Phenology of *Tillandsia purpurea* in association with microclimatic variables in a hyperarid environment of the southern Peruvian coast

Fenología de *Tillandsia purpurea* en asociación con variables microclimáticas en un ambiente hiperárido de la costa sur peruana

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ABSTRACT

Tillandsia purpurea is an endemic species of the Peruvian desert coast, where its main source of water and nutrients is supplied by ocean fog. It is a poorly studied species, and its phenological changes in response to different abiotic factors, including temperature and water availability, are unknown. This study aims to describe the different phenological phases and their relationship with some environmental factors including fog, precipitation, temperature, and humidity. This study was developed in a hyper-arid environment of the southern coast of Peru. We evaluated the fog water available using fog collectors (neblinometers) installed next to each cushion of *T. purpurea*, and also monitored the microclimate conditions at ground level with temperature and humidity sensors. Additionally, phenophases (inflorescence, flowering, fructification, dehiscence, and vegetative stage) were evaluated within ten cushions of *T. purpurea* for a period of eleven months. As for water availability, the average fog water collected by the fog collectors was 5.11 L•$0.25m^2$ month^{-1} and the accumulated precipitation was 35.8 mm. In the microclimate, the mean temperature was 18.4ºC and humidity was 62.5%, and seasonality was observed in the evaluated variables. The T. purpurea phenological phases recorded showed a certain synchrony with some microclimate variables and water availability. The vegetative and dehiscence stages were associated with lower-frequency months, fog volumes, and also with less-warm periods Moreover, the phenophases of inflorescence, flowering, and fructification occurred in the months with higher water availability from fog, precipitation, and associated with warmer periods; in the specific case of fructification, it was more associated with periods of maximum or medium relative humidity.

Keywords: Phenophase, fog desert, Atacama Desert, coastal lomas, *Bromeliaceae*.

RESUMEN

Tillandsia purpurea *es una especie endémica de la costa desértica peruana, donde su principal fuente de agua y nutrientes provienen de la neblina del océano. Se trata de una especie poco estudiada, es así que los cambios fenológicos en respuesta a distintos factores abióticos, entre ellos, la temperatura y la disponibilidad hídrica, son desconocidos. Por lo que este estudio tiene como objetivo describir las distintas fases fenológicas y su relación con algunos factores ambientales como la niebla, precipitación, temperatura y humedad. El estudio se realizó en un ambiente hiperárido de la costa sur del Perú. Se evaluó el agua de neblina mediante neblinómetros colocados a un costado de cada cojín de* T. purpurea *y se monitoreo las condiciones del microclima a nivel del suelo con sensores de temperatura y humedad. También, se evaluó las fenofases (inflorescencia, floración, fructificación, dehiscencia y estado vegetativo) dentro de diez cojines de* T. purpurea *por un periodo de once meses. En la disponibilidad hídrica, el promedio de agua de niebla captada por los neblinómetros fue de 5.11 L•$0.25m^2$ mes^{-1} y la precipitación total acumulada fue 35.8 mm. En el microclima la temperatura promedio fue 18.4 ºC y la humedad promedio fue 62.5%, en las cuales se observó cierta temporalidad. Las fases fenológicas registradas mostraron cierta sincronía con algunas variables del microclima y disponibilidad hídrica. Los estados vegetativo y dehiscencia se asociaron con meses de menor frecuencia y volúmenes de neblina, además que con periodos menos cálidos. Por otro lado, las fenofases de inflorescencia, floración y fructificación, se presentaron en los meses donde se obtuvo captaciones más altas de agua de neblina, precipitación y estuvieron más asociados a periodos más cálidos, en caso específico de la fructificación estuvo más asociado con periodos de máxima o mediana humedad relativa.*

Palabras clave: Fenofases, desierto de niebla, desierto de Atacama, lomas costeras, Bromeliaceae.

