently high rates of capsule set were observed in *Eulophia clavicornis* var. *clavicornis*, *E. c.* var. *inaequalis*, *E. c.* var. *nutans* and *E. tenella*. A breeding system experiment showed that *E. c.* var. *nutans* is capable of autonomous self-pollination. Emasculated flowers of this taxon did not set fruit, suggesting that agamospermy is unlikely. The likely mechanism of autonomous self-pollination in these taxa was identified as the partial or complete absence of rostellum tissue, allowing contact between pollinia and stigmatic fluid, and thus for pollen tubes to grow from *in situ* pollinia to the ovules. In some individuals, basal flowers on an inflorescence possess intact rostellae and functional pollinaria, whereas distal flowers lack pollinia. Neither of these two flower classes set capsules. A few individuals of the otherwise outcrossing *E. zeyheriana*, which normally have well-developed rostellae, show evidence of autonomous self-pollination resulting from interrupted rostellae in these plants. Other outcrossing *Eulophia* species (*E. speciosa* and *E. streptopetala*) sometimes show high levels of fruit set, seemingly without insect visitation. However, investigations showed that these are pseudo-fruits lacking seeds and are a result of insect parasitism. Therefore, high levels of fruit set alone should not be used to infer autonomous self-pollination in orchids.

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1. Introduction

Darwin (1867) wrote extensively about adaptations such as pollinarium reconfiguration (Peter and Johnson, 2006a) that prevent self-pollination in orchids, and was especially troubled by the situation in *Ophrys apifera* and 23 other species of orchids known at that time to undergo autonomous self-pollination. He did, however, recognise that self-pollination in plants might be adaptive, providing reproductive assurance under conditions of pollinator and mate limitation (Darwin, 1876; Lloyd, 1992), although there is conflicting empirical evidence to support this contention (Herlihy and Eckert, 2002; Kalisz et al., 2004). Such conditions, particularly pollen limitation, are known to be frequent among deceptive orchids (Neiland and Wilcock, 1998; Tremblay et al., 2005; Smithson, 2006).

Automatic (i.e. vectorless) self-pollination, which usually occurs when anthers come into contact with stigmas or when pollen falls onto the stigma, is normally referred to as “autonomous autogamy” or “autonomous self-pollination” (Richards, 1986). The use of the more general term “self-pollination” is equivocal, including both autonomous self-pollination as well as self-pollination within single hermaphrodite flowers mediated by pollinators. Self-pollination between different flowers on an individual is unambiguously known as geitonogamy. Cleistogamy is widely and consistently used to describe automatic self-pollination within unopened buds. However, self-pollination within a single flower, either through the services of a pollinator or through the action of the floral organs, is often referred to under the catch-all term “autogamy”. Thus we use the term “autonomous self-pollination” throughout this paper to refer to within-flower self-pollination that occurs without the aid of an animal vector.

Autonomous self-pollination has been known in orchids since 1833 when Brown described the phenomenon in *O. apifera*

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(Catling, 1990). Catling's (1990) review of the incidence of autonomous self-pollination in the orchids showed that autonomous self-pollination occurs in all orchid subfamilies and the majority of tribes and subtribes, with 350 species known at that time to possess mechanisms of autonomous self-pollination. A review of subsequent peer-reviewed articles, combined with the list of autonomously self-pollinating species compiled by Catling (1990) and Van der Cingel (1995, 2001), provides a more complete estimate of the importance of autonomous self-pollination in the Orchidaceae (Peter, 2009). This analysis suggests that autonomous self-pollination is common in the family, making up 31% of the species in which pollination systems are known, and raises the number of autonomously self-pollinating orchid species to 395 (Peter, 2009).

In the tribe Cymbidieae, autonomous self-pollination has been recorded in a number of species including *Oeceoclades maculata* (Gonzalez and Ackerman, 1988) and *Eulophia alata* (Catling, 1990). In these species the stipe of the pollinarium bends sufficiently for the pollinia to be deposited over the rostellum (the small flap of tissue separating the stigmatic cavity from the area under the anther cap housing the two pollinia) and onto the stigma. In addition, Williamson (1984) documented autonomous self-pollination as a result of the absence of rostellar tissue in eight *Eulophia* species from west Africa, although two of these taxa were subsequently reduced to synonymy by Thomas (1998).

