A TEST OF BAKER'S LAW: BREEDING SYSTEMS AND THE RADIATION OF *TOLPIS* (ASTERACEAE) IN THE CANARY ISLANDS

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Baker's law posits that self-compatible (SC) plants will be more successful than self-incompatible (SI) plants in long-distance colonization because a single propagule can establish a viable population. Oceanic islands represent ideal systems to test Baker's law because insular lineages have, without question, originated from long-distance dispersal. The dilemma of Baker's law is that one propagule of an SC plant would establish a population with low genetic diversity, which could limit subsequent evolution. By contrast, a single propagule from an SI ancestor, having originated from an outcrossing source population, would provide more diversity but could not undergo sexual reproduction. We examined this issue by studying the breeding system of members of the flowering plant genus *Tolpis* (Asteraceae), a small (nine to 13 species), monophyletic lineage in the Canary Islands archipelago. A combination of floral morphology, pollen-ovule ratio, autogamous seed set, and genetic data indicates that only one endemic species (*T. coronopifolia*) is effectively SC. The remainder of the endemics are pseudo-self-compatible, i.e., are largely SI but capable of low levels of seed set from self-fertilization. Pseudo-self-compatibility remedies the dilemma of Baker's law: a single propagule can establish a sexual population and yet have sufficient variation to facilitate diversification.

Keywords: Baker's rule, colonization, diversification, pseudo-self-compatibility, sporophytic self-incompatibility.

Introduction

Baker (1955) noted that self-compatible members of plant groups where self-incompatibility is otherwise prevalent often occur in localities they most likely reached by long-distance dispersal. He offered a hypothesis for the correlation between distribution and self-compatibility: a single propagule of a self-compatible plant can initiate a sexually reproducing population, and this is more likely than the independent long-distance dispersal and establishment of two self-incompatible (yet cross-compatible) plants close enough spatially and temporally for cross pollination and seed set. Baker (1955) also stated that self-compatible flowering plants are generally able to set some seed even in the absence of specialized pollinators. Stebbins (1957) strongly endorsed Baker's hypothesis by citing several examples in support of it and considered the correlation between long-distance dispersal and self-compatibility of "such great significance for studies of the origin and migration of genera of flowering plants . . . that it deserves recognition as Baker's law" (p. 344). Plants endemic to oceanic islands represent an ideal system to test Baker's law because they clearly owe their origin to long-distance dispersal from a continental source area.

Carlquist (1966c) was keenly aware of the relevance of Baker's law to discussions of the origin and evolution of oceanic island plants when he observed that long-distance dispersal to an island is "a drastic event in the history of a species, an event which begins a train of consequences" (p. 434). One of the major consequences of dispersal of colonizers to remote oceanic islands is that they lose contact permanently with conspecific continental populations. Therefore, persistence and evolution in the insular setting must be accomplished with the genetic diversity carried to the island during the dispersal event, and a variety of factors will determine the level of diversity in the founding population. Genetic evolution of the island population will be limited by the heterozygosity of the founder and new mutational variation. For any single propagule, factors such as the breeding system of the parental population and ploidy of the colonizers are important determinants. The number of dispersals and the number of propagules per dispersal event could also influence diversity in the initial founding population(s). Each of these factors, acting alone or in concert, determines the total genetic diversity dispersed to an island.

Carlquist (1966c; 1974, p. 510) questioned the generality of Baker's law for island lineages and argued that the descendants of a propagule from a selfing population would be at a severe disadvantage after establishment. Their limited genetic diversity would preclude the generation of the recombinants necessary for diversification and radiation of the lineage beyond the habitats where they initially became established. Not surprisingly, he listed self-sterility as one of the factors of "prime importance" in promoting outcrossing. While a single propagule from a self-incompatible colonizer would provide enhanced genetic diversity because of its origin from an outcrossing source population, the inability to produce progeny by selfing precludes sexual

reproduction after establishment. Given that self-compatible colonizers are favored for establishment while self-incompatible colonizers are favored for diversification of progeny, there is the question of how strictly Baker's law applies to the ancestral colonists of endemic oceanic island plants and how island lineages have coped with the dilemma.

Members of family Asteraceae are the most prevalent endemic angiosperms on oceanic islands (Skottsberg 1921; Wiggins and Porter 1971; Wagner et al. 1990; McMullen 1999; Cronk 2000), because of attributes such as efficient dispersal mechanisms, good colonizing ability, and not requiring specialist pollinators (Carlquist 1966c, 1974). For example, the fruits of Asteraceae are single-seeded cypselas, which often have been modified in ways that promote dispersal to (and among) oceanic islands (Carlquist 1966a, 1966b; 1974, chaps. 2, 11). The prevalence of endemic lineages of insular Asteraceae provides many opportunities to test theories of breeding-system evolution in the island setting. Surprisingly, very few such studies have been carried out. Carr et al. (1986) documented exceptions to Baker's law by demonstrating that some members of the silversword alliance (also Asteraceae) are highly self-incompatible, whereas others exhibit various levels of self-compatibility. These Hawaiian endemics represent arguably the most spectacular plant radiation in any island system. Although Carr et al.'s (1986) taxonomic sampling was not extensive, they carefully documented variation in levels of self-compatibility among several species. *Scalesia* is the largest endemic genus of plants in the Galápagos Islands (McMullen 1999). Rick (1966), McMullen (1987, 1990), and McMullen and Naranjo (1994) reported several species of *Scalesia* as self-compatible and autogamous. Subsequent detailed investigations have demonstrated that two species of *Scalesia*, including one that had previously been reported as self-compatible, are partially self-incompatible (Nielsen et al. 2000, 2003). Results from these two archipelagos demonstrate not only that exceptions to Baker's law exist but also that there is variation in the breeding system among species within lineages. This study advances research on this problem by providing the first exhaustive species-level survey of breeding systems in a monophyletic group endemic to an oceanic archipelago.