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Introduction

The coastal lomas of Peru and Chile are biological communities located in the coastal mountain range and are characterized by being located in hyperarid zones. The presence of fog is a characteristic associated with these desert areas, predominating during the austral winter. This fog is the main source of water for the subsistence of the flora and fauna that reside in these areas. The lomas vegetation in this desert has received different classifications; however, one of them, the tillandsias, stands out, since they are perennial plants that survive almost exclusively on water provided by fog (Pinto, 2005). Commonly, these tillandsias are monotypic (dominated by the Tillandsia genus) or even monospecific formations, where the most recurrent species are *T. purpurea* (endemic to Peru), *T. latifolia*, *T. werdermannii* (endemic to the department of Tacna), *T. paleaceae*, and *T. capillaris* (Aponte and Flores, 2013; Pauca-Tanco *et al.*, 2020). These tillandsias have developed adaptations to extremely arid conditions, including the absence of functional roots and the presence of small serous trichomes or scales on their stems and leaves, which protect them from solar radiation and help them to benefit from the surrounding humidity (Pinto, 2005; Pauca-Tanco *et al*., 2020). The spatial pattern of these plants is another peculiar aspect, presenting two general patterns, the first with a predominance of hemispherical or spherical cushions, and the second pattern forming bands or lines (Pauca-Tanco *et al*. 2020), which would be associated with the orientation and slope of the terrain and would also increase the efficiency of water capture in fog interception.

Fog on the coast of Peru and Chile usually occurs between 500 and 1000 m.a.s.l., although its influence on vegetation develops mainly between 300 and 1200 meters, and this vegetation is often used as an indicator for fog occurrence (Cereceda *et al*., 1999). In the case of tillandsias, this dependence on fog-supplied water, as in *T. purpurea* (Pinto *et al*., 2006), makes them very vulnerable under a climate-change scenario. This would be explained by the fact that advective fogs, which occur along the Peruvian coast, could modify their spatial and temporal patterns, particularly their altitudinal position, due to possible changes in atmospheric temperature and sea-surface temperature (Cereceda *et al*. 1999, Koch *et al*. 2019). Therefore, a dramatic decrease in water availability for these tillandsias could result in the reduction or extinction of their populations (Schulz 2010) and negatively affect coastal fog-dependent communities, either in terms of population or function (Pinto *et al*. 2006; Schulz *et al*. 2010).

Regarding the events inherent to the vegetation, phenology is considered an important component of which changes have been documented, e.g., desynchronization between the phenological phases and the life cycle of the pollinating agents (Gordo and Sanz 2010, Fitchett *et al*. 2015). In addition to that, phenology is not only regulated by genetic factors, but also by some environmental variables, like precipitation, radiation, temperature, humidity, water evaporation, among others (Arroyo *et al*. 1988). Therefore, we consider it important to characterize the plant phenology of these communities, since they can be presented as potential bioindicators of climate change (Gordo and Sanz 2010). The aim of this research is the characterization and association of environmental conditions (fog, precipitation, relative humidity, and temperature) and the phenological cycle related to *T. purpurea* (endemic species of Peru), in a hyperarid zone of the coastal desert of Arequipa, in southern Peru.

Material and Methods

Study area

This study was performed in a hyperarid area of the Peruvian coastal desert, located in the locality of Pampa del Toro, Majes, Caylloma (Arequipa, Peru) (16º32'15.19.19'' S, 72º27'13.24 W), in the thermotropic bioclimatic zone and the ultra-hyperarid precipitation range. The climate in this area is characterized by two seasons: The dry season, which occurs between January and March, and the wet season during the remaining months. The terrain is mostly plain with some undulations and slight elevations, where soils are mostly clayey and loamy, with some dispersed rocks. The surveyed tillandsia is located 15 km from the Pacific coast, along a gradient from 950 to 1050 m.a.s.l., and the vegetation in this area is composed of *Tillandsia purpurea* and *Tillandsia capillaris* species.

