

RESEARCH PAPER

Variation in floral longevity in the genus *Leptosiphon*: mating system consequences

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ABSTRACT

Pollination or fertilisation trigger floral senescence in a wide range of flowering plants, and yet little attention has been given to the implications of this phenomenon to mating system evolution. We examined the effects of pollination on floral senescence in the genus *Leptosiphon*. Species in the genus exhibit a wide range of breeding systems. In all cases, compatible pollination induced senescence; emasculated flowers lived longer than hand-outcrossed flowers. In the self-compatible species, *Leptosiphon acicularis* and *L. bicolor*, and in one highly selfing population of *L. jepsonii*, unmanipulated flowers had reduced longevity compared to emasculated flowers, suggesting that autonomous self-pollination limits floral longevity in these species. Limited floral longevity in these highly selfing taxa may reduce opportunities for male outcross success, representing a possible source of selection on the mating system. In turn, the mating system might influence how selection acts on floral longevity; obligately outcrossing taxa are expected to benefit from longer floral longevity to maximise opportunities for pollination, while selfing taxa might benefit from earlier floral senescence to reduce resource expenditure. Overall, the longevity of unpollinated flowers increased with the level of outcrossing in the genus *Leptosiphon*. Our results taken together with those of a previous study and similar results in other species suggest that floral longevity may represent a largely unexamined role in mating system evolution.

INTRODUCTION

In many angiosperms, floral senescence is triggered by pollination (Gori 1983; Stead 1992; Yasaka *et al.* 1998; Arathi *et al.* 2002; Underwood *et al.* 2005); this may be an adaptive trait that minimises resource expense and water loss, costs incurred by maintaining open flowers (Stead 1992; Ashman & Schoen 1994; Abdala-Roberts *et al.* 2007) or allows plants to optimise floral display sizes (Harder & Johnson 2005). Pollination-induced floral senescence also has potential evolutionary consequences for plant mating system evolution (Marshall *et al.* 2010). In an obligately cross-fertilising hermaphrodite species, male and female fitness depend on the same pollen vector. Fitness through ovule fertilisation and pollen dispersal therefore is correlated to some extent, although they may accrue at different rates (Ashman & Schoen 1994; Schoen & Ashman 1995; Ishii & Sakai 2000). In an outcrossing species, therefore, pollen deposition is expected to trigger floral senescence only after substantial pollen dispersal has been achieved. In contrast, autonomous self-pollination (self-fertilisation that occurs without a pollinating vector) that occurs early in floral anthesis may trigger floral senescence before opportunities for pollen dispersal by a vector occur. If selfing-induced floral senescence reduces male outcross success in autonomously self-fertilising species, then it may be a potential source of pollen discounting (Holsinger *et al.* 1984; Weber & Goodwillie 2007), defined as

a reduction in the pool of pollen available for cross siring events associated with self-fertilisation (Holsinger *et al.* 1984; Harder & Wilson 1998). Pollen discounting can counteract the ecological and genetic benefits of self-fertilisation. Thus, if early floral senescence limits pollen dispersal, it might represent a cost to male fitness that influences how selection will act on a selfing mutation when it arises.

Floral longevity is itself an adaptive trait that is shaped by selection, and might evolve with the mating system (Bell 1985; Blair & Wolfe 2007). In general, floral longevity reflects a selective balance between the costs of maintaining flowers and the male and female fitness gained by keeping flowers open (Ashman & Schoen 1994; Schoen & Ashman 1995; Ishii & Sakai 2000). While maintenance costs should select to limit floral lifespan in both selfing and outcrossing species, the benefits of long-lived flowers are greater in outcrossing species that depend on pollinator visitation for both male and female fitness than in species that produce seeds primarily by autonomous selfing. Thus, outcrossing taxa would be expected to have longer floral longevity than selfing taxa of the same genus or family (Morin 1983; Primack 1985).