We define several terms for clarity of later discussion. Asteraceae are one of a handful of flowering plant families with a sporophytic self-incompatibility (SSI) system instead of a gametophytic self-incompatibility (GSI) system; the expression of SSI is pervasive throughout the family (de Nettancourt 1977; Lane 1996). With SSI, the diploid, or sporophytic, genotype of the parental anther determines compatibility (Hiscock and Tabah 2003). As a result, if the S-alleles are codominant, two S-alleles (rather than one) control incompatibility in SSI. However, the situation is usually more complex because there are often dominance relationships among S-alleles, including varying influence of alleles in the pistil versus those in the pollen (Brennan et al. 2003; Hiscock and Tabah 2003). We distinguish between pseudo-self-compatibility (PSC, sometimes designated "leaky SI" or "pseudo-self-fertility") and true self-compatibility (SC, often designated "true self-fertility"); the differences were discussed by Mulcahy (1984) and Levin (1996). We use PSC and SC to designate both noun (pseudo-self-compatibility and self-compatibility) and adjective (pseudo-self-compatible and self-compatible); the meaning will be clear from the context of the

sentence. One of the fundamental distinctions between PSC and SC is that PSC is quantitative in nature and amenable to selection for increased or decreased self-fertility (Bixby and Levin 1996); one explanation for this is that, in addition to the S-locus, modifier loci influence the level of PSC (Hiscock 2000a, 2000b; Hiscock and Tabah 2003). By contrast, SC plants cannot revert to either PSC or complete SI, ostensibly because a dominant mutation at the S locus confers SC (or prevents SI). Another distinction that has been made between PSC and SC plants is that cross-pollen will outcompete self-pollen in the former but not the latter (Levin 1996).

This study examines the evolution of breeding systems in an oceanic lineage using *Tolpis* (Asteraceae: Cichorieae) in the Canary Islands as the model system for testing Baker's law. Canarian *Tolpis* was selected for several reasons. Complete taxon sampling is possible because it is a relatively small clade with nine to 13 species (depending on one's taxonomy; Jarvis 1980; Archibald et al. 2006; Crawford et al. 2006). With limited sampling, Jarvis (1980) reported a rather wide range of seed set after self-pollinations; his results are sufficient to motivate a more complete study of breeding system. There is morphological variation in floral features among species of *Tolpis* (Jarvis 1980; D. J. Crawford, J. K. Archibald, M. E. Mort, and A. Santos-Guerra, unpublished data) that is indicative of differences between SI (or PSC) and SC species in other Asteraceae (Ornduff 1966; Gibbs et al. 1975; Parker 1975; Ortiz et al. 2006). In addition, Cruden (1977) showed that pollen-ovule (P-O) ratios may be good indicators of breeding system, and we wished to see whether P-O ratios had evolved together with the other floral features typical of SI and SC plants. Thus, we wanted to (1) determine the current breeding systems of Canary Island *Tolpis* and assess the level of PSC, (2) determine whether the evolution of SC is associated with changes in floral morphology, and (3) explore how the evolution of breeding system within this lineage compares with the conflicting hypotheses of Baker (1955, 1967) and Carlquist (1966c, 1974) with regard to the reproductive traits of island colonizers.

Material and Methods

Seed Sources

Seeds were collected from natural populations and served as the sources of plants cultivated in the greenhouses at the University of Kansas. All described species of *Tolpis* occurring in the Canary Islands (including one nonendemic species, *T. barbata*), as well as several undescribed taxa, were included (table 1). Three traits were examined in 43 populations: seed set, P-O ratio, and stigma length, with all three characters measured in 28 of the populations (table 1). The two morphologically variable species, *T. laciniata* and *T. lagopoda*, were sampled from each of the islands on which they occur. Voucher specimens collected in the field are deposited in the herbarium of the Jardín de Aclimatación de la Orotava (ORT).