Environmental Variables and Phenological Data

We randomly selected 10 cushions of *T. purpurea* (a name given to the grouping of

several spatially-isolated individuals) within an area of approximately 12 800 m², ensuring that each selected cushion was separated from another by at least 10 meters. Furthermore, to eliminate the altitude-difference effect on the phenological response of the selected plants, the selected cushions were located between 996 and 1004 m.a.s.l. For the measurement of fog water, a fog collector having an area of 50 x 50 cm was installed laterally to each selected cushion. This fog collector consisted of a 35% raschel mesh of sun shading, combined with a system of water collection ducts, which were connected to storage reservoirs. The fog collectors were installed 20 cm from the cushion, facing southwest (SW) and perpendicular to the predominant wind direction. Evaluations were conducted monthly, recording the total water collected. For the precipitation variable, a DAVIS Rain Gauge (tipping bucket type), connected to a data logger (HOBO Pendant UA-003-64), was installed on a cushion of *T. purpurea* in the central zone of the study area.

As for the microclimatic variables, temperature and relative humidity measurements were taken at ground level with an environmental sensor (PCE-HT-71N), which recorded information every 10 minutes during each day and month of the evaluation. The sensor location was randomly changed among the different cushions during the study period, to determine the temporal variation of these variables and their possible relation with the phenological response of the *T. purpurea*. The phenological phases were recorded through monthly observations in the different cushions of *T. purpurea*. Five phenological phases or stages were considered: Vegetative, inflorescence, flowering, fructification, and dehiscence (the criteria for determining each phenological phase are shown in Table 1). The evaluation period of the environmental variables and the phenological cycle was from February to December 2018.

Results and Discussion

Fog Water and Precipitation Catchment and precipitation

The monthly average of water collected by the fog collectors was 5.11 L•0.25m²., The catchment among these fog collectors showed significant differences after applying an ANOVA (*df* = 9, *F* = 2.25, *P* = 0.03) on data normalized through Johnson transformation (*type* = SB, *Z* = 0.66). Likewise, the fog collectors that reported the greatest catchment were N1 and N7, with a mean catchment of 11.82 and 7.37 L•0.25m² respectively. In contrast, the lowest water catchment was in N2 and N4 (Figure 1a). The total volume of water collected by the fog collectors was 556.01 L, where fog collector N1 collected the largest volume (129.99 L, 23.38%) followed by fog collector N7 with 81.08 L (14.58%), the total monthly average fog water capture being 55.60 L⁻¹ (Table 2).

Concerning the monthly catchment values, seasonality of the fog catchment was observed, increasing from June until October, and then decreasing, August being the month with the greatest fog water catchment (11.85 L•0.25 m²) and also with the greatest variability in water catchment; October ranked second (9.66 L•0.25 m²). Meanwhile, the lowest catchment was from February to April, with less than 1.50 L•0.25 m² (Figure 1b). Significant differences were found in the monthly catchment (ANOVA, *df* = 10, *F* = 28.7, *P* < 0.01), the greatest difference being in February, March, and August.

These results are consistent with the expected temporal pattern that occurs in other areas of

Table 1. Parameters considered to define each phenological phase in the *Tillandsia purpurea* cushions.

