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RESEARCH ARTICLE

Large flowers can be short-lived: Insights from a high Andean cactus

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Abstract

Long-lived and large flowers signify high floral maintenance costs. Species of arid/semiarid climates with large flowers are expected to have short flower life spans and pollination-induced flower longevity in order to curb high floral water and other maintenance costs. We explored the context-dependent large flower/short flower longevity hypothesis in *Eriosyce curvispina* (Cactaceae), a large-flowered species of the semiarid central Chilean Andes. We determined breeding system, flower visitation rates, and open-pollination fruit set and quantified floral water content. In a temperature-controlled field manipulative experiment, we measured potential flower longevity and tested for the presence of pollination-induced floral senescence. We measured the time span of the complete flower cycle defined as from when the flowers began to open to when they were totally closed, and the time span of fully open flowers defined as from when they were totally open until they began to close. The potential flower life span averaged 2.8 days (complete flower cycle) to 2.3 days (fully open flower). The complete flower cycle lasted 21.5 h, but flowers were fully open for only 10.1 h across days. Flower longevity in days was far shorter than reported for a large sample of species in the area. No evidence was found for pollination-induced flower senescence as a complementary means for reducing floral maintenance costs. *Eriosyce curvispina* is self-incompatible and abundantly pollinated by two megachilid bees. The level of pollen limitation ($L = 0.36$) was lower than the average reported for self-incompatible angiosperms. Thus, the short flower life span in *E. curvispina* is not an impediment for high fruit set. Flowers contain >5 g of water of which >2 reside in >40 petaloid tepals. The amount of water is far higher than in another large-flowered, non-cactus species in the area, but only about 15% of that reported in the giant saguaro cactus which has larger flowers than *E. curvispina*.

KEYWORDS
Andes, Cactaceae, floral water content, flower longevity, pollen limitation, pollination

TAXONOMY CLASSIFICATION
Botany; Phenology

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1 | INTRODUCTION

Angiosperm flowers show substantial variation in their potential flower longevity. The potential flower longevity is the maximum period of time the flower is able to remain open and in functional (receptive) state in the absence of pollination (Steinacher & Wagner, 2010). Some flowers last less than 24 h, whereas others remain open and functional for as long as 2 or 3 months (Franchi et al., 2014; Prokop & Neupauerova, 2014; van Doorn & Kamdee, 2014; Zhang et al., 2017). Concomitantly, flowers may remain continuously open over one to several days or re-open over several days (van Doorn & Kamdee, 2014). Flowers also show significant variation in size spanning around a thousand-fold difference (Moyroud & Glover, 2017). Flower longevity is a floral trait that directly affects the probability of pollen import and export in flowers (Arroyo et al., 2006; Ashman & Schoen, 1994; Primack, 1985), whereas flower size is intimately related to breeding system and the attraction of pollinators in outcrossing species (Barrett & Harder, 1996; Karron et al., 2012). How these two fitness-relevant traits are combined under different ecological contexts is of great interest yet has been scarcely investigated.

The construction and maintenance of flowers and therefore of the corolla, entails water, respiration, and carbohydrate costs (Ashman & Schoen, 1997; Dudley et al., 2018; Roddy et al., 2021; Zhang et al., 2017). With respect to water, initial corolla expansion out of the flower bud and the subsequent maintenance of the turgid corolla depends on turgor pressure (Beauzamy et al., 2014). To maintain turgor, flowers draw on water from other plant parts via the xylem or phloem to replace daily transpiration losses (Chapotin et al., 2003; Feild et al., 2009; Galen et al., 1999; Roddy et al., 2016). Species with large and long-lived flowers found in dry climates are expected to be exceptionally water-demanding (Teixido & Valladares, 2014) because in these kinds of habitats, water lost through transpiration is expected to be high. For example, it is estimated that the large flowers of the saguaro cactus (*Carnegiea gigantea*) of dry habitats lose a third of their 33 g of floral water content in a day (Nobel, 1977). Under very dry conditions, plants can lose more water via their flowers than via their leaves (Lambrecht, 2013). Indeed, in several species and in different ecosystems, plant water status and corolla size are directly related or correlated (Carroll et al., 2001; Gallagher & Campbell, 2017; Herrera, 2005, 2009; Kuppler & Kotowska, 2021; Teixido et al., 2019) and water can affect floral abundance (Phillips et al., 2018). These last kinds of observations have led to the hypothesis that small flowers should be favored in dry environments (Galen, 2000; Kuppler & Kotowska, 2021; Teixido et al., 2016). Yet, species with large flowers are common in arid and semiarid climates raising the question as to how high floral maintenance costs are dealt with.

If water in general is scarce, as in arid and semiarid areas, selection should favor traits and mechanisms that minimize the drain on a plant's water budget by flowers. In large-flowered species/lineages, two possibilities are: (1) the possession of an overall short intrinsic flower life span (reduced potential flower longevity; cf., figure 2a in Roddy et al., 2021), and, (2) the presence of pollination-induced flower senescence leading to further shortening of the flower life span. Flower longevity has been shown to be reduced following pollen deposition in many species (Ashman & Schoen, 1994; Giblin, 2005; van Doorn, 1997; Webb & Littleton, 1987) and also following pollen export in some (e.g., Clayton & Aizen, 1996). In the present study, the possession of short-lived flowers in which pollen deposition further shortens flower longevity was investigated in *Eriosyce curvispina*, a large-flowered cactus species of the semiarid Andes of central Chile. Previous work showed the large flowers of *E. curvispina* contain by far the largest amount of dry biomass (475 mg) among 130 simple-flowered species sampled (Arroyo et al., 2019), which is expected to translate into high per day maintenance costs. This finding raised the question as to whether the flowers of *E. curvispina* are short-lived in relation to other species in the area, and if so, whether they are pollen-limited. It also brought up the question as to how much water is contained in flowers of *E. curvispina* in their turgid state. In this paper, we address the following questions: (1) To what degree is *E. curvispina* reliant on external pollination; (2) How much water is contained in the whole flower and how much water is required to maintain corolla turgor; (3) How long are the flowers able to remain open in the absence of pollinators; (4) Is the flower life span plastically truncated following pollination; (5) Is there any evidence for pollen limitation. Several studies have experimentally shown or inferred that temperature affects flower longevity (e.g., Arroyo et al., 2013; Blionis et al., 2001; Giblin, 2005; Steinacher & Wagner, 2010; Teixido & Valladares, 2015). We, therefore, also considered temperature in our analyses. With respect to (3) and (4), we expect the large flowers of *E. curvispina* to be water-demanding, short-lived, and characterized by pollination-induced floral senescence. With respect to temperature, higher temperatures are expected to reduce the flower life span plastically.

