Rev. FCA UNCUYO. 2020. 52(1): 148-160. ISSN (en línea) 1853-8665.

Spatial and temporal synchronicity in the phenological events of *Prosopis flexuosa* in the Central Monte Desert

Sincronización espacial y temporal de los eventos fenológicos de *Prosopis flexuosa* en el Desierto del Monte Central

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Originales: *Recepción:* 25/02/2019 - *Aceptación:* 23/05/2019

Abstract

Some desert plant species are capable of using underground water and are therefore independent of rainfall events. Species of the genus *Prosopis* are thought to be facultative phreatophytes, since they have deep and shallow roots that allow them explore water from underground layers and from sub-surface soil horizons. We created a seven-year series of phenological data in order to make comparisons between two natural Reserves of Mendoza province (Ñacuñán and Telteca) with different rainfall regimes and accessibility of *Prosopis flexuosa* trees to water. Percentage of trees in each phenological phase, date of maximum expression, and intensity of each phenological phase were recorded. We found that the trees had a similar date for leafing and flowering across years and sites, even with very different rainfall regimes. However, pod maturation dates varied significantly, ocurring 37 days sooner in Telteca. A second peak of leaves and flowers were recorded at both sites, being highly variable and non-synchronous in most cases, suggesting a quick response to rainfall events. The ability of *P. flexuosa* to respond to unpredictable rainfall pulses could be an important adaptation to keep ecosystem services functioning, even though associated pollinators and seed dispersers could get decoupled from changes in phenological events.

Keywords
phenological pattern • fruit set • phenological intensity • blooming pattern • synchronization • facultative phreatophyte

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RESUMEN

Algunas plantas desérticas pueden utilizar agua subterránea volviéndose independientes de los eventos de lluvia. Se cree que las especies de *Prosopis* son freatófitas facultativas ya que tienen raíces profundas y superficiales que les permiten explorar capas subterráneas y sub-superficiales del suelo en busca de agua. Creamos una serie de datos fenológicos de siete años para comparar dos Reservas naturales de la provincia de Mendoza (Ñacuñán y Telteca) con diferentes regímenes de precipitación y accesibilidad de *Prosopis flexuosa* al agua. Se registraron: porcentaje de árboles en cada fase fenológica, fecha de máxima expresión, e intensidad de cada fase fenológica. El inicio del desarrollo de hojas y flores fue similar a través de años y sitios, incluso con diferentes regímenes de lluvia. La fecha de maduración de los frutos sin embargo, fue significativamente (37 días) más corto en Telteca. Una segunda cohorte de hojas y flores, muy variable y no sincrónica en la mayoría de los casos, se registró en ambos sitios, sugiriendo una rápida respuesta a pulsos de lluvia. Esta capacidad de respuesta de *P. flexuosa* puede jugar un papel importante al mantener funcionando los servicios ecosistémicos, aunque los polinizadores y dispersores de semillas asociados podrían desacoplarse de los eventos fenológicos.

Palabras clave
patrones fenológicos • producción de frutos • intensidad fenológica • patrón de floración • sincronización • freatófito facultativo

INTRODUCTION

Water availability is one of the main factors that determines productivity in the Monte Desert, triggering a new flush of leaves in most perennial woody plants and germination of annual herbs and grasses (34). Some plant species are capable of using underground water (phreatophytes and other deep rooted plants), and are therefore independent of rainfall events. These plants can produce fruits and seeds during dry years, when most other species barely survive. Species of the genus *Prosopis* are thought to be facultative phreatophytes, because they are characterized by deep roots that allow them to obtain water from deep soil layers, as well as from shallow soil horizons (3, 14, 17, 18). Thus, *Prosopis* trees can maintain their maximum leaf area during the hottest and driest months of the year (26).

Prosopis flexuosa D.C. is the most important tree growing in the central Monte (2). Trees of *P. flexuosa* are very important for subsistence of native people from the Monte, where wide temperature fluctuations between winter and summer (-10°C to 48°C) are frequent, providing shade to domestic animals and people, wood for house and corral construction, and fire for cooking and heating. However, one of the most important services of *P. flexuosa* is fruit production. Fruits are consumed as food and used to prepare beverages. In addition, they are important source of feed for domestic animals when there is no enough grass (19). *Prosopis flexuosa*, like other species of the genus, has stable water potential values, which indicates that this species could be independent of rainfall (7). This idea is reinforced by the fact that its roots reach a depth of more than 10 meters, allowing this species to use underground water (17, 18). Studies carried out on this species for two years at Andalgalá (Catamarca) demonstrated high synchronization in foliage and flowering dates between years (24, 35). In spite of this, research on the development of phenological events in *P. flexuosa* are very scarce, and long series of phenological data on this tree in the Monte desert are lacking.

