THE GENETICS OF SELF-COMPATIBILITY AND ASSOCIATED FLORAL CHARACTERS IN *TOLPIS* (ASTERACEAE) IN THE CANARY ISLANDS

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Members of the genus *Tolpis* (Asteraceae) endemic to the Canary Islands comprise a monophyletic group with the dispersal of one species to the Cape Verde Islands. Most species are self-incompatible or pseudo-self-compatible perennials. However, one species, *Tolpis coronopifolia*, consists of self-compatible annual plants with several floral features typical of the selfing syndrome. The evolution of self-compatibility and the selfing syndrome was studied by producing synthetic hybrids between self-incompatible/pseudo-self-compatible and self-compatible plants to determine the genetic architecture of breeding system and floral trait differences. There was a correlation between self-compatibility and selfing floral traits in the F_2 generation. Self-incompatibility in *Tolpis* appears to be controlled by a locus of major effect but with modifier loci affecting seed set. Segregation of floral traits indicates that they are controlled by multiple loci. The high molecular similarity between plants with the two breeding systems suggests that divergence of the self-compatible *T. coronopifolia* from self-incompatible/pseudo-self-compatible ancestors has been recent. The association between breeding system and floral features likely results from pleiotropy or close linkage and may have facilitated the rapid evolution of the morphologically distinct self-compatible *T. coronopifolia*.

Keywords: Asteraceae, Canary Islands, self-compatibility, *Tolpis*.

Online enhancements: appendix figures.

Introduction

Self-incompatibility (SI; also used to indicate self-incompatible) is the most common mechanism for enforcing outcrossing in flowering plants (Igic et al. 2008). However, the loss of SI to produce self-compatible (SC; also used to designate self-compatibility) plants is also quite common and has occurred repeatedly in angiosperms (Goodwillie 1999; Barrett 2002; Beck et al. 2006; Igic et al. 2008; Foxe et al. 2010). The two primary advantages commonly attributed to selfers over outcrossers is an inherent transmission advantage (Fisher 1941) and the ability to reproduce sexually without mates (Kaliz et al. 2004; Charlesworth 2006). Higher selfing may also decrease hybridization with closely related sympatric species (Antonovics 1968; Levin 1978, 2000 [p. 11]; Fishman and Wyatt 1999; Wendt et al. 2002; Grossenbacher and Whittall 2011). Potential downsides of selfing include inbreeding depression and reduced genetic variation, since selfing increases homozygosity and lowers the effective population size (Goodwillie et al. 2005; Yang and Hodges 2010).

Selfing facilitates colonization following dispersal because one individual can initiate a sexually reproducing population in the absence of mates and pollination vectors (Baker 1955;

Stebbins 1957; Pannell and Barrett 1998). Stebbins (1957) viewed this idea of such general significance that he called it Baker's law. Selfing ability may be especially critical in the persistence of plants on isolated oceanic islands because ancestral colonizers likely arrived by rare, long-distance dispersal events (Cowie and Holland 2006). However, just as Allard (1965) and others had argued for the importance of genetic variation in selfing species, Carlquist (1966) suggested that Baker's law may not be of general application to the insular situation because of the low genetic variation present in a colonizer originating from a selfing source population. He thus emphasized that the higher genetic diversity typical of outcrossed populations is crucial for the persistence and diversification of insular lineages. Reviews of the literature by Ehrendorfer (1979) and Barrett (1996) supported the Baker (1955) hypothesis because the majority of endemic flowering plants examined from islands are SC. Two well-studied island systems with a high frequency of SC species are the Galápagos (McMullen 1987, 1990) and New Zealand (Webb and Kelly 1993). More recent compilations for the Robinson Crusoe (Juan Fernandez) Islands likewise document the prevalence of SC species (Anderson et al. 2001; Bernardello et al. 2001). However, some of the most successful insular radiations in Asteraceae, the plant family with the highest number of oceanic island endemics (Crawford et al. 2009*b*, 2011), originated from SI ancestors in which there was likely some "leakiness" in the system. That is, the plants were pseudo-

self-compatible (PSC; also used to designate pseudo-self-compatibility; Levin 1996; reviewed in Crawford et al. 2009*b*, 2011). Because PSC colonizers originated from potentially outcrossing source populations, they would likely carry more genetic variation than a propagule from a highly selfing population, yet they could set some selfed seed (Levin 1996; Crawford et al. 2008).