2 | MATERIALS AND METHODS

2.1 | Study species and site

Eriosyce curvispina (Bertero ex Colla) Katt. (Figure 1; Guerrero, Walter, et al., 2019a) is a small globose cactus endemic to central Chile found mostly from 1500 to 2300 m a.s.l. where it inhabits exposed dry rocky terrain. An individual branch bears of ring of solitary funnel-shaped flowers (Figure 1a; Hoffmann & Walter, 2004) varying in color from pale yellow-green to brick and wine red, depending on the population. Each flower contains an indefinite number of spirally arranged, intergrading sepaloid to petaloid tepals (Figure 1b). The flowers are protandrous and shortly herkogamous. The complete daily flower cycle starts in the morning hours and terminates in the late afternoon-early evening. Flowers are fully open for only a part of the complete cycle. The numerous anthers begin to undergo dehiscence before the corollas are fully expanded and the stigmatic lobes (ca. 13–14) are spread. The stigmas are positioned above the level of the anthers. The ovary contains a very large number of ovules. In the definitively closed flowers, the tepals shrink dramatically in size

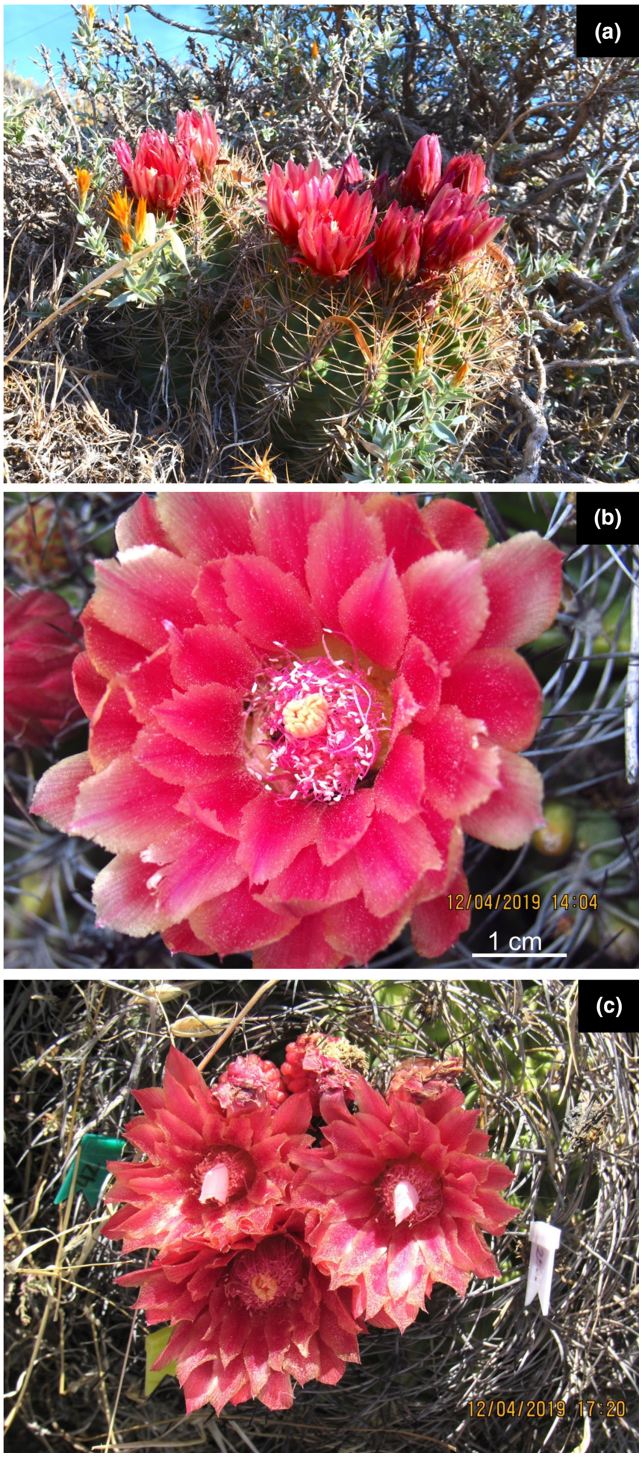


FIGURE 1 *Eriosyce curvispina* on the study site, 2200 m a.s.l. in the central Chilean Andes. (a) Plants showing habit and the typical ring of large solitary sessile flowers. (b) Fully open flower showing the numerous petaloid tepals, stigmatic lobes, and stamens. (c) Flowers (upper two) showing the paper caps used to prevent external pollination in the capped flowers. Scale bar = 1 cm. Images: a – courtesy of K. Bacelli; b, c – M. Cuartas.

and become twisted and thus are easily distinguished from flowers that close temporarily. Flower number per plant for the study population was 5.84 ± 0.37 (Mean ± 1 SE, N = 50 plants). Outer flower diameter and total flower length were 3.3–6 cm (Mean = 4.8 cm) and 2.5–4.6 cm (Mean = 3.6 cm), respectively (N = 30 on 26 plants). Ovule number per flower for the same population is 842.6 ± 66.14 (Mean ± 1 SE; Arroyo et al., 2019). As can be appreciated in Figure 1, the flowers contain a very large number of petaloid tepals.

The present work was carried out on Lomas del Viento (33°21'32"S, 70°19'40"W, 2200 m a.s.l.), east of Santiago, central Chile. The area is characterized by a semiarid climate with a Mediterranean influence. The snow-free period at 2300 m a.s.l. is around 8 months (Arroyo et al., 1981), increasing in length as elevation decreases. At these latitudes in the Chilean Andes, soils undergo intense drying during the warm and practically rainless summer months (Cavieres et al., 2006; Sierra-Almeida et al., 2016; Sierra-Almeida & Cavieres, 2010). Work on flower longevity, pollination, and fruit set was conducted in the late spring of 2019 and austral summer of 2019–2020. Floral water content was measured in early December of 2021. The breeding system work was conducted over the austral summer of 2008–2009.