The humanity is facing climatic change events that have intensified over the last years. Knowing wich factors drive phenological events in perennial plants is useful for testing how these plants may respond to these events.

Objectives

Our objectives were to compare phenological data sets across various years and, in more detail, between two natural reserves with different water availability for *Prosopis* trees. We used data from a seven-year series of two sites in order to describe the phenological pattern of this species. Moreover, a more detailed four-year data series taken simultaneously at both reserves is analysed, in search for similarity on the intensity of each phenological phase. According to the phreatophytic condition of *Prosopis* trees, we expected high synchronization of the beginning of leafing and flowering among years, in each reserve. However, we also expected differences in the degree of expression of phenological events attributable to opportunistic water use from local sporadic rains.

Materials and methods

Study sites

The study was carried out at two natural reserves in the Monte Desert:

Ñacuñán Biosphere Reserve (12 300 ha; 34°02' S, 67°58' W; 540 m a. s. l.)

Situated in the centre of the Monte Desert, it has been excluded from grazing and logging for more than 40 years. The climate is dry and temperate, with cold winters. Annual rainfall averages 337.6 mm (1973-2005 average), however 75% of the rain concentrates in spring and summer. Mean monthly temperature of the coldest month (July) is 6.9°C and 22.4°C for the warmest (January), whereas mean annual temperature is 15.6°C, with an absolute maximum of 42.5°C and an absolute minimum of -13.0°C (12). The vegetation is characterized by an open woodland with sparse trees dominated by *Prosopis flexuosa*, a layer of shrubs (*Larrea divaricata*, *Lycium chilense*, *Junellia aspera*, *Condalia microphylla*, and *Capparis atamisquea*) and a grass layer composed mostly of perennial species (*Pappophorum caespitosum*, *Trichloris crinita*, *Aristida mendocina*, *Digitaria californica*, *Setaria leucopila*, and *Sporobolus cryptandrus*). Several annual grasses and herbs grow in the summer after rain events (33).

Telteca Provincial Reserve (38 500 ha; 32°23' S, 67°54' W; 500 m a. s. l.)

Located within the Monte Desert, is characterized by hot rainy summers and cold dry winters. The absolute maximum temperature reaches 48°C in summer, while the absolute minimum in winter is -10°C, with a mean annual temperature of 18.5°C. Rainfall is variable, ranging between 50 and 200 mm, with a mean annual rainfall of 156 mm (1972-2007 average). The landscape is characterized by a system of dunes and scrublands dominated by *Larrea divaricata*, *Tricomaria usillo*, and *Bulnesia retama*. The herbaceous layer is dominated by perennial (*Aristida mendocina, Panicum urvilleanum*) and annual grasses (*Bouteloua aristidoides, Aristida adscencionis*), with large areas of bare soil between shrubs. Open woodlands of *P. flexuosa* occur mainly in the low-lying areas between dunes, with a shrub layer dominated by *B. retama*, *Capparis atamisquea*, and *Lycium tenuispinosum* (1).

Data collection

Three series of phenological data from Ñacuñán Biosphere reserve and two series from Telteca reserve were used in order to obtain the longest phenological pattern possible. These series were discontinued in time. All trees used in the series were randomly selected and of similar size. At Ñacuñán, ten trees, were selected for the first group of data, and phenological observations were gathered from October 1993 to April 1995. The second group of data was comprised of observations from 10 trees, from October 1998 to May 1999. The last group of data was obtained from a more detailed phenological study, where three sites, each with four trees, and located at least 1 km apart, were selected. This group of trees differs from previous series. The objective was to assess three sites (and two in Telteca, see below) getting a wider representation of spatial variability in phenology. Observations for the last series were made from October 2000 to January 2004. At the Telteca Reserve, two sites with ten trees were observed from October 2000 to January 2004. This series is analogous in detail to that collected at the Ñacuñán reserve during the same period. The second series comprises a three-year study from October 2005 to January 2008, working on two sites, at least 1.5 km apart, with eight trees each.