In a previous study, we examined selfing-induced floral senescence in populations and individuals that varied in the timing of self-compatibility in *Leptosiphon jepsonii* (Polemoniaceae). This annual species exhibits a floral age-dependent form of self-incompatibility that prevents early self-fertilisation in some individuals (transient self-incompatibility),

conferring delayed selfing, while other individuals are self-compatible upon flower opening (Goodwillie *et al.* 2004). The frequency of early self-compatible and transiently self-incompatible individuals varies significantly among populations and is strongly associated with the population outcrossing rate (Goodwillie & Ness 2005). Populations of *L. jepsonii*, therefore, provide a novel opportunity to examine how traits evolve with the mating system. We found that autonomous self-pollination triggered floral senescence earlier in early self-compatible plants than in individuals exhibiting transient self-incompatibility in growth room experiments (Weber & Goodwillie 2007). Similarly, field experiments revealed that flowers in a predominantly early self-compatible population were shorter lived (1.6 days) than flowers of a predominantly transient self-incompatible population (2.5 days). We also found that substantial pollen was available beyond the first day of anthesis, suggesting that early senescence could decrease opportunities for male outcross events. Selfing-induced floral senescence reduces floral longevity and may present a cost to male fitness in populations of *L. jepsonii* that differ in the timing of self-compatibility and outcrossing level.

The current study further explores the potential for selfing to reduce floral longevity and the consequences this may have for the mating system in a comparative study of several species in the annual genus *Leptosiphon*. These species exhibit a range of mating systems from highly selfing to completely self-incompatible. We examine three questions about floral longevity and mating system in *Leptosiphon*: (i) does compatible pollination induce floral senescence in each species? We predict that floral senescence will be induced after cross-pollination in each species, regardless of mating system. (ii) Does autonomous self-pollen deposition induce floral senescence in self-compatible species? We predict that in self-compatible taxa autonomous selfing will limit floral longevity, resulting in reduced longevity for unmanipulated compared to emasculated flowers. For self-incompatible taxa, we predict no difference in floral longevity for unmanipulated compared to emasculated flowers. (iii) Is the longevity of unpollinated flowers higher in outcrossing species? We predict that in the genus *Leptosiphon*, self-compatible taxa will have reduced floral longevity in emasculated flowers compared to self-incompatible, outcrossing taxa.

METHODS

Pollination protocol

Experimental pollinations were carried out on six annual species of *Leptosiphon* (formerly *Linanthus*): *L. latisectus*, *L. androsaceus*, *L. parviflorus*, *L. acicularis*, *L. bicolor* and *L. jepsonii*. In *L. jepsonii*, for which populations exhibit especially wide variation in outcrossing rates, we included two populations, Lake Hennessey (LH) and Ida Clayton Road (IC); in the other five species, within which mating system variation has not been documented, a single population was used. These species and populations were chosen to exhibit a range of breeding systems (fully self-compatible to fully self-incompatible) and outcrossing rates (Table 1). Previous studies used pollen tube data to examine the breeding systems of these species and determined that *L. latisectus*, *L. androsaceus* and *L. parviflorus* are fully self-incompatible, *L. jepsonii* is transiently self-incompatible and *L. bicolor* is self-compatible and highly selfing (Goodwillie 1999, 2000; Goodwillie *et al.* 2004). The two populations of *L. jepsonii*, LH and IC, differ in the timing of self-compatibility (early and delayed, respectively) and outcrossing rates (Goodwillie & Ness 2005; Table 1). Studies of *L. acicularis* suggest that it is either self-compatible (Goodwillie 1999) or transiently self-incompatible (J. Weber, personal observation). In all species studied, stigma receptivity is high upon flower opening and remains so for at least 3 days (Weber 2007; unpublished data). Early anther dehiscence and close spatial arrangement of stigma and anthers result in some autonomous self-pollen deposition in all of the species; spatial overlap and self-pollen deposition is highest in the self-compatible taxa (Goodwillie 1999). Plants of each study population were raised from field-collected seed in a growth room at East Carolina University using cultivation methods described previously (Goodwillie *et al.* 2004).