True SC is achieved via irreversible breakdown of a functioning S-locus, resulting in the potential to produce high levels of selfed seed (Igic et al. 2008; Pettengill and Moeller 2011). In addition, a suite of floral characters often evolves in association with SC (Ornduff 1969; Slotte et al. 2012). Available evidence indicates that many of the SC species that have been studied on oceanic islands originated from SC colonizers (Carlquist 1974, chap. 9; McMullen 1987, 1990; Sun and Ganders 1988; Anderson et al. 2001; Bernardello et al. 2001). Despite the apparent prevalence of SC species, there are at least some reports of various levels of PSC in island endemics, such as the silversword alliance in Hawaii (Carr et al. 1986; Barrier et al. 1999; Baldwin 2003; but see Bainbridge and Baldwin 2010) and *Scalesia* from the Galápagos Islands (Nielsen et al. 2000, 2003). A recent study of the Canarian clade of *Tolpis* (Asteraceae) has shown that, with one exception, species are

SI or PSC (i.e., SI-PSC). The one exception is the SC species *Tolpis coronopifolia* (Crawford et al. 2008), which has several components of the selfing syndrome, including much smaller capitula with fewer, smaller florets (fig. 1). Also, unlike other Canary Island endemic *Tolpis* species, *T. coronopifolia* is an annual (or occasionally biennial) rather than perennial. The SC condition is likely derived, as it is in most other flowering plants (Beck et al. 2006; Igic et al. 2008), and evolved in situ in the Canaries. We are unaware of the in situ evolution of SC and the selfing floral syndrome during the radiation of other island lineages in Asteraceae; one species in the silversword alliance is SC but does not exhibit the selfing syndrome (G. D. Carr, personal communication).

The genus *Tolpis* is a good system to address questions about the evolution of SC and the selfing syndrome in an insular lineage. While the contrasting floral features of closely related outcrossing and selfing species have long been recognized (Ornduff 1969), little is known about the dynamics of change in a variety of floral features associated with the breakdown of SI (but see Slotte et al. 2012). Because the SC *T. coronopifolia* can easily be hybridized with SI-PSC taxa of *Tolpis* (Crawford et al. 2009*a*), it is feasible to study the segregation of characters in F_2 interspecific hybrids. Molecular divergence between *T.*

Fig. 1 Capitula of *Tolpis* sp. nov. 1 (population Santos-Guerra 4; *A*), *Tolpis coronopifolia* (population Crawford et al. 1850; *B*), an F_1 hybrid (*C*), and two F_2 hybrids (*D*) showing the range of size variation in this generation.

coronopifolia and the other species in the Canarian clade is minimal to nonexistent, using data sets normally effective in resolving relationships among congeneric species. These include inter-simple sequence repeat markers (Archibald et al. 2006), allozymes (Crawford et al. 2006), and nuclear internal transcribed spacer (M. E. Mort, unpublished data; R. K. Jansen, personal communication) and noncoding plastid DNA sequences (Mort et al. 2010), suggesting that it has diverged from its SI ancestors recently and rapidly.

Available data from reproductive biology, floral morphology, and molecular markers suggest that SC and several floral traits typically associated with selfing have evolved rapidly in *Tolpis* in the Canary Islands. The purpose of this study was to examine the pattern of inheritance of SC and floral morphology in hybrids between SC and SI-PSC plants of *Tolpis*. Of particular interest was testing the hypothesis that rapid evolution of an SC species of *Tolpis* may have been facilitated by the genetic architecture of the selfing suite of traits.