| Phenophase	Code	Feature
Vegetative	Veg	Cushion with no branchlets (no presence of new stems, evidencing that there is no asexual reproduction) or inflorescences.
Inflorescence	Inf	Cushion with presence of formed branches and inflorescences without formed flowers.
Flowering	Flo	Cushion with branches and inflorescence and open and fresh flowers.
Fructification	Fru	Cushion with branches with fruits in growth and maturation.
Dehiscence	Deh	Cushion with branches and with seeds released from the fruits and/or dispersed on the leaves of the cushion.
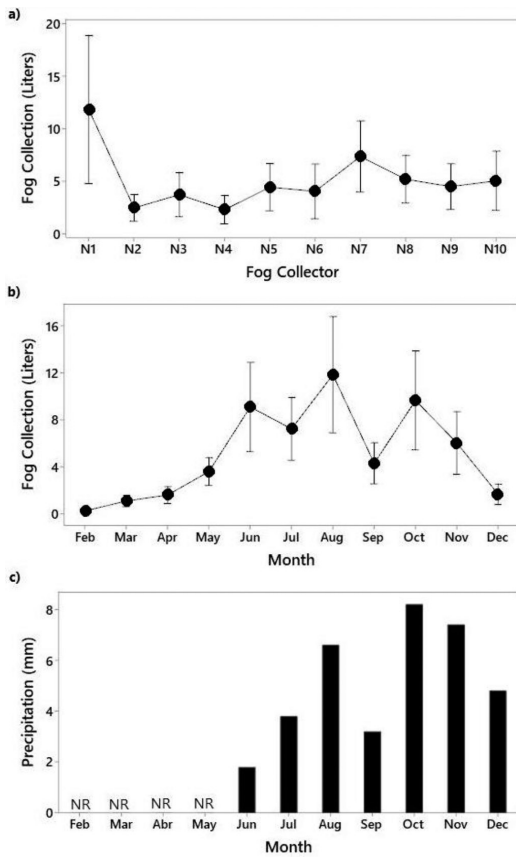
Figure 1. Fog water volume collected per catchment by a) installed fog collector (0.25 m^2) and b) average monthly variation of fog water collected, also showing the c) total precipitation during February to December 2018 in a *Tillandsia purpurea* formation, Pampa del Toro, Arequipa, Southern Peru. NR = not recorded.

Peru and Chile (Cereceda *et al.* 1999, Cereceda *et al.* 2008). This Gaussian bell-shaped pattern corroborates that, during the first months of the year, corresponding to the austral summer, the volumes of water collected are low, in agreement with the general climatic characteristics of coastal ecosystems in South America. Then, fogs become more frequent and with them water collection, which steadily increases towards the months of June, with a maximum in August, and then decreases until December (Figure 1b). The different volumes of fog water collection by each fog collector could be mainly attributable to the soil microtopography, since there are no significant differences in the orientation and altitude of each fog collector; Pinto (2005) verified this case through experiments with pairs of fog collectors placed in front of and behind Tillandsia cushions, where those placed in front of the cushion collected, on average, twice as much water as those placed behind it, considering that the cushions, as three-dimensional objects, modify the shape of the ground, thus modifying the microtopography.

Regarding the water supply from precipitation in this locality (Figure 1c), an accumulated precipitation of 35.8 mm was recorded, where the period without records (NR) occurred between February and May, and the remaining months had a precipitation of more than 1.80 mm. The months with the highest precipitation records were October (8.20 mm) and November (7.40 mm), the average precipitation for the study period was 3.26 mm. These records showed

Table 2. Mean and accumulated volume of water collected by fog collector during the measurement period (February to December 2018) in a *Tillandsia purpurea* formation, southern Peru.

Fog Collector	Coordinates		Elevation (m.a.s.l.)	Orientation	Accumulated volume of water (L/0.25 m^2)	Average fog water catchment (L/0.25 m^2)	Group (*)	
	Latitude	Longitude						
N1	16°32'16.03"S	72°26'14.60"O	1004	189° (SO)	129.99	11.82	A	
N2	16°32'15.63"S	72°26'13.94"O	1003	199° (SO)	27.45	2.50		B
N3	16°32'15.14"S	72°26'13.60"O	1003	165° (SO)	41.24	3.75	A	B
N4	16°32'15.19"S	72°26'13.24"O	1002	223° (SO)	25.65	2.33		B
N5	16°32'15.81"S	72°26'11.19"O	996	208° (SO)	49.03	4.46	A	B
N6	16°32'14.28"S	72°26'11.64"O	999	194° (SO)	44.67	4.06	A	B
N7	16°32'13.70"S	72°26'11.25"O	998	218° (SO)	81.08	7.37	A	B
N8	16°32'13.18"S	72°26'11.36"O	999	196° (SO)	57.29	5.21	A	B
N9	16°32'12.49"S	72°26'12.43"O	1002	193° (SO)	49.66	4.51	A	B
N10	16°32'13.85"S	72°26'13.41"O	1004	194° (SO)	55.70	5.06	A	B

(*) Means that do not share a letter are significantly different.

a similar pattern to that of the fog recorded, with a level increase during winter and none during the summer, a pattern similar to other coastal lomas communities, like Lomas de Atiquipa in southern Peru. When comparing these results with fog collection data, the fog variable is also present in all months of the evaluation period, making it the only water resource available throughout the whole year.

