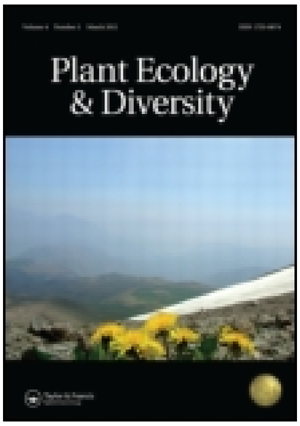

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SHORT COMMUNICATION

Pollination biology and floral longevity of *Aristolochia chilensis* in an arid ecosystem

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Background: In *Aristolochia* species the pollination process involves temporary imprisonment of pollinators. Floral longevity is an essential trait for pollination biology, influencing the total number of pollinator visits. Floral longevity should balance costs of flower maintenance and time to fulfil reproduction. For *Aristolochia* species there is an extra factor: survival of trapped insects. Environmental conditions may affect floral longevity because pollinator visits are likely to be less frequent in stressful habitats.
Aims: Our aim was to study the pollination biology of *A. chilensis* in an arid ecosystem and to determine the relationship between floral longevity in *Aristolochia* and aridity.
Methods: We measured floral longevity, pollinator quantity and identity and tested the viability of self-fertilisation in *A. chilensis*. We also compiled information on floral longevity and habitat characteristics of *Aristolochia* species using published literature.
Results: Dipterans were the only effective pollinators of *A. chilensis*, which required pollinators to set fruit. *A. chilensis* had the greatest floral longevity recorded for the genus and the study population was located in the most arid and least productive environment reported for any *Aristolochia* species. When data from nine *Aristolochia* species were analysed, floral longevity increased with habitat aridity and decreased with habitat productivity.
Conclusions: Floral longevity varies consistently with habitat aridity and productivity in *Aristolochia*. Further research should determine the relative importance of biotic and abiotic factors in the evolution of floral longevity in *Aristolochia*.

Keywords: aridity; *Aristolochia*; environment; floral longevity; pollinators; reproductive ecology

Introduction

Flower longevity is defined as the length of time an individual flower remains open and functional, from anthesis until senescence (Primack 1985; Ashman and Schoen 1996). It is an essential trait for pollination biology because it affects the total number of pollinator visits, and thereby the quantity and diversity of pollen that flowers receive (Ashman and Schoen 1996). There is evidence that the type of habitat affects floral longevity. Plant species in tropical ecosystems typically show shorter floral longevities, presumably because favourable conditions allow increased pollinator visitation (Primack 1985), and floral longevities are extended in environments where pollinators are scarce, which might increase the probability of effective pollination (Fabbro and Körner 2004). In fact, floral longevity is negatively correlated with pollinator visitation rate across species (Ashman and Schoen 1996). The fitness benefits of extended floral longevity via increased probability of pollinator visits (Evanhoe and Galloway 2002; Rathcke 2003; Itagaki and Sakai 2006; Makrodimos et al. 2008) must be balanced against the metabolic and ecological costs of floral maintenance (Ashman and Schoen 1994; Harder and Barrett 1995; Galen et al. 1999; Galen 2000; Celedón-Neghme et al. 2007). Thus, from an adaptive perspective, floral longevity is a life history trait that results from the interplay between the costs of maintenance of a flower and how rapidly it can fulfil its reproductive function (Primack 1985; Ashman and Schoen 1996).