Material and Methods

Hybrids were made between an undescribed SI-PSC species of Canarian *Tolpis* and the SC species *Tolpis coronopifolia* (Crawford et al. 2008). The SI-PSC species belongs to the *Tolpis laciniata* complex and has been designated *Tolpis* sp. nov. 1 (Crawford et al. 2009*a*). The methods for determining the breeding systems of the parental species were described by Crawford et al. (2008). Briefly, capitula were enclosed in fine netting before anthesis, and pollen was distributed over the stigmatic surfaces of the same capitula on successive days until the capitula closed. Self seed set was determined by the proportion of plump, black fruits with embryos. Plants grown from wild-collected seed served as the parents for hybridization, including seeds from population Santos-Guerra 4 (on La Palma) for the SI-PSC parent and seeds from population Crawford et al. 1850 (on Tenerife) for the SC parent. These seeds and all subsequent progeny were reared in consistent environmental conditions in the University of Kansas greenhouses. Plants used to generate F_1 hybrids had proportion pollen viability exceeding 0.80. Crosses were effected by bagging capitula before anthesis and rubbing them together on successive days until fruit was set, which is indicated by the onset of senescence of the peduncle below the capitulum. The seedlings of F_1 hybrids could be detected by intermediate leaf morphology (fig. 2). When SI-PSC plants were the egg parent, nearly all progeny were hybrids, but with SC *T. coronopifolia* as egg parent, fewer than 15% of the progeny were
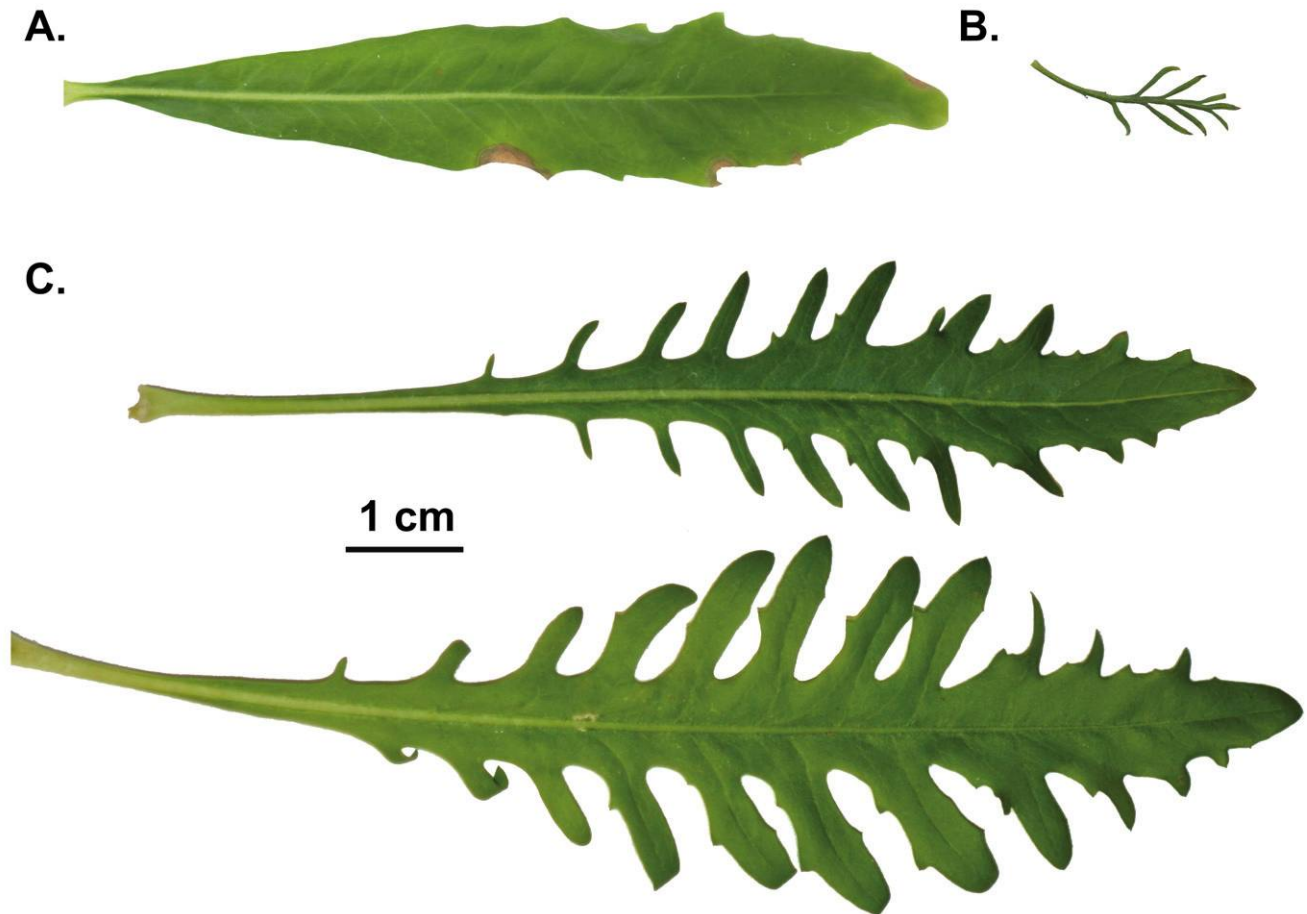