Pollination treatments were designed to examine if compatible pollination triggers floral senescence in each of the species, if autonomous self-pollination limits floral longevity, and if maximum (unpollinated) and unmanipulated floral longevity varies significantly among species. In the growth room, three treatments were applied to newly opened flowers: (i) hand-outcrossed, (ii) unmanipulated and (iii) emasculated. Hand-outcrossed flowers received pollen from two to

Table 1. Characteristics of six species of the genus *Leptosiphon*, including two populations of *L. jepsonii* used in experiments examining floral longevity. Species were chosen that exhibit a range of breeding system characteristics.

	Abb.	SI type	Mean (<i>t</i>)	N	Locality
<i>L. latisectus</i>	LA	SI		6	Pepperwood Ranch, Sonoma County, CA
<i>L. androsaceus</i>	AN	SI		12	Near Lake Hennessey, Napa County, CA
<i>L. parviflorus</i>	PA	SI		12	Pope Valley, Napa County, CA
<i>L. jepsonii</i> (IC)	IC	tSI	0.69	10	Along Ida Clayton Rd, Sonoma County, CA
<i>L. acicularis</i>	AC	SC/tSI		11	Near Maacama Creek, Sonoma County, CA
<i>L. jepsonii</i> (LH)	LH	SC	0.06	12	Near Lake Hennessey, Napa County, CA
<i>L. bicolor</i>	BI	SC	0.04	11	Tuttletown, Tuolumne County, CA

Abb. indicates the abbreviation used to identify each taxon. SI type indicates self-incompatible (SI), self-compatible (SC) or transiently self-incompatible (tSI), mean (*t*) indicates the multi-locus outcrossing rate averaged across years, where available, N indicates the sample size of individuals used in pollination experiments and geographic distribution are provided for each study species or population. All data from (Goodwillie 1999, 2000; Goodwillie *et al.* 2004; Goodwillie & Ness 2005).

three pollen donors and were emasculated in the bud to prevent self-pollen deposition. Hand-pollinations occurred in the morning on the first day of anthesis. Flowers were observed at noon on each day after treatments were applied, and the longevity of each flower was recorded in increments of days. A flower was considered senesced when petals were closed or the flower was no longer upright, and therefore not available to pollinators. The number of plants per population ranged from six to 12. Each treatment was repeated on five flowers of each individual for a total of 15 experimental flowers per plant.

Statistical analyses

A comparison of outcrossed and emasculated flowers tested the hypothesis that compatible pollination triggers floral senescence. A comparison of unmanipulated and emasculated treatments quantifies the extent to which autonomous selfing reduces floral longevity. Finally, emasculation treatments provide an estimate of maximum floral longevity when compatible pollination does not occur. An analysis of variance with Games-Howell *post-hoc* tests was performed within each species or population to test hypotheses about pollination-induced senescence; both taxa and floral treatments were treated as fixed effects (SPSS 2004). An additional analysis of variance with Games-Howell tests was performed on data for individual treatments to examine how maximum (emasculated) and unmanipulated floral longevity vary across these species and populations (SPSS 2004).

RESULTS

In all species and populations, ANOVA revealed significant differences in floral longevity among pollination treatments. Games-Howell tests indicated that outcrossed flowers were significantly shorter lived than emasculated flowers in all

populations (Fig. 1, Table 1), which indicates that floral senescence is induced by compatible pollination in these species. In the self-incompatible species and in the IC population of *L. jepsonii*, which is transiently self-incompatible with a high outcrossing rate, unmanipulated flowers were significantly longer lived than outcrossed flowers, and the longevity of emasculated and unmanipulated flowers did not differ (Fig. 1, Table 2). Unmanipulated flowers were significantly shorter lived than emasculated flowers of *L. acicularis*, the LH population of *L. jepsonii*, and *L. bicolor*, all of which are self-compatible (Fig. 1, Table 2). Furthermore, in *L. acicularis* and the LH population of *L. jepsonii*, floral longevity was not significantly different in unmanipulated and outcrossed treatments, indicating that autonomous selfing is as effective as hand cross-pollination for inducing floral senescence in these taxa. In *L. bicolor*, however, the longevity of unmanipulated flowers (1.6 days) was significantly higher than that of outcrossed flowers (1.1 days), indicating that selfing was less effective than outcrossing in inducing senescence in that species. The three fully self-incompatible species exhibited greater unmanipulated floral longevity than the two transiently self-incompatible populations of *L. jepsonii*, *L. acicularis* and the highly selfing *L. bicolor* (Fig. 2, Table 3).