While working on the pollination biology of the South African species of *Eulophia* and *Acolophia*, we have examined 29 taxa (mostly species but also including a number of subspecies or varieties as defined by Hall (1965)), many of which are pollinated by beetles or bees (Peter and Johnson, 2006b; Peter and Johnson, 2008; Peter, 2009; Peter and Johnson, 2009, this issue). Four taxa consistently showed very high levels of fruit set across different sites and different years, suggesting the possibility that these species might undergo autonomous self-pollination as has been described in other species of *Eulophia* (Williamson, 1984). In addition, very high fruit set indicative of autonomous self-pollination was also observed in some individuals or populations

of species known to be outcrossing. We therefore set out to determine 1) the occurrence and 2) the mechanism of autonomous self-pollination in these taxa.

2. Materials and methods

2.1. The study taxa and sites

This study deals with four taxa that appear to undergo autonomous self-pollination. Three of these taxa were treated at varietal level by Hall (1965), namely *E. clavicornis* Lindl. var. *clavicornis* (Fig. 1A), *E. c.* var. *inaequalis* (Schltr.) A. V. Hall and *E. c.* var. *nutans* (Sond.) A.V. Hall (Fig. 1B) and the fourth, *E. tenella* Rchb. f. (Fig. 1C), at species level.

Some individuals of a number of species that are known to be outcrossing were seen to develop numerous capsules, seemingly without being pollinated as there is no evidence of pollinator mediated pollinia deposition on the stigmas of these flowers. These include *E. speciosa*, *E. streptopetala* and *E. zeyheriana*. These are all species known to be primarily insect-pollinated, as described by Peter (2009) and Peter and Johnson (2008). The basis for this phenomenon was also investigated.

Observations were conducted at a variety of sites in the Eastern Cape and KwaZulu-Natal provinces of South Africa (Table 1). In most cases these study sites were recently burnt grasslands with large to very large population of the study taxa although some populations of *E. clavicornis* var. *clavicornis* and *E. c. inaequalis* were small or dispersed (smaller populations are indicated in Table 1). *E. streptopetala* occurs in scrubby vegetation along the margins of forests.

2.2. Mechanisms of autonomous self-pollination

The gnostemia of all flowers on either fresh or preserved unbagged inflorescences were examined with a dissecting microscope and imaged digitally. Additional images were collected using scanning electron microscopy and macro photography.

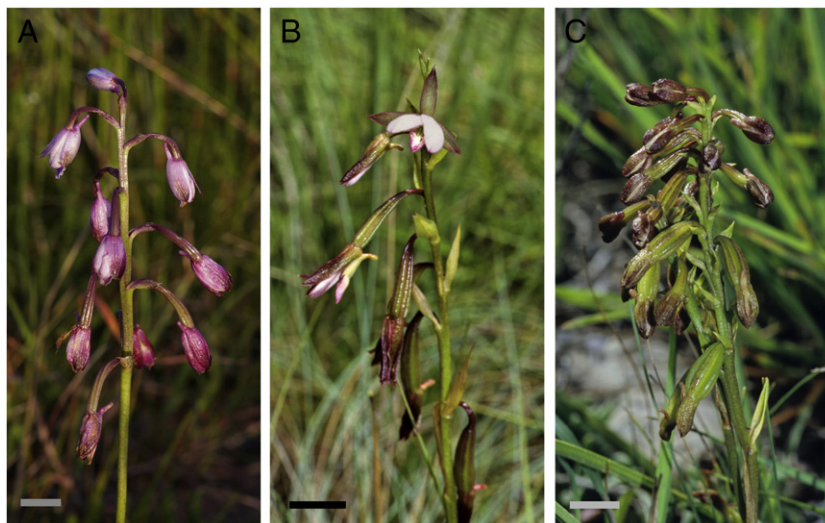


Fig. 1. Inflorescences of (A) *Eulophia clavicornis* var. *clavicornis*; (B) *E. clavicornis* var. *nutans* and (C) *E. tenella* showing very high rates of fruit set consistent with autonomous self-pollination. Bar=10 mm.

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