Fig. 2 Leaves of *Tolpis* sp. nov. 1 (population Santos-Guerra 4; *A*), *Tolpis coronopifolia* (population Crawford et al. 1850; *B*), and two F_1 hybrid individuals (*C*).

hybrids, and the rest were selfs. Proportion pollen viability of the F_1 hybrids used to generate the F_2 generation was higher than 0.90. Vouchers for parental and F_1 hybrids are deposited in the McGregor Herbarium (KANU) at the University of Kansas.

Nine F_2 families were generated by bagging F_1 plants before anthesis, collecting the resulting fruits, and germinating them. From the resulting plants, a total of 129 individuals were measured for the following floral characters: number of florets per capitulum, diameter of capitula, and floret, anther, and stigma lengths. For the first two characters, the average of two capitula per plant was used, and for the latter three characters, the average of five florets from each of two capitula was taken. Pollen viability for each plant was determined by examining at least 200 pollen grains stained with lactophenol aniline blue (Kearns and Inouye 1993; Crawford et al. 2008). Self seed set for F_2 individuals was determined by the same methods used to assess self seed set in the parental species. Large, plump, black to brown-black fruits containing viable embryos were easily distinguished from shriveled, light brown to tan fruits with no embryos (Crawford et al. 2008). Five tan, shrunken fruits from two plants of each of the nine F_2 families were dissected, and there was no evidence of embryos. The pollen : ovule ratio (average of two capitula) was determined for 126 plants, and proportion pollen viability and proportion self seed set (in 124 plants) were calculated by pooling from two or more capitula.

We used general linear models (regression and ANOVA) to determine whether measurements differed among F_1 families. The proportion variables, proportion self seed set and pollen viability, were arcsine square root transformed for these analyses. Calculations were done using Minitab (ver. 14).

Results

The F_2 generation segregated roughly into SI-PSC and SC classes in a 3 : 1 ratio, regardless of the specific criteria used to define the classes (fig. 3A). For example, if ≤0.10 seed set and ≥0.70 are used to define SI-PSC and SC classes, respectively, then the ratio is 3.16 : 1, whereas using ≤0.30 and ≥0.50 results in a 2.94 : 1 ratio. The segregation is bimodal, with most individuals having very low or relatively high self seed set. A substantial proportion of the variation in self seed set may be due to the availability of viable self pollen (fig. 3B). The regression of self seed set onto pollen viability is highly significant ($F_{1, 122} = 24.3$, $P < 0.001$). However, the abundance of plants with high pollen viability yet low self seed set indicates that pollen viability does not fully account for differences in self seed set (fig. 3B). Pollen viability differed significantly among families within the F_2 generation ($F_{8, 119} = 7.83$, $P < 0.001$), but self seed set did not ($F_{8, 115} = 1.86$, $P = 0.07$). All five of the morphological traits differed significantly among families.

