Comparative phenology and floral patterns in Larrea species (Zygophyllaceae) in the Monte desert (Mendoza, Argentina)

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Phenological patterns and floral stages are described for Larrea divaricata, L. cuneifolia, and L. nitida in the Monte desert. In addition, floral structures and their relation to self-pollination levels are compared. Rainfall events and/or microclimatic conditions resulted in phenological differences between sites and years. Seven floral stages were determined and protogyny was detected in the early stages. Larrea divaricata, L. cuneifolia and L. nitida were observed to have a range of large to small floral structure sizes, respectively. This coincides with an increase of autogamy, while at the same time an increase in the percentage of flowers with protogyny.

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Keywords: Larrea; Monte desert; autogamy; self-pollination; floral morphology; phenology; floral stages; floral development; protogyny

Introduction

The genus Larrea (creosotebush) comprises five evergreen xerophytic shrub species with an amphitropical distribution in the warm deserts of America (Hunziker et al., 1972, 1977). The highest diversity is found in South America, where four species (Larrea divaricata Cav., L. cuneifolia Cav., L. nitida Cav., and L. ameghinoi Speg.) occur, showing differences in habitat preference, morphology, phenological patterns, and mating systems (Barbour et al., 1977; Simpson et al., 1977; Ezcurra et al., 1991). In Argentina, Larrea is dominant in the phytogeographical province of Monte that stretches from 24° 35’S in Salta to 44° 20’S in Chubut, and from 62° 54’W on the Atlantic coast to 69° 50’W in the pre-Andean region (Morello, 1958). It is also found in the phytogeographical provinces of Chaco and Patagonia (Ezcurra et al., 1991). Moreover, isolated populations of L. nitida and L. divaricata occur in arid and semi-arid areas of Chile, Bolivia and Peru (Hunziker et al., 1972).

Phenological events in desert plants are triggered mainly by rainfall and suitable temperature (Noy Meir, 1973; Beatley, 1974). The vegetative growth of Larrea species occurs whenever conditions are favourable (Chew & Chew, 1965; Cunningham
et al., 1979), while reproductive growth takes place in response to rainfall events (Barbour et al., 1977; Bowers & Dimmit, 1994). Phenological differences may reflect genetic variations and subtle microgeographic conditions, and may be highly influenced by year-to-year climatic variability (Martínez Carretero & Dalmasso, 1992).

Although similar in floral morphology, Larrea species differ in the size of their floral structures, corolla unfolding, and the degree of contact between anthers and stigma (Simpson et al., 1977; Porter, 1979). These characters have been considered to be related to self-pollination levels. Simpson et al. (1977) demonstrated using experimental crosses with L. tridentata (the North American species), L. cuneifolia and L. divaricata a decrease in the degree of natural self-pollination corresponded with an increase in flower size. Although the mating systems of L. nitida and L. ameghinoi was not studied, the authors suggested that an increase in autogamy might occur in these two species with smaller flowers. To date, a detailed comparative study of floral structure size has not been made of the South American species of Larrea.

This work is part of a broad study focusing on the mating system of all three species of Larrea in Mendoza Province, Argentina. Our main objectives are: (1) to describe the phenological pattern of L. nitida, L. cuneifolia, and L. divaricata in representative areas of the Monte, (2) to characterize and describe their floral development, and (3) to make a comparative study of the floral structure of each species and relate these data to self-pollination levels.

**Materials and methods**

**Study sites**

Field work was conducted on populations of L. divaricata and L. cuneifolia in the Nacuñán Biosphere Reserve. Larrea nitida was studied in two localities in the piedmont near Mendoza city where a population of L. divaricata was also studied. The Biosphere Reserve of Nacuñán (34° 02' S, 67° 54' W; 570 m) is located 200 km SE of Mendoza, in a vast quaternary eolic plain. The reserve is part of the phytogeographical province of Monte, which is characterized by xerophytic vegetation. An open forest of Prosopis flexuosa D.C. with a shrub layer dominated by L. divaricata, and a shrubland of L. cuneifolia (Roig, 1971) are the main plant communities within the reserve. Mean annual rainfall is 329.4 mm (1972–1992), concentrated in spring (24% in September to December) and summer (48% in January to March) (Estrella, 1995).