2.2 | Breeding system

The degree of compatibility and autonomous self-fertilization capacity were investigated by comparing fruit production and the number of seeds formed in flowers subjected to three pollination treatments. Twenty plants each containing several well-developed unopened flower buds were pollinator-excluded with semi-transparent bridle fabric mounted over metal frames. Similar numbers of flowers per treatment were hand self-pollinated and cross-pollinated. These came from 10 or more individuals in each case (not necessarily the same ones), to bring the total numbers of treated flowers to a minimum of 20 in each treatment. For cross-pollination, pollen was collected from other plants in the population. For hand self-pollination, pollen was obtained from the same flower and/or from a neighboring flower on the same plant to ensure sufficient pollen. The remaining flowers on the plants were left unmanipulated to test for autonomous selfing capacity. Resultant mature fruits were collected around 1 month later and the seeds were counted.

2.3 | Potential flower longevity and the effect of pollination on the flower life span

During 2 days in the first week of December 2019, well-developed flower buds were marked on 33 plants. Equal numbers of open flowers were haphazardly assigned to one of two treatments: (1) Stigma of flower capped to prevent external pollination (CAP, N = 42); (2) flower subjected to hand cross-pollination (POL, N = 42). The stigmas were capped with a small piece of folded white paper affixed onto the stigma with silicone grease (Figure 1c). Capping took place early in the flower cycle as the flowers began to open and before the stigma lobes had spread. POL flowers were hand-pollinated around midday on the day of anthesis with large quantities of fresh

pollen collected from several plants growing at least 5 m distance from the experimental plants. In view of the fact that some cross-pollinated flowers failed in the earlier breeding system work (see Results, Section 3.1), we pollinated the flowers minimally over 2 consecutive days. The CAP flowers were purposely not bagged. This mode prevented altering the light intensity and facilitated making observations. Light is known to be involved in flower opening (van Doorn & van Meeteren, 2003). As we were interested in comparing the number of hours flowers remained open in CAP and POL flowers, controlling for this possible effect was important. All treatment flowers were monitored three times a day during the flower cycle: early in the morning, around midday, and late in the evening until they became definitively closed. With the objective of pinning down the total number of hours the flowers were fully open over their life spans, over the first 4 days of the experiment, we monitored all flowers (CAP and POL) at least five times a day between 08:30 and 18:00 h. All treated flowers (CAP and POL) were examined for fruit formation around 2 weeks later.

Upon closer inspection in the field, four buds assigned to the CAP treatment early in the experiment showed signs of already having been open the previous day. Additionally, seven CAP flowers formed fruits. Fruit set in these flowers is likely the result of accidental cross-pollination caused by bees entering the flowers and jostling the paper caps while foraging for pollen. Alternatively, bees entered the flowers very early in the morning before we capped the stigmas. Self-pollination is unlikely (see Results, Section 3.1). Likewise, one POL flower did not set fruit. The 12 problem flowers were eliminated prior to analysis of the data. Maintaining fertilized flowers and vice versa would have decreased the possibility of detecting pollen-induced flower senescence, especially if the latter were subtle. The final sample sizes were $N = 31$ (CAP) and $N = 41$ (POL).

To quantify the potential flower life span and assess the presence of pollination-induced flower senescence, we considered flower longevity in two ways: (1) the time span of the complete flower cycle defined as from when the flowers began to open to when they were totally closed; (2) the time span of fully open flowers defined as from when they were totally open until they began to close. Both measures were expressed in terms of days open, and total hours open summed across all days the flowers were open. To calculate longevity expressed in days, we used the full data set (CAP, $N = 31$; POL, $N = 41$). For hours, we used the data for flowers that were monitored at least five times a day (CAP, $N = 18$; POL, $N = 19$, complete flower cycle; $N = 20$, fully open flower).

2.4 | Water content of flowers

Flowers were harvested to examine water content in early December of 2021. The same flowers were used to quantify the number of petaloid tepals (hereafter PTs) per flower which is not easily established in the intact flowers. We marked 40 fresh flowers (1 per plant) on a warm day around midday (Standard Time) when the flowers were fully open. Half of the flowers were immediately harvested. Material was placed over commercial ice packs in a cooler and transported back to a field lab within less than an hour of harvesting. The PTs were separated from the remaining flower parts (hypanthium, ovary, stigmas, stamens, tepaloid tepals) and counted. The PTs and the remaining flower parts were weighed separately. The second 20 flowers were harvested around midnight when they became temporarily closed overnight and processed in the same way. At this stage, the PTs become erect and closed, but remain similar in size to those of daytime flowers. During the night, flowers and especially the PTs are expected to experience less surface evaporation of water than during the day, resulting in a higher proportion of water in nighttime flowers. All floral material once collected, was immediately processed and weighed on a field balance (Ohaus Scout STX223 model, 220 × 0.001 g) to obtain fresh weights. It was then dried at 70°C for 3 days and weighed on a precision balance (Denver Instrument Company) in g to four decimal places to obtain dry weights. To prevent hygroscopic changes in water content after removing the material from the oven, the paper packets were placed over a bed of silica gel in a desiccator prior to final weighing. To obtain the water content of the whole flower, the weights of the two floral components (PTs and other floral parts) were summed together.

2.5 | Pollinator visitation and open-pollination fruit set

With the objective of quantifying pollinator visitation rates, in the same year as the manipulative experiment, pollinator visits were observed on counted numbers of flowers for periods of 20 min by two independent observers on 9 days spread across the flowering period. Observations took place from 9 to 18 h, intercalated with the other work that was underway. In addition, while monitoring the flowers and carrying out other tasks, we noted down any flower visits observed on the experimental and nearby plants. In total, we accumulated 77 × 20 min (= 25.7 h) of quantified observations and 63 point observations the latter of which included one or more flower visits. Open-pollination fruit set was assessed in 201 flowers. One hundred and fourteen of these flowers corresponded to pollinator-exposed flowers on the original set of marked plants that had not been capped or hand cross-pollinated. The remaining flowers pertained to additional plants in the study population. Overall, the 201 flowers were drawn from a total of 46 plants.