The summary statistics for measurements of floral traits in F_2 individuals are given in table 1, and their frequency distributions are provided in figures A1–A5 (available in the online edition of the *International Journal of Plant Sciences*). Each trait displays continuous variation, suggesting that multiple—and perhaps many—loci contribute to differences between the
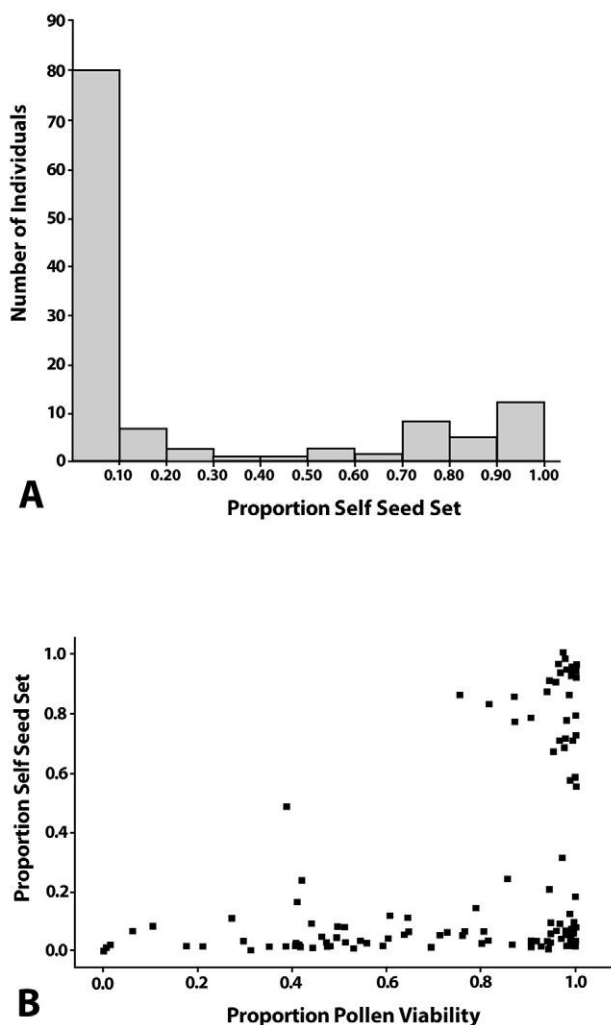

Fig. 3 *A*, Histogram showing number of individuals at each proportion of self seed set in the F_2 generation. *B*, Scatter plot of proportion pollen viability versus proportion viable seed set for F_2 generation.

parental genotypes. As expected, mean floral dimensions (i.e., florets per capitulum, capitulum diameter, and floret, anther, and stigma lengths) are positively correlated (table 2). Pollen : ovule ratio is significantly correlated with floret, anther, and stigma length but not with self seed set (table 2). Interestingly, the floral dimensions exhibit significantly negative correlations with self seed set and pollen viability. The relationship between mean anther length and self seed set is illustrated in figure 4. Anther length shows no relationship with self seed set for anthers less than 28 μm. However, self seed set drops to nearly 0 for plants with anthers longer than 28 μm. Similar but less extreme patterns are observed for other floral dimensions.

Discussion

The roughly 3 : 1 ratio for SI-PSC versus SC individuals in the F_2 generations suggests that the breeding system in *Tolpis*

Table 1

Summary Statistics for Floral Traits Measured in *Tolpis* F$_2$ Hybrids

Variable	N	Mean	SD
No. florets/capitulum	129	88.41	18.94
Capitulum diameter (cm)	129	1.5155	.2920
Floret length (cm)	129	.9030	.1554
Anther length (μm)	129	26.627	3.123
Stigma length (μm)	129	5.6885	.8926
Proportion pollen viability	129	.7608	.2902
Proportion self seed set	124	.2447	.3469
Pollen : ovule ratio	128	1904.5 : 1	499.7

Note. *N*, number of plants.