The Andean Precordillera piedmont is covered by a homogeneous shrub steppe, interrupted by temporary rivers with a taller and more abundant riparian vegetation (Roig, 1976). Larrea divaricata forms an altitudinal belt that ranges from 1200 to 1800 m, dominating the rest of the shrub community. Larrea cuneifolia occupies the lowest and driest belt (800–1200 m), constituting mixed Larrea shrublands with L. divaricata in narrow ecotonal zones. Larrea nitida is a characteristic species of the Andean Precordillera riparian communities, where there is more soil water availability. Plants of this species sometimes occur as low as 900 m, and in some places they are sympatric with the other two species (Roig, 1976).

Two field sites were chosen in the piedmont: Puesto Chamhón (32° 54' S, 68° 69' W; 1470 m) and Puesto La Obligación (32° 55' S, 69° 00' W; 1570 m). Mean annual rainfall at both sites is 300 mm (Station 600, Puesto Chamhón 1983–1996*), concentrated in spring and summer, 26% and 41%, respectively.

*Source: Centro Regional Andino, Instituto Nacional de Ciencia y Técnica Hídricas (CRA-INCYTH).*
Species description

Larrea species rarely exceed 2.5 m height, and can be differentiated by leaf characters. Larrea nitida has compound leaves, while L. divaricata and L. cuneifolia have only two leaflets with a small filiform mucron. The latter present a greater degree of leaflet fusion.

Flowers are solitary and axillary, with five partially fused green sepals and five imbricated free yellow petals. Filaments are partially fused with a basal scale, forming a cup-shaped receptacle where nectar is accumulated.

The ovary is superior, pentacarpellate, globose and pubescent, with a basal nectariferous tissue. The style and the stigma are simple in all species, and the presence of an early female stage (protogyny) has been reported (Simpson et al., 1977). The fruit is a schizocarp that dehisces into five one-seeded mericarps.

Phenological patterns

Ten individuals of each species were randomly selected and phenological events were observed at least once a month in different growing periods. For L. divaricata observations were made in Nacuña during the reproductive periods of 1993–94 and 1994–95, and in Puesto Chambón during 1995–96. For L. cuneifolia similar observations were made in Nacuña during 1993–94, 1994–95 and 1996–97. Larrea nitida was observed in Puesto La Obligación during the 1995–96 reproductive seasons. Four phenological phases were monitored: vegetative growth, presence of flower buds, flowers and fruits. Plants were considered flowering or bearing fruits at the first appearance of the respective organs.

Flowering phenology and floral patterns

Floral development was evaluated by monitoring flowers at the first stage (see Results, floral stages) of L. divaricata and L. nitida in Puesto La Obligación. A total of 117 flowers from four plants of L. divaricata, and 74 flowers from three plants of L. nitida, were monitored. Seven floral stages were considered. Observations were made 24, 30, 48, 55 and 96 hours after flowers were first observed in L. divaricata, and at 24, 32, 48 and 122 hours for L. nitida.

Ten individuals of L. cuneifolia, L. divaricata and L. nitida were selected in order to compare floral morphology. Many flowers in stage 2 or 3 from each plant were collected and fixed in FAA (formalin: acetic acid: ethyl alcohol). Sepal length and width, petal length and width, style length, ovary length, and stamen length were measured for 10 flowers per individual (i.e. 100 flowers per species). Measurements were taken with a digital caliper. Results were analysed using a two-way ANOVA for stamens data (whorls × species), a one-way ANOVA for the other measurements and Tukey’s test for mean’s contrast. In the field, stigma receptivity was determined for different flower stages using the peroxidase test, a positive reaction indicated by the presence of bubbles due to enzymatic activity.

Pollen tube growth was observed in L. nitida. Flowers were bagged and emasculated, and pollinated with individuals of the same population. Three flowers for three different stages were collected after 3, 8, 24 and 32 hours and were fixed in ethanol : lactic acid (2 : 1). The gynoecium was stained with aniline blue (0.1%), and pollen tube growth was observed with fluorescence microscopy.