Self-Fertilization and Seed Set

Two or more capitula from a total of 83 plants from 33 populations were used in the selfing experiments (table 1). Capitula in the bud stage were covered with fine netting. Pollen from the

Table 1

Localities, Selfing Categories, Percent Seed Set, Pollen-Ovule (P-O) Ratios, and Stigma Lengths for Sampled Populations of Canarian *Tolpis*

Species, populations[a]	Locality[b]	Selfing category[c]	Percent seed set	P-O ratio	Stigma length (mm)
T. barbata		SC			
1. 1840	T: between Santiago del Teide and Masca		66.75 (4)	818 (6)	. . .
2. 1849	T: near Arafo		55.5 (2)	460 (1)	.22 (2)
3. 1866	H: between El Pinar and La Restinga		68 (2)	870 (1)	.20 (2)
T. calderae		SI			
4. 1982	P: Mirador de la Cumbrecita		.00 (2)	3387.5 (2)	.57 (2)
T. coronopifolia		SC			
5. 5	T: Arafo		91.5 (2)	866 (2)	.49 (2)
6. 1833	T: Puerto de La Cruz		76.5 (2)	404.5 (2)	.35 (2)
7. 1834	T: La Guancha		58.8 (7)	492 (2)	.28 (2)
8. 1841	T: along road near Chio		44 (1)	460.5 (4)	.28 (3)
9. 1848	T: road near Arafo		83 (3)	706 (4)	.33 (1)
10. 1850	T: road to Badajoz		65 (3)	775 (2)	.34 (2)
11. 1983	T: road to Arico		96 (1)	778 (3)	.37 (1)
T. crassiuscula		SI			
12. 8	T: tunnel W of El Fraile		1.5 (2)	3380.5 (2)	.55 (2)
T. glabrescens		SI			
13. Mesa s. n.	T: Anaga, Roque de Enmedio		77.4 (7)	3116.7 (3)	.52 (3)
T. laciniata		SI			
14. 14	H: near Tábano		3.0 (1)	3450 (1)	.46 (1)
15. 16	P: Los Andenes		.50 (2)	3089 (2)	.49 (2)
16. 17	P: road to Roque de Los Muchachos		. . .	3400 (1)	.53 (2)
17. 1851	H: Valverde to Mocanal		. . .	2969 (2)	. . .
18. 1869	H: road above Frontera		.5 (1)	3300 (1)	.56 (3)
19. 1879	P: Mazo		1.0 (1)	3800 (1)	.60 (1)
20. 1886	P: S of Jedey		4.0 (2)	3400 (1)	.56 (2)
21. 1908	G: road to Enchereda		54 (2)	2590 (1)	.47 (1)
22. 1917	G: road to Vallehermoso		.0 (2)	3400 (4)	.53 (3)
23. 1918	G: road near Epina		. . .	. . .	.75 (2)
24. 1921	G: Mirador de Igualero		.0 (1)	3620 (1)	.55 (3)
25. 1958	H: old road to Sabinosa		. . .	3337 (1)	. . .
26. 1963	H: near Tábano		. . .	3262 (2)	.47 (1)
27. 1979	P: near La Bucarón		. . .	2670 (1)	. . .
T. lagopoda		SI			
28. 1941	T: above Esperanza		. . .	3475 (1)	.52 (1)
29. 1946	T: near Gaitero		.0 (1)	3400 (1)	.38 (2)
30. 1948	T: Fuente de Joco		. . .	2687.5 (2)	.49 (2)
31. 1949	T: near Mirador Ayosa		2.0 (1)	3338.0 (3)	.60 (2)
32. 1966	T: near Aquamansa		. . .	3100 (1)	. . .
33. S.-G. s. n.	GC: near Artenara		3.25 (4)	3400 (3)	.51 (2)
T. proustii		SI			
34. 10	H: Mirador de Bascos		.0 (2)	3660 (3)	.55 (1)
T. webbii		SI			
35. 6	T: above Vilaflor		.50 (2)	2475 (2)	. . .
36. 9	T: near Zapatito de la Reina		.0 (4)	3625 (1)	.44 (3)
37. 11	T: Las Cañadas, Refugio de Montañeros		16.1 (4)	3375 (1)	.42 (2)
T. sp. nov. 1[d]		SI			
38. 4	P: Playa de Nogales		23.5 (5)	3332.5 (2)	.50 (2)
39. 1890	P: El Peñón		. . .	4100 (1)	.58 (2)
T. sp. nov. 2[d]		SI			
40. 13	T: Masca		1.0 (1)	2460 (1)	.45 (1)
T. sp. nov. 3[d]		SI			
41. 1975	T: Barranco Seco		.25 (4)	3249 (2)	.55 (2)
42. 1987	T: Barranco del Infierno		7.5 (4)	3748 (2)	.48 (4)
T. sp. nov. 4[d]		SI			
43. 1984	T: road near Arico		0 (1)	3019 (2)	.42 (4)

Note. Mean values are given when more than one plant was examined per population, and the number of plants studied is given in parentheses.

[a] Numbers 4–17 and the S.-G. s. n. population collected by A. Santos-Guerra; Mesa s. n. population collected by Ricardo Mesa; numbers 1833–1921 collected by D. J. Crawford, M. E. Mort, and A. Santos-Guerra; numbers 1941–1987 collected by D. J. Crawford and A. Santos-Guerra.