The genus *Aristolochia*, with over 300 species, is the most diverse genus in the Aristolochiaceae, a family belonging to the basal angiosperms (Huber 1993). Most *Aristolochia* species are of tropical distribution, but there are also some species in subtropical or temperate regions (Endress 1994; Kelly and González 2003). *Aristolochia* flowers are protogynous, and during the female phase they attract pollinators – mainly dipterans – into a sac-like flower by carrion/dung scents that mimic brood sites of dipterans. Insects are kept imprisoned inside the flower by downward-oriented trichomes located at the inner surface of the flower. During the male phase, insect pollinators are released via the loss of turgor in the trichomes (Fuller 1924; Burgess et al. 2004; Trujillo and Sérsic 2006; Rulik et al. 2008; Berjano et al. 2009; Oelschlägel et al. 2009). Being protogynous is a successful strategy to avoid self-pollination in self-incompatible species, which is generally the case for *Aristolochia* species (Fuller 1924; Sakai 2002; Burgess et al. 2004; Trujillo and Sérsic 2006; Valdivia and Niemeyer 2007; Nakonechnaya et al. 2008). Nonetheless, there is evidence of self-compatibility for some *Aristolochia* species (Razzak et al. 1992; Sakai 2002; Berjano et al. 2006).

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It may be postulated that outcrossing rates decrease with environmental stress, with populations at the edges of species' ranges or in arid habitats showing autonomous self-fertilisation (Schoen 1982; Holtsford and Ellstrand 1992; Kalisz et al. 2004; Levin 2010). With regard to floral longevity and the interplay between flower maintenance costs and successful pollination (Primack 1985; Ashman and Schoen 1996), for *Aristolochia* species there is a potential ecological cost of extended floral longevity: the survival of trapped insects. Insects kept longer inside the flower have a higher risk of dying from starvation because the deceptive *Aristolochia* flowers lack pollinator rewards (Burgess et al. 2004; but see Murugan et al. 2006 for an exception). If insects die inside long-lived flowers, pollen will not be carried to other flowers, thus limiting plant reproduction in the population.

In the present study we describe the pollination biology of a population of the perennial herb *A. chilensis* in a dry habitat (annual rainfall: 78 mm), by reporting floral longevity and pollinator quantity and identity. In addition, we tested whether this population showed some degree of autonomous self-fertilisation. Furthermore, we reviewed the literature on the reproductive ecology of *Aristolochia* in order to evaluate the association between floral longevity in the genus and habitat aridity. The latter allowed us to gain insights into the possible abiotic modulation of floral longevity in *Aristolochia*, a feature that is important to secure plant reproduction under stressful conditions. Knowledge of the interplay between abiotic and biotic selective pressures acting on floral longevity is of value to understand the pollination system in *Aristolochia*.

Materials and methods

Study system

Aristolochia chilensis (Bridges ex Lindl.) is a perennial herb endemic to Chile that is distributed from a Mediterranean-type climate in central Chile (33° 29′ S) to an arid climate in the northern limit of its range (27° 30′ S), which is located in the Atacama Desert (Ruiz 2001). It has dark green, reniform leaves (3–10 cm) and foul-smelling purple-brownish 3–5 cm-long flowers. Flowers have a tubular perianth, subdivided into a utricle, a balloon-like sac that contains the gynostemium, a tube and the limb. The gynostemium results from the fusion of the styles, stigmas and stamens. Downward-oriented white trichomes cover the inner wall of the perianth tube and thus permit the entry but impede the exit of insect visitors. The only published study on the pollination biology of *A. chilensis* was conducted in a population close to the southern limit of its distribution (average annual rainfall of 262 mm; Chilean Meteorology Service 2011: www.meteochile.cl) and reported that it was self-incompatible species, lacking nectaries or any pollinator reward, and that dipterans were the only effective pollinators (Valdivia and Niemeyer 2007).

This study was carried out in a population of *A. chilensis* in the Coquimbo region (29° 58′ S; 71° 22′ W). This region has no rainfall during most of the year (8–10 months), and is classified as an arid Mediterranean-type climate (Di Castri and Hajek 1976). Average annual rainfall is 78 mm (Chilean Meteorology Service 2011), but during dry years it can be <10 mm (Pérez 2005). The study area shows substantial inter-annual variation in rainfall (Chilean Meteorology Service 2011). The study population was located on a rocky, east-facing slope amid a plant community dominated by small shrubs and cacti.