Series of climatological data are also scant and mostly incomplete in the Monte Desert. We had a good representation of data for Ñacuñán for all years assessed. However, for Telteca we only had data starting in 2001, with some gaps in 2001 and 2004. All data were gathered from meteorological stations located at each Reserve.

Definition of variables and data analysis

Phenological patterns

Percentages of trees were calculated, showing different reproductive phenological phases along the growing season: flower buds, inflorescences, juvenile pods, mature pods, and vegetative growth. In this last phase, we only considered non-expanded leaves. Presence of those plant components was enough to consider that a tree was going through a phenological phase, without considering its intensity. For this variable, we used all the available data, seven years for each site that overlapped during 2000-2004 reproductive periods.

Date of phenological maximum expression

We used the date in which most trees demonstrated a phenological event, expressed as Julian day. The phenological phases observed were: flower buds, inflorescences, juvenile pods, and mature pods. We tested differences in the time at which most important phenological events occurred between Ñacuñán and Telteca. Since Julian day was also used as a variable, differences between sites were tested using Generalized Linear Models (GLM) with Poisson error, taking years as replicates. Analyses of GLM were done under the R environment (30), and testing significance of interactions was done by likelihood ratio tests (LRT), comparing models with and without interaction (*i.e.*, nested models) (9).

Intensity of phenological events

Previously used by Debandi *et al.* (2002), this variable accounts for the proportion of the canopy covered by a phenological event in each individual plant. The percentage recorded was assigned to a numerical value according to the following scale: 1 (1-20%), 2 (21-40%), 3 (41-60%), 4 (61-80%), and 5 (81-100%). The mean of each phenological event across all trees was calculated for each date. The phenological phases considered were: non-expanded leaves, flower buds, inflorescences, juvenile pods (not yet mature, greenish pods), mature pods (brownish to yellow fruits, still on the tree), and fallen pods (mature fruits fallen on the ground).

RESULTS

Phenological patterns

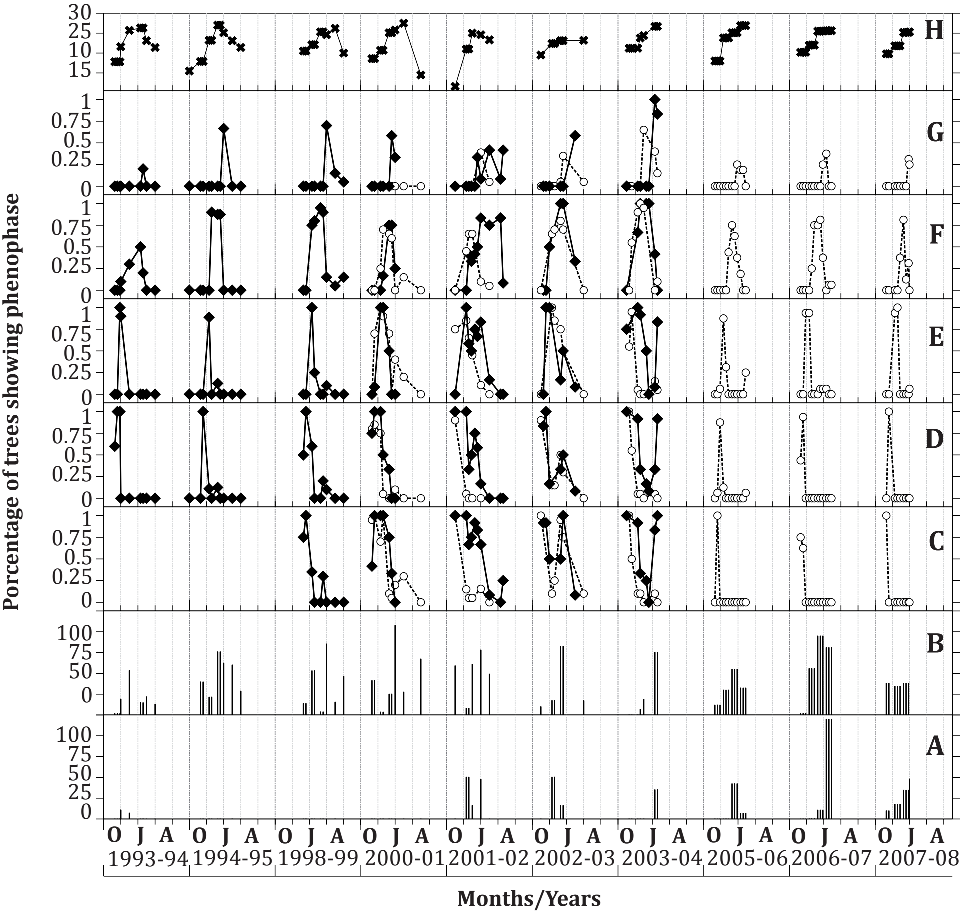
Vegetative growth of *P. flexuosa*, measured by a new flush of leaves, started in early October, with the highest percentage of trees by mid-October (figure 1C, page 153). These leaves quickly expand and all trees are fully covered by new, recently expanded leaves by late October (data not shown). These events were very similar at both sites and for all assessed years. At the time when new non-expanded leaves appear, flower buds are also observable, peaking by mid-October (figure 1D, page 153), and becoming fully flowered trees by late October (figure 1E, page 153).