[b] G = La Gomera; GC = Gran Canaria; H = El Hierro; P = La Palma; T = Tenerife.

[c] SC = self-compatible; SI = self-incompatible. Species were assigned to a category on the basis of two criteria: (1) the diameter of capitula and (2) the level and apportionment of allozyme diversity within and among populations.

[d] Undescribed species (A. Santos-Guerra, unpublished data).

same capitulum was distributed over the receptive stigmas for successive days until the capitulum closed. Capitula were collected when mature, which in *Tolpis* is indicated by the formation of a brown "abscission" zone on the peduncle just below the capitulum. Pollen viability was determined for all plants used in the selfing experiments by staining at least 200 grains in lactophenol aniline blue (Kearns and Inouye 1993). The large, plump, darkly stained pollen grains were easily distinguished from the shriveled, very lightly stained grains. Only plants with more than 70% viable pollen were used in the selfing experiments so that low pollen viability would not limit seed set. The percentage of viable seeds (number of seeds / total number of florets) was determined for each plant, and the mean was calculated for each population. The large, plump, dark (dark brown to black) fruits containing viable embryos were easily distinguishable from the light tan, shrunken fruits lacking embryos (fig. 1).

Pollen-Ovule Ratios

Pollen-ovule ratios were determined for 81 plants from 42 populations (table 1) by extracting a single anther (or rarely all five) from one floret from two different capitula before dehiscence but after microsporocytes had divided and individual pollen grains could be observed. The anthers were gently squashed in lactophenol aniline blue, and pollen was counted
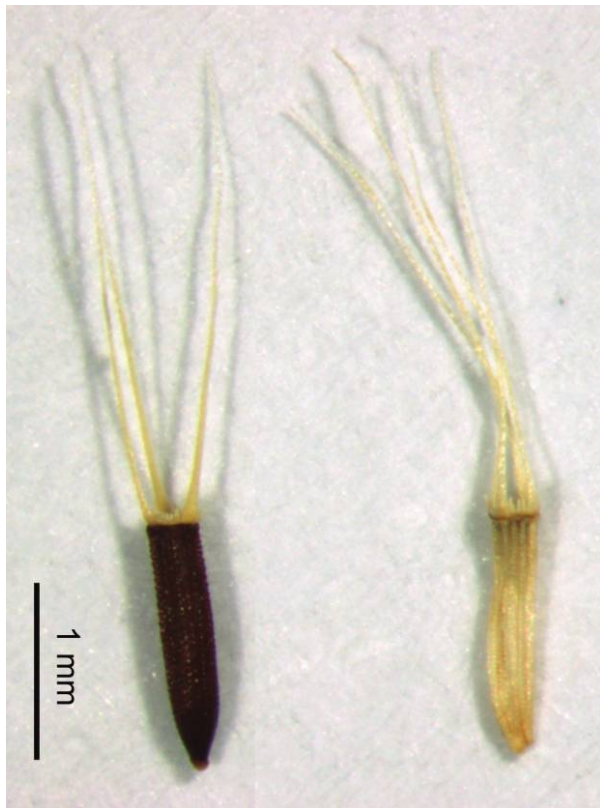
Fig. 1 Fruits from the self-compatible, nonendemic species of Canarian *Tolpis* (*T. barbata*). Dark fruits (left) contain viable embryos, whereas light tan fruits (right) do not.

Table 2

Nested ANOVA for Seed Set, Pollen-Ovule (P-O) Ratio, and Stigma Length

Variable, source	df	F	P	Variance (%)
Seed set:				
Selfing category	1	23.39	.001	85.66
Species (selfing category)	11	4.31	.003	8.84
Error	19	...	...	5.50
P-O ratio:				
Selfing category	1	259.24	.000	96.43
Species (selfing category)	11	1.16	.359	.21
Error	28	...	...	3.37
Stigma length:				
Selfing category	1	33.73	.000	76.52
Species (selfing category)	11	1.25	.311	2.29
Error	24	...	...	21.19

Note. Populations of Canarian *Tolpis* are grouped according to selfing-ability category (i.e., self-compatible or self-incompatible) and species. Assignments to selfing categories were based on capitula diameter and level and apportionment of allozyme diversity.

with a compound microscope. When one anther was used, the number of pollen grains per anther was then multiplied by five (i.e., the number of stamens per floret) to estimate the total number of pollen grains per floret. This gives the P-O ratio as well, because Asteraceae have one functional ovule per floret. The means were calculated for capitula from the same plant and for plants in each population.

Stigma Length

In the tribe Cichorieae, of which *Tolpis* is a member, the entire length of the style branches is stigmatic (receptive to compatible pollen), and thus style branch length can be equated with stigma length. The style branches of 76 individuals from 37 populations were measured with an ocular micrometer on a dissecting microscope (table 1). Style branches were measured when they had diverged from each other and were perpendicular to the style. Most measurements were made from fresh flowers or from flowers preserved in FAA. In a few instances, dried flowers were rehydrated and measured. Comparisons of fresh flowers that were measured and then dried, rehydrated, and measured again showed that results were similar regardless of the material used. Only flowers with style branches fully opened were used. Five to 10 florets per plant (including both style branches of each floret) were measured, and the mean for each plant was calculated. Means were determined for plants within each population.