Floral longevity of emasculated flowers (maximum floral longevity) varied significantly among species and populations (Fig. 3, Table 3). It was greater in the three fully self-incompatible species (*L. androsaceus*, *L. latisectus* and *L. parviflorus*) than in the highly selfing LH population of *L. jepsonii* and the highly selfing *L. bicolor*. *Leptosiphon androsaceus* (a self-incompatible taxa) also had higher maximum floral longevity than the IC population of *L. jepsonii* (a transiently self-incompatible species; Fig. 3). Maximum longevity for the transiently self-incompatible IC population of *L. jepsonii* was shorter than in *L. androsaceus* and marginally shorter than in *L. latisectus* (two self-incompatible taxa; $P = 0.051$; Fig. 3).

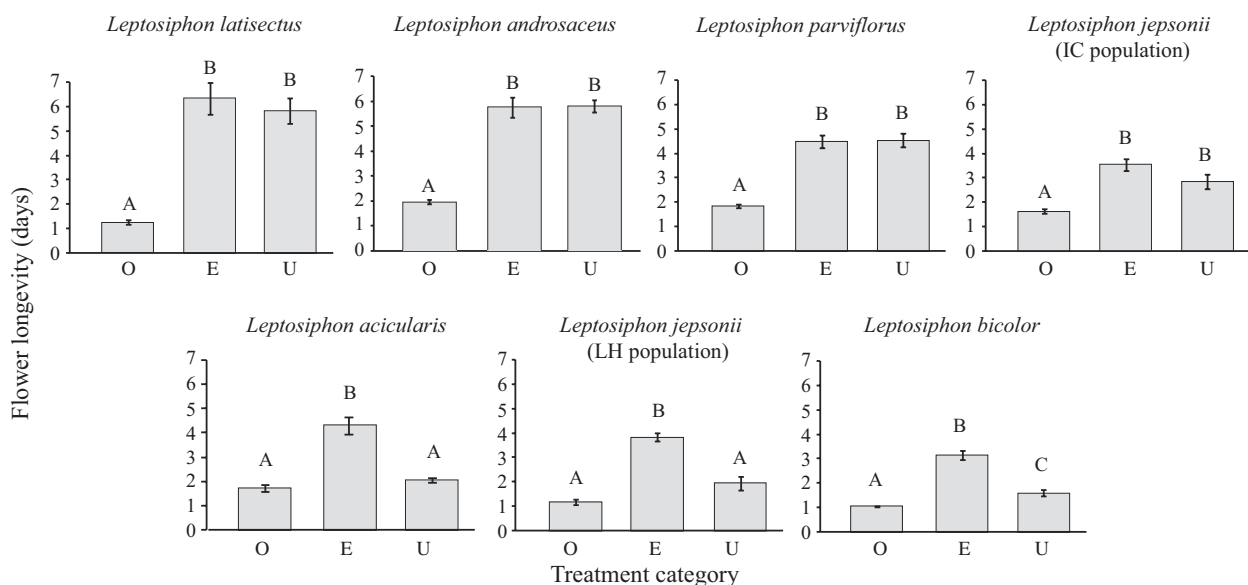
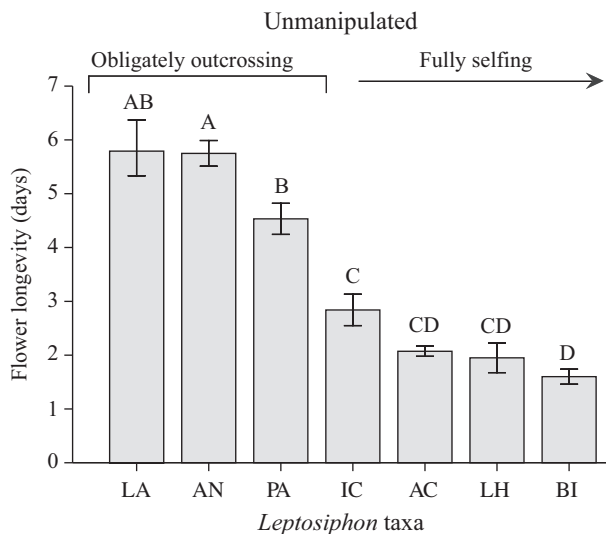