In some years a second peak of leaves and flowers was recorded at both reserves; being, however, more frequent at Ñacuñán. This was more evident by mid December 2002 at both sites, and by mid-January 2004 at Ñacuñán (figure 1C, D, E; page 153). There was a different number of trees fructifying across the years assessed, and the duration of the period of pods maturation was also variable. In a similar way, the peak of trees fructifying was different among years and between sites. To find a coincidence in the date and percentage of trees between sites was only possible during the period 2003-2004. Pods maturation begins by the end of December or mid-January at Ñacuñán, and some weeks earlier at Telteca. Data from complementary phenological series (those data not assessed simultaneously at both sites), were very useful to confirm that the appearance of leaves and flowers occurs at very similar dates, regardless of rainfall.

Date of phenological maximum expression

Maximum expression of phenological phases resulted in subtle differences between sites. On average, new leaves had their maximum expression around October 14th (± 9 days) at Telteca, and around October 20th (± 10 days) at Ñacuñán (figure 2, page 154), having no statistical differences between sites ($\chi^2 = 0.28$; df = 1; $P = 0.59$). Flower buds reached their maximum, on average, four days sooner at Telteca (October 19th ± 7 days) than at Ñacuñán (October 23th ± 3 days), showing no statistical differences ($\chi^2 = 0.23$; df = 1; $P = 0.62$). Flowering reached its maximum by November 5th (± 7 days) at both reserves ($\chi^2 = 0.0009$; df = 1; $P = 0.97$), while immature pods reached their maximum by December 4th (± 8 days) at Telteca and eight days later at Ñacuñán (December 12th ± 21 days), which is not significantly different ($\chi^2 = 0.72$; df = 1; $P = 0.39$).

Date of maximum expression of mature fruits however, did vary significantly, occurring on average 37 days sooner at Telteca (December 27th ± 8 days) than at Ñacuñán (February 1st ± 17 days; $\chi^2 = 11.77$; df = 1; $P = 0.0006$; figure 2, page 154).

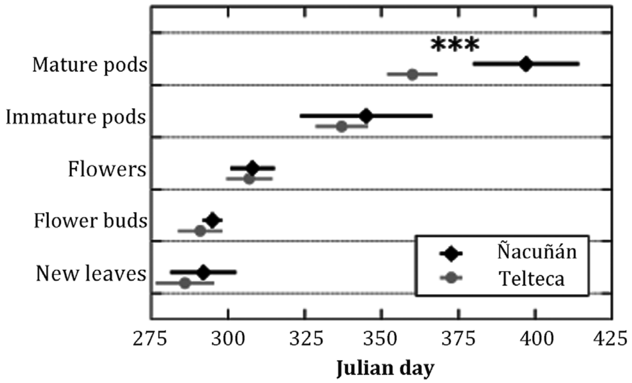


A: monthly rainfall at Telteca; B: monthly rainfall at Ñacuñán; C: non-expanded leaves; D: flower buds; E: inflorescences; F: immature pods; G: mature pods; H: temperature (°C) recorded at the Mendoza meterological station. On the x axe, each reproductive period is shown from October (O) of one year to April (A) of the next year.

A: Lluvia mensual en Telteca; B: lluvia mensual en Ñacuñán, C: hojas no expandidas; D: yemas florales; E: inflorescencias; F: vainas inmaduras; G: vainas maduras; H: temperatura (°C) registrada en la estación meteorológica de Mendoza. En el eje x se muestra los períodos reproductivos desde octubre (O) de un año a abril (A) del siguiente.