Breeding-System Categories

Selfing ability was divided into two categories (designated "SC" and "SI" in table 1) on the basis of two criteria: (1) the diameter of capitula and (2) the level and apportionment of allozyme diversity within and among populations. These groupings were used for a nested ANOVA (see "Statistical Analyses," table 2). In Asteraceae, capitulum size has been shown to be a reliable indicator of breeding system in some genera (Ornduff 1966; Ortiz et al. 2006), as has the apportionment of allozyme diversity (Hamrick and Godt 1997). Jarvis (1980) and D. J.

Crawford (unpublished data) documented that two species of *Tolpis* (*T. barbata* and *T. coronopifolia*) have capitula with diameters of 6–10 mm, while capitula of all other species have diameters of 11–35 mm, with most larger than 15 mm (fig. 2). Crawford et al. (2006) reported low total (species) diversity and a high proportion of the diversity among populations in the two species with smaller capitula. By contrast, species with larger capitula have higher total diversity, and a much smaller proportion of that diversity is apportioned among populations.

Statistical Analyses

A nested ANOVA was used to determine whether the classification of taxa based on capitulum size and allozyme variation accurately predicts seed set, P-O ratio, and stigma length. Here, species is nested within breeding-system category. Where there were measurements from multiple plants within a population, these were averaged. Thus, population-specific values for each trait were the response variables in the ANOVA. The number of populations per species and the number of species per selfing-ability category both varied, and as a consequence, the design is unbalanced. The calculations were conducted using MINITAB, version 14.1.

Results

Seed Set

Seed set resulting from self-fertilization was much higher in populations of *Tolpis barbata*, *T. coronopifolia*, and *T. glabrescens* than in populations of the other species, with all but one of the 11 populations of these three species having means higher than 50% (table 1). Mean seed set in 22 populations of the other 10 species was less than 5%, and only three of those populations (each from a different species) had a mean seed set above 15% (table 1). There is, however, rather wide variation in seed set among plants of some populations of those species with generally low seed set: in population 37 (*T. webbii*), seed set varied from 0% to 38%, and seed set among individuals of population 38 (*Tolpis* sp. nov. 1) varied from 0% to 69%. More than 85% of the total variance in seed set was

between the two classes (SI vs. SC; fig. 3), whereas less than 9% was among species (table 2).

Pollen-Ovule Ratios

Mean P-O ratios for populations of the two species designated SC (*T. barbata* and *T. coronopifolia*) are all below 1000, with those of most populations between 450 and 800 (table 1). In contrast, mean ratios for populations of the other species are mostly greater than 3000 (including *T. glabrescens*; table 1). More than 96% of total variance in P-O ratio was between the two classes (SI vs. SC; fig. 3), whereas almost none of the variance was accounted for between species (table 2).

Stigma Length

Mean stigma lengths for populations of *T. barbata* and *T. coronopifolia* are, with one exception, less than 0.40 mm; mean lengths for populations of the other species are nearly all greater than 0.40 mm (table 1). More than 76% of total variance in stigma length occurred between the two classes (SI vs. SC; fig. 3), and slightly more than 2% was among species (table 2).

Discussion

Baker's Law and Tolpis: The Colonizing Ancestor and Evolution in the Canaries

Inference of the breeding system of the common ancestor of Canarian *Tolpis* has been complicated by the apparent rapid diversification of this clade. Very low levels of sequence divergence in nuclear ITS (R. K. Jansen, personal communication) and noncoding plastid regions (Mort et al. 2007), as well as a paucity of DNA restriction site variation (Moore et al. 2002), have precluded robust resolution of phylogenetic relationships in Canary Island *Tolpis*. Archibald et al. (2006) employed inter–simple sequence repeat (ISSR) markers to infer relationships and found that the two populations of the only SC endemic species of *Tolpis* (*T. coronopifolia*) are strongly supported as a clade and nested high within the tree, suggesting that this species is derived from PSC ancestors and that the colonizing