2.6 | Air temperature

In the central Chilean Andes, warm temperatures are known to reduce both potential and actual flower longevity (Arroyo et al., 2013; Pacheco et al., 2016). When flower buds open on different days, the resultant flowers are likely to be subject to different temperatures over their life spans. For example, a flower that opened over a period of very cold days compared with one that opened during a warmer period could stay open longer as a result

of the cooler conditions. To assess for possible effects of this kind, we recorded temperature (°C) with three HOBO U23 Pro v2 battery-powered sensors (Onset Computer Corp., Cape Cod, MA, USA) equidistant along the study ridge. The sensors were leveled to 15 cm above ground level (a.g.l.) which is representative of the temperature conditions under which *E. curvispina* flowers open. These data also allowed us to characterize the weather conditions during the experiment.

2.7 | Data analysis

All statistical analyses and preparation of figures (excepting images) were carried out in R version 4.0.3 (R Core Team, 2020).

2.7.1 | Breeding system and floral water content

To test the effect of pollination treatment on the number of seeds produced per flower, data were analyzed with a generalized linear model (GLM) with quasi-Poisson error distribution and log link function using the glm function in the "stats" version 4.0.3 package (R Core Team, 2020). Absolute amount of water (expressed in g) contained in the floral parts was the difference between the fresh and dry weights. Percent water content was obtained by dividing the difference between fresh weight and dry weight by fresh weight. Prior to statistical analysis, the percentage values were arcsine transformed. Floral water content for flowers harvested during the daylight and night-time hours was compared using a GLM with normal error distribution and identity link function.

2.7.2 | Potential flower longevity and the effect of pollination on the flower life span

The effect of pollination and temperature on flower longevity measured in hours of the complete flower cycle a flower was open and hours when it was fully open was analyzed with a Generalized Linear Model (GLM) with a quasi-Poisson error distribution and a log link function. Temperature was the mean hourly temperature based on the data from the nearest data logger to each plant. Models including temperature, treatment, and the interaction between temperature × treatment were tested. The best-fit model was selected according to the Akaike Information Criterion (AIC), the amount of variance explained, and the variance inflation factor (VIF). Analyses were carried out using the stepAIC and vif functions of the "MASS" and "car" packages, respectively (Fox & Weisberg, 2019; Venables & Ripley, 2002). In a broader approach, GLM was also used to assess the effect of the pollination treatment on the total number of days (and percentage of hours in those days) over which a flower was open. Daily temperature was not considered in this analysis because the flowers are not open over the night hours. Box plot graphs to visualize the results of the effect of pollination on flower longevity expressed in days, hours, and percentage of hours over which the flowers remain open, were plotted using the ggplot function of the "ggplot2" package version 3.3.5 (Wickham, 2016).

2.7.3 | Pollinator visitation and pollen limitation

Flower visitation rates were calculated as visits × flower^{-1} × 20 min^{-1} (Arroyo et al., 2017). Animals that entered the flowers and made contact with the anthers and stigmas were considered as effective pollinators. Beetles and occasional ants that foraged on the anthers for prolonged periods of time were not considered to be important pollinators (c.f., Bowers, 2002). Visitation rates were compared for the morning and afternoon hours with a generalized linear model (GLM) with quasi-Poisson error distribution and log link function. The total number of visits expected over the flower lifetime was calculated from the visitation rates and the total number of hours the flowers were fully open. To determine whether *E. curvispina* is pollen-limited, we calculated the standard pollen limitation index $L = 1-(P_o/P_s)$ where P_o was the percent fruit set under open-pollination and P_s the percent fruit set under supplemental cross pollen (Larson & Barrett, 2000). $L = 0$ indicates a complete lack of pollen limitation, whereas values of L approaching 1 indicate very high pollen limitation. For P_s, we used the data for the non-bagged pollen-saturated hand-pollinated flowers in the manipulative experiment. P_o was measured fruit set (see Section 2.5).

3 | RESULTS

3.1 | Breeding system

A high proportion of the cross-pollinated flowers (70.0%) set fruit (Table 1). In contrast, only 4.3% of the hand self-pollinated flowers and none of the unmanipulated flowers set fruit. As the unmanipulated flowers failed to produce any seed, only the hand self- and cross-pollination treatments were included in the statistical analysis. The GLM (quasi-Poisson distribution and log link function) indicated that the number of seeds obtained under hand self-pollination flowers was significantly lower than under hand cross-pollination (t value = −2.98, d.f. = 1, $p < .005$). The last result indicates that

TABLE 1 Results of breeding system tests in *Eriosyce curvispina*, Lomas del Viento, 2200 m a.s.l., Andes of central Chile

Treatment	Plants	Flowers	Fruits	Seed/fl (Mean ± SE)
Cross-pollination	11	20	14	375.5 ± 63.3^{a}
Self-pollination	12	23	1	1.5 ± 1.5^{b}
Unmanipulated	19	62	0	0

Note: Different letters indicate significant differences among treatments (GLM, quasi-Poisson distribution, and log link function). Seed/fl: number of seeds produced per flower.

E. curvispina is highly self-incompatible and thus dependent on pollinators.

3.2 | Potential flower longevity and the effect of pollination on the flower life span

The weather conditions over the study period were stable. The mean daily temperature ranged from 14.2 to 19.2°C. The days were sunny and rainless. The flowers began to open between 9 and 12 h and close around 15–16 h. However, in a few cases, flower opening commenced in the late afternoon. Flowers were not seen to be open at night. Flowers opened between 2 and 4 days when the number of days was calculated on the basis of the complete daily flower cycle and averaged less than 3 days (Table 2). When calculated on the basis of the time the flowers were fully open, the flowers remained around half a day less (Table 2). In terms of hours open, on average CAP flowers were partially to fully open (complete flower cycle) for less than 22 h but fully open for only around 10 h (Table 2). The latter boils down to 4.4 h day^{-1}. The number of hours the flowers were fully open was less than 20% of the total hours summed over all the days that a flower was open at some time (Table 2).

Generalized linear models (GLM) showed that temperature had no significant effect on the two measures of flower longevity expressed in hours. The best-fit models did not include the interaction between temperature and treatment (Table 3). Contrary to expectation, pollination had no effect on flower longevity, either when considered as length of the complete flower cycle or as the time span of fully open flowers (Tables 2 and 3; Figure 2). The potential flower life span in days when the flowers are completely open (mean of CAP and POL flowers) boils down to around 2.4 days. Overall, the results show that individual flowers of *E. curvispina* open for relatively few days, are fully expanded for a relatively small number of hours, that pollination does not induce flower senescence and that the flower life span is not affected by temperature, at least in the range experienced over the study period.