Figure 1. Percentage of *Prosopis flexuosa* trees showing different phenological phases along ten reproductive periods at two sites: Ñacuñán reserve (continuous lines and filled markers) and Telteca reserve (dashed lines and empty markers).

Figura 1. Porcentaje de árboles de *Prosopis flexuosa* mostrando diferentes fases fenológicas durante diez períodos reproductivos en dos sitios: Reserva Ñacuñán (línea continua y marcador lleno) y Reserva Telteca (línea discontinua y marcador vacío).



Asterisks (***) indicate significant differences in developing time between sites (probability at P < 0.001).

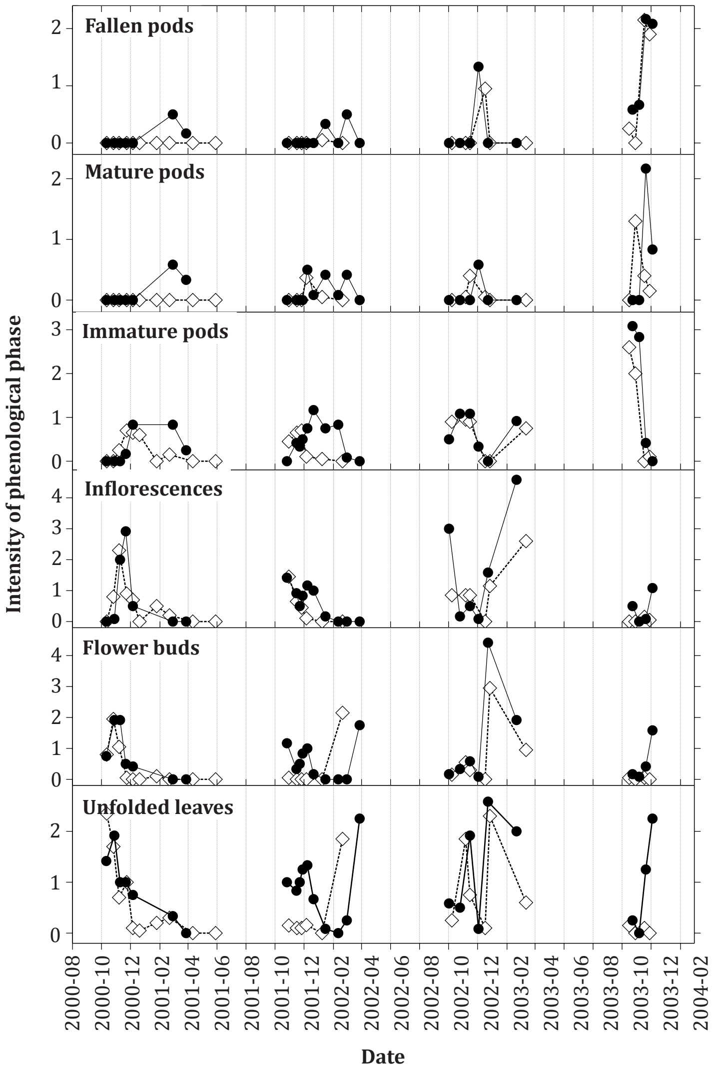
Los asteriscos (***) indican diferencias significativas en el tiempo de desarrollo entre sitios (con probabilidad P < 0,001).

Figure 2. Development of phenological phases of *Prosopis flexuosa* along the year. Values are means for seven years of Julian days (± SD) when maximum expression was detected (see text for details), taken at two sites of the Monte Desert.

Figura 2. Desarrollo de las fases fenológicas de *Prosopis flexuosa* a lo largo del año. Los valores representan el día juliano cuando se detectó la máxima expresión, promediado a lo largo de siete años de observación (± SD), en cada uno de los dos sitios estudiados del desierto del Monte.