Fig. 2 Capitula from two populations of *Tolpis*, as well as a capitulum from their F$_1$ hybrid. From left to right: *Tolpis coronopifolia* (population 6, categorized as self-compatible), F$_1$ hybrid, and *Tolpis* sp. nov. 1 (population 39, categorized as self-incompatible; see table 1).
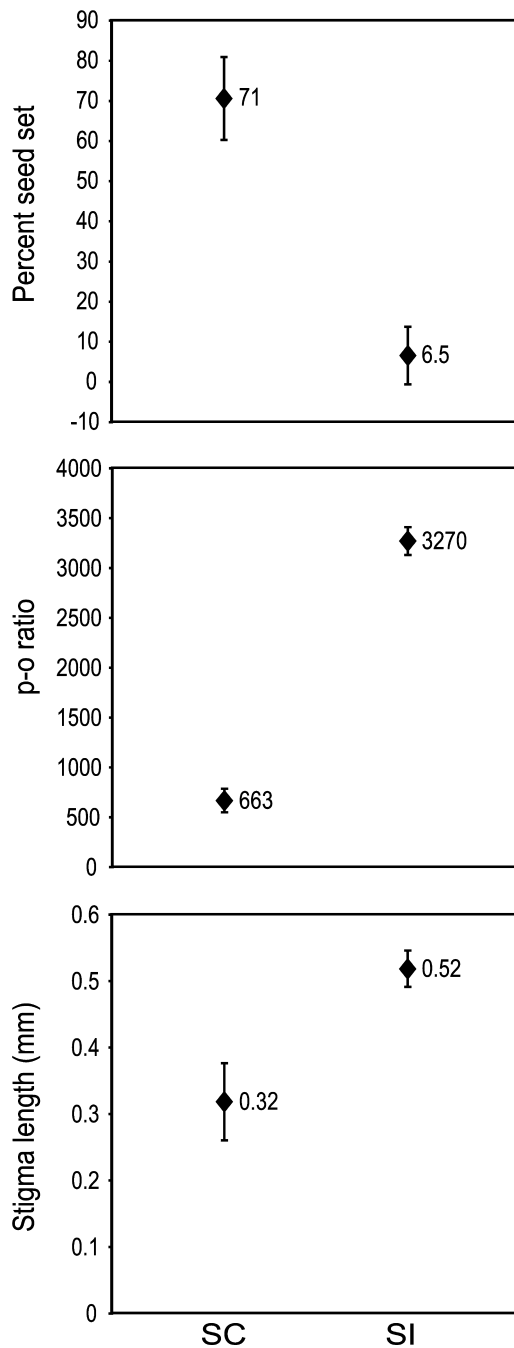
Fig. 3 Means and 95% confidence intervals for seed set, pollen-ovule ratio, and stigma length (mm) of the selfing-ability categories (SC = self-compatible; SI = self-incompatible).

ancestors were PSC. In addition, the preponderance of other available evidence, both morphological and genetic, suggests that the colonizing ancestor of the *Tolpis* lineage in the Canary Islands was PSC. *Tolpis* thus is supported as an exception to Baker's law, but the intermediate nature of PSC between SC and SI may provide some of the benefits for island colonizers proposed by both Baker (1955, 1967) and Carlquist (1966c, 1974; see below). Very limited data are available on pollina-

tors of *Tolpis* in the Canary Islands; a species of small bee has been observed heavily pollinating one population, and honeybees have been seen visiting capitula in several populations (J. K. Archibald, D. J. Crawford, A. Santos-Guerra, and M. E. Mort, unpublished data). Like many Asteraceae, including other insular endemics (Philipp et al. 2004), *Tolpis* is probably a generalist with a variety of pollinators (Lane 1996; Fagua and Gonzalez 2007).

A broader survey of breeding-system evolution within Asteraceae also supports the hypothesis that PSC (rather than SC) was ancestral in Canarian *Tolpis*. The widespread and common occurrence of SSI in Asteraceae (de Nettancourt 1977; Charlesworth 1985; Lane 1996) and the sporadic occurrence of SC at the species, population, or intrapopulation levels throughout the family suggest that SSI is the ancestral condition within the family. Within the tribe Cichorieae, of which *Tolpis* is a member, there are rare occurrences of SC species (or populations within species) in genera that otherwise are comprised of SI species (Parker 1975; Wells 1976; Gallego 1983; Brauner and Gottlieb 1987; Izuzquiza and Nieto Feliner 1991; Cheptou et al. 2000; Ruiz de Clavijo 2001). Phylogenetic studies have inferred SC as the derived condition within small, monophyletic groups such as insular lineages (Barrett et al. 1997; Schoen et al. 1997; Goodwillie 1999; Beck et al. 2006). The most definitive support for SI or PSC being the ancestral condition for an island clade is provided by the Hawaiian silversword alliance, because it is known that their continental ancestors were SI (Barrier et al. 1999; Baldwin 2003). These phylogenetic studies support the hypothesis that the change from SI to SC is unidirectional (Charlesworth and Charlesworth 1979; Mulcahy 1984), and they provide compelling indirect evidence for PSC as the ancestral condition in Canary Island *Tolpis*, with SC being the derived condition. However, as discussed below, there can be selection for increased selfing or outcrossing in both PSC and SC plants.

In addition to the findings of this study of Canary Island *Tolpis*, apparent exceptions to Baker's law among island Asteraceae have been identified in the aforementioned silversword alliance in Hawaii (Carr et al. 1986) and *Scalesia* on the Galápagos Islands (Nielsen et al. 2000, 2003). There is also evidence that suggests PSC in the large genus *Argyranthemum* in the Macaronesian islands (Francisco-Ortega et al. 1997; M. Olangua-Corral, personal communication) and *Commidendron* in St. Helena (Cronk 2000; Eastwood et al. 2004; A. Eastwood, personal communication). In those genera, some reports indicate SC for taxa, whereas others report SI for the same taxa or for congeners, which is suggestive of variation within and among species.