Fig. 1. Mean floral longevity of six species, including two populations of *Leptosiphon jepsonii*, of hand outcrossed (O), emasculated (E) and unmanipulated (U) flowers. Letters above bars indicate treatments that were significantly different in Games-Howell *post-hoc* tests. Error bars represent ± 1 SE.

Table 2. ANOVA results and Games-Howell *post-hoc* tests for the effect of pollination treatment on floral longevity for each species (or population).

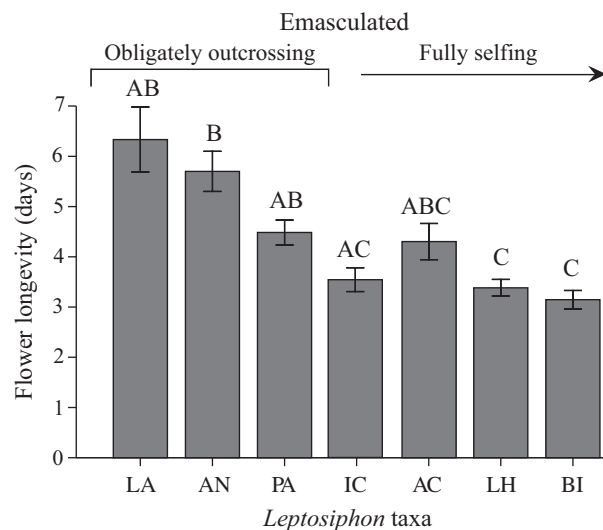
Species or population	Source of variation	df	MS	F	Games-Howell comparison
<i>L. latisectus</i>	Treatment	2	47.80	34.38***	E × U
	Error	15	1.39		E × O** U × O**
<i>L. androsaceus</i>	Treatment	2	57.51	64.65***	E × U
	Error	33	0.89		E × O*** U × O***
<i>L. parviflorus</i>	Treatment	2	28.27	47.43***	E × U
	Error	33	0.60		E × O*** U × O***
<i>L. acicularis</i>	Treatment	2	21.09	35.76***	E × U***
	Error	29	0.60		E × O*** U × O
<i>L. jepsonii</i> (IC)	Treatment	2	9.23	18.05***	E × U
	Error	27	0.51		E × O*** U × O**
<i>L. jepsonii</i> (LH)	Treatment	2	14.96	32.65***	E × U**
	Error	33	0.46		E × O*** U × O
<i>L. bicolor</i>	Treatment	2	12.939	64.54***	E × U***
	Error	30	0.200		E × O*** U × O**

E, emasculated; U, unmanipulated; O, outcrossed.
** $P \leq 0.01$, *** $P \leq 0.001$.

**Fig. 2.** Mean floral longevity of six species, including two populations of *Leptosiphon jepsonii*, of unmanipulated flowers. Letters above bars indicate treatments that were significantly different in Games-Howell *post-hoc* tests. Abbreviations and breeding systems are as follows: LA for *L. latisectus*, self-incompatible; AN for *L. androsaceus*, self-incompatible; PA for *L. parviflorus*, self-incompatible; IC for the Ida Clayton population of *L. jepsonii*, transient self-incompatible; AC for *L. acicularis*, self-compatible or transient self-incompatible; LH for the Lake Hennessey population of *L. jepsonii*, transient self-incompatible; and BI for *L. bicolor*, self-compatible. Error bars represent ± 1 SE.**Table 3.** ANOVA results for the effect of species (or population) with different outcrossing rates and levels of self-incompatibility on floral longevity in emasculated and unmanipulated flower treatments.