TABLE 2 Flower longevity measures for *Eriosyce curvispina*: complete flower cycle and fully open flower expressed in days, hours, and percentage of hours in which the flowers remain open.

	Treatments			
	CAP		POL	
Flower longevity	Mean ± SE	*N*	Mean ± SE	*N*
Complete flower cycle				
Days	2.77 ± 0.10[a]	31	2.93 ± 0.08[a]	41
Hours	21.50 ± 1.03[a]	18	22.71 ± 0.98[a]	19
% of total hours	32.95 ± 0.87[a]	18	32.68 ± 0.75[a]	19
Fully open flower				
Days	2.29 ± 0.12[a]	31	2.51 ± 0.08[a]	41
Hours	10.08 ± 0.69[a]	18	10.78 ± 0.68[a]	20
% of total hours	18.69 ± 0.89[a]	18	18.39 ± 0.93[a]	20

Note: Different letters indicate significant differences among treatments (GLM, quasi-Poisson distribution, and log link function). There were no significant differences.

Abbreviations: CAP, pollinator-excluded flowers; POL, hand cross-pollinated flowers.

3.3 | Floral water content

The petaloid tepal (PT) number per flower was large (41.2 ± 0.9; Mean ± SE; $N = 40$) and variable (29–51 per flower). Individual whole flowers of *E. curvispina* contained more than 5 g of water (the equivalent of >5 ml of water; Table 4). The >40 PTs of a single flower contained an average of over 2 g of water (the equivalent of >2 ml of water). Overall, around 90% of the whole flowers and their parts were comprised of water (Table 4). We found no significant difference in the absolute amount of water between night-time and day-time flowers (whole flower: t value = 0.22, d.f. = 1, $p = .828$; PTs: t value = 0.65, d.f. = 1, $p = .522$; other floral parts: t value = −0.11, d.f. = 1, $p = .912$). With respect to % water content, no difference was found between the PTs for day- and night-time flowers (t value = 1.90, d.f. = 1, $p = .065$). However, % water was slightly higher in the night-time flowers considering the whole flower (t value = 2.93, d.f. = 1, $p = .006$) and the remaining parts (t value = 3.11, d.f. = 1, $p = .004$). One interesting aside was the large amount of variation in the volume of water per individual PT (day-time flowers: 31.5–83.2 mg; night-time flowers 34.5–88.3 mg). Such variation could be due to water being distributed differently in flowers with different numbers of PTs. However, there was no significant correlation between the amount of water per PT and PT number per flower ($r = -0.165$, $p = .309$, $N = 40$). Such variation is likely to relate to differences in the physiological state of the plants due to microsite variation and plant age. Both of these factors are not easily controlled for in field-based studies.

3.4 | Pollination and pollen limitation

Eriosyce curvispina was visited by two megachilid bees, *Trichothurgus dubius* (Figure 3a,b) and *T. herbsti* (Figure 3c), both endemic to Chile (Montalva & Ruz, 2010), the large high Andean hummingbird, *Oreotrochilus leucopleurus*, and a small unidentified bee. Considering all bee and hummingbird visits recorded ($N = 292$), the highest proportions pertained to *T. dubius* (50.3%), followed closely by *T. herbsti* (48.6%). Only two visits (0.7%) were recorded for the hummingbird and one for the unidentified bee (0.3%). Specialized *T. dubius* lands abruptly on the flower on its abdomen. It proceeds to dig deep into flowers to collect pollen which it scrapes backward onto the abdomen. In the process, the pollen-laden abdomen makes contact with the stigma (Video S1). The foraging habit in the smaller *T. herbsti* was similar, but the fit with flower morphology was less precise than for *T. dubius* (Video S2). Flower visitation rates varied widely from 0 to a maximum of 5 visits × $flower^{-1}$ × 20 min^{-1} (equivalent to

TABLE 3 Results of the Generalized Linear Models (GLM, quasi-Poisson distribution, and log link function) in *Eriosyce curvispina* to test for the effect of temperature (°C) and pollination on flower longevity expressed in days, hours, and percentage of hours in which the flowers remain open.

Flower longevity	Model effects	Estimate	Std. error	*t* value	*p*-Value
Complete flower cycle					
Days ($N = 72$)	Intercept	1.020	0.034	29.756	**<.000**
	Treatment	0.054	0.045	1.192	.237
Hours ($N = 37$)	Intercept	3.574	0.346	10.343	**<.000**
	Temperature	−0.020	0.014	−1.473	.150
	Treatment	0.056	0.063	0.891	.379
% of total hours ($N = 37$)	Intercept	3.495	0.025	140.045	**<.000**
	Treatment	−0.008	0.035	−0.238	.814
Fully open flower					
Days ($N = 72$)	Intercept	0.829	0.044	18.968	**<.000**
	Treatment	0.092	0.057	1.628	.108
Hours ($N = 38$)	Intercept	3.148	0.449	7.013	**<.000**
	Temperature	−0.031	0.017	−1.877	.069
	Treatment	0.085	0.090	0.944	.352
% of total hours ($N = 38$)	Intercept	2.928	0.050	57.996	**<.000**
	Treatment	−0.017	0.070	−0.237	.814

Note: See Section 2.3 for definitions of flower longevity measures. Significant values are shown in bold.

0.25 visits × flower^{-1} × min^{-1}). In spite of the fact that no visits were recorded in 57.1% of the 20 min observations, the mean flower visitation rate was high (0.505 visits × flower^{-1} × 20 min^{-1}, which is equivalent to 0.025 visits × flower^{-1} × min^{-1}). Visitation rates in the morning (Mean ± 1SE: 0.53 ± 0.15) and afternoon (Mean ± 1SE: 0.49 ± 0.15) hours were not significantly different (t value = −0.17, d.f. = 1, $p = .869$). Extrapolated over the time flowers were seen to remain fully open, an average flower is predicted to have received an outstanding 16 visits over its life span. Fruiting in open-pollination flowers was 62.2%; in the pollen-saturated hand cross-pollinated flowers fruit set was 97.6%. Therefore, the pollen limitation index (L) was 0.36, indicating that only around 1/3 of the flowers did not produce fruit.