While data are still limited for lineages of insular Asteraceae, the emerging picture is that PSC of island colonizers may be more common than previously thought. Levin (1996) discussed the advantages of PSC plants as founders and cited Lloyd's (1992) observation that PSC maximizes the advantages of both outcrossing and SC. That is, if a colonizer originated from a highly outcrossing population, then it would carry more genetic diversity than a propagule from a highly selfing population. Given the opportunity, it is likely that PSC populations will be outcrossing rather than selfing because outcross pollen will outcompete self-pollen (Levin 1996). This would help alleviate Carlquist's (1966c, 1974) concern about

the limited evolutionary future of the progeny of colonists due to low diversity. However, a single PSC colonist could initiate a sexually reproducing population and thus would follow Baker's law in one sense, but in another sense it would be an exception because the colonizer is not strictly SC (Baker 1955, 1967). It appears that a PSC ancestor of the Canarian *Tolpis* lineage would have many advantages for colonizing and diversifying on the archipelago.

Several factors can increase the autonomous seed set of PSC plants. Diploid control of pollen incompatibility in plants with SSI allows for dominance relationships among alleles. These relationships may range from total dominance to codominance among alleles, but there also may be tissue-specific dominance in either the pollen or stigma (Brennan et al. 2003). Forced inbreeding (Hiscock 2000*b*) and bottlenecks, which could occur in the founding of small island populations, could increase PSC in small populations (Reinartz and Les 1994). The extensive studies of *Senecio squalidis* (Asteraceae) have demonstrated the complexity of S-allele dominance relationships and the effectiveness of the species as a colonizer despite very low S-allele diversity (Hiscock 2000*a*, 2000*b*; Brennan et al. 2003; Hiscock and Tabah 2003).

PSC in the colonizing ancestors of *Tolpis* could facilitate the founding of new sexual populations within and among the islands by dispersal of single propagules to new areas or habitats. The higher the level of PSC, the more rapidly population sizes could be built up, because there would be more compatible matings, both by selfing of progeny and by crosses among progeny. However, the effective population sizes would be lower for PSC plants than for SI plants with similar histories and numbers of individuals (Levin 1996). One result of smaller effective population sizes is that novel features could be more rapidly fixed in populations by stochastic processes or high levels of selfing (Levin 1996). These mechanisms could be producing the wide divergence seen among congeneric species in oceanic islands (Carlquist 1974). There are at least two examples in *Tolpis* where PSC may have been a factor in the differentiation of morphological variants. High PSC was observed for one population (38, table 1) of *Tolpis* sp. nov. 1. Individuals of this population form a strongly supported group, according to ISSR markers (Archibald et al. 2006), and there is a highly significant deficiency of heterozygotes at allozyme loci (D. J. Crawford, J. K. Archibald, M. E. Mort, and A. Santos-Guerra, unpublished data). Another example is the very small population 42 (table 1) of *Tolpis* sp. nov. 3. Individuals from this population, as with *Tolpis* sp. nov. 1, are identified as a group by ISSR markers and have a deficiency of heterozygotes at allozyme loci.

The only polyploid species of *Tolpis* in the Canary Islands is *T. glabrescens*. It represents one of the few examples of the origin of a polyploid during the diversification of a plant lineage in an oceanic archipelago (Stuessy and Crawford 1998). There has been a long-held view that there may be an association between polyploidy and the breakdown of SI (Stebbins 1950, p. 306), but recent reviews by Mable (2004) and Barringer (2007) have questioned the validity of this assumption. The evidence for the association is even less compelling for plants with SSI than it is for plants with GSI (Mable 2004; Barringer 2007). In studies of artificial populations, Cook and Soltis (2000) found higher selfing rates in a recently evolved tetraploid *Tragopogon* (Asteraceae) than in one of its diploid progenitors. However, studies of natural populations of the same species found higher outcrossing in the tetraploid than in the diploid (Cook and Soltis 1999). Despite equivocal results for other taxa with SSI, there does appear to be some support for the association between polyploidy and selfing within our data set. The mean seed set for the one sampled population of *T. glabrescens* is comparable to seed set in the SC species; however, capitulum sizes, P-O ratios, and stigma lengths of *T. glabrescens* are similar to those of populations of diploid species with high levels of SI. Within the population of *T. glabrescens*, seed set for the seven plants varied from 42% to 100%; Jarvis (1980) also found variation (0.5%–57%) in seed set of selfing plants of *T. glabrescens*, but it is not clear how many plants he examined. This species is very rare and is known from several small populations on the paleoisland of Anaga on the island of Tenerife (Jarvis 1980; A. Santos-Guerra, unpublished data). It has been suggested that increased self-fertility could be advantageous for newly arisen polyploids because it would increase reproductive success by enhancing crosses between otherwise rare polyploid gametes (Levin 1975; Miller and Venable 2000). Increased selfing thus would be advantageous for the growth and persistence of a population after the initial origin of polyploidy, and this could explain the higher PSC in *T. glabrescens*.