Treatment	Source of variation	df	MS	F
Emasculated	Species	6	13.21	12.92***
	Error	67	1.02	
Unmanipulated	Species	6	33.27	47.01***
	Error	67	0.71	

** $P \leq 0.01$, *** $P \leq 0.001$.

**Fig. 3.** Mean longevity of emasculated flowers of six species, including two populations of *Leptosiphon jepsonii*. Letters above bars indicate treatments that were significantly different in Games-Howell *post-hoc* tests. Abbreviations and breeding systems are the same as for Fig. 2. Error bars represent ± 1 SE.

DISCUSSION

Floral senescence triggered by pollination is widespread in angiosperms (Stead & Moore 1979; Gori 1983; O'Neill 1997; Yasaka *et al.* 1998; Arathi *et al.* 2002; van Doorn 2002; Rathcke 2003; Underwood *et al.* 2005; Rogers 2006; Castro *et al.* 2008) and may play a role in the evolution of self-fertilisation in self-compatible species. For all of the species and populations of *Leptosiphon* studied, floral senescence was induced by compatible pollination, as outcrossed flowers senesced earlier than emasculated flowers. Our experimental protocol did not allow us to determine the specific trigger for floral senescence. Pollen tubes can reach the base of the style in only 3 h in *Leptosiphon* species; therefore, fertilisation itself could be the signal for the rapid senescence observed. Pollen germination and pollen tube growth may also trigger senescence, as has been described in many other species (*e.g.* Stead & Moore 1979; Karle & Boyle 1999; Underwood *et al.* 2005; Castro *et al.* 2008; reviewed in: O'Neill 1997; Rogers 2006). In petunia, both pollen tube growth and ovule fertilisation appear to trigger stages of floral senescence (Hoekstra & Weges 1986; Underwood *et al.* 2005). Incompatible pollen deposition does

not appear to trigger senescence in *Leptosiphon*; some autonomous self-pollen deposition occurs in all of the *Leptosiphon* species studied since stigma and anthers show little spatial separation, yet in self-incompatible populations, unmanipulated flowers were as long-lived as emasculated flowers. Moreover, in a previous study of *L. jepsonii*, hand self-pollinated flowers were longer lived in an inbred line with delayed self-compatibility relative to one with early self-compatibility, despite the fact that pollen was deposited upon flower opening in both lines (Weber & Goodwillie 2007).

We showed that autonomous self-pollination limits floral longevity in self-compatible species of the genus *Leptosiphon*. Our results are consistent with previous work in which we examined populations of *L. jepsonii* that differed in the relative proportion of early and late self-compatible plants (Weber & Goodwillie 2007). We found in that study that unmanipulated flowers in plants with early self-compatibility were shorter lived than those with delayed self-compatibility. By expanding our study to the genus level, we were able to provide further evidence that autonomous selfing limits floral longevity. Based on the comparison of emasculated and unmanipulated flowers, autonomous self-pollination reduced maximum floral longevity in a highly selfing population of *L. jepsonii* (LH) and two other self-compatible species. In two of these cases, *L. acicularis* and LH population of *L. jepsonii*, flower longevity of unmanipulated flowers was not different from the longevity of flowers hand cross-pollinated on the first day of anthesis. This suggests that autonomous self-pollination can reduce opportunities for cross pollen receipt in low or intermediate pollinator environments for these taxa (when pollinators may not visit on the first day of anthesis). For *L. bicolor*, hand cross-pollinated flowers senesced earlier than unmanipulated flowers, showing that autonomous selfing does not reduce floral longevity as much as cross-pollination on the first day of anthesis, despite deposition of self pollen upon flower opening and complete self-compatibility (Goodwillie 1999). This somewhat surprising result might reflect differences in the abundance of pollen deposited. Pollen production is low in *L. bicolor* (unpublished data), as is common in many highly selfing species (Cruden 2000), and hand cross-pollinations may have more thoroughly covered the stigma surface than after autonomous selfing.

In species comparisons, longevity of unmanipulated flowers in self-incompatible species was as much as three times that of the most selfing species (Fig. 2). Although similar trends were seen in emasculated flowers, the difference between selfing and outcrossing species was less extreme (Fig. 3). This suggests that the lifespan of flowers in selfing species is limited both by evolved differences in floral longevity and senescence induced by autonomous self-pollination.