is controlled by a major locus, as it is in the sporophytic SI (SSI) system of other Asteraceae such as *Senecio squalidus* (Hiscock and Tabah 2003), and that SI (at least with regard to the alleles present in the parents of the hybrids) is dominant to SC. The match to a 3 : 1 ratio is even closer if one excludes those plants with low pollen viability. Although not always explicitly considered in studies of seed set, low pollen viability can clearly reduce the level of self seed set even in fully SC individuals (Gottlieb 1973). The complexity of the SSI system in Asteraceae has been documented though not fully elucidated. A major factor conferring complexity is the possible dominance relationships among S-alleles with SSI (Brauner and Gottlieb 1987; Levin 1996; Hiscock and Tabah 2003; Busch and Schoen 2008; Brennan et al. 2011). Dominance among alleles may differ in pollen and stigma, resulting in different compatibility results for reciprocal crosses (Hiscock and Tabah 2003). Another source of complexity in elucidating the genetics of SSI is the occurrence of modifier loci unlinked to the S-locus (Good-Avila and Stephensen 2002; Brennan et al. 2011). These loci may alter dominance relationships among S-alleles or increase compatible matings not interpretable in the context of S-alleles in an SSI system (Hiscock 2000; Brennan et al. 2003, 2011). One or more of these factors as well as others may have influenced results in this study. For example, among the F$_2$ plants in the SI-PSC category, only five had no viable seed, indicating that SI is leaky, with modifier loci a possible cause. Only two of the SC plants had 1.0 proportion self seed set, and in some instances, reduced self seed set of SC plants co-occurs with low pollen viability (fig. 3*B*). Resource limitation may also have been a cause of reduced seed set, although this is not likely because only vigorous hybrid plants were selected for study. While much remains to be determined about the genetics of

SI in *Tolpis*, present data indicate that a single major locus influences seed set, with alleles for SI dominant to those for SC but with other factors likely involved.

The loss of SI has been documented between sister or progenitor-derivative species (Ornduff 1966; Gottlieb 1973; Beck et al. 2006; Busch and Urban 2011; Slotte et al. 2012), between sister subspecies (Pettengill and Moeller 2011), among populations of a species (Busch 2005; Koelling et al. 2011), and among individuals within populations (Brauner and Gottlieb 1987; Tsukamoto et al. 1999; Mable et al. 2005). The breakdown of SI may be associated with one or more floral features collectively known as the selfing syndrome (Ornduff 1969), so that closely related SI-PSC and SC species differ by several of these floral characters (Ornduff 1966; Foxe et al. 2009; Slotte et al. 2012). Components of the selfing syndrome typically include fewer, smaller flowers and loss of floral rewards for pollinators, ostensibly because of reduced selection for features attracting pollinators (Ornduff 1969). Also, there may be selection for features promoting autonomous autogamy, such as anthers and stigmas in close proximity and synchrony of anther dehiscence and stigma receptivity (Ornduff 1969).

A major result of this study is that five floral traits that are part of the selfing syndrome are associated with viable self seed set (SC) in the F$_2$ individuals. This might be expected if plants with these traits have higher seed set because of more efficient autonomous autogamy. However, preliminary observations have not confirmed this hypothesis; selfed seed set in *Tolpis* does not differ whether capitula of a plant are unmanipulated or florets are manually pollinated with pollen from the same capitulum (D. J. Crawford, M. E. Mort, and A. Santos-Guerra, unpublished data). Thus, while more data are needed, there is no evidence at present that the selfing syndrome in *Tolpis* increases seed set by more efficient autonomous selfing. It may be that selection for pollinator attraction has precluded development of the selfing syndrome in some PSC plants, whereas outcrossed seed production is not an issue with SC plants. However, this does not explain the correlation of selfing morphological features and seed set in these F$_2$ plants, where the influence of selection on co-occurrence of traits has been removed. This correlation may instead be due to either genetic linkage or pleiotropy. The measured floral dimensions appear to be controlled by multiple loci (figs. A1–A5). This suggests that genetic linkage is unlikely, since it would mean that several loci (involved in floral morphology) would coincidentally have to be genetically proximate to each other and to the major locus responsible for SI/SC. Pleiotropy remains as a possibility, although we are aware of no precedents for an SI locus directly influencing morphology.