SC in Tolpis*: Evolution of Related Traits and Evidence for Selfing*

Levin (1996) reviewed studies suggesting that SC has evolved from PSC. While various models exist for the transition from one state to another, the key factor for our discussion is the aforementioned irreversibility of the transition to SC. Although we have documented that *T. coronopifolia* is SC, this does not address the question of the mating system of the species in nature. Insular endemics may be SC yet have high outcrossing rates and largely fail to set seed in isolation (e.g., *Bidens* in Hawaii; Ritland and Ganders 1985; Sun and Ganders 1988). Several lines of evidence argue that *T. coronopifolia* is highly selfing in natural populations. First, the species has a suite of floral characters typical of selfers (Ornduff 1966, 1969; Anderson 1995; Barrett et al. 1997; Ortiz et al. 2006); these include smaller capitula (fig. 2), shorter stigmas, and capitula open for only about 2 d, as compared to 7–15 d for the capitula of other endemic species of *Tolpis* (Jarvis 1980; D. J. Crawford, unpublished data). Second, average seed set for 53 isolated, unmanipulated capitula from seven plants of *T. coronopifolia* in the greenhouse was 77.7% (D. J. Crawford, unpublished data), suggesting that the species is highly autogamous. Third, the very high apportionment of allozyme diversity among populations of *T. coronopifolia* (0.828; Crawford et al. 2006) even exceeds the values (0.510 and 0.591 for selfers and selfing endemics, respectively) given in the reviews of Hamrick and Godt (1989, 1997). These values are several times higher than those for endemics with mixed mating systems (Hamrick and Godt 1997). The P-O ratios for *T. coronopifolia*, while several times lower than those for the endemic PSC species of *Tolpis* and the xenogamous (primarily SI) species given by Cruden (1977), are higher than the ratios given by Cruden (1977) and others (Philbrick and Anderson 1987; Mione and Anderson

1992) for autogamous species. In fact, the mean population P-O ratio for *T. coronopifolia* falls near Cruden's (1977) value for facultative xenogamy. It is possible that the recent evolution of SC and selfing in *T. coronopifolia* has not provided adequate time for "adjustment" of P-O ratios to those typical of selfers, as has been suggested for an SC species in the Juan Fernández Islands (Anderson et al. 2001) and for aquatic angiosperms (Philbrick and Anderson 1987).

Associated with the evolution of SC in *Tolpis* is the switch to the annual (or weak biennial) habit in *T. coronopifolia*. Phylogenetic studies indicate an association between selfing and the annual habit (Barrett et al. 1997), something suggested by Stebbins (1957). Annual, highly selfing species have the capacity to become effective colonizing weeds (Stebbins 1957; Ruiz de Clavijo 2001). While *T. coronopifolia* is restricted to the island of Tenerife and cannot be classified as an aggressive weed, it is the only endemic species that is found in open, rather dry, and somewhat disturbed sites (Jarvis 1980; D. J. Crawford, J. K. Archibald, M. E. Mort, and A. Santos-Guerra, unpublished data). Allozymes (D. J. Crawford, J. K. Archibald, M. E. Mort, and A. Santos-Guerra, unpublished data) and morphological data indicate differentiation among populations of *T. coronopifolia*. Populations are fixed for alternative allozyme alleles and differ in features such as color of ligules and leaf dissection (Jarvis 1980; A. Santos-Guerra, personal observation). Evidence suggests that dispersal and the founding of new populations have occurred on Tenerife, with high selfing facilitating the fixation of different combinations of characters.

In contrast to *Tolpis coronopifolia*, the other SC species of *Tolpis* in the Canary Islands, *T. barbata*, has spread throughout the archipelago (Jarvis 1980). This species shares several characters with *T. coronopifolia*, in addition to SC. It has small stigma lengths, low P-O ratios, and small capitula that remain open for a short time. Isolated capitula have a mean of 70% seed set, suggesting that *T. barbata* is highly autogamous (D. J. Crawford, unpublished data). Also, the species has a high proportion of allozyme diversity among populations (Crawford et al. 2006). However, *T. barbata* is not endemic to the Canaries and is widespread in southern Europe, North Africa, Medi-

terranean islands, and the Azores and Madeira (Jarvis 1980); it is not clear whether the species originated on a continent or in an oceanic archipelago (Moore et al. 2002). The species is extremely variable over its geographic range, with the habit varying from annuals to basally woody perennials (Jarvis 1980); within the Canary Islands, the species is largely annual. Although both *T. barbata* and *T. coronopifolia* share several floral features associated with SC and a selfing breeding system, the nonendemic former species is much weedier than the endemic latter species.

In summary, the genus *Tolpis* in the Canary Islands is an exception to Baker's law. The colonizing ancestor was most likely PSC, not SC, and highly selfing. A PSC colonizer that originated from an outcrossing source population ostensibly was able to form a sexually reproducing population while carrying sufficient genetic diversity for the subsequent evolution of the lineage in the Canaries. SC and autogamy have evolved at least once in the Canary Islands and are associated with a suite of floral features (including decreased stigma length and P-O ratio) and the annual habit.

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