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Breeding system and pollination of selected orchids of the genus *Chloraea* (Orchidaceae) from central Chile

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Abstract

The breeding system determines different ways whereby seeds will be produced, and the degree of dependency of plants on pollinators for seed set. The genus *Chloraea* (Orchidaceae) has its main center of diversity in southern South America. There is only poor knowledge concerning its breeding system and pollination. We determined the breeding system of *C. crispa*, *C. chrysantha*, *C. galeata*, and two color forms of *C. bletioides* (yellow- and white-flowered forms). None of the species in this study produced fruits through apomixis or autogamy, thereby indicating a complete dependency on pollen and pollinators. Geitogamy did not differ significantly with respect to xenogamy excepting in the yellow-flowered form of *C. bletioides.* Thus, the indexes of self-incompatibility for the white- and yellow-flowered forms of *C. bletioides*, *C. galeata, C. crispa,* and *C. chrysantha,* were 1.00, 0.56, 0.82, 1.09, and 0.81, respectively; indicating that, excluding the yellow-flowered form of *C. bletioides* which must be regarded as partially self-incompatible, all orchids assessed are totally self-compatible plants. Natural fruiting in the yellow-flowered *C. bletioides*, *C. chrysantha* and *C. galeata* was high, in spite of being nectarless orchids, since the availability of pollinators under natural conditions seemingly resulted unlimited. However, no pollinator was observed visiting *C. chrysantha* and *C. galeata*, whereas the yellow-flowered form of *C. bletioides* was visited by hymenopterans and coleopterans. At contrast, reproductive success of the white-flowered form of *C. bletioides* and *C. crispa* was pollen limited, the former being visited by hymenopterans, dipterans, and colepterans; and the latter by two hymenopterans.

Keywords: *Chloraea*; Orchidaceae; Self-compatibility; Pollinator-dependency

Introduction

The extent to which flowering plants depend on external vectors for outcross pollen transportation is a central question in plant reproductive ecology. The breeding system of a species determines the way whereby seeds will be produced, and the degree of dependency of plants on pollinators for seed set (Lovett-Doust and Lovett-Doust, 1988; Richards, 1997). Reproductive failure in plants can often be attributed to either pollination limitation where the movement of viable pollen between flowers through the absence of pollinators is insufficient (Bierzychudek, 1981; but see Zimmerman and Pyke, 1988), or to resource limitation where insufficient resources are available to allow the

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maximum fruit set to take place (Primack and Hall, 1990; Primack and Stacy, 1998). Among the Orchidaceae, nectariferous orchids produce more successfully fruits and seeds as compared with nectarless orchids (Neiland and Wilcock, 1998; Proctor et al., 1996). During the origin of Orchidaceae evolution in the Cretaceous, most angiosperm flowers would have been visited by unspecialized insects like beetles and flies, which pollinated them while feeding on both floral and vegetative tissues (Neiland and Wilcock, 1998; Proctor et al., 1996). The most likely origin of the highly adapted mechanisms among nectarless orchids is that they arose from primitive orchids, which had even lower levels of fruit set than seen today, probably owing to the existence of unspecialized and largely unrewarding flowering environments (Neiland and Wilcock, 1998). In this sense, a small adaptation that improved pollinator attraction would have had a reproductive advantage and would have increased in frequency.

The most likely shortcut to break away from the ecological and evolutionary limitations imposed by consistent sexual reproductive failures, is the adoption of pollinator-independent fruit production (i.e., autogamy and/or agamospermy), or the provision of rewards in order to entice pollinators (i.e., allogamy) (Neiland and Wilcock, 1998). Nevertheless, agamospermy is infrequent in orchids because it may be inhibited since embryo-sac formation in the family is unusual in requiring the presence of pollen on the stigma as a stimulus (Neiland and Wilcock, 1998). Automatic self-pollination has been reported to be more widespread but is probably morphologically prevented in most orchids by the herkogamous structure of flowers (Proctor et al., 1996). Therefore, the way adopted by orchids in order to ensure a successful fruit set is to produce nectar for pollinator enticing, thus precluding autogamy or agamospermy as possible pathways for seed set (Neiland and Wilcock, 1998; Proctor et al., 1996).

The genus *Chloraea* has its center of diversity in southern South America (Correa, 1969). Its taxonomy and systematics is poorly known (but see Correa, 1969; Lehnebach, 2003) equally than its breeding system and pollination (but see Clayton and Aizen, 1996; Lehnebach and Riveros, 2003). The aim of this work is to determine the breeding system and natural pollination of selected species of the genus *Chloraea* in order to increase our knowledge about the breeding strategies of a part of the endemic orchids of this region. If a great amount of orchids are self-compatible, we expected that self-compatibility in orchids of the genus *Chloraea* is widely represented. Because nectarless orchids are usually limited by pollinators for fruit setting, we also expected that all orchids herein assessed are limited by pollinators for fruit production regarding that all of them are thought to be deceit-pollinated on account of bearing non-rewarding nectaries for attracting nectar-feeding pollinators (personal observations).

Methods

Species and study site

The white- and yellow-flowered forms of *C. bletioides* Lindl., *C. crispa* Lindl., *C. chrysantha* Poepp., and *C. galeata* Lindl., are geophytic orchids that inhabit hillsides in central Chile (Fig. 1; Correa, 1969). All these species exhibit pauciflorous inflorescences with 3–10 flowers per plant in *C. bletioides* (both color morphs), 6–20 in *C. crispa*, 8–20 in *C. chrysantha*, and 10–20 in *C. galeata* (Correa, 1969; Novoa et al., 2006). Flowering and fruiting occur from October to January in the austral spring-time season (Novoa et al., 2006).

The white-flowered *C. bletioides* can be found from ca. 32°S to 38°S and was studied at the Río Clarillo National Reserve (33°S), from October to December 2003, specifically in equatorial-facing slopes neighboring the Clarillo river. *C. crispa* ranges from ca. 38°S to 41°S and was studied in a field placed 20 km away from Yumbel city (38°S approx.) in an area of stabilized sand dunes, which is strongly cultivated with plantations of *Pinus radiata.* Both *C. chrysantha* and *C. galeata* range from 33°S to 38°S, whereas the yellow-flowered *C. bletioides* has been observed only at the 33°S. These three species were studied at the Roblería del Cobre de Loncha National Reserve (34°S approx.) from October 2002 to January 2003, and from October 2003 to December 2003, in equatorial-facing slopes nearby El Chivato hill.

Breeding system and natural pollination

To determine the breeding system of *C. bletioides* (two color forms), *C. crispa*, *C. chrysantha*, and *C. galeata*, four pollination trials and in addition a control for natural pollination were conducted (Kearns and Inouye, 1993). Each treatment was performed in 20, 25, 90, 19, and 22 individual plants in the white- and yellow-flowered forms of *Chloraea bletioides, C. crispa*, *C. chrysantha*, and *C. galeata*, respectively (all treatments equally distributed on each plant). To test whether these orchids are capable of fruit setting in the absence of pollen (i.e., agamospermy), an apomixis test was performed on at least 15 flower buds, which were emasculated (i.e., anther excision) and bagged until seed dispersal in order to prevent any flower–pollinator interaction. Similarly, to test whether these orchids are capable of fruit setting after receiving pollen from the same flower in the absence of pollinators carrying pollen within the flower (i.e., autogamy), an automatic