The percentage of protogynous flowers was calculated from randomly collected flowers of the three Larrea species. Ten plants per species were selected and two flowering branches per plant were bagged to exclude pollinators to determine the degree
of autogamy and geitonogamy. In the first treatment, flowers were unmanipulated to determine spontaneous self-pollination (autogamy). For the second treatment, hand pollination was performed with pollen from flowers of the same plant (geitonogamy). Mature fruits were harvested and the number of seeds produced per flower was counted.

**Results**

**Phenological patterns**

During the three observation periods, 1993–94, 1994–95 and 1995–96, individuals of all three species of *Larrea* exhibited vegetative growth. Reproductive activity of *L. cuneifolia* in the Biosphere Reserve of Nacuñán differed among years. Although flower bud production always began during the first 2 weeks of October in the three periods of observation (Fig. 1), in 1994–95 flowering and fruiting were poorer and delayed compared to the other two periods. This displacement could be attributed to the scarce rainfall recorded during the winter, 1994, and the beginning of the following spring (Fig. 1). In addition, between December and January, 1993–94 and 1994–95, *L. cuneifolia* presented a second bloom closely related to a rainfall peak in December 1993 and 1994. In contrast, although considerable rainfall occurred in winter and spring 1996, and also December rainfall was significant, a second bloom was not observed during the 1996–97 growing period (Fig. 1).

In Nacuñán during 1993–94 and 1994–95 *L. divaricata* started producing flower buds in late September and early October. A second period of flower bud production was observed in 1994–95 at the end of December. In the later cases, however, the percentage of individuals that flowered simultaneously was low (less than 50%) when compared to the 1993–94 bloom period (Fig. 1). Two periods of flower bud production during a single growing season was similarly observed in *L. cuneifolia*.

The population of *L. nitida* studied in the piedmont started producing flower buds by mid-September. However, the growth of these buds was very slow, and flowering did not begin until a month later. Flowering in *L. divaricata*, which coexists with *L. nitida* on this site, occurred approximately 20 days later than in *L. nitida*. Consequently, overlapping of this phase was brief (Fig. 2).

**Flowering phenology and floral patterns**

**Floral stages**

Although floral development is a continuous process, seven floral stages were defined. Figure 3 shows stages 0 to 4 for *L. nitida* and *L. divaricata*.

Stage 0: sepals cover the corolla and petals gradually turn from green to yellowish-green in the globose bud (Fig. 3(a,f)).

Stage 1: sepals and petals begin to separate at the apex. In some cases they expose the already receptive stigma thus starting the female phase (protogyny). At this stage we observed nectar production and the visit of insects, which sometimes succeeded in forcing the opening of the flower (Fig. 3(b,g)).

Stage 2: sepals and petals begin to open during anthesis and the bright yellow corolla unfolds. Androecium and gynoecium are exposed, although the anthers remain indehisced. Stamens of the inner whorl (opposite petals) approach the petals and anthers remain indehiscent, while the anthers of the outer whorl (alternate to petals) move toward the stigma and begin to release pollen. The stigma is receptive and nectar production is observed (Fig. 3(c,h)).
Figure 1. Phenological patterns of Larrea divaricata and L. cuneifolia in Ñacuñán Biosphere Reserve. Mean annual rainfall (1972-1996) and mean monthly rainfall for each period of observation are shown.
Figure 2. Phenological patterns of Larrea nitida and L. divaricata in Puesto La Obligación and Puesto Chambón respectively. Mean annual rainfall (1983–1996) and mean monthly rainfall for each period of observation are shown (ND = no data).

Stage 3: sepals and petals unfold until perpendicular to the axis of the flower, except in L. nitida in which these structures remain partially opened. Petals then rotate 90° on their axis, remaining perpendicular to sepals and resembling the vane of a windmill. Each stamen of the inner whorl remains protected by a petal and its anthers remain indehiscent. The anthers of the outer whorl have little pollen and are whitish, the stigma is receptive and there is nectar secretion (Fig. 3(d, i)).