Pollination biology

To determine the quantity and identity of floral visitors, a total of 111 flowers from different plants were collected during the 2008 and 2009 growth seasons: 58 flowers in the pistillate stage and 53 in the staminate stage. The utricles of all flowers were dissected and all insects were counted. One sample of each insect type was kept in 70% ethanol and identified to family level. Insect visitors collected during 2009 were observed with a magnifying glass to detect pollen on their bodies and thus determine whether they were effective pollinators. We recorded the number of insects per flower, abundance by family, and family dominance, i.e. percentage of the total insect sample.

To assess the possibility of self-pollination in *A. chilensis*, an experiment was carried out during the 2008 growing season. In late September, we randomly chose 20 plants from the study population with unopened flowers. In each plant we carefully covered one flower with a tulle mesh bag to prevent pollinator access, while another flower was left intact, as control treatment. This paired design was free from bias resulting from differences among plants. Two months later all experimental plants were checked for the presence of fruits.

To observe floral longevity, we marked 80 unopened flowers from 40 different plants in the study population during the 2009 growing season. Ten flowers were dissected every day after anthesis until the eighth day, which was considered the end of flower lifetime because by that time all flowers had completely wilted. Both internal and external morphological changes were noted, with special emphasis on the reproductive structures of the flowers. We also recorded the presence of insects inside the flowers.

Aridity and flower longevity in Aristolochia *species*

To relate our results to those from other *Aristolochia* species, articles addressing the pollination biology of *Aristolochia* species were obtained by searching in the Web of Science (ISI) database and checking the references cited by those articles. We included papers reporting floral longevity and duration of the female phase of *Aristolochia* species. We only considered studies carried out in natural populations. We did not take into account articles reporting results from observations made in botanical gardens or in urban settings because environmental conditions there might differ from those in natural populations (e.g. temperature, soil water, nutrient availability) and could affect floral longevity. We retrieved data on temperature (mean maximum temperature of the warmest month, °C) and precipitation (mean annual precipitation, mm) of the sites reported in the studies, or nearby locations, from online climate databases (http://www.worldclimate.com; http://www.meteochile.cl/). We also obtained data on the net primary productivity (NPP, expressed as dry matter (g m^{-2} $year^{-1}$) corresponding to each site coordinate from a database available at http://user.uni-frankfurt.de/~grieser/downloads/NetPrimaryProduction/npp.htm. To assess the relationship between floral longevity, and habitat aridity (precipitation) and NPP, we used regression analyses.

Results

A total of 124 insects from 17 families and five orders were found inside 111 flowers of *A. chilensis* inspected during the 2008 and 2009 growing seasons. Dipterans were the most common visitors and the members of Calliphoridae family were the most frequent, at ca. 42% (Table 1). Up to a maximum of 14 insects were found inside a single flower, but most flowers harboured one individual. The only insect visitors observed carrying pollen were dipterans from the Calliphoridae and Muscidae families. Calliphoridae individuals carrying pollen were observed in both pistillate and staminate stages; Muscidae carrying pollen were observed in the staminate stage. Dipterans showed an average density of 0.6 individuals per flower.

In the self-pollination experiment, none of the bagged flowers – where pollinators were excluded – was able to set fruit; therefore, insects were needed for fertilisation and fruit production to occur. In contrast, 39% of the flowers in the control treatment – where pollinators had access to flowers – had fruits two months later.

There was a sequence of both internal and external morphological changes in the *A. chilensis* flower during its lifetime (Figure 1). On the first day of anthesis, the stigmas were receptive and the trichomes were erect and oriented downwards. On the second day, the gynostemium began to bend its lobes to the inside, starting to fold the stigmas. On the third day of anthesis three out of 10 flowers were not exposing pollen yet, but in seven flowers, the stigmas were already folded and they were already exposing the stamens and pollen. On the fourth day, all flowers had their pollen exposed and the trichomes were flattened; this widened the perianth tube and allowed insects to enter and leave. During the fifth day, many trichomes fell off and the perianth tube was wide open; most insects left the flower by this stage. On the six and seventh days, the flowers started to wither, with the upper parts of the tube decaying and

Table 1. Classification and abundance of insect families found inside the flowers of *Aristolochia chilensis* in a population from an arid environment. For each family, the total abundance (*N*), dominance (*D*, percentage of the total) and the flower stage where insects were found (female or male) are shown.