Results for *Leptosiphon* are consistent with those in other plant taxa. In a study of *Impatiens hypophylla* (Balsaminaceae) varieties, autonomous selfing reduced floral longevity (Sato 2002). Karle & Boyle (1999) found that floral longevity was mediated by breeding system and the stage of floral development in which autogamy commences in self-compatible and self-incompatible clones of the Easter cactus *Hatiora × graeseri* (Cactaceae). Selfing-induced floral senescence could limit opportunities for pollen transfer, and therefore male outcross success. This potential cost of autonomous self-

ing might play a role in the evolution of plant mating systems and warrants further consideration.

In turn, mating systems might influence the evolution of floral longevity (Karle & Boyle 1999; Sato 2002; Marshall *et al.* 2010). An outcrossing species may gain both male and female fitness by allowing flowers to remain open longer to increase the probability of visitation (Bell 1985; Primack 1985; Blair & Wolfe 2007). Empirical support for a fitness gain associated with floral longevity comes from studies of outcrossing species in which fruit or seed set is lower when floral longevity is experimentally reduced (*Kalmia latifolia*, Rathcke 2003; *Roscoea* spp., Zhang *et al.* 2011). Further evidence comes from the finding of longer floral longevity in populations or species found in low visitation environments (Berjano *et al.* 2009), particularly at high elevations (Medan 2003; Giblin 2005). In contrast, highly selfing species should stand to gain less by maintaining flowers and may benefit from pollinating quickly and moving on to fruit development. In this context, selfing species should generally have shorter floral longevity than outcrossing species of the same genus or family (Morin 1983; Primack 1985). We demonstrated that maximum (emasculated) floral longevity generally increases with the degree of outcrossing in species of the genus *Leptosiphon* (Fig. 3). We note that the pattern is independent of phylogenetic relatedness; *L. androsaceus*, a self-incompatible species, is closely related to two of the self-compatible species, *L. jepsonii* and *L. bicolor*, while the self-incompatible *L. latisectus* and *L. parviflorus* are closely related to *L. acicularis*, a self-compatible species (Goodwillie 1999). We hypothesise that mating systems have mediated the evolution of floral longevity in this genus. In a previous study, populations of one of the self-incompatible species, *L. parviflorus*, were found to be significantly pollen-limited (Goodwillie 2001). Moreover, all of the self-incompatible species included in the study have long corolla tubes and are pollinated largely by bees (Grant & Grant 1965; J. Weber personal observation). Specialised pollination systems have been associated with high rates of pollen limitation (Martén-Rodríguez & Fenster 2010). Thus, limited, specialised pollinator service in self-incompatible *Leptosiphon* species might have selected for longer flower duration to maximise seed set. An alternative explanation for this pattern in other plant taxa has been offered: reduction in floral longevity and other life history stages has evolved by selection to limit the length of the life cycle in ephemeral habitats, with selfing a by-product of selection (Snell & Aarssen 2005). However, all of the *Leptosiphon* species sampled are sympatric and occur in fairly similar oak woodland habitats, so this explanation seems unlikely in the present case.

In conclusion, we found evidence that there is potential for autonomous self-pollination in self-compatible species to have both a proximal effect on floral longevity and selective consequences for the evolution of floral longevity. In the genus *Leptosiphon*, highly selfing taxa exhibited shorter floral longevity than self-incompatible taxa in unmanipulated flowers. Reduced floral longevity in autonomously self-fertilising taxa may reduce opportunities for male outcross success. Further, we demonstrate that maximum floral longevity is higher in fully self-incompatible taxa compared to highly self-fertilising taxa, suggesting that floral longevity may be an adaptive trait that evolves with the mating system. The

selective explanations for divergence in the mating and breeding systems in *Leptosiphon* remain largely unknown, although various lines of evidence suggest roles of microhabitat variation in pollinator visitation (Goodwillie 2001; Weber & Goodwillie 2009), wind availability (Goodwillie 1999) and hybridisation with congeneric species (Weber & Goodwillie 2009). However, this study contributes to our understanding of how floral traits have evolved in concert with the mating system in *Leptosiphon*.

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