4 | DISCUSSION

In his seminal paper on flower longevity, Primack (1985) argued that large flowers should last longer than small flowers given the large amounts of resources invested. Indeed, based on a study of 11 species of *Paphiopedilum* (Orchidaceae), flower longevity is significantly positively correlated with floral dry mass area (Zhang et al., 2017). Here, taking environmental context into account, we argued that large and presumably water-demanding flowers of species in arid and semiarid climates are expected to be short-lived. *E. curvispina* turned out to high self-incompatible thus was an appropriate choice for looking at flower longevity in an arid habitat species and its effect on fruit set. The flower life span in *E. curvispina*, with >40 petaloid tepals and the highest floral biomass for the flora of the study area (Arroyo et al., 2019), in terms of potential longevity measured in days (fully open flowers), is 45% shorter than the average flower longevity of 4.2 days recorded for the open-pollinated flowers of 24 species in the montane zone in the central Chilean Andes (Primack, 1985). If potential flower longevity had been looked at in the montane study, the difference with our species would possibly be even larger. With respect to other large-flowered species in the area, both intrinsic potential flower longevity and actual flower longevity are notably longer in *Rhodolirium montanum* (Amaryllidaceae; Pacheco et al., 2016) and *Alstroemeria umbellata* (Alstroemeriaceae; Arroyo et al., 2022). Significantly, dry floral biomass in these last-mentioned species is around an order of magnitude lower than in the cactus species (Arroyo et al., 2019). Clearly, for the amount of resources invested, the flower life span of *E. curvispina* is very short. Flower longevity is best measured in terms of the total hours flowers remain open. However, this kind of data is still rare in the literature. When flower longevity in *E. curvispina* was measured in this way across days, the flowers were partially to completely open (complete flower cycle flowers) for less than 22 h and fully open for less than 11 h. This is similar to the total number of hours open reported for 2-day flowers of *Opuntia engelmannii*, another cactus species (Bowers, 2004). In both species, the amount of time flowers are fully open is about the same amount of time as in bindweed (*Convolvulus arvensis*) which is considered to be a species with a very short flower life span (Prokop & Neupauerova, 2014).

We expected that flowers of *E. curvispina*, in addition to being short-lived, could further lower their maintenance costs by closing after pollination. Floral maintenance costs are considered to be one of three proposed evolutionary drivers of pollination-induced floral senescence (Ashman & Schoen, 1994; Franchi et al., 2014; van Doorn, 1997). Recent evidence for pollination-induced flower

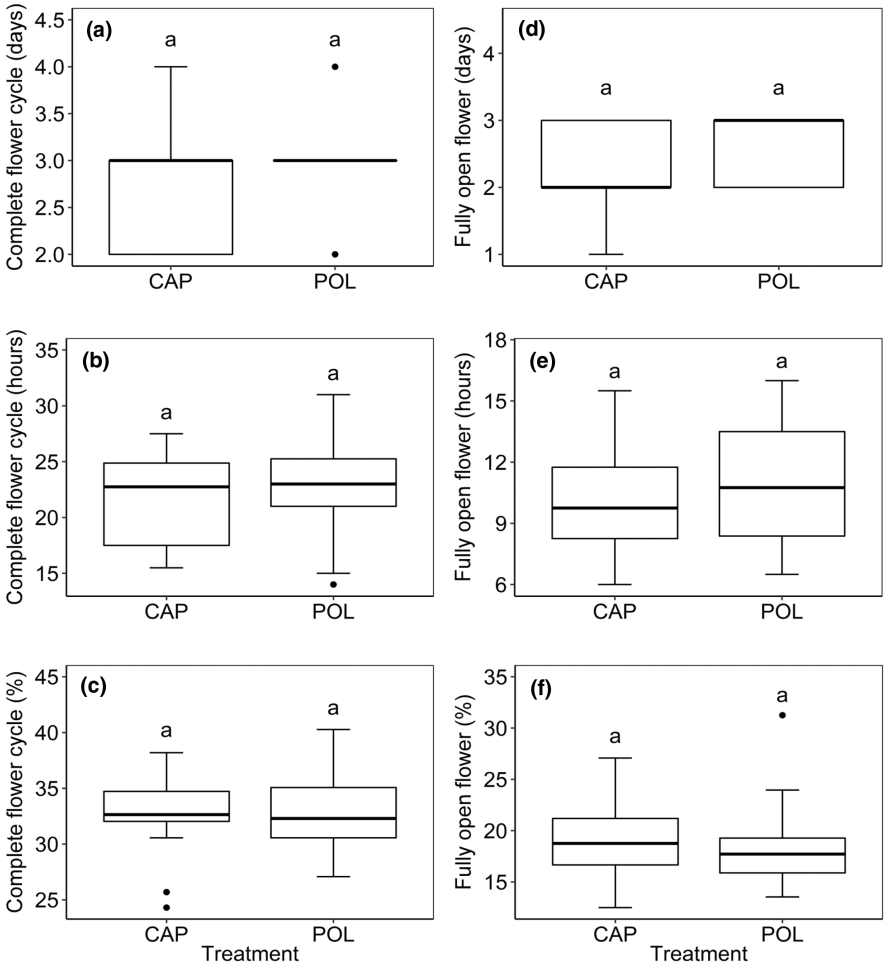


FIGURE 2 Effect of hand cross-pollination on two measures of flower longevity: complete flower cycle (a–c) and fully open flower (d–f). CAP, stigmas of flower capped to prevent external pollination; POL, flower subjected to hand cross-pollination. See Table 2 for statistics and sample sizes. Different letters indicate significant differences between treatments (GLM, quasi-Poisson distribution, and log link function). There were no significant differences.