Stage 4: petals return to their original position, the anthers of the inner whorl approach the stigma and begin dehiscence. At the end of this stage all the anthers remain clustered near the stigma, and the anthers of the outer whorl become dark. The stigma remains receptive, and flowers produce pollen and nectar (Fig. 3(e, j)).
Figure 3. Floral stages of Larrea nitida and L. divaricata. (a) to (e) show stages 0 to 4 of L. nitida. (f) to (j) show stages 0 to 4 of L. divaricata. Bars = 2 mm.

Stage 5: petals lose turgor, turn pale and later, dark. Stamens remain clustered near the stigma, but anthers have no pollen and darken. The stigma also darkens and is no longer receptive.

Stage 6: the calyx and corolla segments are dry and brownish. Stamens dry and abscission occurs. The ovary begins to develop and its external pubescence becomes more noticeable. The style remains attached to the ovary, but begins to dry and also turns brownish.

Protogyny and stigmatic receptivity

The three species of Larrea studied showed different degrees of protogyny at stage 1 (Table 1). Larrea divaricata, L. cuneifolia, and L. nitida showed increases in the
Table 1. Percentage of protogynous flowers and total flowers assessed at stage 1 in three species of Larrea in Mendoza, Argentina

<table>
<thead>
<tr>
<th>Species</th>
<th>Protogynous flowers</th>
<th>N. flowers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Larrea divaricata</td>
<td>35%</td>
<td>127</td>
</tr>
<tr>
<td>Larrea cuneifolia</td>
<td>66%</td>
<td>100</td>
</tr>
<tr>
<td>Larrea nitida</td>
<td>92%</td>
<td>137</td>
</tr>
</tbody>
</table>

Percentage of protogyny, coinciding with decreases in the size of floral structures (Table 2).

The peroxidase test indicated that stigmas were receptive during stages 1 to 4 in all three species. Observations of hand self-pollinated flowers of L. nitida at three different stages (1, 3, 4), indicated that the pollen tubes reach the stylar base in only three hours. Twenty-four and 32 hours after pollination, pollen tubes were observed in the ovary, suggesting that fertilization is likely to occur during the first day.

Flower life-span

Similar floral phenological patterns were observed in the two species of Larrea studied. The reproductive phase began with stage 1 (Fig. 3(b,g)) and anthesis, ending with stage 5 when the calyx and corolla are senescent, the stigma is not receptive and there is little or no pollen remaining. The reproductive period lasts approximately 48 hours and has two phases: one (female stage), when the stigma is receptive and predehiscence pollination may occur, and the other when pollen production begins and stigmatic receptivity continues (bisexual stage).

Twenty-four hours after stage 1 in L. divaricata it was observed that 40-7% of the flowers had reached stage 2, 48-3%, stage 3 and only 11-0% remained at stage 1 (Fig. 4(a)). Larrea nitida showed a slightly different developmental pattern: 20% of their flowers had reached stage 4 24 hours after stage 1, showing more advance development at this stage in relation of L. divaricata (Fig. 4(b)). However, almost 30%

Table 2. Comparison of floral structure means (mm) in three species of Larrea in Mendoza, Argentina