Table 2

Correlations (*P* Value) between Floral Traits in *Tolpis* F$_2$ Hybrids

|	Florets/capitulum	Capitulum diameter	Floret length	Anther length	Stigma length	Pollen : ovule ratio	Pollen viability
Capitulum diameter	.661 (.000)	. . .					
Floret length	.530 (.000)	.904 (.000)	. . .				
Anther length	.503 (.000)	.650 (.000)	.697 (.000)	. . .			
Stigma length	.229 (.009)	.393 (.000)	.405 (.000)	.542 (.000)	. . .		
Pollen : ovule ratio	.091 (.305)	.133 (.135)	.191 (.031)	.252 (.004)	.192 (.030)	. . .	
Pollen viability	−.287 (.001)	−.342 (.000)	−.359 (.000)	−.352 (.000)	−.379 (.000)	−.135 (.128)	. . .
Self seed set	−.224 (.012)	−.292 (.001)	−.376 (.000)	−.443 (.000)	−.257 (.015)	−.108 (.230)	.391 (.000)
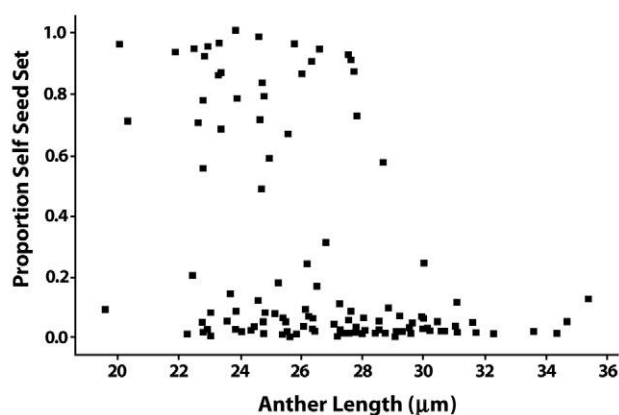
Fig. 4 Proportion self seed set versus anther length in F_2 generation.

Pollen : ovule ratios have been shown to be good indicators of breeding system, with selfers having a lower pollen : ovule ratio than outcrossers (Cruden 1977). Differences are seen between pollen : ovule ratios in the SC *Tolpis coronopifolia* (400–900 : 1) and all of the SI-PSC species (2,500–3,800 : 1) of Canarian *Tolpis* (Crawford et al. 2008), though the pollen : ovule ratios for *T. coronopifolia* are not as low as the means given by Cruden (1977) for obligate or facultative autogamy. Pollen : ovule ratios in the F_2 individuals measured here are correlated with the lengths of florets, anthers, and stigmas (table 2). This may simply be due to the number of pollen grains being constrained by general floret size and especially by the length of anthers, that is, the associations being caused by functional constraints. Causation is not shown here, but reduction of floral size may be the mechanism behind lower pollen : ovule ratios in the SC *T. coronopifolia*; pollen : ovule ratios were not found to be correlated directly with self seed set in these F_2 individuals (table 2).

The low divergence among species of Canarian *Tolpis* for several molecular markers (Archibald et al. 2006; Crawford et al. 2006; Mort et al. 2010) suggests that SC and the selfing syndrome evolved recently and rapidly in *T. coronopifolia*. This is in agreement with other studies in which sequence data indicate that SI-SC species pairs have diverged recently, for example, with estimates of 20,000–50,000 yr for two species of *Capsella* (Brassicaceae; Foxe et al. 2009; Guo et al. 2009). Within members of Asteraceae, molecular, geological, and biogeographical data support recent divergence between SI and SC species of *Lasthenia* (Ornduff 1966; Chan et al. 2001) and *Stephanomeria* (Gottlieb 1973; Lee et al. 2002). The correlation between the floral traits and SC would aid selection on the entire suite of features and facilitate rapid divergence between *T. coronopifolia* and the SI-PSC species of *Tolpis* in the Canarian clade. Similarly, the correlation among floral morphological traits may speed divergence of this suite of characteristics. The latter correlation may be partly due to developmental constraints dictating that smaller flowers will lead to smaller floral parts. The shorter generation time for the annual *T. coronopifolia* could also accelerate divergence compared with perennials.