Order	Family	*N*	*D* (%)	Stage (♀/♂)
Diptera	Calliphoridae	52	41.9	33/19
	Phoridae	4	3.2	4/0
	Trypetidae	4	3.2	3/1
	Pipunculidae	2	1.6	0/2
	Drosophilidae	2	1.6	1/1
	Sciaridae	2	1.6	2/0
	Muscidae	1	0.8	0/1
	Piophilidae	1	0.8	0/1
	Tachinidae	1	0.8	1/0
Hemiptera	Psyllidae	18	14.5	8/10
	Aphidae	8	6.5	7/1
	Miridae	5	4.0	3/2
	Anthocoridae	3	2.4	2/1
	Largidae	1	0.8	1/0
Lepidoptera	Gelechidae	10	8.1	5/5
Coleoptera	Chrysomelidae	9	7.3	0/9
Acariformes	Trombidiidae	1	0.8	0/1

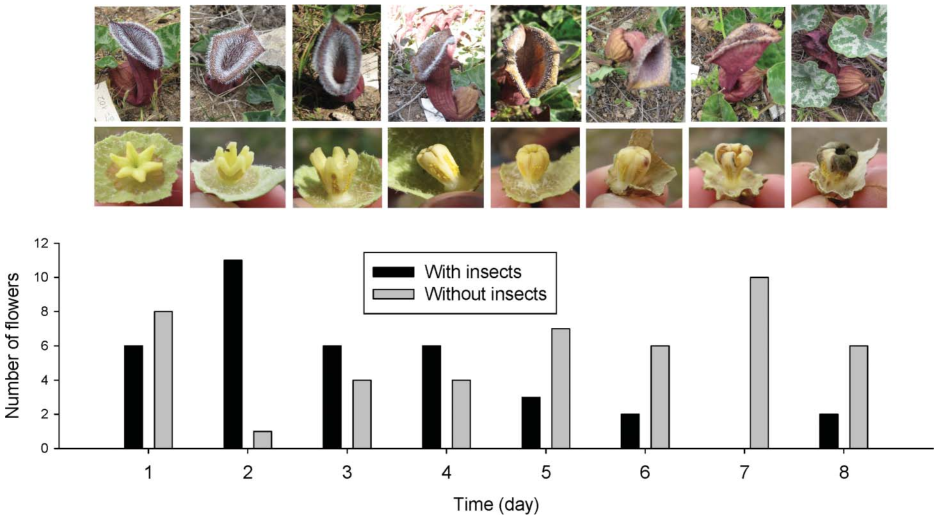

Figure 1. Floral longevity of *Aristolochia chilensis* from anthesis (Day 1) to senescence (Day 8). External morphology of the flower (upper row of photographs) is shown together with changes in the gynostemium (lower row of photographs) during the transition from the female stage to the male stage. The proportion of flowers harbouring insects is shown for each day.

Table 2. Floral longevity and environmental conditions of the habitat of *Aristolochia* species studied under natural conditions to date. Floral longevity, time from anthesis to floral senescence (days); Female phase (days); *P*, mean annual precipitation (mm); $T_{\max}$, mean maximum temperature of the warmest month (°C); NPP, Net Primary Productivity (g m^{-2} $year^{-1}$, dry matter).