<table>
<thead>
<tr>
<th></th>
<th>Larrea divaricata</th>
<th>Larrea cuneifolia</th>
<th>Larrea nitida</th>
</tr>
</thead>
<tbody>
<tr>
<td>One-way ANOVA</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sepal length</td>
<td>3.50 (± 0.41)a*</td>
<td>2.37 (± 0.25)b</td>
<td>2.63 (± 0.60)b</td>
</tr>
<tr>
<td>Sepal width</td>
<td>5.18 (± 0.43)a</td>
<td>4.72 (± 0.49)a</td>
<td>3.98 (± 0.57)b</td>
</tr>
<tr>
<td>Petal length</td>
<td>9.56 (± 0.63)a</td>
<td>8.55 (± 0.71)b</td>
<td>5.76 (± 0.37)c</td>
</tr>
<tr>
<td>Petal width</td>
<td>4.89 (± 0.50)a</td>
<td>5.14 (± 0.74)a</td>
<td>2.96 (± 0.33)b</td>
</tr>
<tr>
<td>Style length</td>
<td>2.96 (± 0.32)a</td>
<td>3.91 (± 0.80)b</td>
<td>3.08 (± 0.74)a</td>
</tr>
<tr>
<td>Ovary length</td>
<td>3.61 (± 0.41)a</td>
<td>2.54 (± 0.22)b</td>
<td>2.06 (± 0.38)c</td>
</tr>
<tr>
<td>Two-way ANOVA</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length of stamens</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Antesepalous</td>
<td>7.37 (± 0.66)a1†</td>
<td>7.29 (± 0.66)a1</td>
<td>6.14 (± 0.70)b1</td>
</tr>
<tr>
<td>Antepetalous</td>
<td>6.48 (± 0.61)a2</td>
<td>6.12 (± 0.53)a2</td>
<td>5.93 (± 0.68)a1</td>
</tr>
</tbody>
</table>

Different letters between columns (*) and different numbers between rows (†) representing significant differences at p < 0.05 (Tukey test).
of flowers of L. nitida remain at stage 1 at 24 hours and 11% at the same stage at 32 hours. Stage 5 was observed after 48 hours, with a higher percentage in L. divaricata (11%) than in L. nitida (1-4%). After 4 days most of the flowers were senescent or in early fruit development.
Morphological analysis and level of autogamy

Different sized floral structures were observed, with the largest structures in L. divaricata, followed by L. cuneifolia and L. nitida. This was not observed in style length (Table 2), however, when considering the length of the ovary and the style together, size differences were consistent with other floral structures. Results of a two-way ANOVA showed that stamen lengths were different between species and whorls \((p < 0.05)\) and the interaction (species \(\times\) whorls) was not significant \((p = NS)\). In both L. divaricata and L. cuneifolia, the inner and outer whorls of stamens differed in length (Tukey test, \(p < 0.05)\). In L. nitida this difference was not statistically significant (Table 2). The mean length of the stamens slightly exceeded the gynoecium level in all three species of Larrea (Fig. 5) indicating that there was some possibility of autogamy. In spite of this, both spontaneous and hand self-pollination treatments yielded low seed production. In L. nitida, seed set was 0.180 and 0.479 seeds per flower in the autogamous and geitonogamous treatments, respectively. In L. cuneifolia seed set was lower than L. nitida, 0.163 and 0.199 seeds per flower, respectively (Fig. 5). In L. divaricata, seed set was lower than that of L. nitida and L. cuneifolia, 0.026 and 0.075 seeds per flower, respectively.

Discussion

Larrea divaricata began flowering by mid-November in the piedmont localities. Martínez Carretero & Dalmasso (1992) recorded a flowering period for this species in the same area that starts in early October and continues sporadically until late April. The late start of the reproductive phase detected in our study could be attributed to microclimatic differences in the area, related to the altitude and exposure of hillsides, as pointed out by Roig & Marone (1982). In other regions like north-eastern Patagonia (42° 48' S, 65° 08' W) the flowering period of L. divaricata extends from mid-November until late December (Bertiller et al., 1991). The flowering period for the North American species, L. tridentata, could extend from spring until autumn in the Sonoran desert, depending on rainfall (Bowers & Dimmit, 1994).

In dry periods like 1993–94 and 1994–95 in Nacuña (40% and 33.5% lower than the 1980–96 average, respectively), we observed a facultative response of creosotebush flowering to water availability. This reproductive phenological pattern agrees with the previously suggested opportunistic growth strategy of creosotebush, which usually blooms in response to rainfall events (Bowers & Dimmit, 1994; Smith et al., 1997). This flowering behaviour has also been observed in populations of L. divaricata from Andalgalá (Cóatamarc, Argentina) and L. tridentata from Silver Bell (Arizona, U.S.A.) (Simpson et al., 1977). Two successive blooming were recorded in association with important rainfall events for L. cuneifolia in 1993–94 and 1994–95, and for L. divaricata in 1994–95 in Nacuña (Fig. 1). A similar response has also been reported for L. tridentata populations in the Mojave, Sonoran and Chihuahuan deserts (Solbrig & Yang, 1977; Ackerman et al., 1980; Kemp, 1983). However, 1996–97 rainfall was slightly above the historical mean (2%), and only one flowering period was observed for L. cuneifolia, probably due to higher and more evenly distributed rainfall events during winter and early spring than in previous years (Fig. 1).