The factors driving evolution of SC in *T. coronopifolia* on the Canary Islands remain obscure, but there are several possible

reasons for loss of SI-PSC and evolution of the floral selfing syndrome. Leaky SI (PSC) is pervasive in species of *Tolpis* in the Canaries (Crawford et al. 2008, 2010). Evidence indicates that PSC can facilitate increased selfing with weakening of SI and the further increase of PSC to eventually produce nonfunctional S-alleles (reviewed in Levin 1996; Busch and Schoen 2008). Levin (1996, p. 326) stated after review of the literature, "I am unaware of any instance in which S_f [self-fertility] alleles increased in a species that was not already pseudo-self-fertile." PSC varies quantitatively, and selection can raise or lower self seed set over generations (Levin 1996). Factors such as strength of S-alleles and modifier loci are likely responsible for the variation on which selection can act. By contrast, once an S-allele becomes nonfunctional, it is highly unlikely, if not impossible, that reversal to the SI-PSC condition will occur (Igic et al. 2008).

One factor that could increase SC is the inherent 50% transmission advantage of selfing over strictly outcrossing plants because selfing plants contribute two sets of gametes to each selfed offspring and can contribute to the next generation by both selfing and siring offspring with other plants (Fisher 1941; Jain 1976). Another factor that could select for increased selfing, both PSC and SC, is the limitation of compatible mates (Busch and Schoen 2008). This could include small populations with very low S-allele diversity and single colonizers founding new populations following dispersal. *Tolpis coronopifolia* occurs on the island of Tenerife in primarily open habitats of the xerophytic scrub zone (Jarvis 1980). This species is an annual and thus has only one season of reproductive opportunity, which might favor the evolution of SC. Unlike several SI-PSC perennial *Tolpis* species that occur on more than one island in the Canarian archipelago, *T. coronopifolia* has not dispersed from Tenerife and become established on any of the four other high islands. However, in the Canaries, frequent colonization events may be likely even within single islands. Disturbances such as landslides and volcanic activity have occurred throughout the history of the Canaries, including recent historical times (Carracedo and Day 2002, chap. 6). Human disturbance, such as development for tourism and road building, are also constantly creating open habitats such as those favored by *T. coronopifolia* (Caujapé-Castells et al. 2010). Species of *Tolpis* are found along roadsides over altitudinal gradients and vegetation types on the island of Tenerife (Arévalo et al. 2005).

Field studies have not detected natural hybrids between *T. coronopifolia* and other endemic species of *Tolpis* in the Canaries (A. Santos-Guerra, unpublished data). Given that experimental hybrids are readily synthesized in cultivation, one or more factors presumably restrict interspecific gene flow in the field. *Tolpis coronopifolia* is known to occur with other species of *Tolpis* on occasion, but it more often occurs in open habitats where other species are much less common (Jarvis 1980). The highly selfing breeding system of *T. coronopifolia* may also reduce gene flow with congeneric species, as has been suggested for other plants (Antonovics 1968; Fishman and Wyatt 1999; Wendt et al. 2002; Grossenbacher and Whittall 2011). Reduced pollen viability of some F_2 plants (fig. 3B) suggests some Dobzhansky-Muller incompa-

tibilities between the parental species (Fishman and Willis 2001), although their role restricting the occurrence of advanced generation or backcross hybrids remains to be elucidated.

In summary, present evidence indicates that *T. coronopifolia* evolved recently from SI or, more precisely, PSC ancestors on Tenerife in the Canary Islands. The correlation of SC with several floral traits likely facilitated the rapid origin of the *T. coronopifolia* phenotype. The most feasible hypothesis is that selection for selfing in the colonization of open areas drove the origin and evolution of *T. coronopifolia*.

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