Microclimatic Variables and Phenology Associated with *Tillandsia purpurea*

The temperature range recorded during the evaluation ranged from 6.5 °C to 40.0 °C, with a mean of 18.4 °C (*sd* = 8.4), showing a clear trend with two periods (Figure 2a), a warmer one from December to April with mean temperatures above 20 °C, and a less warm period from May to November with mean temperatures below 18 °C, the coldest month recorded being August with 15.7 °C. As for relative humidity, the mean values recorded ranged from 13.7% to 98% humidity, with an annual mean of 62.5%. Monthly averages (Figure 2a) showed a variation between 48.6% and 70.8%, with high humidity during May and October, and the lowest average humidity recorded in December. Currently, there is not much information on microclimatic conditions associated with plant species, particularly in hyperarid areas, even though their importance has been recognized, especially to establish their mechanisms and effect on vegetation, chiefly in fog ecosystems (Sotomayor & Drezner, 2019). Temperature ranges recorded during this study are in accordance with temperature ranges reported for other Peruvian desert localities with fog occurrence (Sotomayor & Drezner, 2019), and also above the temperature tolerance ranges of some species, such as *Tillandsia dasyliriifolia*, in which tolerance ranges above the lethal temperature (LT_{50}) are reported to be a minimum of 9.15 °C and a maximum of 43.10 °C (Castillo *et al.* 2016). It is suggested that the density of the trichome layer is one of the factors involved in the survival of tillandsias to such temperature variations and water loss by evapotranspiration, which would vary among different species, and which present an inverse relation to this variable concerning water loss and, consequently, their survival (Ohrui *et al.* 2007).

Regarding phenology, in February, when the evaluations of phenophases began, two phenophases were predominantly observed: Dehiscence (70%)
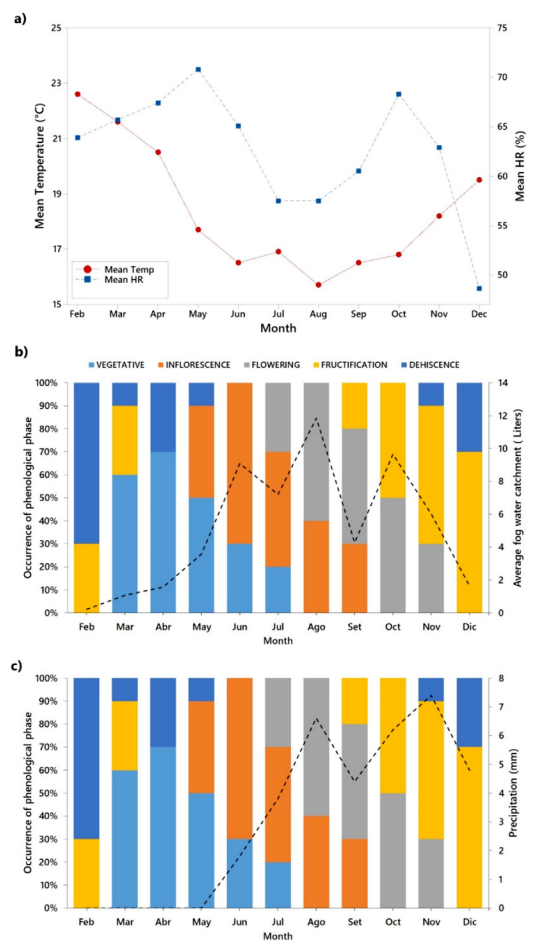

Figure 2. Microclimatic variables and development of phenological phases associated with *T. purpurea* (February to December 2018) in a desert region of southern Peru. a) Monthly means of temperature and relative humidity, b) phenophases and mean fog water collection in fog collectors, c) phenological phases and total monthly precipitation.

and fructification (30%). During the following evaluations, a gradual change was observed among phenological phases (Figure 2b, Figure 2c), vegetative phases occurring from March to July, among which there was also an increase in the inflorescence and flowering phases. Flowering occurred from July to November, followed by the fructification phase from September to December and the increase of dehiscence from November to December, which completed the phenological cycle of this species, since it corresponds to the same phase found during the first month of the study.