Species	Population location	*P*	$T_{\max}$	NPP	Floral longevity	Female phase	Source
A. chilensis	Coquimbo, Chile	78	21.6	146.4	8	2–3	[1]
A. paucinervis	Huelva, Spain	490	31.8	883.9	7.5	5.3	[2]
A. baetica	Huelva, Spain	490	31.8	883.9	7	3.5	[2]
A. argentina	Córdoba, Argentina	837	29.8	1317.4	2	1	[3]
A. littoralis	Gainesville, FL, USA	1316	33.6	1715.4	3	1	[4]
A. maxima	Panama City, Panamá	1907	35.8	2207.0	2	1	[5]
A. inflata	Panama City, Panamá	1907	35.8	2207.0	2	1	[5]
A. pilosa	Las Cumbres, Panamá	1907	35.8	2207.0	2	–	[6]
A. grandiflora	Veracruz, México	1753	31.2	2208.0	3	1	[7]

Sources: [1] This study; [2] Berjano et al. (2009); [3] Trujillo and Sérsic (2006); [4] Hall and Brown (1993); [5] Sakai (2002); [6] Wolda and Sabrosky (1986); [7] Burgess et al. (2004).

partially closing the entrance to the flower. On the seventh day, 20% of the flowers were still completely open and 80% were already closing, but 100% still had the stamens functional and still with pollen. On the eighth day, the flowers were withering. Insects remained inside the flower mostly until the fourth day, less frequently the fifth day, and rarely on days six and seven after anthesis. Only two insects were observed in the flowers on the eighth day, and one of them was dead (Figure 1).

The literature survey yielded data for eight *Aristolochia* species, in addition to *A. chilensis* (Table 2). Their floral longevity ranged from 2–8 days, with most species showing flowers lasting for 2–3 days (Table 2). The female stage lasted only 1 day in five of the species where this information was available, and its duration was correlated with total floral longevity (Pearson correlation, $r = 0.78$). The study population of *A. chilensis* was located in the most arid and least productive habitat and showed the greatest flower longevity (Table 2). When the nine *Aristolochia* species were included in regression analyses, despite the small sample, floral longevity showed statistically significant associations with precipitation and habitat productivity. Thus, floral longevity decreased with increased precipitation ($F = 20.75$, df $= 7$, $R^2 = 0.71$, $P = 0.0026$) and habitat productivity ($F = 25.69$, df $= 7$, $R^2 = 0.76$, $P = 0.0014$).

Discussion

The studied population of *Aristolochia chilensis* was located at the driest of all sites from where reproductive ecology has been reported for the genus, including a species from the Sonoran desert (Crosswhite and Crosswhite 1984). With regard to pollinator abundance (dipterans), this population received 50% less visits per flower (0.6) than that reported for the Mediterranean species *A. baetica* (1.2) (Berjano et al. 2009), or the tropical species *A. pilosa* (2.1–6.0) (Wolda and Sabrosky 1986) and subtropical *A. littoralis* (10.9) (Hall and Brown 1993). Therefore, the studied species not only inhabits a rather stressful habitat in terms of water availability but it also experiences low pollinator availability.

Insects from several families and orders visited the flowers of *A. chilensis,* but only dipterans were observed carrying pollen. This finding agrees with previous work on *A. chilensis* (Valdivia and Niemeyer 2007) and other *Aristolochia* species (Berjano et al. 2009), and is also consistent with the syndrome of sapromyiophily that is typical of Aristolochiaceae and other basal angiosperm families (Sakai 2002; Burgess et al. 2004; Berjano et al. 2009; Bolin et al. 2009; Johnson and Jürgens 2010). Pollinators are necessary for fruit production in *A. chilensis* as seen from the results of the pollinator exclusion treatment. An identical result was reported for a population of *A. chilensis* from a comparatively humid environment (Valdivia and Niemeyer 2007). This suggests that inhabiting a stressful environment has not driven the evolution of self-compatibility to provide reproductive assurance in this species. However, self-compatibility may increase in populations of weakly self-fertile plant species growing in conditions of environmental stress (Levin 2010) or when pollinators are limiting (Kalisz et al. 2004). There are some *Aristolochia* species that are self-compatible, but they are not distributed in particularly stressful habitats (Razzak et al. 1992; Sakai 2002; Berjano et al. 2006). In *Aristolochia* species, changes in floral longevity (see below) are seemingly more feasible than modifications of the mating system in order to cope with pollinator shortage associated with habitats of low productivity. Interestingly, *Convolvulus chilensis*, one of the few herbaceous perennials co-occurring with *A. chilensis* in arid Chile, shows autogamy but extremely short floral longevity (Suárez et al. 2004).