TABLE 4 Water content in fully open (around midday) and closed (around midnight) flowers of *Eriosyce curvispina*

	Water content (g) (Mean ± SE)			Water (%) (Mean ± SE)		
Time	Whole flower	PTs	Other floral parts	Whole flower	PTs	Other floral parts
Midday	5.04 ± 0.29[a]	2.02 ± 0.13[a]	3.03 ± 0.19[a]	89.4 ± 0.2[a]	90.3 ± 0.2[a]	88.8 ± 0.2[a]
Midnight	5.12 ± 0.24[a]	2.13 ± 0.11[a]	3.00 ± 0.16[a]	90.1 ± 0.1[b]	90.7 ± 0.2[a]	89.6 ± 0.2[b]

Note: Different letters indicate significant differences between the harvest times (GLM, normal error distribution, and identity link function).
Abbreviation: PTs, petaloid tepals.

longevity in a dry habitat species of *Alstroemeria* is consistent with this expectation (Arroyo et al., 2022). However, there are many species, including in dry habitats (e.g., Teixido et al., 2019), that do not show this phenomenon. As far as we can tell, pollination-induced floral senescence has been studied on very few occasions in Cactaceae and rarely under carefully controlled conditions as in our study. We found reports for *Mammillaria glochidiata* (van Doorn, 1997), *Mammillaria grahamii* (Bowers, 2002), and one of two self-pollinated variants of the self-incompatible cultivated Easter cactus (*Hatiora* × *graeseri*; Karle & Boyle, 1999). We found no evidence for pollination-induced floral senescence in *E. curvispina* irrespective of whether a coarse- (days) or fine-grain (hours) measure of flower longevity was considered. Therefore, this mechanism is irrelevant for streamlining floral maintenance costs in our species. This result was surprising. Our species is protandrous. Thus, a shortening of the flower life span following pollination would not materially affect pollen export and male fitness as would be the case in protogynous species and species in which pollen export and import overlap in time (c.f., Clayton & Aizen, 1996; Ishii & Sakai, 2000; Weber & Goodwillie, 2007, 2013). It appears that flower longevity in our species is strongly genetically determined. The fact that temperature had no effect (at least under the range of temperatures experienced during the study), also points in this direction.

Theory suggests that the evolution of floral longevity is shaped by natural selection to maximize pollen transfer while minimizing

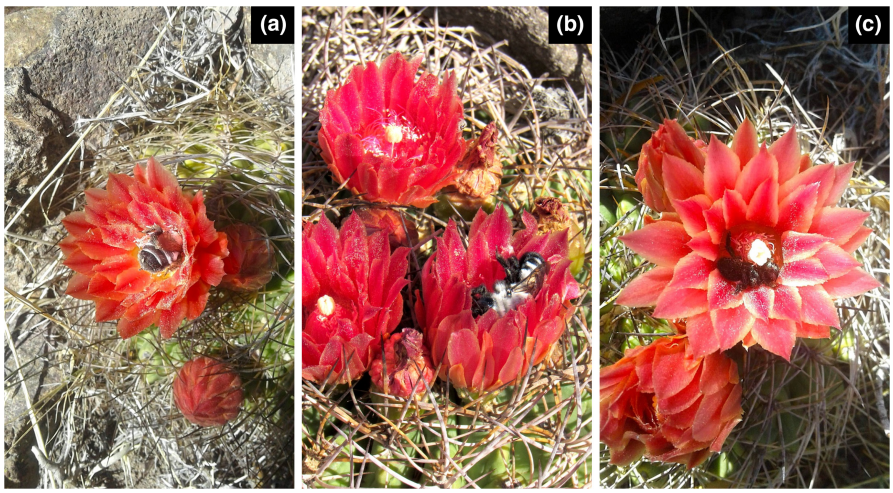


FIGURE 3 Pollinators of *Eriosyce curvispina* observed in the study population. (a) *Trichothurgus dubius* (Megachilidae) actively collecting pollen from the anthers in the fully open funnel-shaped flowers. The foraging habit of the bee brings the abdomen in direct contact with the stigmas. (b) *T. dubius* foraging on a partially open flower early in the daily flower cycle. (c) *Trichothurgus herbsti* (Megachilidae) collecting pollen on a fully open flower. The fit between this bee and the flower for pollination is less precise than in *T. dubius*. Images: a, c – V. Robles; b – M. Cuartas.

floral maintenance costs (Ashman & Schoen, 1994, 1997). Short flower life spans imply greater fitness risk given that less time is available to absorb pollinator-mediated temporal and spatial variation in pollen import and export. This should especially be the case in species that produce few flowers per plant, thereby placing their eggs in a small number of baskets—as in the case in our species. It, therefore, became of interest to know whether the focal species is strongly pollen-limited and especially in view of the fact that pollen limitation has been documented for several species in what is a fairly high-elevation area (Arroyo et al., 2017; Muñoz & Arroyo, 2006; Muñoz & Cavieres, 2008). The flowers were seen to be amply pollinated by two bee species and occasionally by a hummingbird. *Trichothurgus dubius* is known to specialize on Cactaceae (Sielfeld, 1973). It has also been reported on *E. curvispina* var. *mutabilis* and two subspecies of *Eriosyce chilensis* in the central Chilean coastal desert (Guerrero, Antinao, et al., 2019b). *Trichothurgus herbsti* is a polylectic bee (López-Aliste et al., 2021). Although it visits Cactaceae, it has also been collected on other plant species (Luisa Ruz, personal communication). *Oreotrochilus leucopleurus* is known to pollinate several nectar-richness subalpine and alpine species (Arroyo et al., 2020; Pérez et al., 2006).

Although the diversity of bees in the study population was considerably lower than documented in coastal subspecies of *E. curvispina* (Guerrero, Antinao, et al., 2019b), the flower visitation rates in our plant were very high leading to an estimate of around 16 visits per flower over the small number of hours the flowers remain fully open. This is a conservative estimate. The bees were sometimes seen visiting the flowers early in the daily flower cycle before they were completely open and again in the afternoon when they were beginning to close. This effectively tells us flower longevity based on the total daily flower cycle is perhaps a better measure of the flower life span in *E. curvispina*. Of course, many of the visits recorded, as in all data of this kind, will be revisits and some could have occurred before the stigma was receptive. The pollen limitation index ($L = 0.36$) falls well below the mean value of $L = 0.69$ reported for a large sample of self-incompatible angiosperm species analyzed by Larson and Barrett (2000) indicating that *E. curvispina* is considerably less pollen-limited than the average self-incompatible angiosperm. This suggests that the short potential flower life span in our species does not lead to exaggerated fitness loss. An evident shortcoming of our work is not having evaluated pollen limitation over more than one flowering season. In a pilot study conducted in another year, 100% of 12 marked flowers produced fruits suggesting that high fruit set is common (M. T. K. Arroyo, unpublished data). Based on the available information, it appears that *E. curvispina´s* short potential flower life span does not constitute an impediment for high fruit set. To the contrary, we see a relatively small number of large attractive flowers per plant, each containing a very high number of ovules, being very successfully pollinated.