Regarding the main phenological stages, such as inflorescence, flowering, and fructification,

it was observed that they were related to water availability, both from fog water catchment (Figure 2b) and precipitation (Figure 2c); in both cases, the fructification period begins immediately after the months of greater water availability, which corresponds to September (Figure 2c). Overall, the presence of the different phenological phases in this study matches up with the results presented by Türkowsky and López (1983) for *T. purpurea* in the Cajamarquilla valley (Lima, Peru), where the flowering and fructification phases occur when water availability is increased, especially from coastal fogs. However, when these same authors present the results for other Tillandsia species (*T. paleacea*, *T. latifolia Var. major*, *T. latifolia Var. latifolia,* and *T. recurvata*) no demographic synchrony is shown, since the different phenological phases do not match up throughout the year.

The principal component analysis (PCA) based on the phenological phases and environmental variables monitored during the evaluation (Figure 3a) showed that 81.5% of the variability was explained by the first two dimensions (Dim1 = 56.5%, Dim2 = 25.0%). Dim 1 consisted mainly of the variables of minimum humidity, temperature (average and minimum) and fog. In the case of Dim 2, it was mainly formed by the maximum humidity and, to a smaller degree, by the average humidity and precipitation.

On the other hand, some positive associations were observed with the phenological phases of inflorescence and flowering (September to October), with environmental variables of fog and maximum temperature. Meanwhile, the vegetative and dehiscence phases are especially associated with periods of low humidity, and with average and minimum temperatures. The fructification phase (November and December) has a positive association with periods of average and maximum humidity. As for the correlation of the different variables measured (Figure 3b), positive correlations were found in the group of minimum and mean temperatures, and also with minimum humidity; on the other hand, negative correlations were found mainly with fog and minimum humidity, and also with mean and minimum temperatures.

The various phenological phases observed in *T. purpurea* throughout the year did not respond at the same time during each phenophase; this pattern has been presented and reported in other species of *Tillandsia* (Aponte and Flores 2013). There are months when the proportion of plants in a phenophase is predominant, but, in turn, each phenophase extends to other months until it changes to another phase (Figure 2a, 2b), which could indicate some phenotypic plasticity of *T. purpurea* individuals, similar to other plant species (Lenza and Klink 2006, Guerta 2015).

Also, some of the responses of this species may be influenced by changes in climatic and edaphic conditions (Badeck *et al.* 2004) particular to the microhabitat (Borchert 1998). Therefore, the
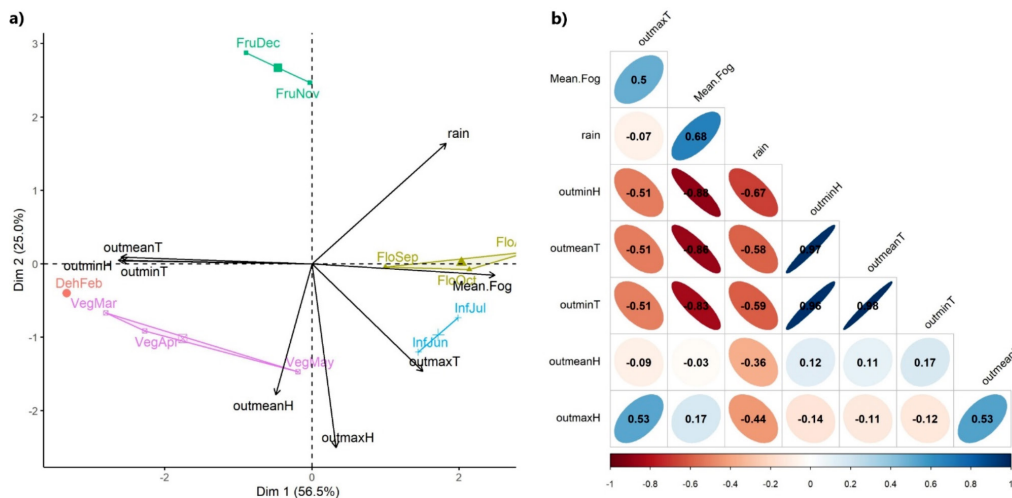