Floral longevity has been reported to vary with environmental conditions, with long-lived flowers often found in stressful habitats (Ashman and Schoen 1994), but it also varies inversely with the rate of pollinator visits across species (Ashman and Schoen 1996). In sympatric populations of two Mediterranean *Aristolochia* species, the one with the lower visitation rate showed longer floral longevity (Berjano et al. 2009). We found that floral longevity in *Aristolochia* species increased with habitat aridity and decreased with primary productivity, supporting the expected relationship between floral longevity and the stressfulness of a habitat. The similar outcome of both regression analyses, with precipitation and productivity as predictors, suggests that water availability is the main factor determining environmental conditions that shape floral longevity. This trait may also be influenced by the species' mating system, with flowers of outbreeders lasting longer than those of inbreeders, and thereby increasing the probability of pollination (Primack 1985). However, within *Aristolochia* there is no clear pattern of variation of floral longevity with species' self-fertilisation ability (Sakai 2002; Burgess et al. 2004; Berjano et al. 2006, 2011; Trujillo and Sérsic 2006).

As expected from its location in a relatively stressful habitat, with low rainfall and high inter-annual variability, *A. chilensis* showed the longest floral longevity recorded for the genus. Whereas long-lasting flowers in *A. chilensis* might enhance the probability of pollinator visit, flower maintenance entails metabolic costs (Ashman and Schoen 1994). Moreover, extended floral longevity might jeopardise the survival of trapped insects. The longer insects are kept inside the flower, the higher the probability of them dying from starvation in the rewardless *Aristolochia* flowers (Burgess et al. 2004; but see Murugan et al. 2006). If insects die within the flower, pollen cannot be transferred to another plant and populations may eventually experience a demographic breakdown because *A. chilensis* requires cross-pollination to set seeds.

The critical period for insect survival is the pistillate stage, where they cannot leave the flower. The longer this stage lasts, the greater the probability of insect mortality. This suggests that floral longevity may exert selection on insect starvation resistance. Interestingly, this could also suggest that starvation resistance of pollinators might determine the observed upper limit of floral longevity (or duration of the pistillate stage) in the genus. Starvation may cause dipteran mortality in about 4 days, but in combination with desiccation 100% mortality occurs in less than 3 days (Weldon and Taylor 2010). This potential for higher mortality during the pistillate stage might explain why *A. chilensis* shows only a slightly longer pistillate stage compared with other *Aristolochia* species, despite having the longest total floral longevity in the genus. Interestingly, the Mediterranean *A. paucinervis* has the longest pistillate stage within *Aristolochia* (Table 2), and high mortality (8–62%) of dipteran visitors within the flower has been reported (Berjano et al. 2009). The possible role of starvation and/or desiccation resistance of pollinators in the evolution of floral longevity in *Aristolochia* species from arid environments deserves further investigation.

Aristolochia species show rather unique pollination features. We have shown that floral longevity in the genus varies consistently with environmental conditions, which are associated with both biotic and abiotic factors that may exert constraints on plant fertilisation. Further research should determine the relative importance of each of these factors across species and identify the selective agents at the population level. *A. chilensis*, which is distributed in semiarid and arid environments, shows the longest floral longevity so far reported for the genus. The study of survival of trapped insects and self-compatibility in populations from the most arid environments are promising research avenues to understand the limits and potentials of the pollination system in this species and the entire genus.

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Notes on contributors

Gisela C. Stotz is generally interested in the evolutionary consequences of plant interactions with other plants, insects and the environment.

Ernesto Gianoli's research interest focuses on functional explanations for ecological patterns and on understanding the ecological and evolutionary consequences of plant–insect interactions influenced by the environment.

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