Intensity of phenological events

Non-expanded leaves reached their peak with high intensity at the beginning of the reproductive season in concordance with bud burst. However, they quickly expanded before the inflorescences began to open. A second peak of non-expanded leaves was observable in some years, which seems to be a response to local conditions, since secondary peaks were different in intensity at both sites. In Telteca, during the 2001-2002 and 2003-2004 periods, no new flush of new leaves ocurred after the main peak of this event, but in Ñacuñán we registered a second peak of non-expanded leaves, that reached the magnitude of the first peak (for example February 2004, figure 3, page 155). In 2002-03 there was a second peak of non-expanded leaves with similar intensity at both sites. Flower buds and inflorescences reached similar intensities in their first peak during the 2000-01 and 2001-02 periods at both sites, but had a higher intensity in Ñacuñán during the last two years recorded (figure 3, page 155). Likewise, a second peak was recorded during the 2001-2002 and 2003-2004 periods with higher magnitude at Ñacuñán (figure 3, page 155). Juvenile pods had a similar intensity during the first three years, but increased considerably in the last year, at both sites (figure 3, page 155). This increase in intensity during the 2003-04 period was subsequently translated into higher intensities of mature and fallen pods, since the magnitude of these events was higher than in previous years.



Intensity follows a subjective scale with values of 0-5 (see text for details).

Los valores de intensidad están expresados acorde a una escala subjetiva de 0-5 (ver texto para detalles).

Continuous lines with filled circles indicate events at Ñacuñán reserve, and dotted lines with empty diamonds indicate events at Telteca reserve.

Líneas continuas con círculos llenos indican eventos en la Reserva de Ñacuñán, mientras que líneas discontinuas con rombos vacíos indican eventos en Reserva Telteca.

Figure 3. Mean intensity of phenological events of *Prosopis flexuosa* at two sites of the Monte Desert.

Figura 3. Intensidad promedio de los eventos fenológicos de *Prosopis flexuosa* en dos sitios del Desierto del Monte.

We observed a gradual increase in fallen pods across the considered years, from 2000 to 2004.

DISCUSSION

Initiation of vegetative and reproductive cycles of *P. flexuosa* can be considered independent from rainfall events, since the observed periods of leafing and flowering always occurred before the rainy season. This pattern had already been observed, for this species by different authors (26, 35, 36), and in other phreatophyte species of this genus: *Prosopis alpataco* (6), *P. articulata* (23), *P. caldenia* (11), *P. chilensis* (35, 36), *P. glandulosa* (25), and *P. laevigata* (29). This independence from rainfall events is possible, at least in part, due to underground water availability. At Telteca, low annual rainfall should not allow the development of *Prosopis* woodlands (16). However, the presence of this tree could be explained by the fact that underground saline water can be found at a depth of 5 to 15 meters (4, 18). By contrast, at Ñacuñán, underground water can be found at a depth of 70-80 meters. According to Roig (1993), this species could likely obtain water from intermediate-depth humid sandy-clay layers that can be observed frequently across the soil profile. Thus, water availability constrains the distribution of mesquite trees and allows them to synchronize their phenological phases over large geographic areas.

In addition to the independence from rainfall events, other local conditions can trigger phenological events. According to Solbrig and Cantino (1975), the photoperiod is an important sign for leafing and flowering initiation in *P. velutina* and *P. chilensis*; while Goen and Dahl (1982) found a relationship between bud-burst and temperature rising during spring in *P. glandulosa*. These environmental conditions can generate in some cases a latitudinal cline (5), indicating an adjustment to local temperature and/or photoperiod, and to the length of the growing season (36). The assessed sites for this study are located 184 km apart from each other (almost 1.5° in latitude), and the date of maximum expression of most phenological events was very similar at both sites, or a bit earlier at Telteca, the northernmost site. Leafing started by early to mid-October. However in northern latitudes like Andalgalá (27°34' S; 66°18' W-Catamarca, Argentina (35)) and Chancaní (31°24' S; 65°27' W-Córdoba, Argentina) (28), leafing in *P. flexuosa* began in early spring (September) while in southern latitudes it began in early November (38°45' S; 63°45' W-La Pampa) (11). In a similar way, flowering started in mid-to-late October at both Reserves, and 15-30 days earlier in northern latitudes (Andalgalá and Chancaní), while in southern latitudes flowering was recorded in late November-early December (La Pampa).

Although there were similarities in bud burst and flowering dates, reaching their maximum expression at very similar times at both study sites, differences begin to be observable when trees start fruiting. Immature pods appear, in average, sooner at Telteca, with similar maximum expression dates across the years. However, this difference becomes more evident when fruits reach maturity, as the time needed to reach maturity is significantly longer in the southernmost site. This difference may be due to climatic reasons, since Telteca has a hotter and dryer climate than Ñacuñán. It might also be due to genetic differences, at is has been demonstrated that the genus *Prosopis* maintains a genetically fixed phenological pattern when individuals from separate geographical areas are grown under uniform conditions (8, 22, 24).