Our main argument for a short flower life span (and our prediction for the presence of pollination-induced floral senescence) in *E. curvispina* hinged on the supposition that its high biomass flowers are resource demanding and that such demands would be alleviated in flowers that last for few days. We, therefore, decided to look at the water content of flowers. The absolute amount of water in the PTs in *E. curvispina* flowers is around 6 times higher than in the large tepals of a single flower of *Alstroemeria umbellata* (mentioned earlier); comparing whole flowers, it is 8 times higher (Arroyo et al., 2022). A single flower of *E. curvispina* contains far more water than a whole inflorescence of *A. umbellata*. Notably, the PTs of a single flower of *E. curvispina* contain over 22 times as much fresh biomass as an average species in a large sample of species from Spain with a Mediterranean-type climate (Herrera, 2009). Thus, in relative terms, it is reasonable to conclude that the flowers of *E. curvispina* would consume a large amount

of water if they remained open for a large numbers of days in the dry high Andean habitat where transpiration rates (and presumably surface evaporation) tend to be high (Dudley et al., 2018). Of course, the exact amount of water involved still remains to be determined. Here, we provided a snapshot of the amount of water necessary to maintain the corolla turgid. Detailed physiological work is needed to determine the absolute volume of water lost and consumed daily, and thus the real effect of a relatively short flower life span.

Despite the generally high water content of *E. curvispina* flowers, the >5 g of water per whole flower pales alongside the 33 g of water contained in a single huge flower of the giant saguaro cactus (*Carnegiea gigantea*; Nobel, 1977) and the 41.8 g of water in the giant flowers of *Magnolia grandiflora* (Feild et al., 2009). Interestingly, in terms of flower longevity measured in days, the flowers of *Carnegiea gigantea* are open for only one night. Similarly, short flower life spans have also been reported in other columnar Cactaceae with very large flowers (e.g., Fleming et al., 2001; Gorostiague & Ortega-Baes, 2017; Martins et al., 2016; Ossa & Medel, 2011; Walter, 2010). This is highly consistent with the large flower/short flower longevity hypothesis which predicts the largest flowers in Cactaceae are expected to have the shortest flower life spans. Nevertheless, it must be cautioned that all these records, with the exception of that for *Echinopsis leucantha* (Gorostiague & Ortega-Baes, 2017), pertain to flower longevity measured in open-pollinated flowers. If such species are characterized by pollination-induced flower longevity, their potential flower life spans could be longer.

Although percentagewise the amount of water was slightly higher in night-time flowers, this was not the case for the PTs per se. Neither did the absolute amount of water in day- and night-time harvested PTs differ. The latter could have to do with the fact that the tepals (and hypanthium) of cactus flowers (Erdelská & Ovečka, 2004; Garcia de Almeida et al., 2010; Rosas et al., 2022), like the vegetative body (Nobel et al., 1992), contain mucilage which is comprised of soluble sugars with osmotic properties (Saag et al., 1975) important from drawing water into cells. The apparent lack of functional stomata in cactus flowers (Nobel, 1977), which in the vegetative body open at night in cacti, could be another factor. Indeed, the presence of mucilage might go a long way toward explaining why cactus species can support very large flowers under dry and desiccating arid and semiarid conditions. However, this does not mean that their flowers do not represent a large draw on a plant´s water budget. This is something that needs to be studied. Corolla dry mass per area has been proposed as an adaptation to maintain water in petals, an effective water conservation strategy to dry conditions (Teixido et al., 2019; Zhang et al., 2017). Although we did not measure dry mass per corolla area, according to these studies, this metric is predicted to be high in our species.

5 | CONCLUDING REMARKS

We argued that flower longevity should bear a relation to ecological context. Although flowers may be large, in arid habitats, short-lived flowers can be expected so as to reduce water and other maintenance costs. Moreover, selection to reduce flower longevity following pollination could be expected as a further means for reducing flower life length. Even though pollination does not shorten the flower life span, our work shows that the large, water-rich flowers of *E. curvispina* have a short flower life span compared to a large number of species in the same area for which data are available. It sets a framework for looking at flower longevity and flower size in other large-flowered species/lineages of arid and semiarid climates. Additional studies along the 100° of latitude and 5000 m of elevation covered by the cactus family are needed to verify whether a trade-off between large flowers and short flower life spans is a general ecological rule in this important plant family of arid and semiarid climates. The Cactaceae are characterized by a huge diversity of pollination mechanisms, some more specialized than others (Cavalcante-Cardoso et al., 2019). Flower longevity affects the probability of pollen import and export. Consideration of the level of pollination specialization as an additional factor driving flower longevity would be interesting. Evidently, a useful piece of information for evaluating our hypothesis in *E. curvispina* with greater precision concerns exactly how much water is lost from flowers on a daily basis compared with other parts of the plant. This requires measuring floral transpiration rates which was beyond the scope of the present study. A non-destructive way to calculate the amount of water in the overall plant body, necessary to determine the draw of flowers on the overall plant water budget, should be found. Finally, in undertaking this study, we were struck by the general lack of basic information on the water and biomass content of flowers across the angiosperms in general. General surveys are not common in the ecological literature of today. This is one area in which a general survey in different ecosystems using a common protocol is likely to lead to novel hypotheses.

AUTHOR CONTRIBUTIONS

Marcela Cuartas-Domínguez: Data curation (equal), formal analysis (equal), investigation (equal), methodology (equal), visualization (equal), writing – review and editing (equal). **Valeria Robles:** Investigation (equal), methodology (equal), supervision (lead), writing – review and editing (equal). **Mary T. K. Arroyo:** Conceptualization (lead), data curation (equal), formal analysis (equal), funding acquisition (lead), investigation (equal), methodology (equal), visualization (equal), writing – original draft preparation (lead), writing – review and editing (equal). All authors have read and agreed to the published version of the manuscript.

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with the work on flower water content. Ítalo Tamburrino provided useful comments on the manuscript. Paola Jara-Arancio collaborated in producing the figures. Karina Bacelli edited photos and Santiago Cuartas edited the pollination videos. We thank Luisa Ruz for her help with the identification of the two bee species and Pablo Guerrero for his advice regarding the name of the cactus species studied.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data have been archived in Dryad: https://doi.org/10.5061/dryad.qfttdz0kv.

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