Distyly and heteromorphic incompatibility in oceanic island species of *Erythroxylum* (*Erythroxylaceae*)

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**Abstract:** Surveys of oceanic island floras have shown that heterostyly is usually absent in such regions, probably because this floral polymorphism is often associated with a self-incompatibility system. In this context we describe the floral biology of three species of *Erythroxylum* on La Réunion island and examine the compatibility relationships of one of these species, *E. laurifolium*. All three species are distylos but differ in relative stigma-anther separation in the different morphs. In general, short-styled flowers have greater stigma-anther separation than long-styled flowers, which are often homostylous in appearance. This lack of stigma-anther separation in long-styled flowers is due to style twisting which improves reciprocity at the high organ level. The reduced stigma-anther separation does not appear to be associated with the evolution of selfing as *Erythroxylum laurifolium* shows heteromorphic self-incompatibility. The presence of heteromorphic incompatibility in a group of species that have colonized an oceanic island is discussed.

Heterostyly is a genetically controlled floral polymorphism known to occur in 25 families of flowering plants, distyly being present in at least 23 families (GANDERS 1979a, BARRETT 1993) and tristyly in six families (BARRETT 1993, THOMPSON & al. 1996). For a species to be considered heterostylos, the floral morphs must differ reciprocally in stamen and style length (LLOYD & WEBB 1992). In many species, the two morphs also differ in pollen size, pollen production and in other ancillary features (DULBERGER 1992). A common associated feature of heterostyly is the presence of a self- and intramorph-incompatibility system which allows only legitimate (between anthers and stigmas of the same level) pollination to set fruit. This is usually termed heteromorphic incompatibility (BARRETT 1988).

Surveys of oceanic island floras have shown that heterostyly is often absent in such communities, e.g. Hawaii (CARLQUIST 1974), New Zealand (GODLEY 1979) and the Galapagos (McMULLEN 1987). This absence of heterostyly from oceanic islands may be due to the fact that many heterostylos species are self-incompatible and that according to "Baker's Law" self-compatible species are more likely to establish populations after long distance dispersal due to their ability to reproduce.
in the absence of pollinators (Baker 1955, 1967; Stebbins 1957). Indeed, Baker (1967) used the lack of heterostylosus species on Hawaii as evidence for this idea. Alternatively, the added constraint for heterostylosus species is that they often show heteromorphic incompatibility in which only “legitimate” pollination between morphs causes fruit set. This means that each plant is only compatible with half the population when the morph ratio is 50/50. This could be a major constraint for the colonization of oceanic islands where populations sizes may be small.

In several cases heterostyly has been shown to break down in a pattern that appears to be related to both stochastic and selective pressures during island colonization. Colonisation of the Carabbean islands by *Turnera ulmifolia* appears to have involved the breakdown of distyly since islands are populated by self-compatible long-homostylosus individuals derived from distylosus self-incompatible populations in central- and South-American (Barrett & Shore 1987). In *Eichhornia paniculata* most populations in Brazil and central America are tristylosus, whereas on Jamaica the short-styled morph is absent and many populations are monomorphic for mid-styled plants. Many of these are dominated by modified selfing variants of the mid-styled morph which have at least one anther placed adjacent to the stigma (Barrett & al. 1989).

The Mascarene islands of La Réunion, Mauritius and Rodrigues are tropical oceanic islands that have never been connected to continental land masses (MacDougall 1971). In contrast to other oceanic islands, we have found that heterostyly occurs in several families, notably the Linaceae (Thompson & al. 1996), Rubiaceae (Paillet & Thompson 1997) and Olacaceae (Paillet, unpubl.). The distylosus *Gaertnera vaginata* (Rubiaceae) endemic to La Reunion island shows heteromorphic incompatibility (Paillet & Thompson 1997).

*Erythroxylum* (Erythroxylaceae) is a genus of about 190 species centered mostly in the neotropics but distributed in all tropical regions (Friedmann 1987). The genus is represented by distylosus (Ganders 1979b), dioecous (Bawa & Opler 1975), and (at least one) agamospermous species (Berry & al. 1991). Detailed studies of distylosus *Erythroxylum* species have shown that both self-compatible and self-incompatible species occur (Ganders 1979b). In the southern Indian Ocean the genus *Erythroxylum* contains 27 species indigenous to Madagascar, two species endemic to the Seychelles and four species endemic to the Mascarene archipelago. Most of the Madagascan, Seychelles and Mascarene species have been reported to be morphologically heterostylosus but no study confirming the presence of reciprocal herkogamy and heteromorphic incompatibility have been performed.

The purpose of the present paper is to quantify variation in floral traits in three *Erythroxylum* species endemic to the Mascarene islands and to quantify whether one species (*Erythroxylum laurifolium* Lam.) has a heteromorphic incompatibility system on La Réunion island. The objectives of our study are thus as follows: (1) to confirm whether the species present on La Réunion island show style length and anther height polymorphisms typical of distylosus species, (2) to quantify any pollen size and number variation associated with heterostyly, (3) to quantify female fecundity in a natural population of *Erythroxylum laurifolium* and (4) to examine whether *E. laurifolium* on La Réunion island shows a heteromorphic incompatibility system.