While it is clear that *P. flexuosa* can flower independently from rainfall events, the main blooming period was very short. At both sites, mesquite bloomed from October to December, although bloom never lasted for the three months. Long periods in which *P. flexuosa* have visible flowers, have been attributed to early and late flowering individuals that overlap their blooms for many weeks (28). However, in our case, blooms were very short in time and a second and discrete bloom was observable, especially in Ñacuñán, in most of the study years. The flush of new leaves and flowers could be correlated to the cambial growth found by Giantomasi *et al.* (2012). According to this finding, *P. flexuosa* has an immediate growth response to short-term rainfall, evidenced by the production of new derivative cells linked to rains occurring a few days before any manifestation of cambial cell division (13). What is not clear is the advantage of these low intensity secondary peaks, especially those related to reproduction. Of the 10 reproductive periods assessed, only in 2003-04 at Ñacuñán, the secondary bloom was of high intensity. The 2003-04 period also had the highest fruit intensity (juvenile, mature, and fallen pods). On average, fallen fruits had an intensity equivalent to 20-40% of the ground beneath the trees, regularly covered by pods. This last reproductive period studied, yielding the highest pod production, also had the lowest annual rainfall of the last 10 years prior to 2004, in Ñacuñán. This is in accordance with Nilsen *et al.* (1991), and Lee and Felker (1992). Their findings for *P. glandulosa*, recorded an increase of flowers per branch and pod production as water stress increased. This lack of rainfall during the main bloom of mesquite has an important positive effect in the reproductive success of this species. Many authors have documented this relationship (11, 21, 35), also well known by local people.

Finally, we intend to point out the importance of long series studies on phenology, given that they provide valuable data for inferring phenological responses to environmental conditions. In this paper, we present the first descriptive phenological aspect of *P. flexuosa* in the central Monte Desert. Moreover, some surprising events like the intensity of flower buds in Ñacuñán during January 2004, open a series of questions about water use by *P. flexuosa* trees. Is it possible that mesquite trees use superficial water to produce the secondary flush of leaves and flowers? This question has been party answered by the cambial growth research done by Giantomasi *et al.* (2012). However it is still necessary to focus on the effect of rainfall events and other environmental conditions that promote a large flush of new flowers during summer, *i.e.*, after the main reproductive event of spring, and to determine the fate of these flowers. The response of cambial growth to short-term rainfall events should be viewed as an adaptation to the sporadic and convective nature of rains in this region (13, 32). Undoubtedly, the ability to take advantage of rains in a desert must be important for these plants. However, if this adaptation is beneficial from a reproductive point of view is not clear, given the low production efficiency of mature fruits.

In the context of climate change in the Monte Desert (20), facultative phreatophytes, like *P. flexuosa*, can play an important role in ecosystem response and continue to provide ecosystem services. They, not only contribute with a surplus of productivity in arid environments, but also have the capacity to respond to the unpredictable pulses in water availability. In the future, we expect higher frequency and magnitude of secondary pulses of leafing, flowering, and fruiting that will extend these phenological events in the growing season. If pollinators and seed dispersers will adapt to these changes and take advantage of them, remains to be know.

CONCLUSIONS

Prosopis flexuosa can flower independently from rainfall. During all assessed years flowering initiated before rainfall events. The main blooming period was very short at our study sites, with high synchronicity of leafing and flowering among trees at each site, as well as among sites. Differences in the extension of flowering periods can be attributable to secondary peaks related to rainfall events. The highest pod production year, also had the lowest annual rainfall of the 10 years prior to 2004, corroborating the relationship of high pod production with rainfall decreases.

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ACKNOWLEDGMENTS

We want to thank Juan Alvarez, Gualberto Zalazar, Erica Cesca, Valeria Corbalán and Mariano Cony for field assistance. Nelly Horak and Anabela Bonada for assistance in the English version, the Dirección de Recursos Naturales Renovables of Mendoza, and IADIZA for allowing us to conduct the studies at Telteca and Ñacuñán reserves, respectively.

This research was supported by Agencia Nacional de Promoción Científica y Tecnológica under grant PICT 03220-PICTR 2002 00200; and IAI - Interamerican Institute for Global Change Research under grant CRN3.