Figure 3. a) Principal component analysis on phenological phases of *T. purpurea* and climatic variables (precipitation and fog) and microclimatic variables (temperature and relative humidity), b) correlogram of the variables used in the phenological and environmental analysis.

changes observed in the different phenological stages throughout the year, as we expected and in contrast to other ecosystems, are closely associated with water availability, which in this case comes predominantly from fog or precipitation, or both. Clearly, the most important ecological limiting factor in these hyper-arid ecosystems is water, since other factors, such as photoperiod, do not differ significantly throughout the year, especially in tropical regions. Some authors (Borchert and Rivera 2001) agree that in some species occurring in low latitudes (tropical zones) where changes in photoperiod may also be an important factor in phenological changes (Körner & Basler 2010, Piao *et al.* 2019). Another significant variable associated with this is temperature, which is one of the main controllers of plant phenology, where its effect would be mainly related to the accumulated temperature of the previous season to the present phenological event (Piao *et al.* 2019).

Furthermore, between February and April, the dehiscence and vegetative phases predominated, in association with a period without precipitation records and with the lowest volumes of fog water. This could indicate that *T. purpurea* plants decrease their metabolic activity, like other species, and survive the months of drought using some mechanism to resist this environmental condition (Borchert and Rivera 2001), but this is still unknown for this species. Subsequently, in May, the first inflorescences appear and remain until September; in July, the first flowers appear, which, from September onwards, turn into fruit (70% of cushions correspond to this phenological stage), initiating the dehiscence phase (Figure 2). Inflorescence and flowering, which are closely related to greater availability of water, and temperatures, would generate a response of the reproductive phases of *T. purpurea*.

Finally, the evaluation of the phenological stages and their relation with some climatic and microclimatic variables continues to be important, since these interactions help to explain some characteristics, like growth form, leaf shape, and, most importantly, plant physiology (Adams 2010). This, in addition to the current global climate change and its effects on the Pacific coast of South America, especially in the presence of fog layers which are the main source of water for *T. purpurea*, and consequently on the survival of this species and others in the Atacama Desert. The limited research on climate change in the arid South American coast was focused on northern Chile, revealing plant mortality in some communities of the Chilean coastal desert (Schulz *et al.* 2010, Schulz *et al.* 2011), and explaining a decrease in the cover of stratocumulus clouds since the mid-1970s, particularly in Arica, northern Chile, as well as a decrease in the frequency of precipitation and fog. According to Schulz *et al.* (2011), these changes in coastal climate of Chile may be reducing the cover of some plant communities, caused by a decrease in water availability and an increase in the impact of direct solar radiation in places where cloud cover has been reduced. (Schulz *et al.* 2011). Even now there is insufficient scientific evidence on the future of arid zones in the context of climate change, and even more so for fog-dependent deserts, such as the phenological processes that occur here (Adams 2010, Fitchett *et al.* 2015, Piao *et al.* 2019); thus, it is still important to continue monitoring arid zones and species that can be used as indicators of change (Morisette *et al.* 2009), both in the ecosystems and in the services provided.

Conclusions

The phenological cycle of *T. purpurea* was documented, the dehiscence and vegetative phases being associated with periods of lower water availability (February, March, and April) and less warmth, while the flowering and fructification phenophases occur in the months of greater water availability (June to October), and the inflorescence phases were recorded between May and September, when the frequency of fog increases and temperature values are higher. Therefore, the availability of water from fog and precipitation, as well as temperature, would be the most important variables in the phenological cycle of this species.

Additionally, seasonality was identified in the environmental variables of precipitation and fog, and in the microclimate, in terms of relative humidity and temperature for this desert area with fog-dependent communities.

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