Lack of flowering and a high proportion of shrivelled flower buds were observed during 1995 in Nacuña, where annual rainfall values were 21% lower than the mean (period 1980–96). During this period only a few individuals produced flowers and these usually presented malformations including abortion of the gynoecium, reduced anthers with little pollen and underdeveloped buds. This phenomenon may be a consequence of drought and continuing extreme conditions that also influence leaf and stem loss (Barbour et al., 1977).
Figure 5. Stamen-gynoecium relationships and self-pollination levels in three species of *Larrea*. (a) Seed set per flower under hand self-pollination (HSP) and natural self-pollination (NSP) treatments (Mean ± S.D.); (b) comparative length of stamens antepetalous (SAP), stamens anteseptalous (SAS), and gynoecium. Mean (figures) ± S.D. (bars).
The model proposed by Bazzaz (1987) predicts that vegetative growth occurs when resources are not limited and that under stress conditions there would be a change of resource allocation toward the production of reproductive structures. *Larrea tridentata* seems to fit in this model since resource allocation toward reproductive structures like buds, flowers, and fruits appears to be greater in years of low rainfall (Cunningham et al., 1974; Barbour et al., 1977; Cunningham, 1979). Although this hypothesis was not specifically assessed in this study, our data seem to contradict Bazzaz's prediction. Observations made in populations of *L. divaricata* and *L. cuneifolia* suggest that in years of high temperatures and extreme drought, especially if preceded by dry years, the reproductive phase does not develop normally. On the other hand, *L. nitida* exhibits a marked preference for relatively humid and cool places like the streams flowing down the piedmont (Morello, 1956; Roig, 1972, 1976) which suggests that its reproductive phenology might be less influenced by unpredictable rainfall events.

In some species the degree of anther–stigma separation affects the frequency of self-pollination (Lloyd & Schoen, 1992). The size and position of floral structures of the three species of *Larrea* studied indicate that self-pollination is possible. On average, the two staminal whorls always exceed the style height permitting contact of the anthers with the stigma during stages 2, 3 and 4. However in all three taxa, we have found a temporal separation in the development of male and female phases, detecting protogyny at floral stage 1. In this stage, the receptive stigmas have an opportunity to receive outcrossing pollen first. Similar floral stages and flower maturation occur in *L. tridentata*, where most flowers have the stigma exposed during some time while the anthers are still indehiscent, and predehiscence pollination accounts for allogamy in 19% of the observed flowers (Boyd & Brum, 1983). The *Larrea* species could be considered as incompletely protogynous (Lloyd & Schoen, 1992). Selfing may compete with outcrossing for ovule fertilization when the anthers of the antepetalous stamens begin to dehisce and approach the stigma (Lloyd & Schoen, 1992). Our research supports the hypothesis proposed by Simpson et al. (1977) that in *Larrea* species decreasing flower size corresponds with increasing levels of autogamy. In our study *L. nitida*, with the smallest flower structures of the three species observed, had the highest levels of autogamy. Despite the possibility of anther–stigma contact the three species studied produced very low seed sets in both autogamy and geitonogamy treatments, suggesting that an incompatibility mechanism favours xenogamy and discriminates unequally between the two modes of selfing. Boyd & Brum (1983) observed a similar pattern in *L. tridentata*. The existence of protogyny at stage 1 in *Larrea* flowers, in combination with a higher rate of pollinator visits during this phase (Debandi et al., unpubl. data) favours cross-pollination. The characteristics and the high seed set registered under outcross treatments for the populations of *Larrea* (Peralta et al., unpubl. data), suggest that while some seed sets are produced through autogamy, especially when pollinators are scarce or isolated plants, allogamy may play a prevalent role in the *Larrea* species reproductive biology.

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